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

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Chapter 5. The Production Ecology of Macrofaunal Gastropods.

5.1. Introduction.

5.1.1. Hydrobia ulvae (Pennant).

Hydrobiid snails, which include Hydrobia ulvae; H. ventrosa, Montagu; H. neglecta (Muus); and Potamopyrgus jenkinsi (Smith), are one of the most abundant intertidal, invertebrate groups in north European estuaries (Clay, 1967a). The interspecific distribution of these species in Danish waters has been considered in detail (Muus, 1967; Fenchel, 1972, 1975a, b; Fenchel et al, 1975; Kofoed, 1975a, b; Fenchel and Kofoed, 1976) but whereas H. ulvae and H. ventrosa have been commonly found in the British Isles (Clay, 1967a), H. neglecta has only recently been discovered (Muus, 1967; Bishop, 1976) and may previously have been mistakenly included with the other species. H. ulvae, however, is the most common Hydrobiid and, as it is the only species of importance within the Forth estuary, is included in the present study.

(i) Distribution.

Within a wide geographical range the distribution of H. ulvae is largely determined by temperature and salinity. The species is eurythermic although temperature changes affect its salinity tolerance (Muus, 1967). Its intertidal distribution suggests that it is euryhaline with a salinity tolerance range of 10 > 33⁰/oo, i.e. it is polyhalophilous (Muus, 1967), although within a confined area its distribution is influenced by other abiotic and biotic factors. The species is euryoecious with respect to substrate although it probably prefers a muddy sediment (e.g. Spooner and Moore, 1940; Fretter and Graham, 1962) it rarely occurs on clean sand (Stopford, 1951) and never occurs on black,

strong-smelling mud (Muus, 1967). However other workers suggest that it occurs in polluted water and foetid mud (Blegvad, 1915; Fraser, 1932; Stopford, 1951).

Hydrobiae are considered to be more susceptible to the amount of water movement accompanying a sediment type than to the sediment itself and Wolff (1973) suggests that this may clarify the occurrence of the species in such varied habitats. H. ulvae prefer a shallow area with quiet water, especially if such an area occurs in the upper tidal zone (Thamdrup, 1935; Spooner and Moore, 1940; Raymont, 1955), although the animals have been found at low water (Rees, 1940) and occasionally reported from the sublittoral on muddy bottoms which are indicative of slight water movement (Wolff, 1973). Within an intertidal area, the maximum vertical distribution of H. ulvae has usually been found to be H.W.S.T. (Stopford, 1951) which may have a fortnightly tidal cover, although the animals will usually find better conditions lower on the shore (Green, 1968).

It has previously been suggested, therefore, that whilst substrate and vegetation are important in determining the distribution of H. ulvae, it is the amount of water movement that is the deciding factor (Muus, 1967). Within an overriding salinity regime, H. ulvae prefers large water movements compared with other Hydrobiae species (Muus, 1967) and this, together with its salinity preference, may account for its recorded occurrence in the outer, more saline parts of the estuaries (Wolff, 1973). However, although the species could survive on a moderately exposed beach during the summer it would not necessarily survive the winter. It may be stated, therefore, that although within lentic biotopes there exist many degrees of water movements which

Hydrobiae tolerate, they are not found in lotic biotopes.

The literature suggests that although local occurrences of combinations of the abiotic environmental-limiting master-factors (i.e. salinity, temperature, O₂ and exposure) will determine to a large extent the composition and distribution of Hydrobiae, the substrate (a part biotic and part abiotic factor) and other factors such as light, pH and vegetation will also affect the distribution.

(ii) Feeding and Behaviour.

The feeding and diet of Hydrobiae has often been linked to their distribution. They have been classed as herbivores and detritus feeders (Blegvad, 1915; Stopford, 1951; Perkins, 1958; Newell, 1965; Muus, 1967; etc.) although it is likely that they have an omnivorous diet of macroalgae, meiofauna, diatoms, macrophytes (Zostera, etc.), microflora, microfauna and sediment (Clay, 1967a). Although early research (cited in Newell, 1965) suggested that H. ulvae fed predominantly on Enteromorpha or Ulva, current research has shown this to be untrue. Newell (1962) suggested that when floating the animals feed upon a mucous raft which traps detritus but whilst on the mud surface they utilize the microflora attached to the sediment and detrital particles.

The unusual floating behaviour exhibited by H. ulvae may also contribute to their success. Although the animals float at certain times of the tidal cycle, life cycle or year (Linke, 1939; Holme, 1949; Smidt, 1951; Newell, 1962; Muus, 1967; Wolff, 1973), the reason for this has not been determined. Where young Hydrobiae have been observed to float by either producing a

mucous raft or air bubble or subsequent to the shell becoming dry, the behaviour has been described as effecting dispersal such that the animals are passively transported to other parts of an estuary (Muus, 1967; Wolff, 1973; Little and Nix, 1976). Anderson (1971), however, found predominantly large animals floating at high tide from the top of objects on the upper-shore and suggested that this behaviour was only performed to aid in the dispersal of the newly hatched young. However, he could not correlate floating behaviour with the breeding season. Recent work has shown that in a population of size classes up to 4.95mm, the majority of floating animals were smaller than 1.45mm. This behaviour was only found during the summer when floating of the young or adults with egg masses would lead to greater dispersal (Little and Nix, 1976).

(iii) Life Cycle, Reproduction, Growth and Mortality.

This species is bisexual, with copulation preceding fertilized egg laying by the female. Each female produces about 300 eggs per season (Linke, 1939) which are laid in capsules on the shells of other Hydrobiae and on other objects on the shore; this prevents the eggs from being covered by silt. Capsules usually contain between 5 and 25 eggs (up to 60 maximum) with an average of between 8 to 15 (Muus, 1967; Anderson, 1971; Warnes, pers. comm.). Although the breeding season varies with latitude, the spawning maximum in Britain occurs during the period April to July (Rothschild, 1940; Stopford, 1951; Muus, 1967; Green, 1968; Warnes, pers. comm.) although egg capsules have been found during most months. The eggs hatch after 8-10 days to produce veliger larvae which are, to a lesser or greater extent, mobile and which then stay close to the sediment and metamorphose after a short

time, possibly 8-10 days (Thamdrup, 1935; Muus, 1967). Veliger larvae have been found in the plankton at the same time as egg capsules found on adults (Thamdrup, 1935; Anderson, 1971; Fish and Fish, 1977).

The species probably matures at the end of the first year (Rothschild, 1941) or second year (Anderson, 1971) and has a normal life cycle of one and a half to two and a half years leading to a maximum size of 4.5 - 5mm for the species (Smidt, 1951; Muus, 1967; Anderson, 1971). The growth of H. ulvae may be correlated with the availability of diatoms of a particular size range (Fenchel and Kofoed, 1976) or the presence of fine, as opposed to coarse, substrate (Anderson, 1971; Fish and Fish, 1974; Fenchel, 1975b) and may be density dependent (Anderson, 1971). This latter author also found that the smaller animals at the lower part of the shore on coarse substrate grew more slowly and matured later than the high-shore animals living on fine, thixotrophic mud.

Several authors have suggested that the large densities of Hydrobiae are a result of their high fecundity and low mortality rate after the juvenile stage (Muus, 1967; etc.) and that after this stage, mortality is due to senility. However H. ulvae has many predators including Nereis and Carcinus (Clay, 1967a) while Ankel (1936) (in Clay, 1967a) states that the opisthobranch Retusa truncatula is its characteristic predator on mud-flats and Muus (1967) suggested that large populations of R. obtusa would perceptibly influence the mortality of H. ulvae. H. ulvae is also an important prey item for wading birds and shelduck (Davidson, 1971; Prater, 1972; Bryant and Leng, 1976; Goss-Custard

and Jones, 1976; and J.M. Warnes, pers. comm.) and large flounders (Summers, 1974). However, in some of these studies a large proportion of intact or only partly digested H. ulvae have been found in the predators' faeces.

The literature, reviewed above, shows that although many workers have studied certain aspects of the biology of H. ulvae, the causes of the variation in the animals' distribution and abundance within an intertidal area have not been studied. Similarly, although many workers have suggested that the animals play a large part in the transfer of energy along estuarine food chains, until recently (Wolff and De Wolf, 1976) the role of H. ulvae had not been quantified in terms of the production and potential food available to the predators in the ecosystem. The present study was designed to elucidate these latter aspects of this species' ecology.

5.1.2. Retusa obtusa (Montagu).

Members of the opisthobranch genus Retusa were at first thought to be uncommon in muddy estuarine areas. However, the literature suggests that once identified they are common. The species R. mammilliata (Philippi), R. retusa (Maton and Rackett) and R. obtusa have been recorded from south west England (M.B.A., 1957). Ankel (1936) (in Clay, 1967a) found R. truncatula (Bruguière) in Danish waters and Hurst (1965) found R. obtusa, R. umbilicata (Montagu) and R. truncatula in the Øresund, Helsingør, Denmark and R. obtusa in the Barry Inlet, South Wales. McMillan (1968) describes R. retusa, R. alba (Kamacher) (i.e. R. obtusa), R. mammillata and R. subcylindrica (Brown) in British waters. The last two species are described as local but widely

distributed whereas the former two are more common. The species R. retusa is more common on shallow sublittoral muddy ground whereas R. obtusa is more common intertidally in muddy estuaries and brackish waters (McMillan, 1968) and has been recently studied in north European waters (Muus, 1967; Smith, 1967a, b; Wolff, 1973; Thompson, 1976).

R. obtusa, the only species encountered in the Forth estuary, is the most familiar of the Retusae although there is a typical form which has a distinct tapering spire to the shell and a flat-topped variety pertenuis which lacks such a spire and is probably more common in finer deposits (Thompson, 1976). Individuals of both the normal variety of R. obtusa and the variety pertenuis were recovered from Torry Bay. It is possible that the combined treatment of both varieties may lead to some of the ambiguities in the population dynamics of the species.

Smith (1967a) suggests that R. obtusa is only found intertidally in sheltered areas and that its normal habitat is sublittoral. Hurst (1965), however, found this species both intertidally and sublittorally; furthermore the species has been observed intertidally in Danish estuaries (Muus, 1967), Dutch estuaries (W.J. Wolff, pers. comm.), the Dovey estuary (J.D. Fish, pers. comm.), the Ythan estuary (Anderson, 1971), the Solway Firth (Perkins, 1974). It has not been found however, on the Tees estuary (J.S. Gray, pers. comm.) or the Lyhner (R.M. Warwick, pers. comm.). It is considered that this species is present in most estuarine areas where H. ulvae is present, although its absence from some areas may be the result of slow recolonisation of areas because of the species' non-pelagic mode of reproduction. Sublittoral findings of R. obtusa may be of the similar R. retusa.

Muus (1967) recorded R. obtusa from an unpolluted shallow bay, with a soft-sandy-clay bottom covered with dense Zostera and other macrophytes and with a salinity in the range 23-28⁰/oo. Hurst (1965) found the species on fine silty-mud intertidally in the area subsequently studied by Smith (1967a, b), the Barry Inlet, South Wales, which had a dominant macrofauna composed of Corophium, Hydrobia, Nereis and Macoma. Wolff (1973) found R. obtusa only in the marine reaches of estuaries, areas of > 12⁰/oo salinity during normal river discharge, in areas of fine and muddy sands M.P.D. 1.61 - 3.02 ϕ (125-332 μ m) with the bulk of observations in sediments 125-166 μ m M.P.D. He found it intertidally as well as in tidal channels, but it was lacking from the zone just below mean H.W. level where H. ulvae was abundant and suggested that it was not able to tolerate the long period of immersion at that zone.

It has long been suggested that R. obtusa feed on Hydrobiae (Jeffreys, 1867; Muus, 1967; Smith, 1967a; Anderson, 1971; Wolff, 1973), on foraminiferans (Pruvot-Fol, 1954; Hurst, 1965; Smith, 1967a; Wolff, 1973) together with copepods, R. obtusa juveniles and Rissoids (Hurst, 1965; Wolff, 1973). This feeding pattern is similar to that given for other shelled opisthobranchs by Hurst (1965). However, the feeding of R. obtusa is somewhat different to that of other shelled opisthobranchs in that it does not have a proboscis, buccal mass or radula and probably feeds by suction. Retusae compensate for this loss by having a large crop and well developed gizzard with internal plates which allows for the ingestion and digestion of large amounts of food (Hurst, 1965). Smith (1967a) found that an adult Retusae of 2.5mm length would ingest Hydrobiids of up to 0.5mm in length.

The life cycle and breeding of R. obtusa, have been investigated by Smith (1967a) who found that it has an annual life cycle with the adults dying after spawning in the spring and is a protandrous hermaphrodite with each adult producing a mean of 33 eggs in one to four egg masses (Smith, 1967a). The onset of breeding occurs in late March in South Wales and early summer in the Netherlands (Wolff, 1973). Thompson (1976) suggests that tiny egg masses are produced which are attached to the shells of the adults and that this is an unusual occurrence in opisthobranchs. There is no planktonic larval stage, again an unusual occurrence, and the microscopic young, miniature adults hatch after a few weeks (Thompson, 1976).

Therefore, although the ecology of this species has been studied to some extent, the role of opisthobranchs in general, and R. obtusa in particular, in the estuarine food web has not been previously studied. The present work was undertaken in order to quantify the production ecology of this species, to study its relationship within the intertidal area, and to study the production of this carnivore in relation to that of one of its prey species, H. ulvae.

5.2. Materials and Methods.

The populations of H. ulvae and R. obtusa were monitored in the field (see Section 2.2.2.). Information on the population dynamics, abundance and distribution was obtained.

At each station and sampling occasion, total numbers and dry weight of H. ulvae retained in 2 x 5x5x5cm cores and sieved over a 500µm sieve were obtained. During July, 1975, the calculated animal densities obtained from 2 x 125cm³ cores were compared with those obtained from 5 x 125cm³ cores and found to be within 10% of the latter. It was decided therefore that only two cores would be used for H. ulvae population determination.

The animals were removed from the sediment under low magnification, dried at 60°C for 14 days and the total sample weight obtained. Thus for each station at each month the total numbers m⁻², dry weight g m⁻², and mean individual weight (M.I.D.) were obtained. In addition, at each station from March to June, 1975, the individual lengths were measured and the proportion of dry flesh weight (fdw) in the total dry weight (tdw) was obtained by decalcifying the animals in 10% hydrochloric acid; this latter proportion was then applied to specimens in which only the tdw was known. After this initial four-month period it was decided that, because of the importance of the bivalve molluscs on Torry Bay and of the research being performed on other areas of the Forth estuary, the research effort in this study was concentrated on the bivalves and the analysis of the H. ulvae population was reduced.

As estimates of the size and weight distribution of individual H. ulvae were not made for each sampling occasion and

station, it was not possible to use the conventional methods of calculating production (see Section 3.2.3.). Therefore the production of this species was calculated utilizing estimates of the population respiration and biomass. Englemann (1966) initially quantified the relationship between the population annual respiration (R) and annual production P, including somatic growth, eggs and exuvia) of terrestrial species by regressing data from studies where both parameters had been determined. McNeil and Lawton (1970) developed this logarithmic relationship further by including studies on aquatic animals, omitting some atypical data and correcting other data used by Englemann. It has been suggested that the respiratory costs at any level of production in a long lived poikilotherm population tend to be higher than in short lived poikilotherms. McNeil and Lawton (1970), therefore, differentiated the data for P on R for poikilotherms into long and short lived species; the latter having a life span of less than two years.

Miller et al (1971) further revised the P/R relationship for long lived marine invertebrates to include additional data for larger poikilotherms. Their equation, given below, was therefore thought to be more accurate than the initial equation and was considered suitable for H. ulvae :

$$P = 0.6640 R^{0.8517}$$

where P and R are in Kcal m⁻² yr⁻¹. This method, of estimating production by determining population respiration, produces final estimations in which the confidence intervals, if measured by taking into account the errors over each step of the method, are rather large (McNeil and Lawson, 1970; Phillipson, 1970; Miller et al, 1971), however it is still considered that major

conclusions are not affected by these inaccuracies and that the final estimates are of the appropriate magnitude.

Determination of the respiration rates of Hydrobiids have been made by Negus (1968) and Fenchel (1972), together with an estimation cited by Fretter and Graham (1962) which appears to be four orders of magnitude greater than that for other comparable invertebrates. The respiration rate in the first study was determined with many animals placed in water in a vessel such that few values are given for the size/ O_2 uptake relationship. The size/ O_2 uptake relationship given by Fenchel (1972) was considered comparable with rates for other marine or estuarine animals of approximately the same size and has therefore been employed in the present study.

A Q_{10} value of 2.05 has been used to determine the O_2 uptake of animals at different environmental temperatures. This value was determined by Miller et al (1971) by regressing respiration on temperature data from published data regarding fourteen species of temperate marine poikilotherms. A correction for temperature fluctuations is necessary as respiration rates in poikilotherms, unless acclimated in which case there is constant O_2 uptake with temperature variation, are temperature dependent.

The individual respiration rates at each field temperature were calculated from the data of Miller et al (1971) and Fenchel (1972)(Table 5.1). Utilizing the data of mean size, respiration rate, temperature and time, the monthly population respiration rates were summed for each station and converted to litres of O_2 uptake by the factor :

$$1 \text{ g } O_2 \equiv 0.7 \text{ l } O_2 \quad (\text{Crisp, 1971}).$$

Table 5.1 The Calculation of the Respiration Rate of Hydrobia
ulvae (as $\mu\text{g O}_2/\text{mg tdw/hr}$) at Each Temperature Using
the Data of Miller et al (1971) and Fenchel (1972).

tdw (mg)	temperature	5°C	10°C	15°C	20°C
0.25		0.109	0.156	0.223	0.320
0.5		0.086	0.127	0.182	0.260
1.0		0.082	0.117	0.168	0.240
1.5		0.078	0.112	0.161	0.233
2.0		0.077	0.110	0.157	0.225
2.5		0.075	0.107	0.154	0.220
3.0		0.072	0.102	0.147	0.210
3.5		0.071	0.101	0.145	0.208
4.0		0.070	0.100	0.143	0.205

The annual population respiration was then converted to energy units by the oxycalorific equivalent :

$$1 \text{ l } O_2 \text{ respired} \equiv 4.825 \text{ Kcals} \quad (\text{Crisp, 1971})$$

The annual population production was then determined using the equation given by Miller et al (1971) as $\text{Kcals m}^{-2} \text{ yr}^{-1}$. However, although it is considered more valid to give parameters of an animals' energy budget in energy units (Crisp, 1971; Grodzinski et al, 1975) as the study is ultimately concerned with the energy partitioning in the ecosystem, the majority of previous studied concerning intertidal invertebrate ecological energetics have given estimations as weights of total animals or the flesh content of the animals (shell-free or ash-free dry weight)(Burke and Mann, 1974; Chambers and Milne, 1975b; Warwick and Price, 1975; Wolff and De Wolf, 1976; etc.). This trend is continued here although corresponding energy values are given for comparison (see Section 5.3.3.).

The production energy units have been converted into g flesh dry weight by assuming a calorific value of $5 \text{ Kcals g}^{-1} \text{ fdw}$, a value derived from studies on comparable species (Cummin and Wuycheck, 1970; Slobodkin and Richman, 1971; Thayer et al, 1973). Thayer et al (1973) suggest that when compared to estimates based on ash-free dry weight, decalcification of molluscan tissue does not lower the calorific value of a species.

The method used for the calculation of population respiration is as accurate as the "best estimate" method of Phillipson (1970) in which equal weighting is given to all life stages and the oxygen consumption is determined. The determination is probably within 10% and possibly within 5% of an estimation derived from a more detailed knowledge of the size class structure of the

population and the field temperature fluctuations (Phillipson, 1970; McLusky and McFarlane, 1973).

Retusa obtusa individuals were removed from both large and small samples such that 0.1m^{-2} and 0.0125m^{-2} were respectively sampled for large (width $>2\text{mm}$) and small (width $< 2\text{mm} > 0.5\text{mm}$) animals. By combining both types of samples and converting the numbers obtained in the small samples to an equivalent for the large samples, population estimates could be determined. The length of these animals was measured and their individual dry weight obtained. The ash-free dry weight of a random sample of the large animals from September, 1975, onwards was also determined. The population production (P) and elimination (M) of R. obtusa has been calculated using the methods given by Crisp (1971)(see Section 3.2.3.).

5.3. Results.

5.3.1. The Abundance and Biomass of H. ulvae.






The population density of H. ulvae fluctuated both spatially and temporally within wide limits (Fig. 5.1). All stations supported higher levels during the summer months and, if the large influx of animals into each station is assumed to occur subsequent to spat settlement, then the main spatfall in 1975 was during August (for A1, B2, B1, C4, C5 and C2), July (B5) and September - October (A2, B3 and C5). The animals were retained from a length of 600 μ m which, as their settling size is 300 μ m (Fish and Fish, 1976), omitted only the recently settled animals. The spat growth rate would result in the animals being caught with a 500 μ m mesh after a maximum of three weeks.

In 1976, population density maxima were recorded in the August and November samples, possibly missing the majority of spat which settled in August and did not survive until November. However, the monthly sampling at Station B3 indicated that the quarterly sampling did not miss a large spatfall. It may therefore be suggested that at most stations the 1976 spatfall was lower than in 1975 (this has also been found for the upper Forth, J.M. Warnes, pers. comm.), although at A3 and A4 the population density maxima for the two years were similar.

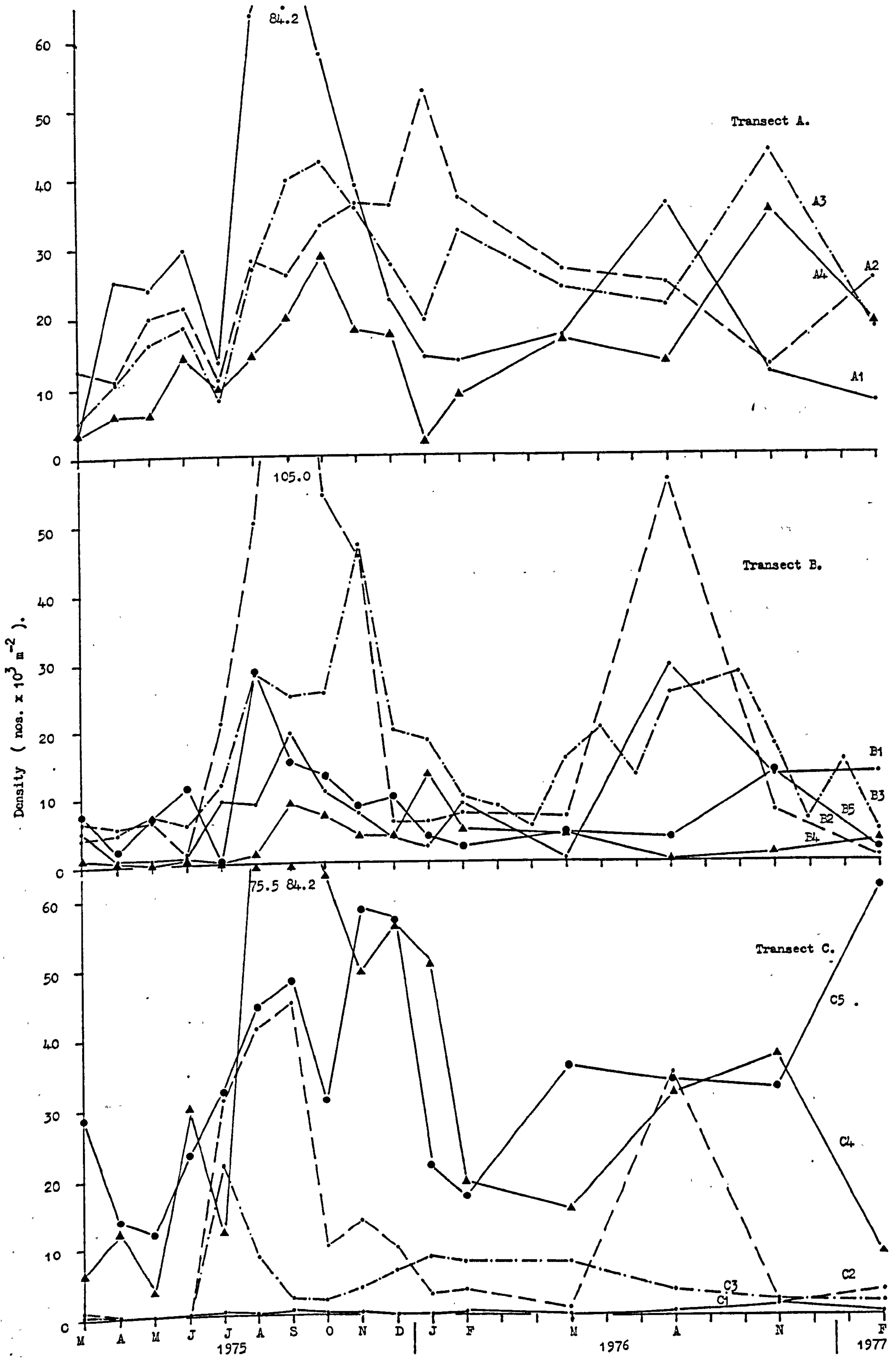
The high-shore stations of Transects C and A had population densities that were more constant than the low-shore stations (Fig. 5.1); the latter generally had high numbers of newly-settled individuals at certain times of the year and low population levels for the remainder of the year, e.g. compare Stations A1 and C2 with C4, C5, A2 and A3 (see Section 5.3.2.). However, A4 also

Figure 5.1 H. ulvae : The Density at Each Station on Each Sampling Occasion.

Legend

Transect	A	B	C
	1	1	1
	2	2	2
	3	3	3
	4	4	4
		5	5





had very high numbers at certain times of the year whilst supporting large populations throughout the year. Transect B stations showed greater fluctuations than Transects A or C and, within the transect, Stations B1-B3 showed much greater fluctuations in population densities than B4 and B5, which had relatively stable Hydrobiid populations. Stations B2 and B3 also supported high levels during the settlement periods and for three months afterwards whilst maintaining low levels for the remainder of the year. Similarly, Stations C4 and C5 also had large fluctuations in numbers whilst continuously supporting high population levels, whereas C1 and C3 had constantly low levels and C2 had high levels only during settlement. On Transect A, A1 also showed much greater fluctuations than the other stations, initially attributable to the large settlement during the period August to September at this station.

In comparing stations, the large inflow of newly settled animals to the dense mussel-bed at Station B2 appeared unusual as the corresponding Station C1, situated on similar substrate and mussel-density, received very few animals. It is suggested that the difference in tidal height (C1 1.27m, B2 2.97m above C.D.) was responsible for this anomaly. It is initially suggested that the settlement of H. ulvae was possibly of a passive nature such that the greatest settlement occurred in fine mud areas but also that the tidal height of an area affected settlement (see below). Station C3 was slightly lower than B2 but had a much coarser substrate type and subsequently received a relatively low spatfall. Additionally, the spat inflow to this station in June, 1975, was considerably earlier than most other stations.

As newly settled spat added proportionally less to the

station biomass than did larger animals, the fluctuations of biomass throughout the year were smaller than those of population density at each station (Figs. 5.1 cf. 5.2). The stations can therefore be grouped into three types according to the size of the populations that they support (Fig. 5.2) :

(i) stations with large biomasses for the year together with summer settling peaks, A2-A4, C4 and C5;

(ii) stations with very low, stable biomasses through the year, B1, B4, C1 and C2;

(iii) stations with low biomasses for most of the year but which have higher biomasses with large spat settlements, B2, B3, B5 and A1, and C3 to a lesser extent.

The observed differences in biomass levels were only slightly lower in 1976 than 1975.

The average population size for Torry Bay (Fig. 5.3; Table 5.2) shows the large differences between the two years sampled and, although the main settling peaks may have been missed during the quarterly sampling of 1976-77, the population levels immediately after that period, in November, were still lower than in 1975. The winter-spring population levels observed over the two sampling years (March-May, 1975, January-May, 1976, February, 1977) suggest that there was a relatively stable population of H. ulvae on Torry Bay, a point especially interesting if the levels of spawning and settling in 1976 were lower than in 1975.

In considering the mean population (in 1975-76)(Table 5.3), some areas on Torry Bay supported up to 40000 Hydrobiids m^{-2} throughout the year whilst others had an average yearly population of less than 200 individuals m^{-2} . Stations which

Figure 5.2 H. ulvae : The Total Dry Weight
Biomass at Each Station on Each
Sampling Occasion. (Legend as
Fig. 5.1.)

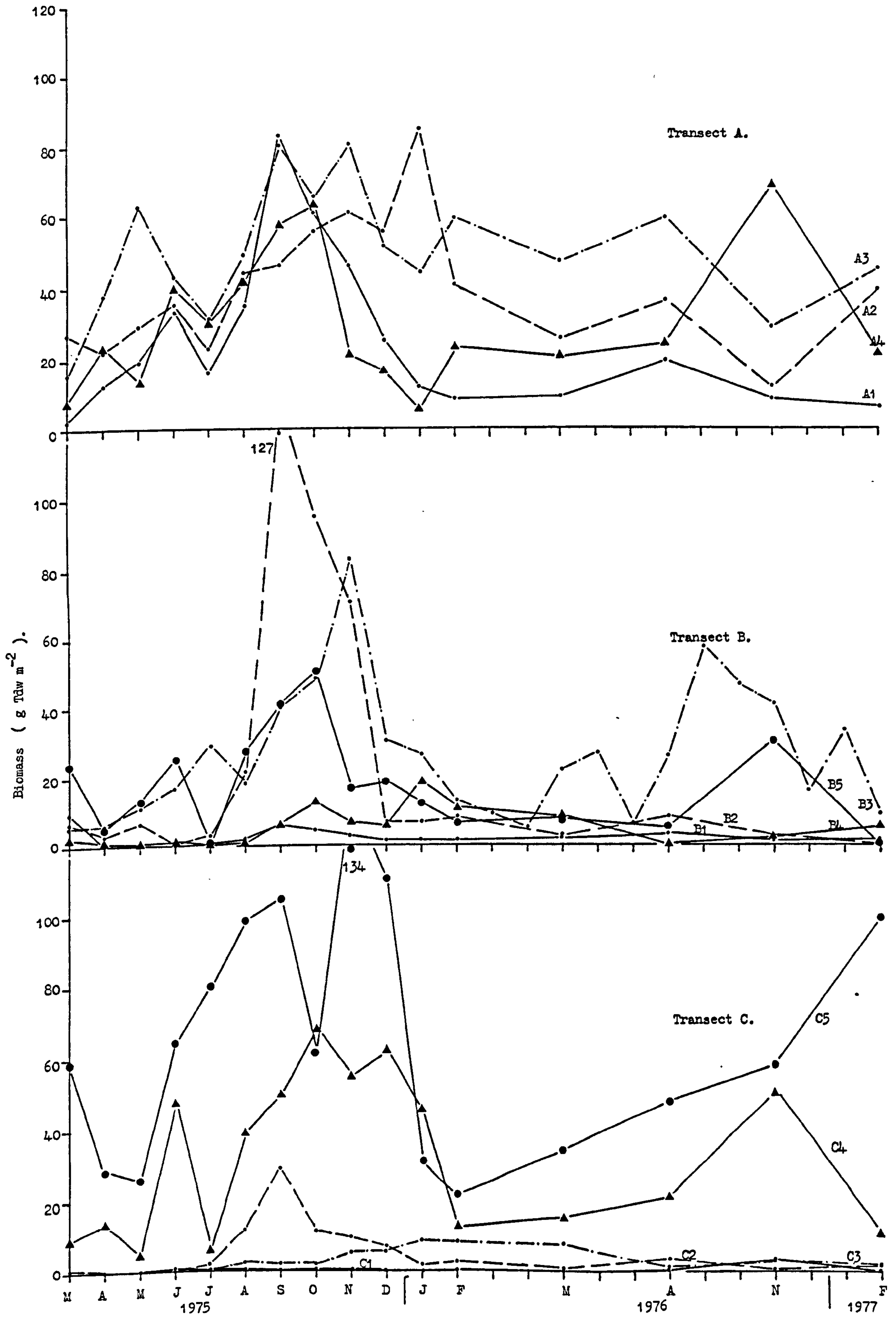


Figure 5.3 H. ulvae ; The Mean Density (Solid Line) and Total Dry Weight Biomass (Broken Line) For the Torry Bay Population at Each Sampling Occasion.

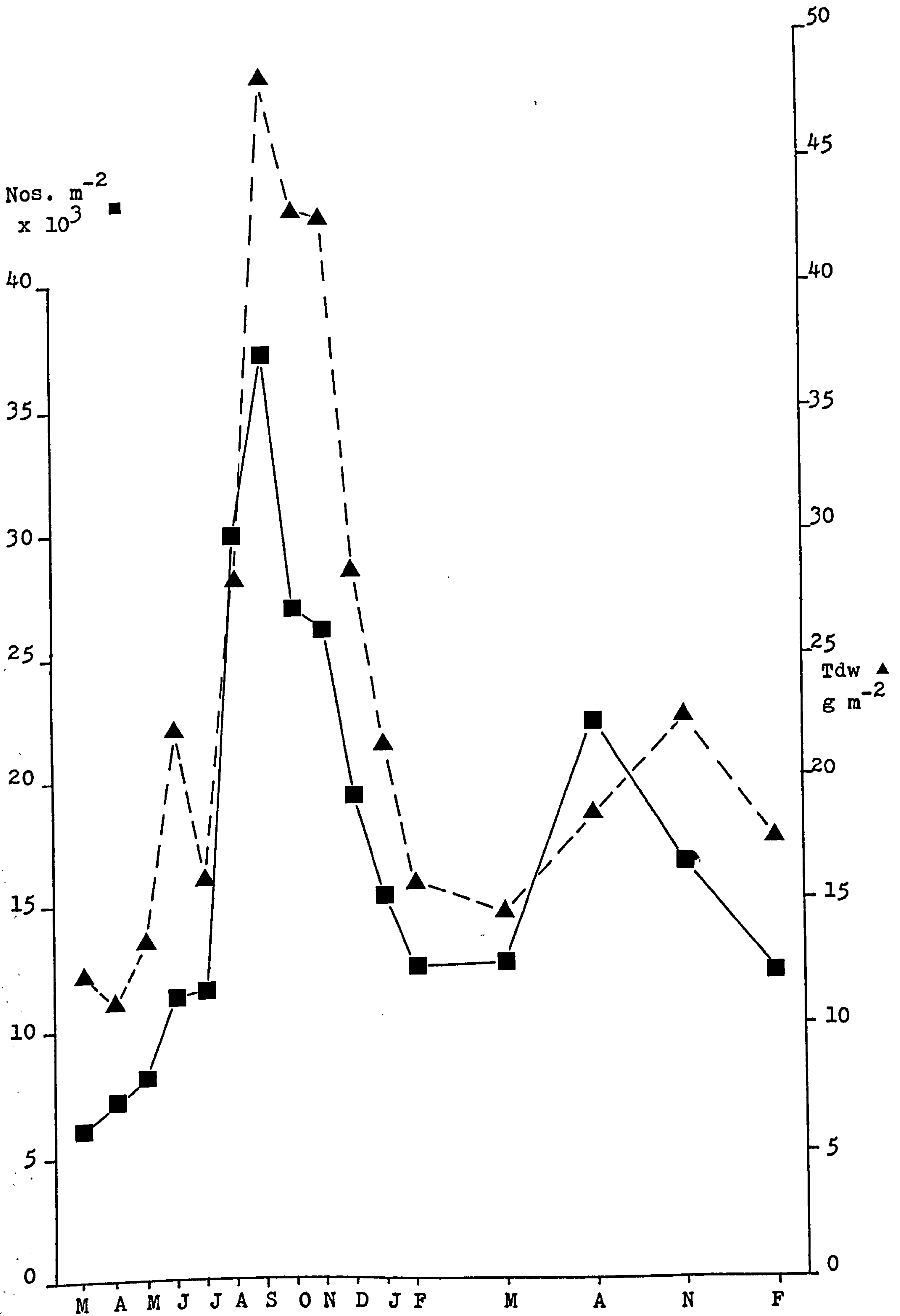


Table 5.2 The Monthly Mean Density, Biomass and M.I.W. of H. ulvae (1975-76 Data). ($\bar{x} \pm 1$ S.D.)

Year	Month	$\bar{N} \text{ m}^{-2}$ x1000	tdw m^{-2} (g)	M.I.W. (mg)
1975	March	6.04 \pm 7.36	15.941 \pm 12.205	1.78 \pm 0.85
"	April	6.67 \pm 7.33	11.044 \pm 12.533	1.78 \pm 1.15
"	May	7.41 \pm 7.92	13.404 \pm 17.431	1.65 \pm 0.99
"	June	11.27 \pm 11.45	22.036 \pm 22.240	1.53 \pm 1.04
"	July	11.55 \pm 10.32	15.925 \pm 22.414	1.40 \pm 1.31
"	Aug.	29.95 \pm 22.87	28.170 \pm 26.720	1.07 \pm 0.84
"	Sept.	37.30 \pm 32.78	48.195 \pm 39.461	1.35 \pm 0.87
"	Oct.	27.01 \pm 21.12	42.906 \pm 30.427	1.60 \pm 0.82
"	Nov.	26.13 \pm 20.13	42.465 \pm 40.267	1.42 \pm 0.61
"	Dec.	19.22 \pm 18.45	28.538 \pm 31.560	1.33 \pm 0.52
1976	Jan.	16.46 \pm 16.95	21.380 \pm 23.628	1.50 \pm 0.86
"	Feb.	12.33 \pm 10.83	15.687 \pm 16.565	1.35 \pm 0.82

Table 5.3 The Mean Density, Biomass and M.I.W. of H. ulvae at Each Station (1975-76 Data). ($\bar{x} \pm 1$ S.D.)

Station	$\bar{N} \text{ m}^{-2}$ x1000	tdw m^{-2} (g)	M.I.W. (mg)
A1	32.48 \pm 24.31	29.774 \pm 23.736	0.93 \pm 0.25
A2	27.19 \pm 12.58	44.061 \pm 18.472	1.70 \pm 0.28
A3	23.15 \pm 12.33	51.948 \pm 19.251	2.51 \pm 0.86
A4	12.27 \pm 7.87	28.795 \pm 18.577	2.56 \pm 0.80
B1	6.48 \pm 5.41	2.604 \pm 2.797	0.44 \pm 0.47
B2	26.24 \pm 31.53	32.158 \pm 44.146	0.95 \pm 0.50
B3	17.15 \pm 12.61	27.489 \pm 21.879	1.67 \pm 0.58
B4	3.74 \pm 4.06	5.664 \pm 6.133	1.54 \pm 0.63
B5	9.06 \pm 7.63	20.117 \pm 14.683	2.50 \pm 0.78
C1	0.17 \pm 0.19	0.117 \pm 0.143	0.78 \pm 0.56
C2	3.60 \pm 2.80	6.282 \pm 8.518	0.57 \pm 0.32
C3	3.51 \pm 3.32	3.214 \pm 3.201	0.82 \pm 0.38
C4	38.45 \pm 28.16	34.347 \pm 23.590	0.99 \pm 0.36
C5	32.20 \pm 16.10	68.444 \pm 37.838	2.08 \pm 0.42

maintained low population for most of the year but had larger populations during settlement, had yearly averages in which $\bar{x} < 1$ S.D. (e.g. B1, B2, B4, C1 and C3). The table also again demonstrates that the stations at the higher tidal levels support larger animals. These points will be considered in more detail below.

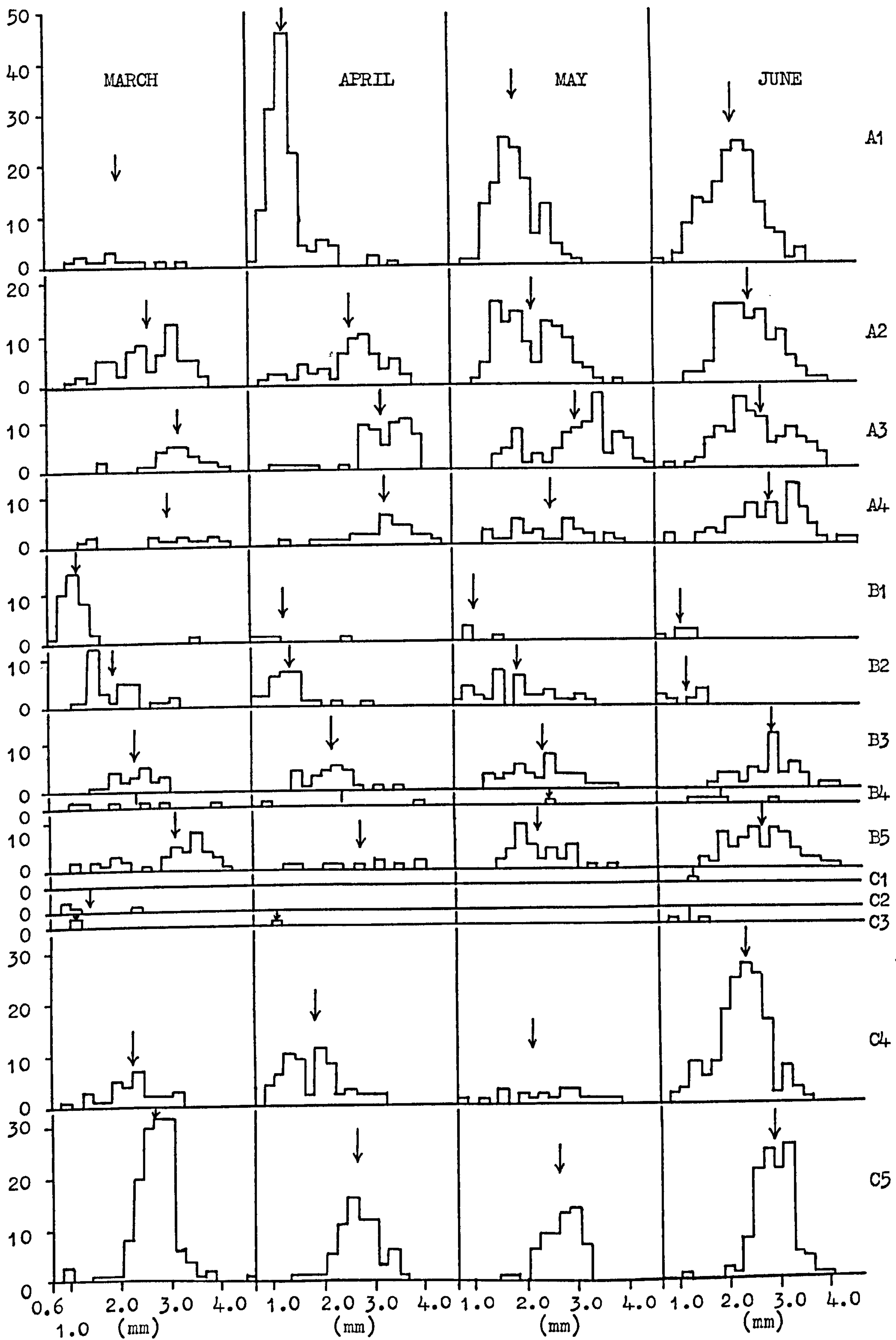
5.3.2. The Spatial and Temporal Variation in the Mean Size and Weight of H. ulvae.

5.3.2.1. The Size-frequency Distribution of H. ulvae.

The size-frequency histograms (Fig. 5.4) for each month during the period March-June, 1975, show that the mean size of H. ulvae at each station increased with an upshore progression along each transect. In addition, whereas the Stations A1, B1, B2, C4 and C5 had a relatively unimodal distribution for each month, others showed a bimodal distribution as expected for a species with a 2+ year life span, e.g. A2, A3, A4, B3 and B5.

On Transect A, A1 was dominated by first year (0+ group) animals (< 2mm length) whereas the Stations A2-A4 were populated by larger animals. However, whereas the mean individual size at the latter stations stayed relatively constant, that at Station A1 increased such that by early summer the mean sizes of all four stations were relatively similar. This may reflect both the position of the first year animals on the sigmoid growth curve and the necessity in the older animals to divert energy into reproduction. A similar situation was found on the other transects where the lower stations supported populations of small animals whereas larger individuals were found at the upper-shore stations; however, stations such as B3, B5 and C4 contained both

Figure 5.4 H. ulvae : The Size-frequency Histograms
For Each Station For the Months March to
June, 1975. Ordinate as Nos. Sampled.
(↓ Denotes Mean Size at Sampling Occasion.)



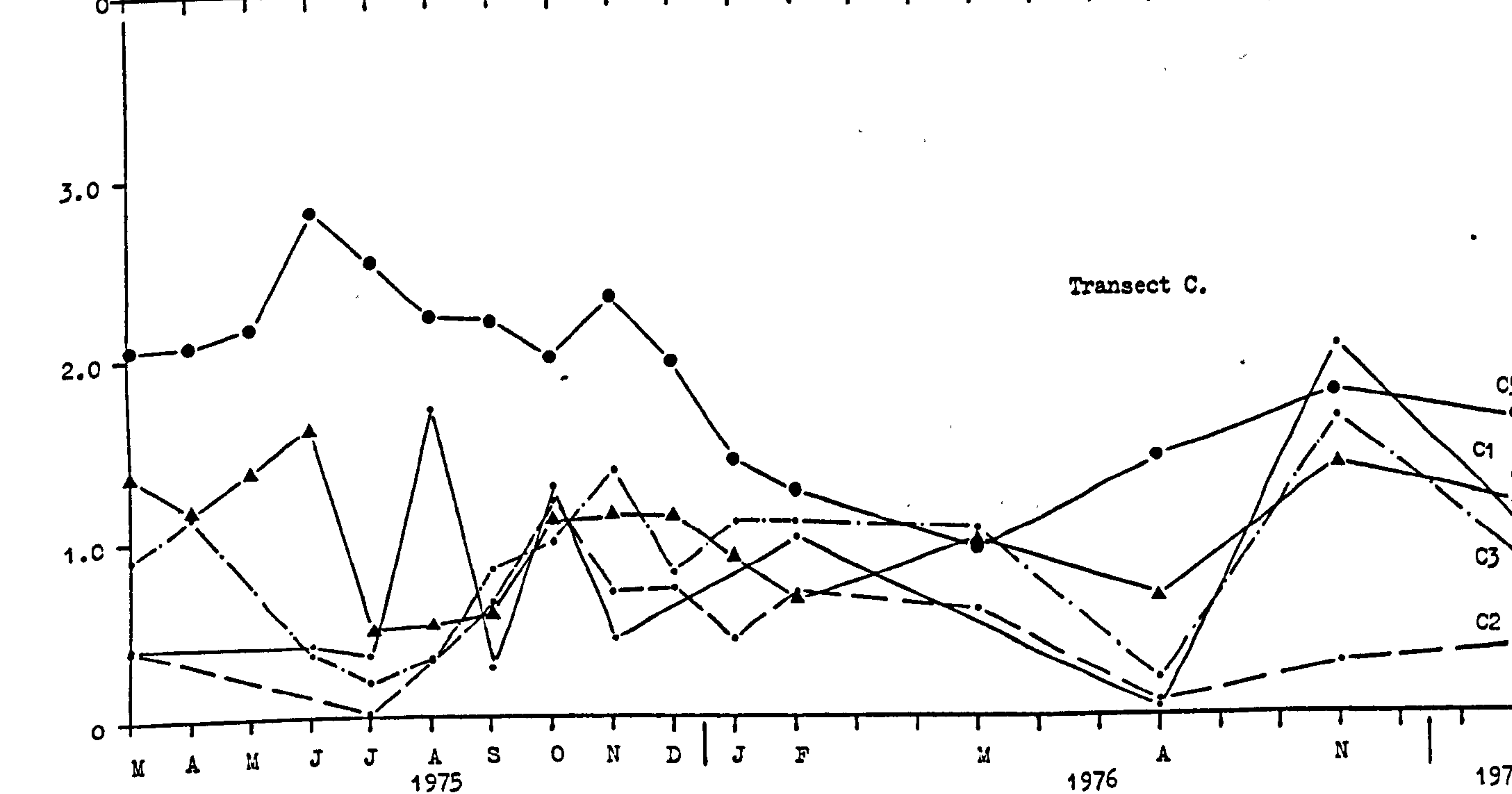
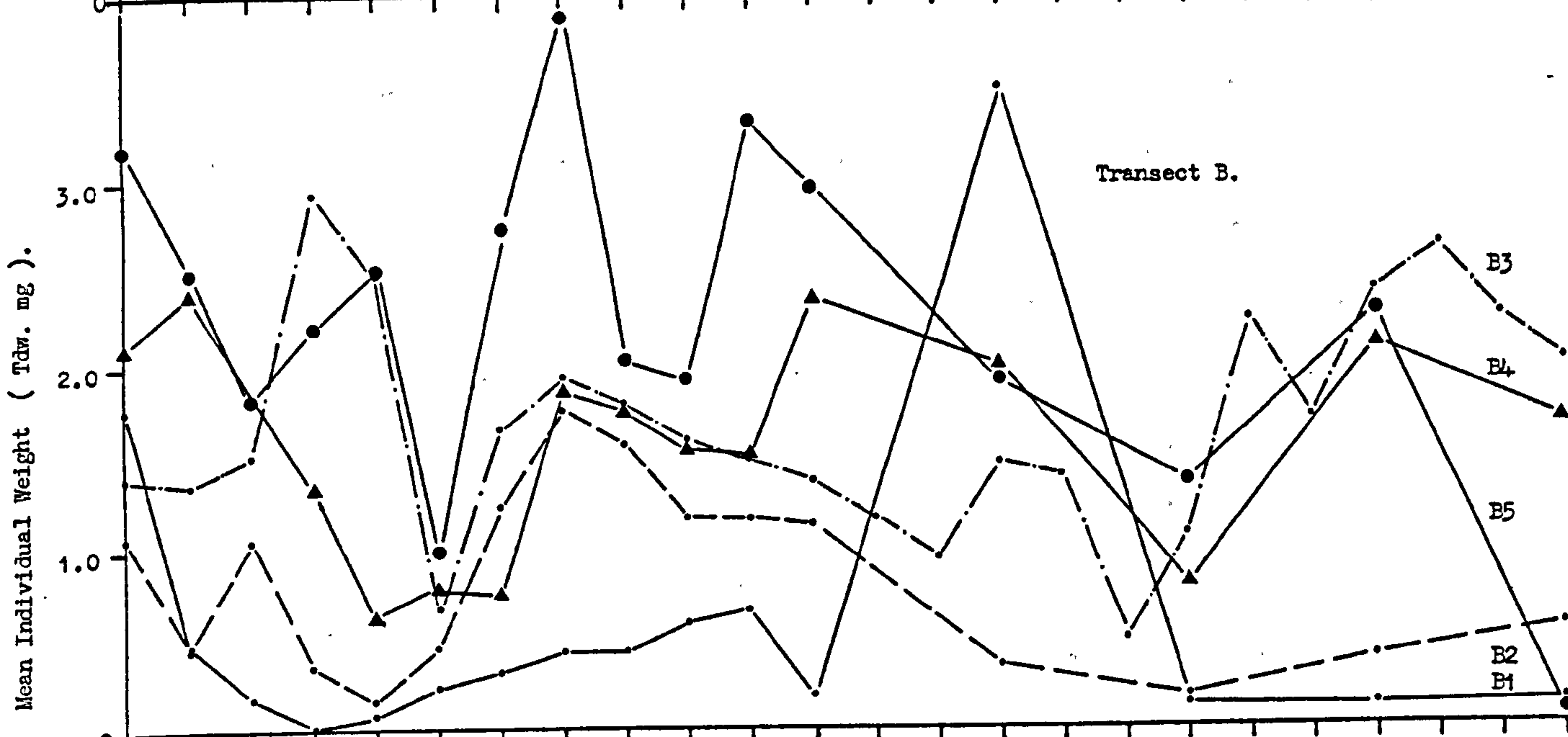
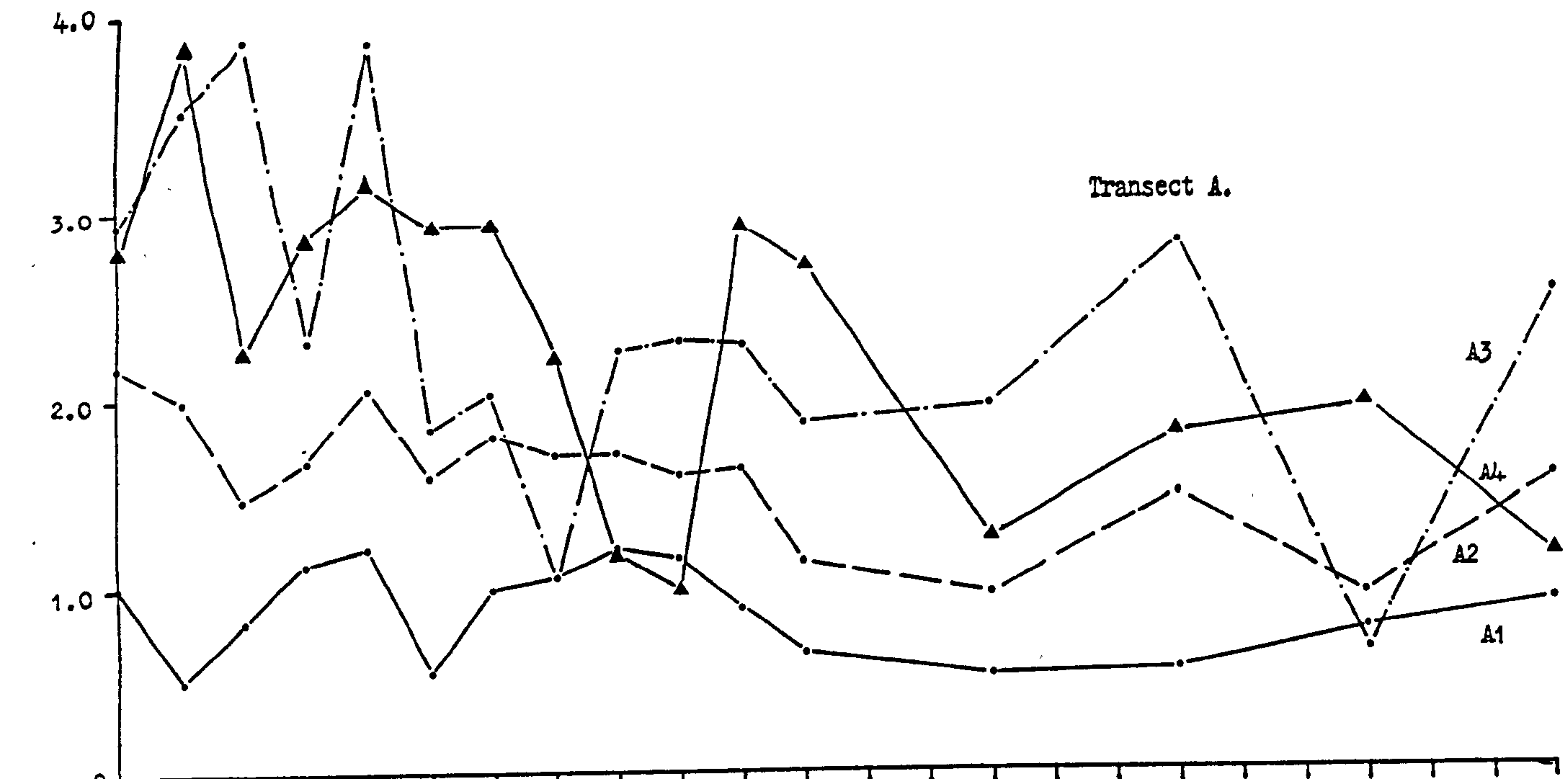
large and small elements in the population. The histograms also demonstrate the population size at each station; the Transect A and upper Transect C stations supported much larger populations than the other stations. However, this is thought to be a seasonal phenomenon and is considered in greater detail below.

5.3.2.2. The Variation in M.I.W. For Each Station and Sampling Occasion (Fig. 5.5).

The M.I.W. for each station population was influenced by weight changes both due to reproduction and emaciation, by the inflow of spat and by the death of larger, senescent animals and is therefore of limited value. At stations with a unimodal population distribution (Fig. 5.4) the M.I.W. accurately indicates the individual weight of the majority of the population at that station; however, at other stations, where there is no such distribution, then the M.I.W. will be less representative.

Many stations (C1-C4, B2-B5, A1 and A2) showed minimal M.I.W. values during the period July to September in each year which may be attributed to settlement at those stations. Of the remaining stations the minimum value at C5 was during the spring, 1976, and that at A2 and A3 was during October to December, 1975. It is likely that at these latter stations, the M.I.W. minima may have been caused by an influx of small animals from other stations; it may be initially suggested that the animals are moved to more favourable stations for the adult population after some growth at the lower stations. Although the graphs show large seasonal variations, an increase in individual size with an increase in tidal height of the stations on each transect is again evident. In addition, for those stations where usually very few and occasionally no animals were found, e.g. C1, B1 and B4, the

Figure 5.5 H. ulvae : The Mean Individual
Total Dry Weight at Each Station
and at Each Sampling Occasion.
(Legend as Fig. 5.1.)



curves show very large amounts of variation; an extrapolation from the preceeding and succeeding months M.I.W. data has been used for those months when no animals were sampled at these stations.

5.3.3. The Production of H. ulvae.

The method of derivation of station production is shown in the example of Station A1 from 1st. March, 1975 to 29th. February, 1976 (Table 5.4). The production and biomass data at each station are summarised (Table 5.5; Fig. 5.6a) for 1975-76 and reflect not only the large variation in H. ulvae populations over the whole of the area but also within restricted transects and between adjacent areas, e.g. A3 cf. A4, C4 cf. C5. The close linearity of the production to biomass relationship initially suggests that the productivity within the bay was relatively uniform. However, the figure 5.6b shows that this was not the case and demonstrates the negative curvilinear relationship between the size of animals found at any particular station and the P/\bar{B} of those animals, i.e. the smaller the animals within a population the higher its productivity. This is a reflection on both the decreasing growth rate with increasing age and size and the fact that respiratory costs in a long lived population increase with age.

The Tables 5.6 and 5.7 give the calculated production and mean biomass data and their conversion as energy units for both sampling years. Although the mean area production and \bar{B} estimates were somewhat lower in 1976-77 than in 1975-76, there was no significant difference between the years. The P/\bar{B} ratios for each year were similar and again there was no significant difference. The effect on the production estimates of sampling on a quarterly as opposed to a monthly basis can be seen from the

Table 5.4 The Computation of H. ulvae Production.
e.g. Station A1, 1975-76 Data.

Month	I	II	III	IV	V	VI	VII
March	2.62	1.008	2600	6.5	0.082	744	159.841
April	12.72	0.505	25200	5.0	0.086	720	787.622
May	19.94	0.831	24000	12.0	0.117	744	1735.737
June	33.72	1.131	29800	14.0	0.168	720	4078.771
July	16.25	1.202	13520	16.3	0.168	744	2031.120
Aug.	35.12	0.554	63400	20.0	0.260	744	6793.613
Sept.	83.024	0.986	84200	15.5	0.168	720	10042.583
Oct.	60.978	1.051	58000	11.5	0.117	744	5308.013
Nov.	46.278	1.193	38800	10.5	0.117	720	3898.459
Dec.	25.550	1.141	22400	7.0	0.082	744	1558.754
Jan.	12.366	0.871	14200	8.0	0.117	744	1076.436
Feb.	8.724	0.641	13600	4.0	0.086	696	522.184
							<u>37993.133</u> <u>mg O₂/m²/yr</u>

Column I = Biomass (tdw g m⁻²)

II = M.I.W. (mg tdw)

III = Population density (nos. m⁻²)

IV = Mean of air and water temperatures for the sampling period (°C).

V = Individual respiration calculated from Table 5.1 using M.I.W. and temperature in µg/mg tdw O₂ uptake per hour.

VI = Length of sampling period (hrs)

VII = Population R for each sampling period (mg O₂/m²)

$$R_{\text{ann}} = 37.993 \text{ g O}_2/\text{m}^2/\text{yr} = 128.322 \text{ K.cals}/\text{m}^2/\text{yr}$$

$$\text{Using } P_{\text{ann}} = 0.6440 R_{\text{ann}}$$

$$P_{\text{ann}} = 40.228 \text{ K.cals m}^{-2} \text{ yr}^{-1}$$

Table 5.5 The Production of H. ulvae at Each Station (1975-76).

Station	R _{ann.} Kcal/m ² /yr	P _{ann.} Kcal/m ² /yr	P _{ann.Fdw.} g/m ² /yr	\bar{B} _{Tdw.} g/m ²	\bar{B} _{Fdw.} g/m ²	\bar{B} Kcal/m ² /yr	P/ \bar{B}
A1	128.322	40.228	8.046	29.774	5.210	26.052	1.544
A2	140.041	43.336	8.667	44.061	7.711	38.553	1.124
A3	184.175	54.725	10.945	51.948	9.091	45.454	1.204
A4	109.995	35.280	7.056	28.794	5.039	25.195	1.400
B1	9.939	4.553	0.911	2.604	0.456	2.278	1.998
B2	123.058	38.818	7.764	32.158	5.628	28.138	1.379
B3	102.101	33.114	6.623	27.489	4.810	24.053	1.377
B4	18.504	7.731	1.546	5.664	0.991	4.956	1.560
B5	75.708	25.666	5.133	20.116	3.520	17.602	1.458
C1	0.541	0.382	0.076	0.117	0.020	0.102	3.726
C2	32.485	12.485	2.497	6.281	1.099	5.496	2.271
C3	10.822	4.896	0.979	3.214	0.562	2.812	1.741
C4	134.930	41.985	8.397	34.347	6.011	30.053	1.397
C5	271.644	76.195	15.239	68.444	11.978	59.889	1.272

Table 5.6 The Production of H. ulvae at Each Station (1976-77).

Station	R _{ann.} Kcal/m ² /yr	P _{ann.} Kcal/m ² /yr	P _{ann.Fdw.} g/m ² /yr	\bar{B} _{Tdw.} g/m ²	\bar{B} _{Fdw.} g/m ²	\bar{B} Kcal/m ² /yr	P/ \bar{B}
A1	47.119	17.138	3.427	11.464	1.949	9.744	1.759
A2	98.045	31.988	6.398	28.401	4.828	24.141	1.325
A3	152.720	46.656	9.331	46.990	7.988	39.941	1.168
A4	98.174	32.023	6.405	34.003	5.780	28.902	1.108
B1	14.912	6.432	1.286	2.280	0.388	1.938	3.319
B2	25.616	10.196	2.039	4.617	0.785	3.925	2.598
B3	84.171	28.090	5.618	25.390	4.316	21.582	1.301
B3*	84.732	28.249	5.650	25.393	4.317	21.584	1.309
B4	13.743	6.000	1.200	4.989	0.848	4.240	1.415
B5	34.325	13.084	2.617	11.955	2.032	10.162	1.287
C1	2.624	1.465	0.293	1.005	0.171	0.854	1.714
C2	10.933	4.938	0.988	1.602	0.272	1.362	3.627
C3	13.209	5.801	1.160	4.209	0.716	3.578	1.621
C4	86.771	28.827	5.765	24.799	4.216	21.079	1.368
C5	164.559	49.719	9.944	50.047	8.508	42.540	1.169

All data based on quarterly sampling except B3* which was based on monthly sampling.

Figure 5.6 H. ulvae : (a) The Relationships
Between the Annual Flesh Production
and the Mean Biomass at Each Station.
(b) The Relationships Between the
Mean Individual Total Dry Weight
and the Annual P/\bar{B} Value at Each
Station. (1975-76 Data.)

$$P/\bar{B} = 2.241 - 0.329 I$$

$$r = 0.725$$

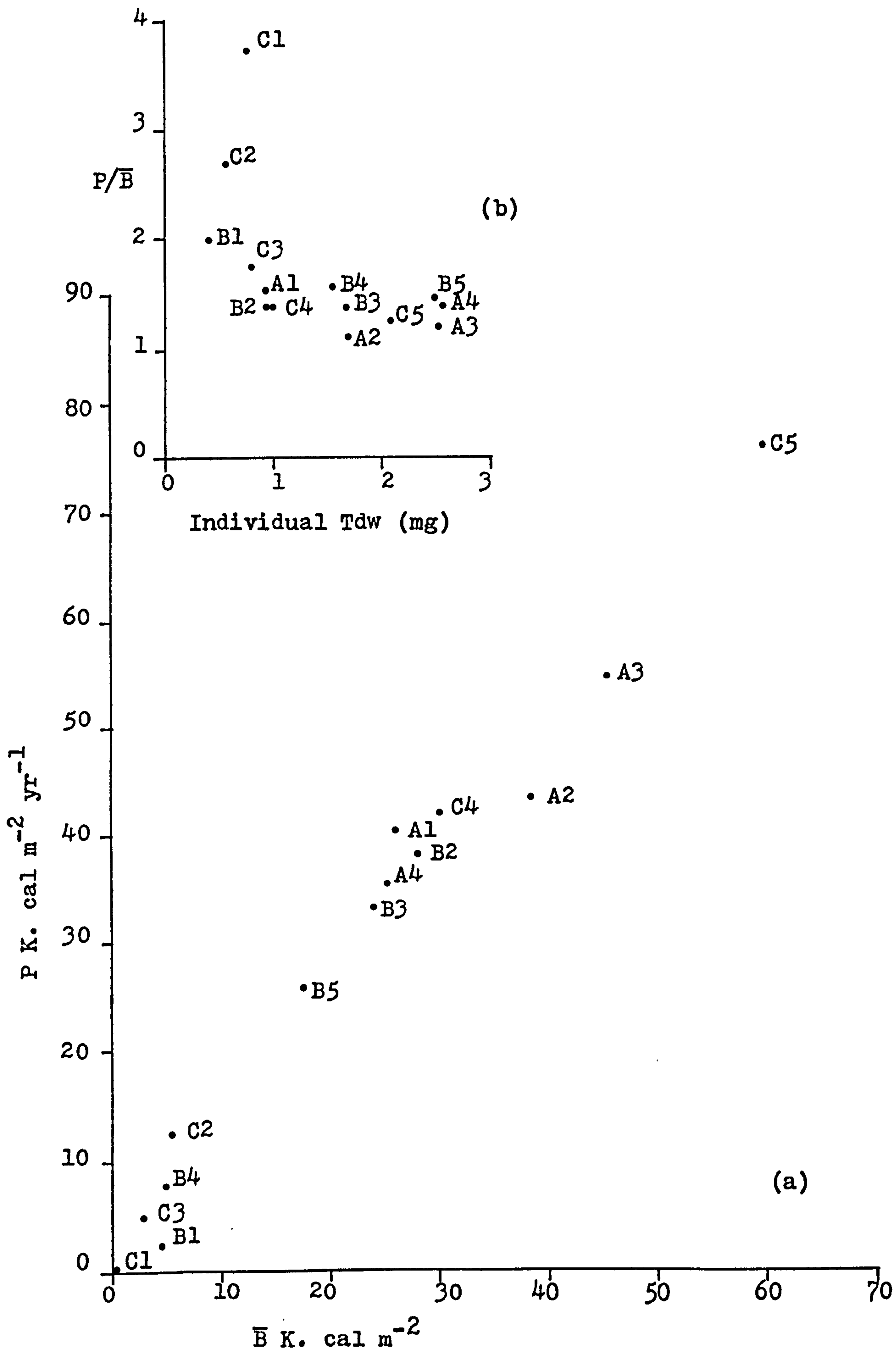


Table 5.7 A Comparison of the Production Data for H. ulvae for Each of the Two Sampling Years.

Station	P_{ann} g fdw m^{-2} yr^{-1}		\bar{B} g fdw m^{-2}		P/ \bar{B}	
	1975-76	1976-77	1975-76	1976-77	1975-76	1976-77
A1	8.046	3.428	5.210	1.949	1.544	1.759
A2	8.667	6.398	7.711	4.828	1.124	1.325
A3	10.945	9.331	9.091	7.988	1.204	1.168
A4	7.056	6.405	5.039	5.781	1.400	1.108
B1	0.911	1.287	0.456	0.388	1.998	3.319
B2	7.764	2.039	5.628	0.785	1.379	2.598
B3	6.623	5.618	4.811	4.316	1.377	1.301
B4	1.546	1.200	0.991	0.848	1.560	1.415
B5	5.133	2.617	3.520	2.032	1.458	1.287
C1	0.076	0.293	0.021	0.171	3.726	1.714
C2	2.497	0.988	1.099	0.272	2.271	3.627
C3	0.979	1.160	0.562	0.716	1.741	1.621
C4	8.397	5.765	6.011	4.216	1.397	1.368
C5	15.239	9.944	11.978	8.508	1.272	1.169
\bar{x}	5.991	4.034	4.438	3.057	1.675	1.770
± 1 S.E.	1.173	0.855	0.962	0.772	0.178	0.218

Using t-tests (in which variances were equal) :-

	t-values	p
P_{ann}	1.348	n.s.
\bar{B}	1.125	n.s.
P/ \bar{B}	0.337	n.s.

estimates from Station B3 during 1976-77 :-

<u>Estimates</u>	<u>P</u>	<u>\bar{B}</u>	<u>P/\bar{B}</u>
Monthly	5.650	4.317	1.309
Quarterly	5.618	4.316	1.301

Although Station B3 was one of the lesser stations affected by settlement in 1975, it is considered that the estimates for 1976-77 determined by quarterly sampling are as valid as those obtained by monthly sampling in 1975-76.

5.3.4. Spatial Differences in H. ulvae Biomass and Production Summary Data.

In order to examine the spatial differences in the H. ulvae population the production summary data, given in Sections 5.3.1. to 5.3.3., has been analysed by the use of correlation and regression techniques against the measured environmental variables (see Section 2.3., data given in Table 2.3).

5.3.4.1. The Relationships Between H. ulvae Production Summary Data and Environmental Variables.

A matrix of the correlation coefficients between the variables was constructed (Fig. 5.7) and three step-wise linear multiple regressions were computed for each dependent variable (Table 5.8).

(i) H. ulvae Mean Annual Biomass.

H. ulvae \bar{B} gave a positive exponential relationship with tidal height, which reached a plateau at higher values of each variable (** on linear basis), and a negative relationship (*) with salinity when both were logarithmically transformed. All environmental variables were included in the equation (Table

	\bar{B} H.	\bar{N} H.	P. H.	M.I.W. H.	\sqrt{B} H.	\bar{B} R.	P. R.	\sqrt{B} R.
T.H.	(***) ⁺ ***	(***) ⁺ **	(***) ⁺ ***	(**) ⁺ ***	(***) ⁻ ***	(**) ⁺		
M.P.D.								
S.C.								(*) ⁺
SK.								
%H ₂ O _F								
%H ₂ O _J						+		
%C.						*		
%N.						+		
%S. & C.						*		
Slope								
C/N.								
Int. Sal.	(*) ⁻		(*) ⁻	(***) ⁻ ***	(*) ⁺ *			
H. \bar{B} .		(***) ⁺ ***	(***) ⁺ ***	(*) ⁺ *	(***) ⁻ **	(***) ⁺ **		
H. \bar{N} .			(***) ⁺ ***		(***) ⁻ *	(***) ⁺		
H. P.				(*) ⁺ *	(***) ⁻ **	(***) ⁺ **		
H. M.I.W.					(**) ⁻ *	(*) ⁺		
H. \sqrt{B} .						(***) ⁻		
R. \bar{B} .							(*) ⁺ ***	(*) ⁺
R. P.								(**) ⁺ *

Figure 5.7 H. ulvae, R. obtusa: Spatial Data Analysis- Pearson Correlation Matrix of Density, Biomass, Production and Productivity With Environmental Variables and Population Variables. (The significance of double-logarithmic correlations are given in parentheses; only significant correlations are given.)

Environmental variable abbreviations and symbols as given in figure 2.9.

H. = H. ulvae parameters; R. = R. obtusa parameters; \bar{N} . = mean annual density ($n\ m^{-2}$); \bar{B} . = mean annual flesh biomass ($mg\ m^{-2}$ for R. obtusa, $g\ m^{-2}$ for H. ulvae); P. = annual flesh production ($mg\ m^{-2}$ for R. obtusa, $g\ m^{-2}$ for H. ulvae); \sqrt{B} . = annual productivity; M.I.W. = mean individual flesh weight (mg).

Table 5.8 H. ulvae : Spatial Data Analysis - Multiple Regression Equations of Production Summary Data With Environmental Variables. (Legend as Fig. 5.7.)

Dependent Variable	Incorporated Variables and Significant Equation	Excl. Variables	Total Variance Accounted For	Main Variables
(1) \bar{B}	TH., M.P.D., S.C., SK., %H ₂ O, %C, %N, %S. & C., Slope, C/N, Salinity. $6.51\%C - 0.414C/N + 4.08TH. + 9.42S.C. - 58.82$	-	97.9%	TH. (56.6%), S.C. (22.8%), Salinity (9.0%).
(2) \bar{B}	TH., S.C., Salinity, %N. $4.574TH. + 5.269S.C. + 0.442Salinity - 58.71$	-	88.5%	TH. (56.6%), S.C. (22.8%), Salinity (9.0%).
(3) \bar{B}	TH., S.C., Salinity, C/N. $4.354TH. + 6.133S.C. + 6.166Salinity - 53.824$	-	89.7%	TH. (56.6%), S.C. (22.8%), Salinity (9.0%).
(1) \bar{N}	TH., M.P.D., S.C., SK., %H ₂ O, %C, %N, %S. & C., Slope, C/N, Salinity. $- 1016991\%N - 209476.7$	-	95.4%	TH. (34.0%), Salinity (25.0%), Slope (13.8%), C/N (10.2%).
(2) \bar{N}	TH., Slope, C/N, Salinity $19828.9TH. + 3128.0Salinity - 1131.4Slope - 326552.2$	C/N	72.8%	TH. (34.0%), Salinity (25.0%), Slope (13.8%).

Table 5.8 Continued.

Dependent Variable	Incorporated Variables and Significant Equation	Excl. Variables	Total Variance Accounted For	Main Variables
(3) \bar{N}	TH., %N, Slope, Salinity. $20128.9_{TH.}^{**} + 3123.13_{Salinity}^{**} - 329006.9$	-	73.1%	TH. (34.0%), Salinity (25.0%), Slope (13.8%).
(iii) (1) P	TH., M.P.D., S.C., SK., %H ₂ O, %C, %N, %S. & C., Slope C/N, Salinity. $11.188_{S.C.}^{**} + 3.88_{TH.}^{*} - 210.15_{%N}^{*} - 49.6$	-	98.0%	TH. (56.9%), S.C. (21.4%), Salinity (9.1%).
(2) P	TH., S.C., C/N, Salinity. $5.401_{TH.}^{**} + 6.892_{S.C.}^{**} + 0.5093_{Salinity} - 67.085$	-	87.8%	TH. (56.9%), S.C. (21.4%), Salinity (9.1%).
(3) P	TH., S.C., %N, Salinity $5.514_{TH.}^{**} + 6.341_{S.C.}^{**} + 0.537_{Salinity} - 70.333$	-	87.3%	TH. (56.9%), S.C. (21.4%), Salinity (9.1%).
(iv) (1) M.I.W.	TH., M.P.D., S.C., SK., %H ₂ O, %C, %N, %S. & C., Slope, C/N, Salinity, \bar{B} , \bar{N} , P, P/ \bar{B} . All n.s. + 1.037	Slope, C/N, P/ \bar{B} .	99.2%	Salinity (79.8%), \bar{N} (7.3%), \bar{B} (6.5%).

Table 5.8 Continued

Dependent Variable	Incorporated Variables and Significant Equation	Excl. Variables	Total Variance Accounted For	Main Variables
(2) M.I.W.	Salinity, Slope, M.P.D., %S. & C. $2.948 - 0.0298^{***} \text{Salinity}$	%S. & C.	81.5%	Salinity (79.8%).
(3) M.I.W.	M.P.D., %S. & C., Slope. All n.s. + 0.409	-	19.8%	%S. & C. (15.9%), M.P.D. (3.6%).
(v) (1) P/B	TH., M.P.D., S.C., SK., %H ₂ O, %C, %N, %S. & C., Slope, C/N, Salinity, \bar{B} , \bar{N} , P, M.I.W. $1.443^{***} \text{M.I.W.} + 0.067^{***} \text{Slope} + 4.851^{***} \%N - 0.847^{***} \text{SK.} - 0.136^{***} \bar{B}$ $+ 1.362^{***} \text{S.C.} - 0.00004^{***} \bar{N} - 0.00402^{**} \%S. \& C. - 0.217^{**} \text{TH.}$ $- 0.0957^* \text{P} - 0.67313$	M.P.D., %H ₂ O, C/N.	ALL	TH. (71.1%), M.I.W. (5.3%).
(2) P/B	M.P.D., %N, Slope, \bar{N} , M.I.W. $1.891 - 0.00003^* \bar{N}$	-	69.3%	\bar{N} (36.5%), %N (21.3%), M.I.W. (8.9%).

5.8(i)) as independent variables and accounted for the total variation in H. ulvae \bar{B} data. However, the variables tidal height, sorting of sediment and salinity accounted for 88.5% of that variance and, on the elimination of the less significant variables, were included in the equation at highly significant levels. The sediment related variables of % C, N, H₂O, S & C and slope of shore became non-significant in the equations.

(ii) H. ulvae Mean Numbers.

This parameter showed the same relationship with tidal height as the H. ulvae \bar{B} although the relationship had greater variability. The variation in H. ulvae abundance was mainly accounted for by tidal height, salinity and shore slope, with the organic content of the substrate playing a less important role (Table 5.8(ii)).

(iii) H. ulvae Annual Production.

This variable was positively related to tidal height (***) and negatively related to salinity (*) on a logarithmic basis. The multiple regression equation produced for this dependent variable was similar to that for the H. ulvae biomass as 87.3% of the variation was accounted for by tidal height, sorting coefficient and salinity (Table 5.8(iii)).

(iv) H. ulvae Mean Individual Weight.

This variable produced a linear, positive correlation with tidal height (***) and a similar negative correlation to interstitial salinity as a percentage of the overlying salinity, i.e. the larger animals tolerate lower interstitial salinities. This may possibly have been a result of the relationships between tidal height and salinity (-ve ***) and tidal height and H. ulvae

size (+ve ***). The first multiple regression equation suggests that the larger animals tolerated the lower salinities and produced areas with high numbers and biomasses. This variable was also regressed against substrate linked variables in order to show whether or not the size of the animal found at a station was correlated with particle sizes at that station. A large proportion (15.9%) of the variation was accounted for by the amount of silt and clay in the sediments (Table 5.8(iv)).

(v) H. ulvae P/ \bar{B} .

The productivity was related to tidal height on a negative exponential basis (***); this reflects the fact that tidal height and H. ulvae size were positively related and that the smaller animals had a higher P/ \bar{B} . The P/ \bar{B} was also positively related to the sediment %C, %N and %H₂O (all *) but not with M.P.D.; this would be expected from the inter-relationships between the sediment variables.

The first multiple regression was significant for most of the variables, possibly suggesting that this variable was influenced by many factors, although the major part of the variance of the P/ \bar{B} was attributed to tidal height. However, when many variables were eliminated in order to assess the influence of the sediment parameters and the H. ulvae population parameters on the P/ \bar{B} , then 66.7% of the variance was attributed to H. ulvae mean numbers (36.5%), sediment %N (21.3%) and mean individual weight (Table 5.8(v)).

5.3.4.2. Interactions Between the H. ulvae Population Variables.

The production and mean biomass and density of H. ulvae were positively intercorrelated as expected. The M.I.W. of H. ulvae

was also positively related to P and \bar{B} , i.e. areas inhabited by large animals produced more than the others, but not to population density. The P/\bar{B} was negatively correlated with biomass (**), numbers (*) and production (**). The productivity gave a curvilinear relationship with H. ulvae numbers, with the ratio decreasing with increasing population density, which became more significant when logarithmically transformed. This relationship may indicate that the P/\bar{B} of the population was density dependent. It is more likely, however, that this merely reflects the spat and large animal distribution and productivity.

In addition, there was a negative curvilinear relationship between H. ulvae production and P/\bar{B} , suggesting that areas with a high P/\bar{B} have a low production. This again may reflect the low production by the younger animals which had a high P/\bar{B} ratio. This latter phenomenon is demonstrated by the significant, negative curvilinear correlation between M.I.W. and P/\bar{B} .

5.3.4.3. The H. ulvae/Sediment Relationship and the Importance of Zostera marina.

It is suggested that the most important factor affecting the ecology of H. ulvae on Torry Bay was tidal height, therefore the relationships between this variable and the population production summary data were considered in greater detail. The stations could be placed in three discrete groups according to the major environmental factors (Fig. 5.8 (a), (b), Fig. 5.9 (a)) :

Group I : stations at the lowest parts of the transects, with soft mud as substrate and with or without M. edulis beds - Stations C1, C2, B1, B2, B3 and A1.

Group II : areas of intermediate to high tidal height, with

Figure 5.8 H. ulvae : The Relationships Between
(a) Mean Annual Flesh Biomass and
(b) Mean Density With Tidal Height.

Group I Soft mud, lowshore stations,
some with M. edulis beds.

Group II Stations of clean bare
sand, little or no attached
macroflora, at or near high
shore region.

Group III Stations with Z. marina on
sand or sandy-mud.

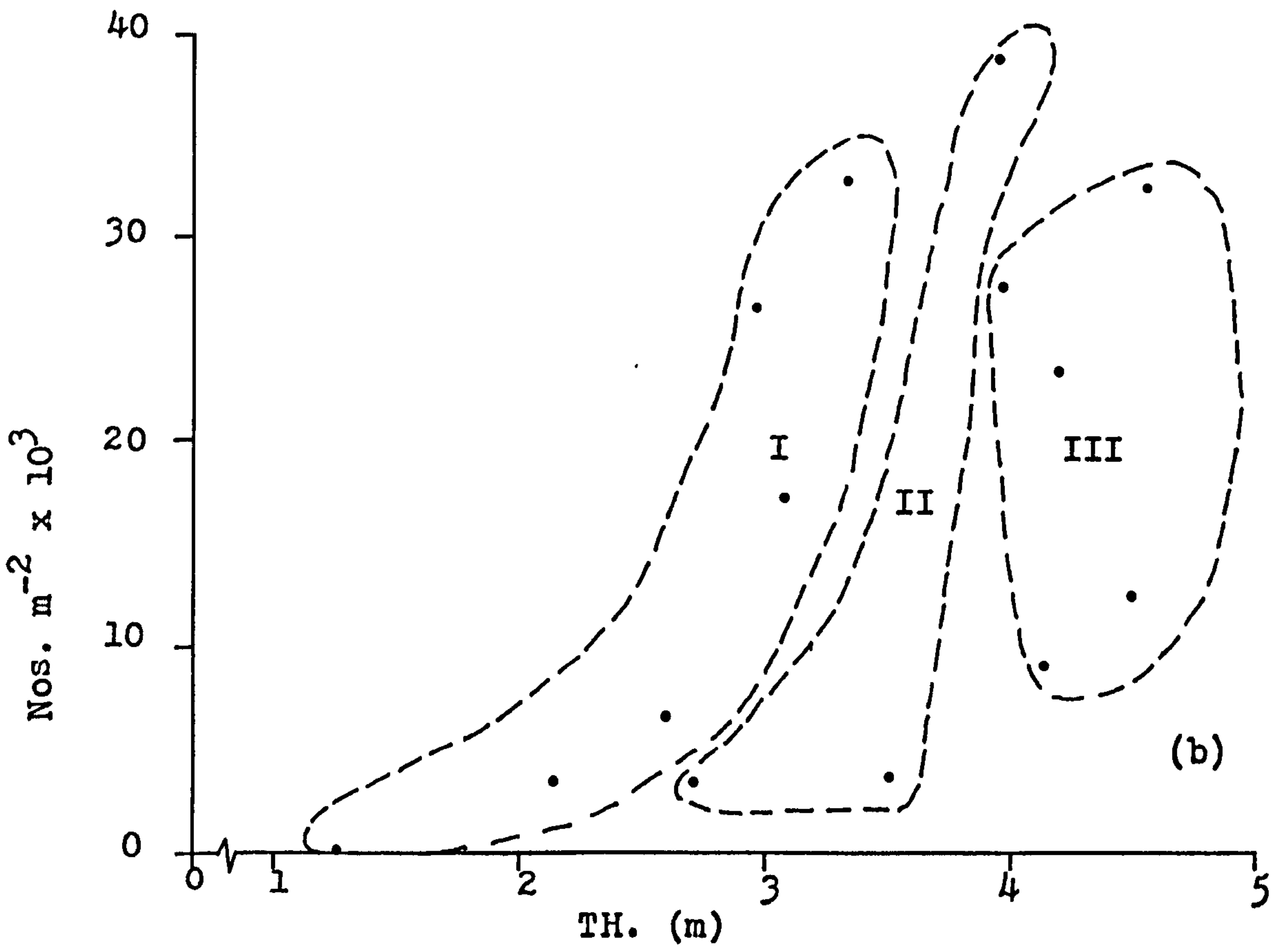
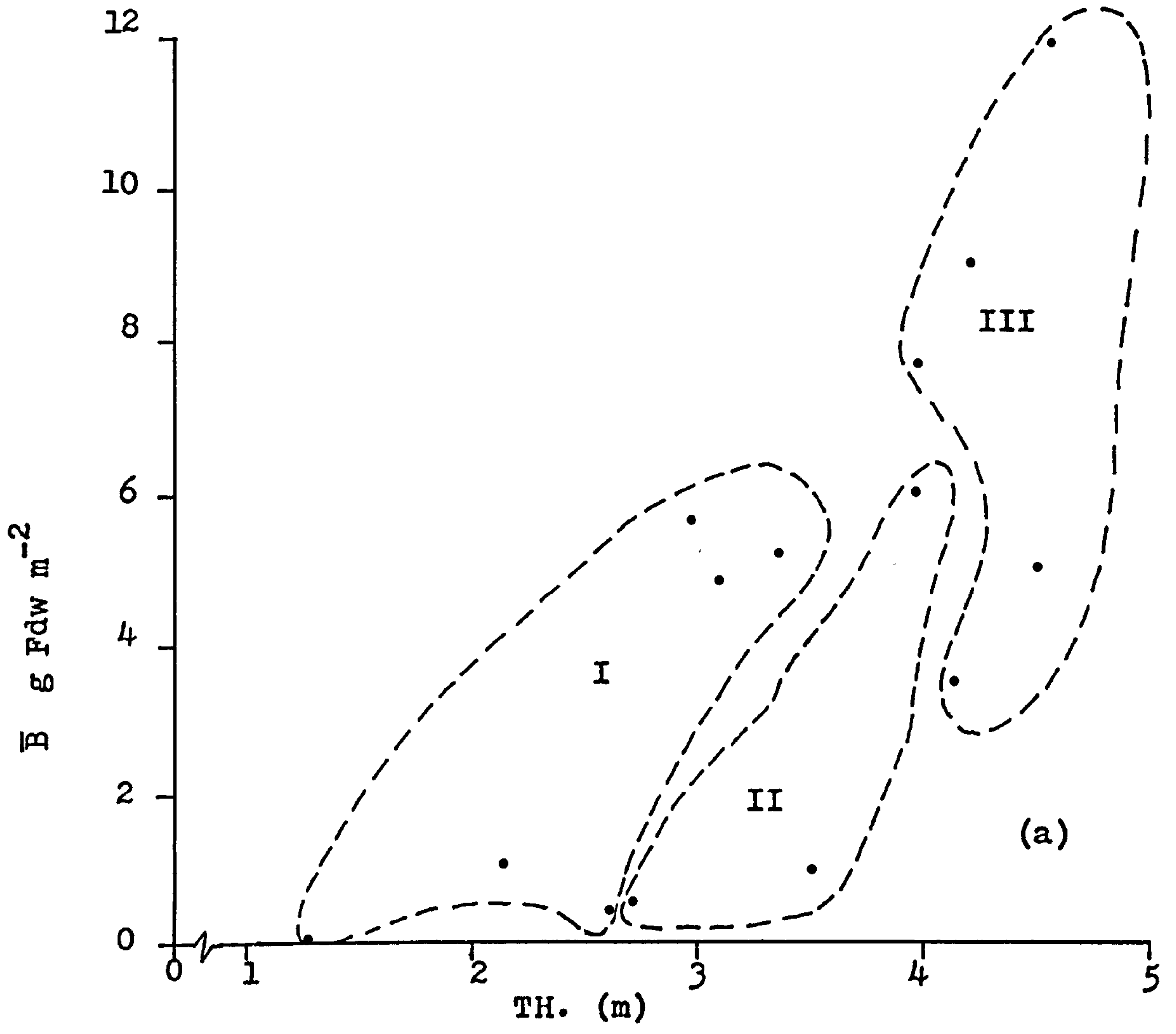
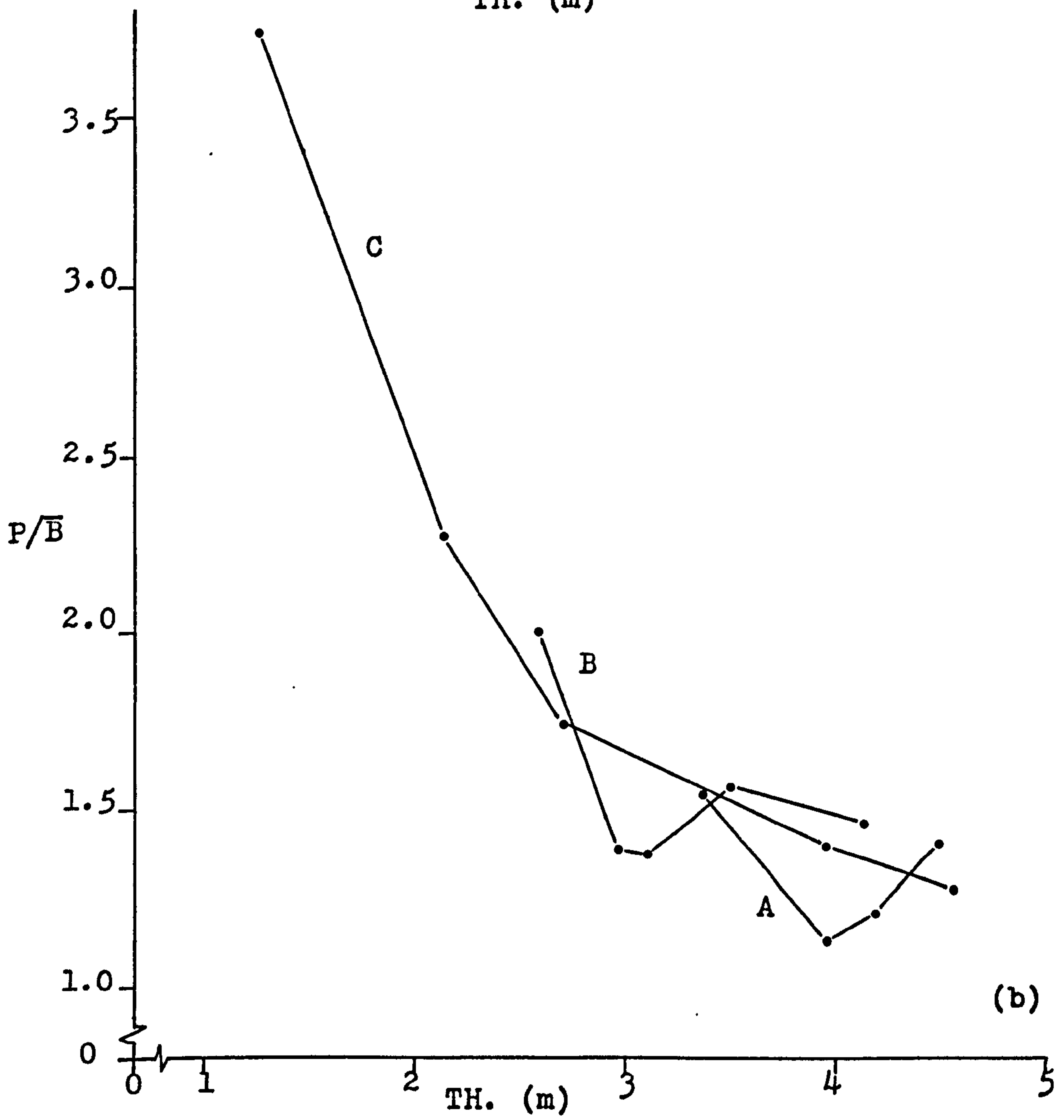
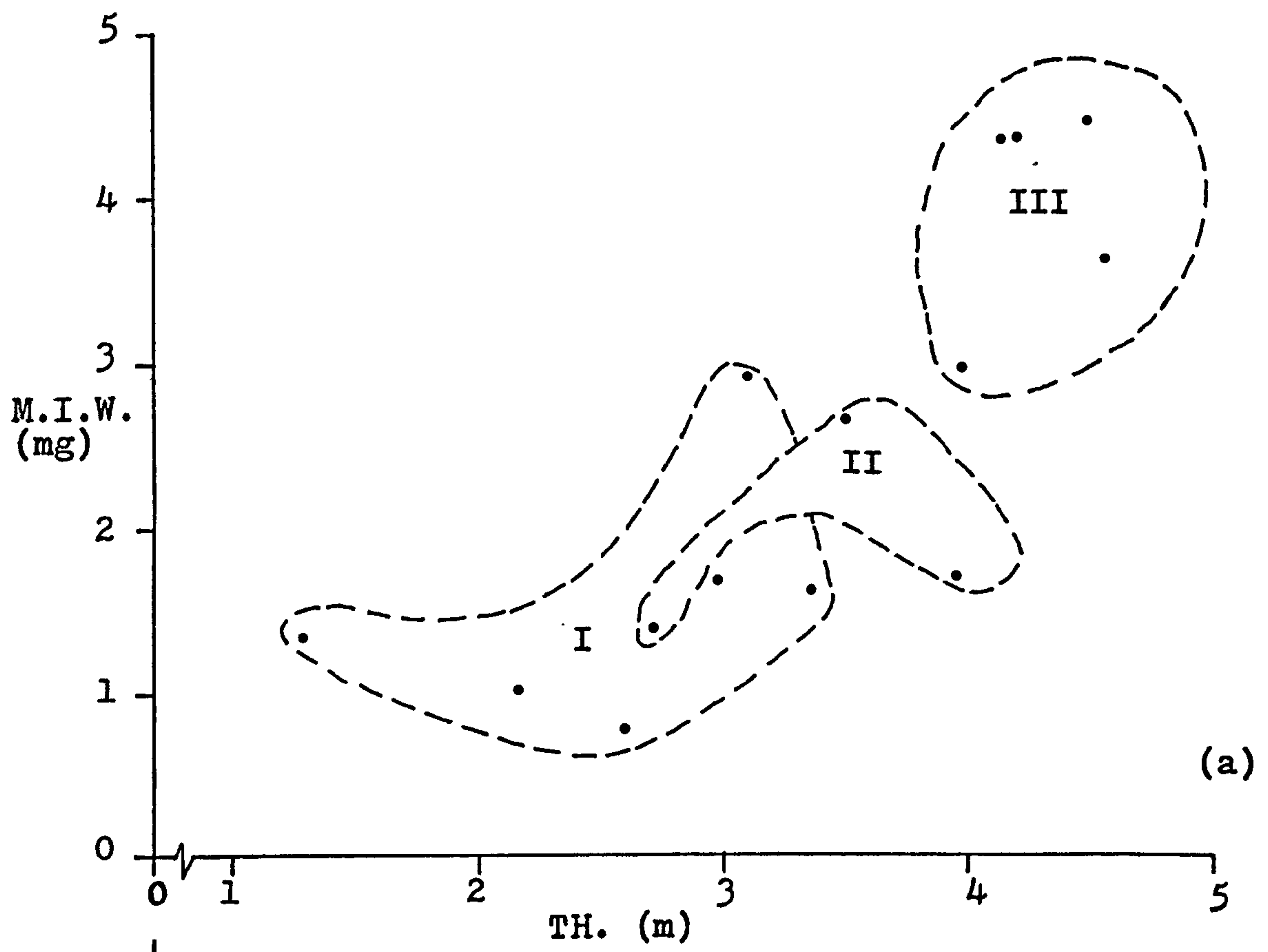


Figure 5.9 H. ulvae : (a) The Relationship Between the Mean Individual Flesh Weight and Tidal Height at Each Station. Groups are Given in Fig. 5.8. (b) The Change in P/\bar{B} Value With Tidal Height. The Individual Transects are Delimited.



a clean sand substrate which had no deposit-attached macroflora although rock-attached macroflora may be present - Stations C3, C4 and B4.

Group III : high tidal areas of sand or sandy-mud which supported Z. marina beds to a lesser or greater extent - Stations A2, A3, A4, B5 and C5.

This grouping of the stations appeared to be the most straightforward and the groups can be easily delimited in the Principal Components Analysis of stations (see Fig. 2.12). Within each group, there is a curvilinear pattern of increasing mean biomass or population density with tidal height (Fig. 5.8). (The relationship between H. ulvae production and biomass (Fig. 5.6b) suggests that there would be similar relationships between tidal height and production.) An overall curvilinear relationship is evident in Fig. 5.8 (b), although high population densities at spat settling periods result in the Stations C4, A1 and B2 deviating slightly from such a pattern. Therefore, within each group there is a large amount of variation which supports the suggestion that although the Hydrobiae population parameters were mainly influenced by tidal height, they were also influenced by many minor variables.

The curvilinear relationship between H. ulvae M.I.W. and tidal height (Fig. 5.9 (a)) also reinforces the conclusion that the larger animals occurred at higher levels on the shore (Figs. 5.4 and 5.10). The observed decrease in P/\bar{B} with an increase in tidal height (Fig. 5.9 (b)) therefore reflects the negative curvilinear relationship between P/\bar{B} and H. ulvae M.I.W. (Fig. 5.6a).

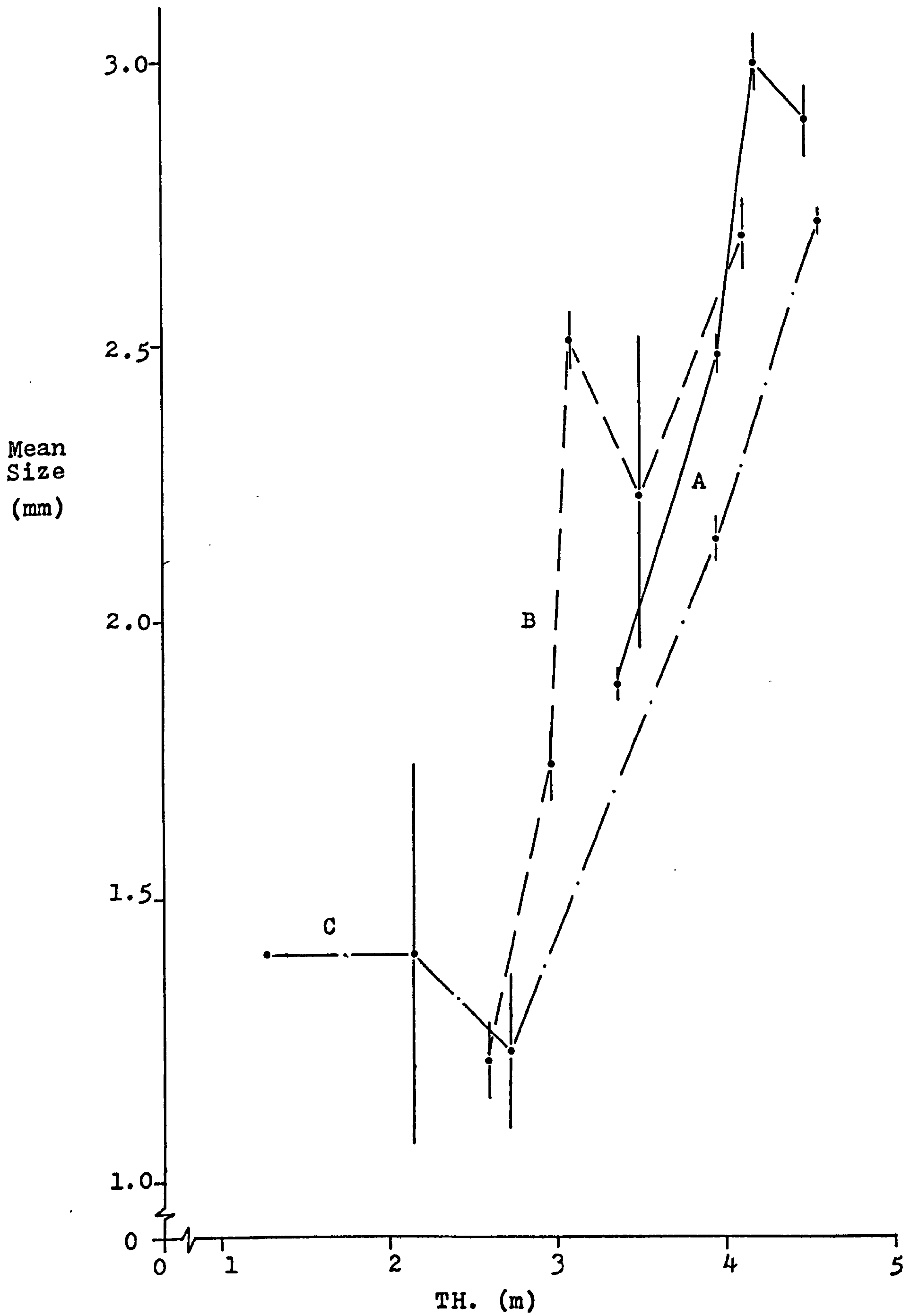
It has also been shown that the H. ulvae mean length and individual weight were correlated with tidal height (Fig. 5.10) and also that M.P.D. was related to tidal height (Section 2.4.1.4.). As deposit-feeding Hydrobiae may utilize a mean food particle size which is related to its size (Fenchel, 1975b; Fenchel et al, 1975), it may be suggested that the size of animal would be related to the M.P.D. of the sediment. The present study shows no such relationship (Fig. 5.11a) but demonstrates that large and small H. ulvae occur over all sizes of substrate particle size, although, by definition, the three major groups described above are still discrete. In addition, a correlation matrix (Fig. 5.11b) was constructed for the H. ulvae production summary variables against the percentage of each size class of sediment particles at each station. Little further detail regarding the sediment preference of H. ulvae was gained from this analysis except that whilst there were positive relationships between the mean biomass, numbers and annual production and the larger sizes of particles, there were negative relationships with the finer particle sizes. However, the majority of these relationships were not statistically significant.

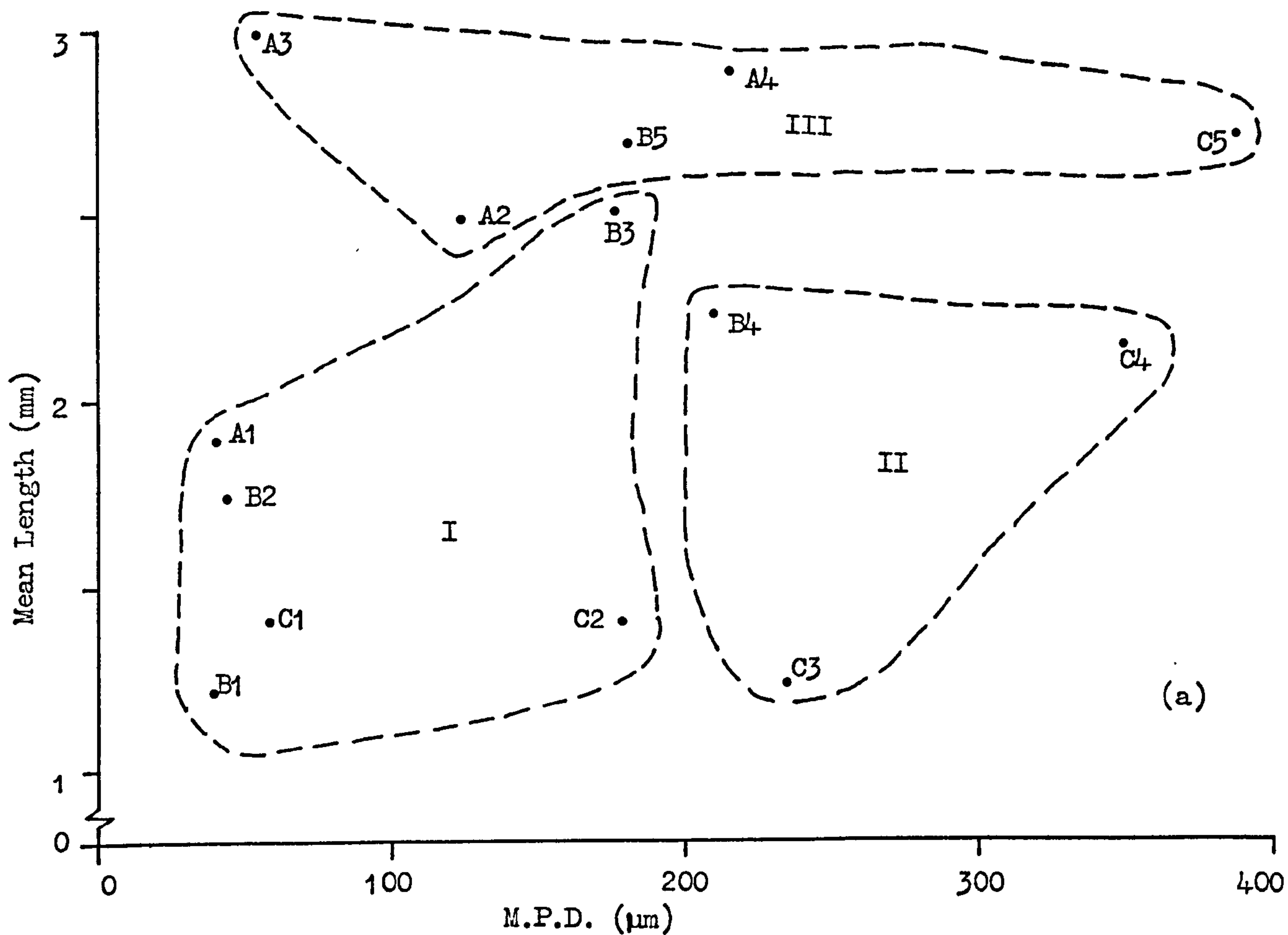
The regression equation :

$$y = 15.8x - 2.1 \quad p < 0.001$$

of length of Hydrobiid (x) against its median food particle size (y), calculated from data given by Fenchel (1975b), was then used to calculate the possible particle size taken by the size of H. ulvae found at the stations (Table 5.9). No significant correlations were found between the numbers or biomass of H. ulvae found at a particular station and either the percentage of preferred particles in the sediment at that station or the per-

Figure 5.10 H. ulvae : The Relationship Between
the Mean Size (\pm 1 S.D.) at Each
Station and the Tidal Height.
(March-June, 1975 Data.)





Particle Size Class	> 5.6mm	2-5.6mm	1-2mm	0.5-1mm	250-500μm	125-250μm	63-125μm	31.2-63μm	15.6-31.2μm	7.8-15.6μm	3.9-7.8μm	< 3.9μm
<u>Hydrobia</u> Variables												
$\bar{B}_{ann.}$	+	+	+	+	+	-	-	-	-	-	-	+
	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
$\bar{Nos.}$	+	+	+	+	+	-	-	+	-	+	+	+
	*	*	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
$P_{ann.}$	+	+	+	+	+	-	-	-	-	-	-	-
	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
M.I.W.	+	-	+	+	+	+	+	-	-	-	-	-
	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
P/\bar{B}	-	-	+	-	-	-	+	+	+	+	+	+
	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.

Figure 5.11 (a) H. ulvae Mean Size at Each Station.

(b) Pearson Correlation Matrix : H. ulvae Production Summary Variables with Percentage of Each Size Class of Particles.

Table 5.9 The Mean Length and Expected Particle Size Preference of H. ulvae.

Station	Mean Length (mm)	* ¹ (µm)	* ² %	* ³ %
A1	1.89	27.7	16.8	14.6
A2	2.48	37.1	12.8	19.1
A3	2.99	45.2	27.3	27.4
A4	2.89	43.6	7.9	6.1
B1	1.21	17.0	21.1	12.8
B2	1.74	25.3	14.9	8.1
B3	2.51	37.5	10.2	19.6
B4	2.23	33.1	2.3	0.6
B5	2.69	40.4	2.1	0.6
C1	1.40	20.0	8.7	15.8
C2	1.40	20.0	8.1	6.1
C3	1.22	17.2	1.6	1.0
C4	2.15	31.9	1.1	0.1
C5	2.72	40.8	1.3	0.6

where *¹ = Median food particle size (from Fenchel, 1975b, see text).

*² = Percentage by weight of deposit smaller than the preferred size range of particles.

*³ = Percentage by weight of deposit at the preferred size range of particles.

centage of particles smaller than the preferred size. The data obtained, however, would not indicate whether individuals of differing sizes utilize different particle sizes within the substrate at a station. Additionally no consideration of the role of diatoms in the diet of H. ulvae has been taken into account in this study.

The importance of the presence of Z. marina may now be considered. The effect of Z. marina beds on the H. ulvae population estimates has been shown briefly (Figs. 5.8 (a), (b); 5.9 (a)). An estimate of the standing crop of Z. marina at each station was made in June, 1975, which gave a linear relationship with the H. ulvae biomass for that month :

$$y = 0.474 \pm 0.139x + 13.755$$

$$p < 0.05, n = 14$$

where $y = \text{H. ulvae biomass g (fdw) m}^{-2}$

$x = \text{Z. marina standing crop g (afdwt) m}^{-2}$

The curvilinear line fitted by eye may be a more accurate description of the relationship (Fig. 5.12).

Although the importance of Z. marina has been stressed by many authors (Hunt, 1925; etc.) as a source of detritus and subsequently food for detritivores, it is possible that the same major environmental factors regulate the occurrence of both Z. marina and H. ulvae and that this situation is not strictly one of cause and effect. However, as this and previous studies indicate that H. ulvae shows a preference for Z. marina zones, it may be suggested that Z. marina is used both as a source of detritus and an additional substrate.

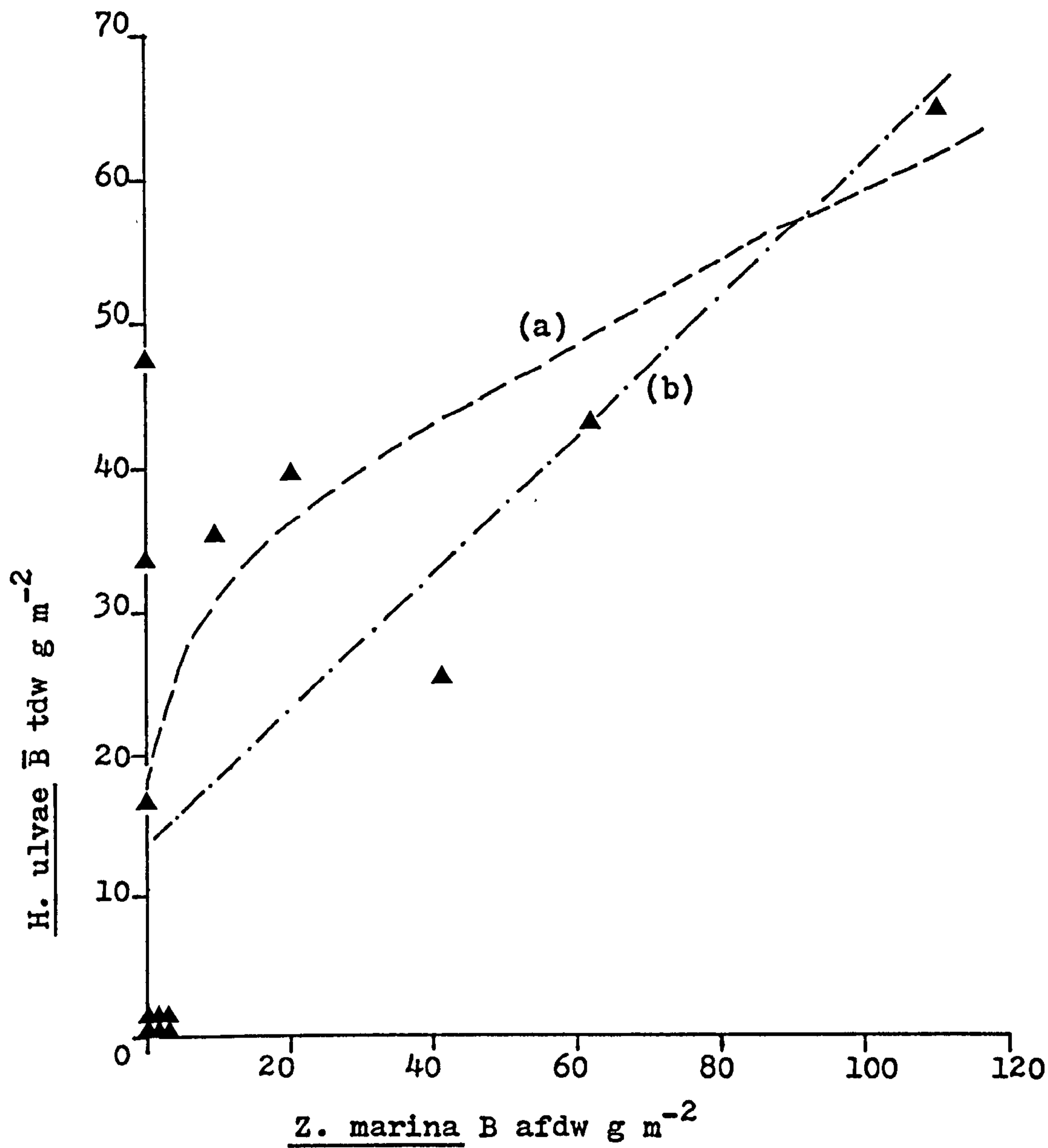


Figure 5.12 H. ulvae : The Relationship Between the Biomass of Z. marina (June '75 Data) and H. ulvae Mean Annual Biomass.

(a) Line Fitted by Eye.

(b) Linear Regression Line (See Text).

5.3.5. The Production Ecology of R. obtusa.

5.3.5.1. The Population Dynamics and Growth of R. obtusa.

5.3.5.1.1. The Total Population.

The percentage flesh weight determinations of R. obtusa did not show any seasonality (Fig. 5.13a) and described a normal distribution when plotted against length (Fig. 5.13b). The mean monthly value of 13.6% afdw of tdw has therefore been used where a conversion factor was required. The total numbers and biomasses for each station for each month are given in Table 5.10. In addition, size-frequency histograms for the population were constructed (Fig. 5.14).

The age cohorts present in the population were then defined by estimating maxima in size groups on the histograms. No attempt was made to distinguish the age cohorts by any other method (e.g. Harding, 1949; Cassie, 1950, 1954) as the combination of large and small samples possibly introduced error to the estimates. The nomenclature of each cohort has been derived from the year of the autumn appearance of that cohort.

The population data, presented in Figs. 5.15, 5.16, 5.17, show that R. obtusa had an annual life cycle although there was usually a period of about fifteen months from the first appearance of the young of a cohort to the disappearance of that year class. There appeared to be an extremely long period over which the young were produced from October-November, when the first young appeared, until mid-summer when the year class reached a maximum in numbers; the maximal biomass, however, was reached slightly later in the year during September-November.

The individual flesh weight and length demonstrated a

Figure 5.13. R. obtusa : (a) The Change in Flesh Dry Weight (as 1% of Total Dry Weight) at Each Sampling Occasion. Mean Value at Each Month and Over Whole Sampling Period Denoted. Bar = Mean \pm S.D. \pm S.E.

(b) The Relationship Between Length and Flesh Dry Weight (as 1% of Total Dry Weight). (L.H.S. Frequency Distribution.)

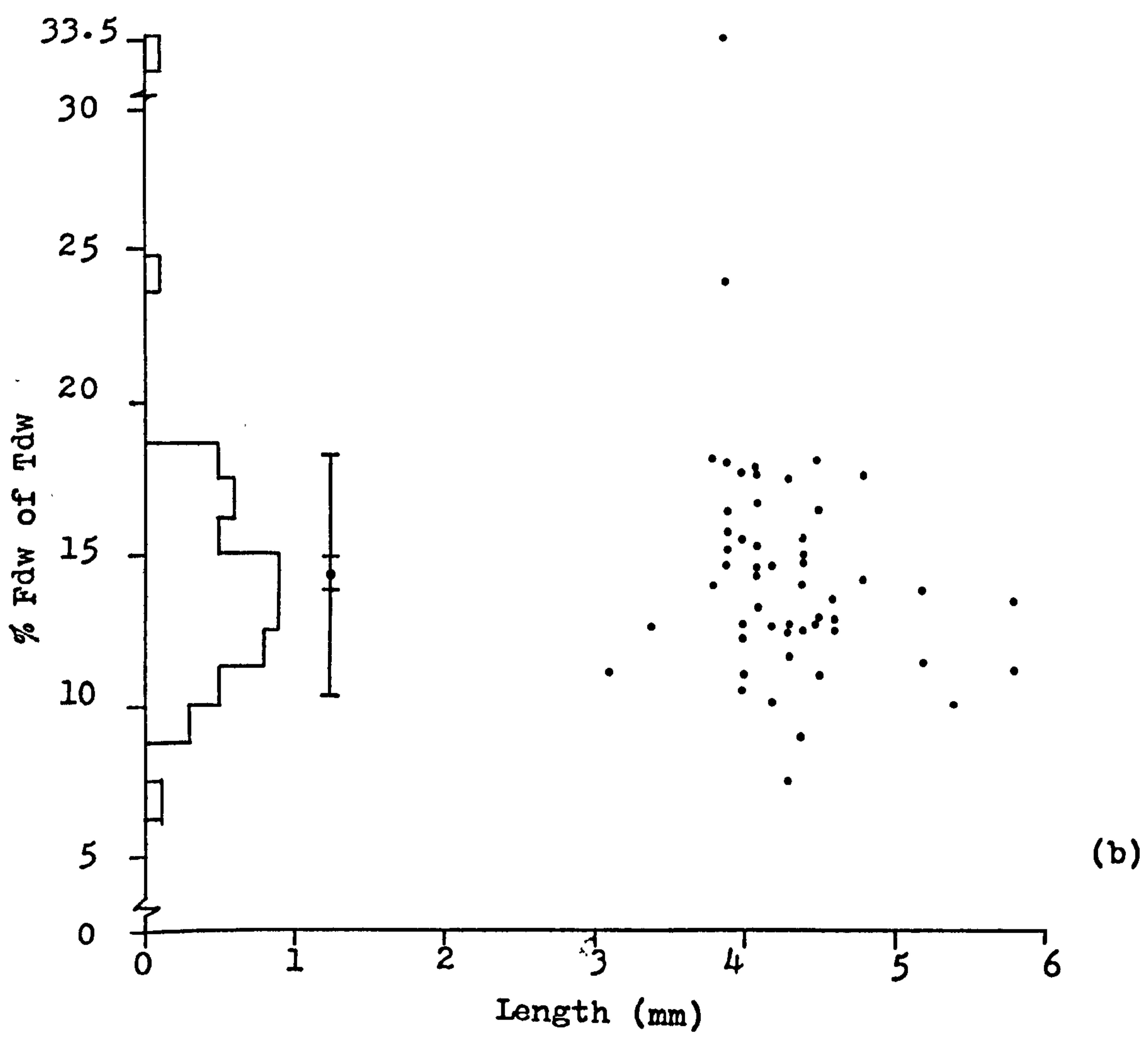
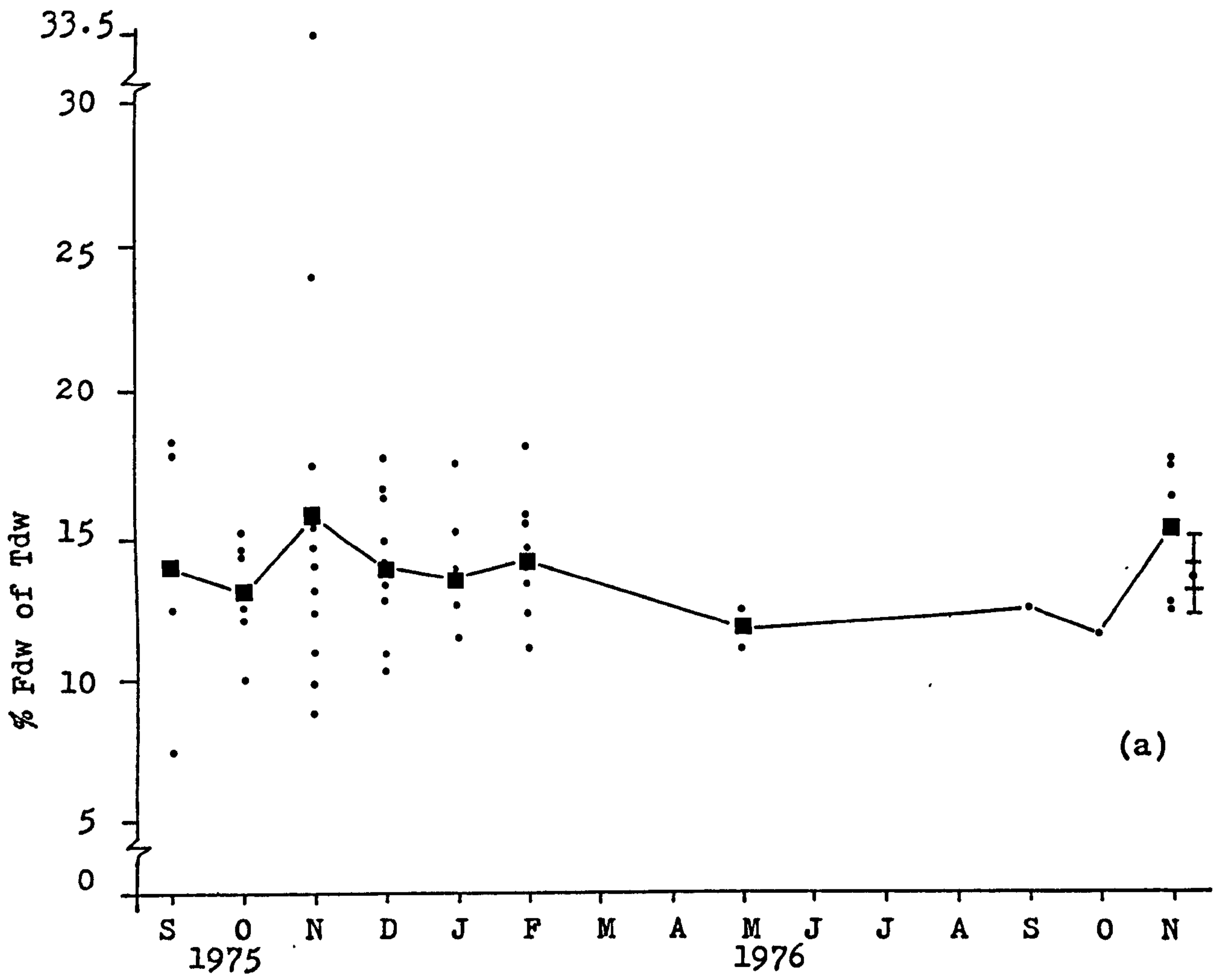


Table 5.10 Retusa obtusa: The Density and Biomass (Tdw.) at each Station and Sampling Occasion.

(Upper figure: $n\ m^{-2}$; lower figure: Tdw. $g\ m^{-2}$).

Station	1975												1976					1977	
	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	May	Aug.	Nov.	Feb.			
A1	-	-	-	10	-	320	160	80	200	330	-	10	160	-	90	-			
				0.095		0.134	0.196	0.272	1.102	1.689		0.084	0.026		0.254				
A2	-	20	200	400	320	240	240	20	400	260	-	120	160	560	-	80			
		0.168	0.020	0.560	0.056	0.165	0.336	0.104	1.604	0.253		0.394	0.081	0.321		0.030			
A3	40	40	460	420	160	480	490	210	250	330	160	90	600	160	190	-			
	0.451	0.340	0.544	0.285	0.013	0.240	0.979	0.563	1.145	1.122	0.685	0.295	0.465	0.162	0.313	-			
A4	20	-	-	-	160	160	-	10	100	90	-	-	170	80	-	-			
	0.219	-	-	-	0.008	0.120	-	0.055	0.414	0.214	-	-	0.074	0.009	-	-			
B1	-	20	-	-	-	-	-	-	-	-	-	-	-	-	10	-			
		0.185	-	-	-	-	-	-	-	-	-	-	-	-	0.068	-			
B2	200	-	600	200	640	240	480	10	570	-	240	170	560	400	-	-			
	0.700	-	0.560	0.240	0.205	0.178	1.236	0.080	1.915	-	0.060	0.069	0.114	0.384	-	-			
B3	400	13100	210	1000	1280	970	860	440	420	50	240	250	320	1040	430	10			
	0.140	1.329	0.222	1.280	1.917	2.565	3.271	1.404	1.950	0.501	0.415	0.526	0.045	1.720	1.623	0.071			
B4	-	-	-	-	-	160	-	-	10	-	10	-	80	-	10	-			
						0.826	-	-	0.055	-	0.158	-	0.003	-	0.099	-			
B5	-	-	-	-	80	80	-	-	10	90	-	-	-	-	-	-			
					0.050	0.066	-	-	0.120	0.148	-	-	-	-	-	-			
C1	-	-	-	-	160	-	-	-	-	-	-	-	80	-	-	-			
					0.171	-	-	-	-	-	-	-	0.008	-	-	-			
C2	-	-	-	-	80	160	-	80	170	-	10	-	800	800	240	80			
					0.018	0.123	-	0.151	0.547	-	0.091	-	0.117	0.337	0.249	0.420			
C3	-	-	-	-	-	80	80	80	90	90	-	10	-	240	-	-			
						0.026	0.108	0.136	0.449	0.196	-	0.076	-	0.295	-	-			
C4	-	-	-	-	80	-	30	-	10	10	20	20	-	-	-	-			
					0.027	-	0.161	-	0.112	0.106	0.258	0.273	-	-	-	-			
C5	220	480	300	440	240	420	190	260	140	110	20	10	100	90	-	30			
	0.620	3.816	2.141	1.298	0.430	0.883	0.585	0.475	0.646	0.250	0.377	0.126	0.403	0.108	-	0.494			

Figure 5.14 R. obtusa : Size-frequency Histograms
at Each Sampling Occasion.

Ordinate (a) All Stations Divisions
in 10m^{-2} . (b) Station B3 1976-77 Data
Divisions in 50m^{-2} .

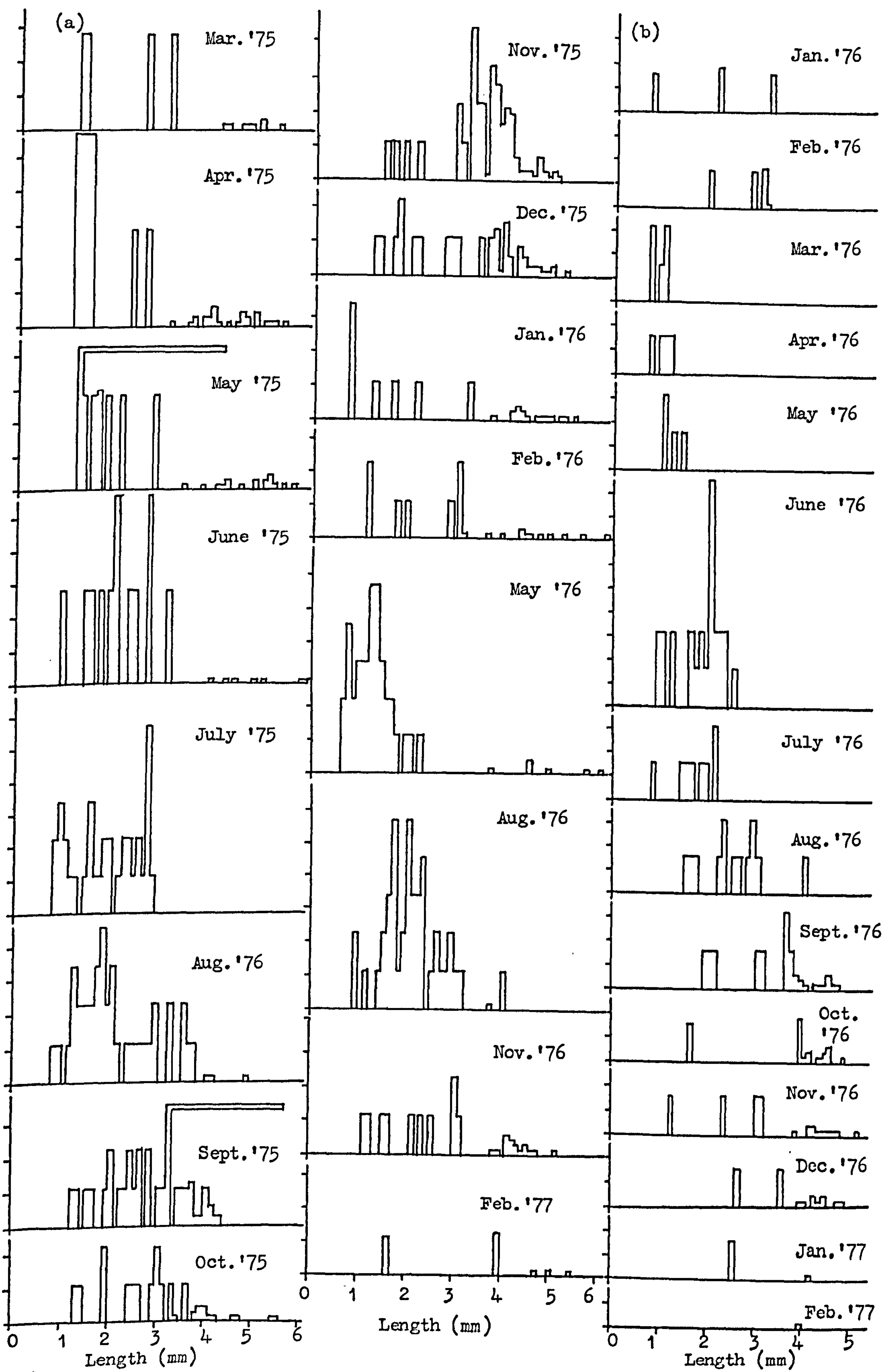


Figure 5.15 R. obtusa : The Mean Length of Each
Cohort at Each Sampling Occasion.
Vertical Bars ± 1 S.D.

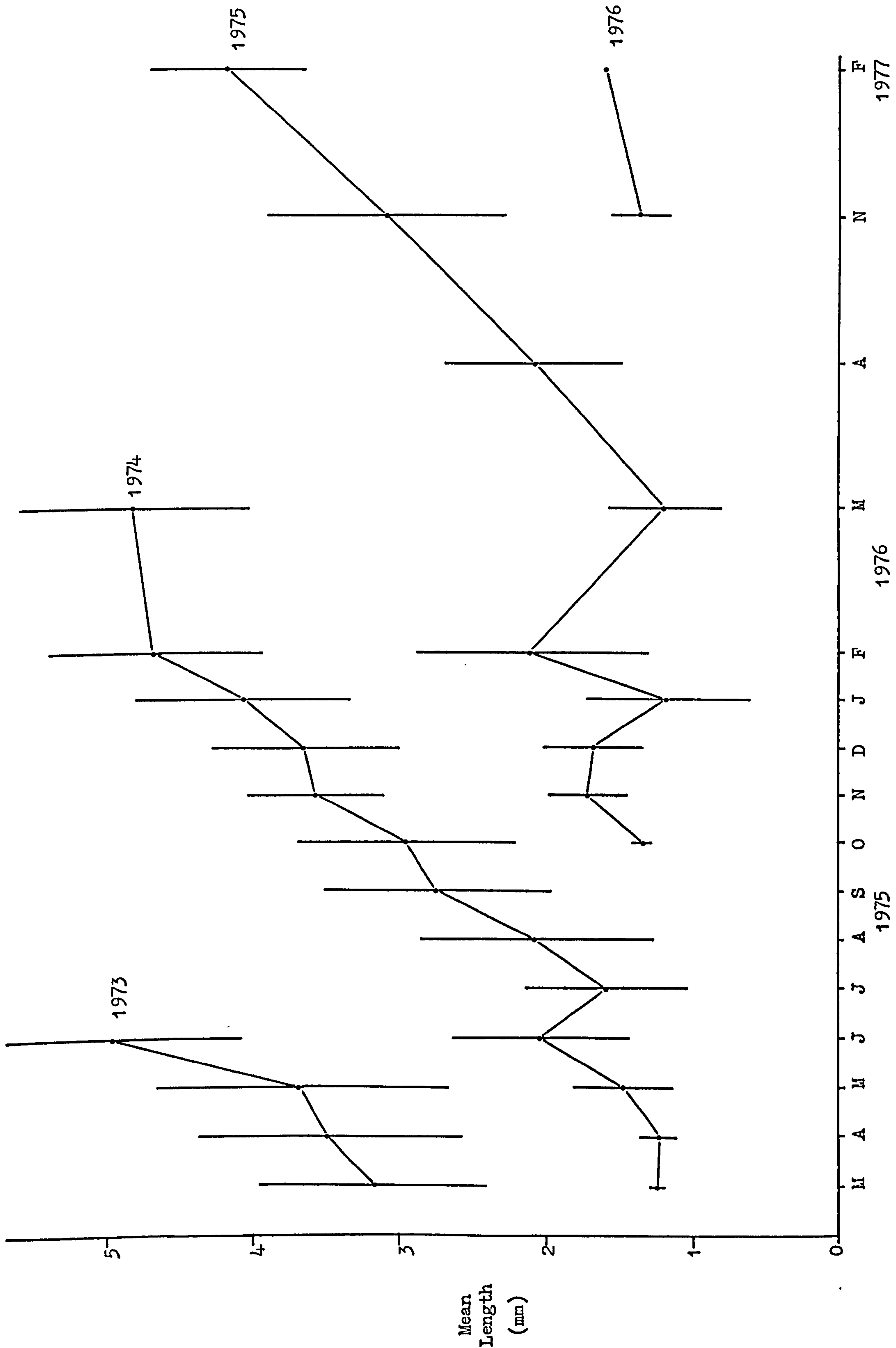


Figure 5.16 R. obtusa : The Mean Biomass
(Total Dry Weight) of Each
Cohort at Each Sampling
Occasion.

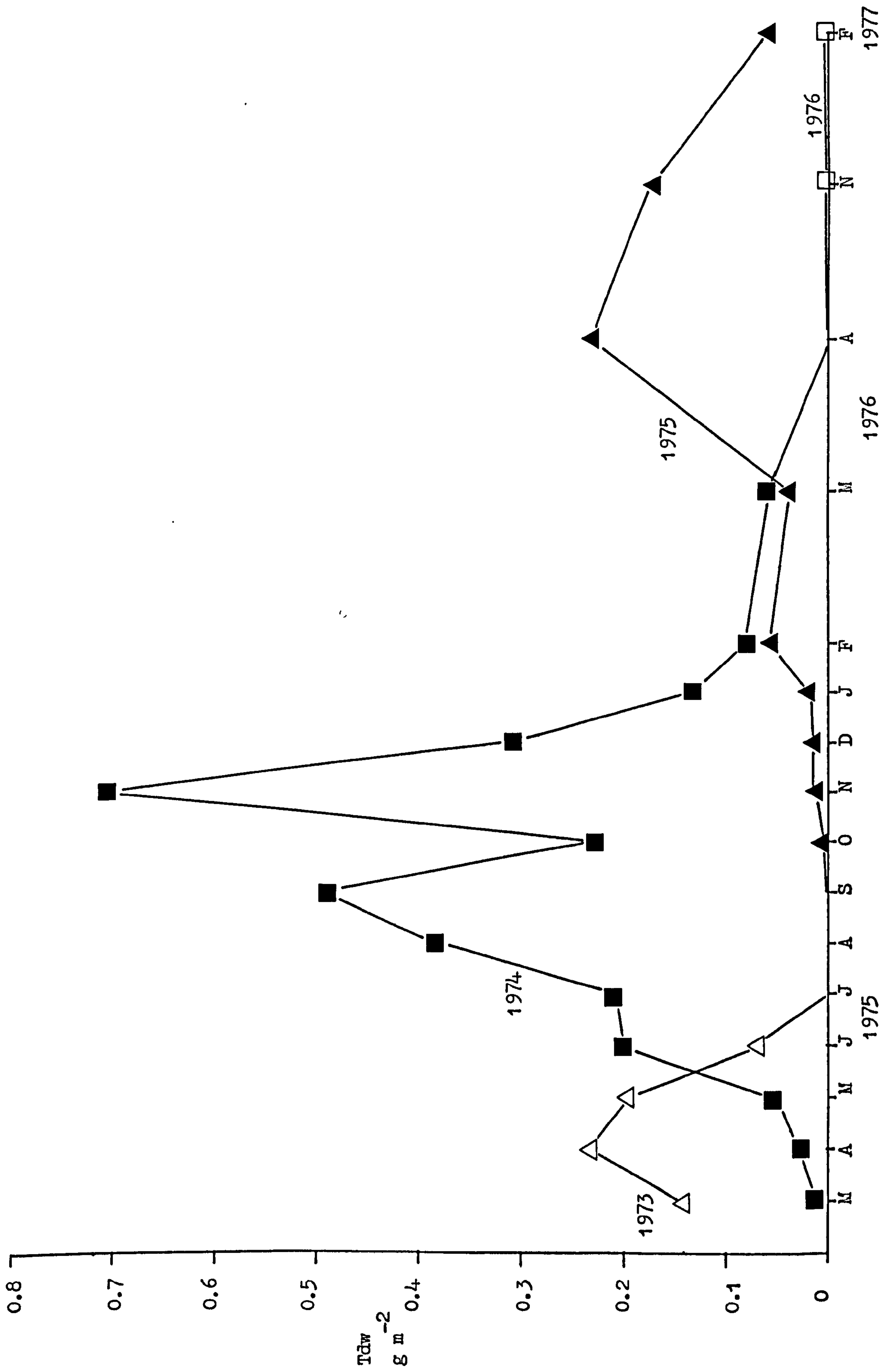
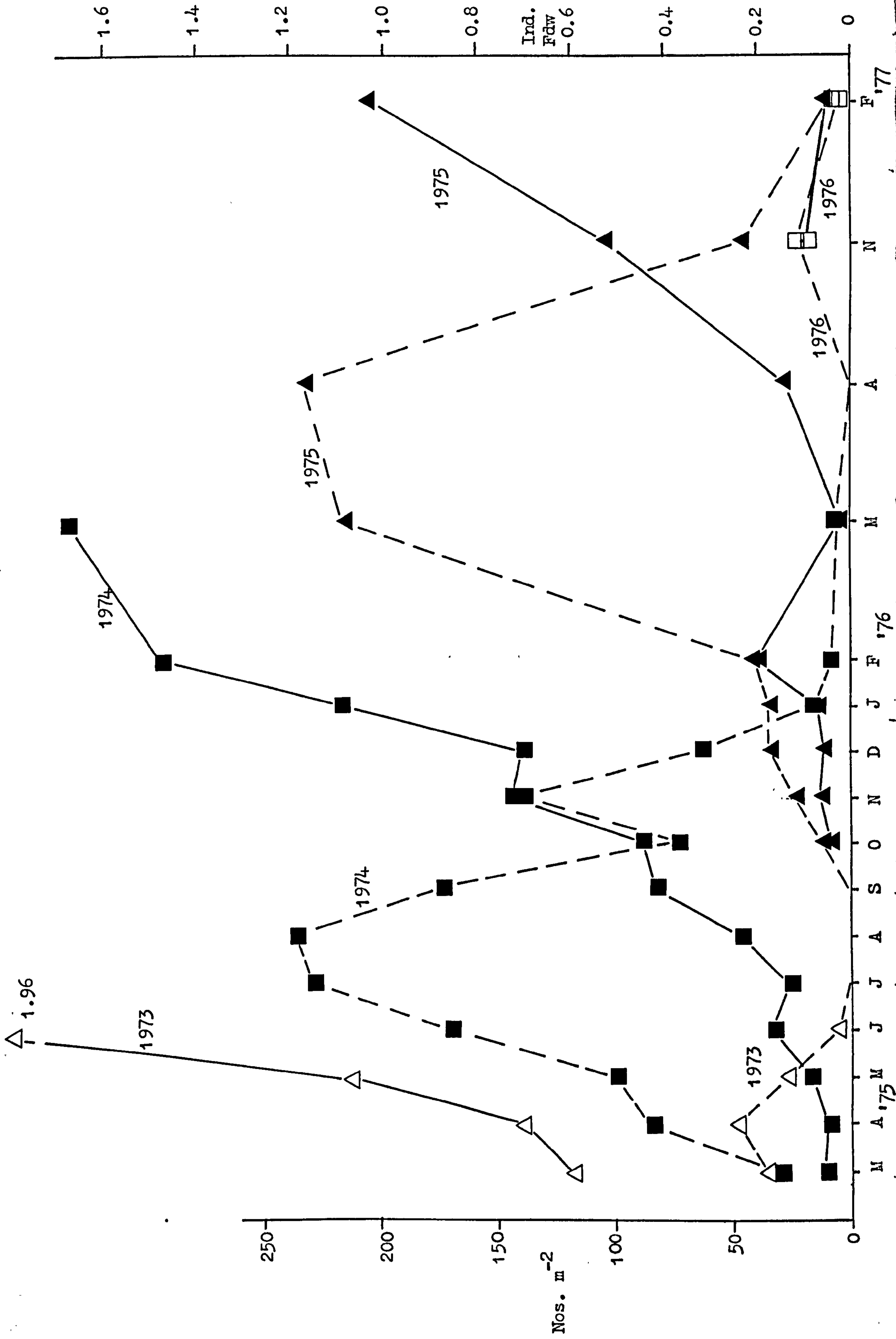


Figure 5.17 R. obtusa : The Individual Mean Flesh
Weight and Density of Each Cohort at
Each Sampling Occasion.
Dotted Lines - Density;
Solid Lines - Mean Weight.



sigmoid growth curve with the major part of the growth occurring during the period June to January which was preceeded and followed by a slower growth rate (Figs. 5.15, 5.17). The lack of growth over the winter may possibly be attributed to both the unfavourable conditions and the onset of maturity. Points of minima in these two graphs can be attributed to an inflow of newly hatched individuals into the cohort.

5.3.5.1.2. The Populations Supported at Each Station.

The diagram (Fig. 5.18) shows the presence of the age cohorts at each station and sampling period and the mean sizes of those cohorts. It is evident that those stations which support constant adult populations also support the progeny of those adults; this demonstrates the limited ability of R. obtusa to colonise new areas, either locally or geographically, because of the mode of reproduction employed. It may also be suggested that some stations did not support breeding populations of R. obtusa and that only individuals washed from neighbouring areas were found at those stations, e.g. B1, B4, B5 and C1.

At many stations, the mature 1973 cohort animals survived until July, 1975 and produced the 1974 cohort; the latter was the dominant cohort throughout 1975 and survived until the spring of 1976. The cohort produced by the 1974 group, i.e. those immature individuals present from October, 1975 onwards, showed a decrease in their mean size during the spring and early summer period 1976. That decrease was attributable to the numbers of young individuals of the main spawning entering the year class.

The growth rates of R. obtusa did not appear to differ with station although the maximum size reached by a cohort varied with

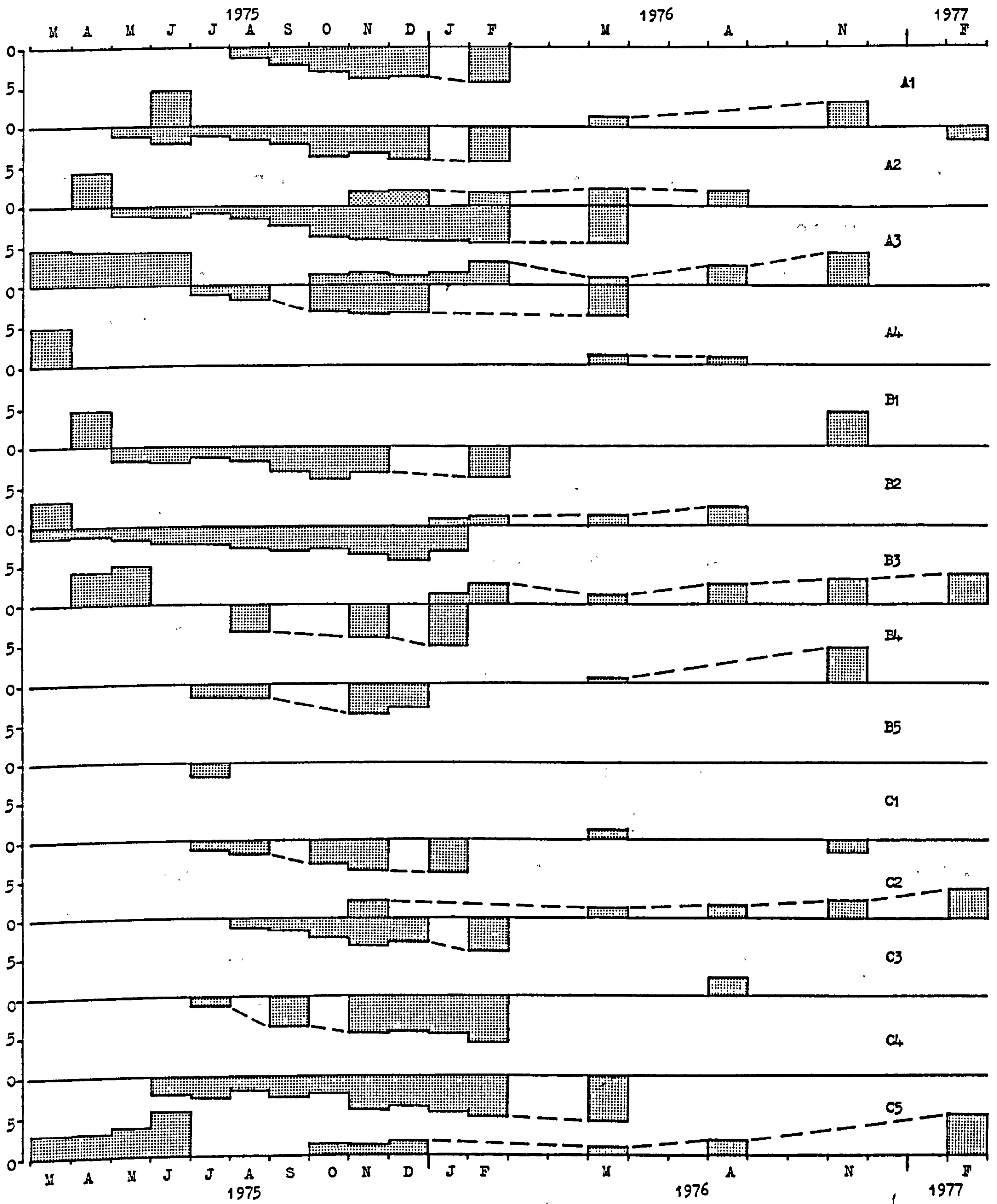


Figure 5.18 *Retusa obtusa*: The Occurrence and Size of Each Year Class at Each Station and on Each Sampling Occasion. (The ordinate is mean size (mm)). Dashed line gives probable pattern where no animals found.

area and the cohorts survived for longer periods in some areas than others. The weight-specific instantaneous growth rates (G) of the 1974 cohort were calculated for each station for each monthly sampling period from May, 1975 until February, 1976, using the regression equation :

$$\text{Log}_{10} \text{ fdw} = 2.849 \text{ Log}_{10} l - 1.7469$$

$$r = 0.9798$$

$$n = 92$$

$$P < 0.001$$

where l = mean length of the cohort at a station.

from which growth rate, G, was computed using the formula :

$$G = \frac{d \text{ Log}_e w}{dt} = 2.303 \frac{d \text{ Log}_{10} w}{dt} \quad (\text{from Crisp, 1971})$$

where w = flesh weight (mg)

t = time (days)

thus giving the rate of change in fdw on a daily basis (Fig. 5.19; Table 5.11). Negative growth rates have not been graphically represented as these were attributable to either the loss of large animals from the population or an influx of small animals, both of which would decrease the cohort mean size.

The highest growth rates for most of the stations occurred during the period July to November. This may be attributed to many factors including the fact that settlement of young and mortality of old Retusae were both minimal during this period such that any increase in the mean size of the cohort was evident. Additionally, the summer to autumn period was commonly the most favourable time for growth following any emaciation due to spawning and preceeding winter emaciation. However, it may also

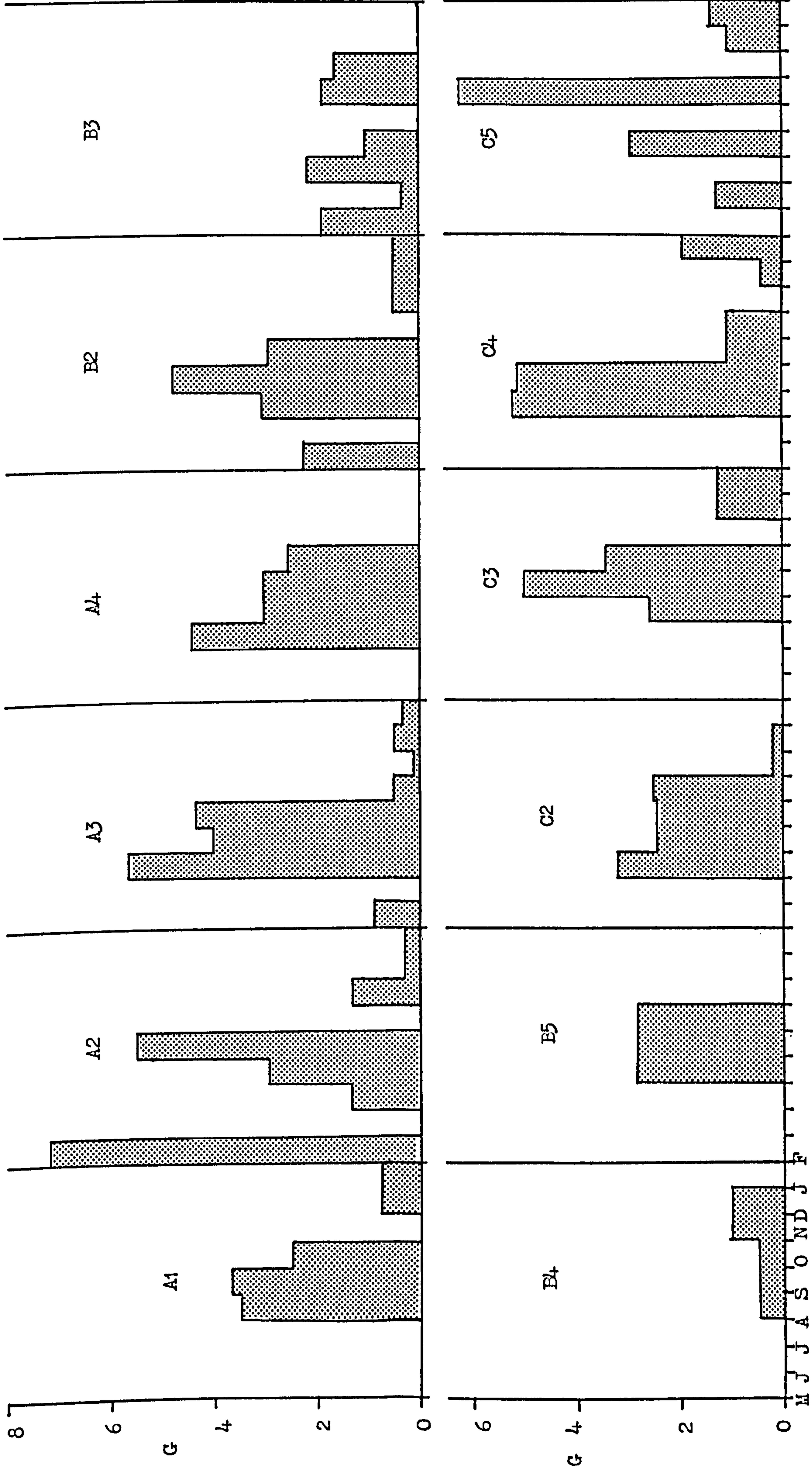


Figure 5.19 R. obtusa : The Weight Specific Instantaneous Growth Rate ($G \times 10^{-2} \text{ days}^{-1}$) at Each Station (1975-76 Data).

Stations B1 and C1 Insufficient Data.

Table 5.11 R. obtusa : The Weight-Specific Instantaneous Growth Rates (as $G \times 10^{-2} \text{ days}^{-1}$, see text),
for Each Sampling Period, 1975-76 Data.

Station	A1	A2	A3	A4	B1	B2	B3	B4	B5	C1	C2	C3	C4	C5
May-June	-	7.131	0.877	-	2.242	1.896	-	-	-	-	-	-	-	-
June-July	-	-6.621	-3.746	-	-4.228	0.329	-	-	-	-	-	-	-	1.246
July-Aug.	-	1.307	5.652	4.403	-	3.048	2.148	-	0	-	3.196	-	5.134	-3.345
Aug.-Sept.	3.484	2.950	4.006	3.020	-	4.784	1.037	0.468	2.821	-	2.427	2.562	5.131	2.928
Sept.-Oct.	3.628	5.507	4.328	3.020	-	2.911	-0.507	0.468	2.821	-	2.427	4.939	1.021	-1.175
Oct.-Nov.	2.493	-1.163	0.433	2.540	-	-2.267	1.870	0.468	2.821	-	2.467	3.403	1.021	6.203
Nov.-Dec.	-0.564	1.261	0.108	-0.346	-	0.511	1.638	0.971	-2.090	-	0.195	-1.379	-0.315	-0.751
Dec.-Jan.	0.754	0.276	0.497	-	-	0.511	-2.524	0.971	-	-	0.195	1.235	0.397	1.055
Jan.-Feb.	0.754	0.276	0.321	-	-	0.511	-	-	-	-	-	1.235	1.907	1.314

be observed that the maximal growth rates by the 1974 R. obtusa cohort occurred during the period of H. ulvae spat settlement when there were maximum numbers of 0+ group H. ulvae in the population (see Section 5.3.5.3.). It is also probable that during this period other prey items of R. obtusa, such as meio-fauna, microfauna and the newly settled spat of other macro-invertebrates, would have been abundant and would also have contributed to the large growth rates.

5.3.5.2. The Production and Elimination of R. obtusa.

Both E (as ΔM) and P have been calculated for the main age cohort in 1975, i.e. the 1974 age class (Table 5.12). During periods when there was a large recruitment into the population, i.e. up until mid-summer, then the estimate ΔM had a negative value. Over the whole life span of a cohort both E and P should be identical as the amount of production is lost as elimination. The respective figures for ΔP and ΔM (E) for the 1974 cohort were 121.416 and 114.473mg (afdw) m^{-2} per 1.167 yr; the survival of a few individuals after this time period accounting for the slightly lower latter value. Therefore, only the production (P) has been used in the further considerations and calculated for the combined populations of the stations on Torry Bay. The production for the period March, 1975 to February, 1976 was found to be 158mg (afdw) m^{-2} yr^{-1} \equiv 1.102g (tdw) m^{-2} yr^{-1} with a P/\bar{B} value of 3.45. This P/\bar{B} value, although approaching the recorded values for similar populations of macroinvertebrates with an annual life cycle, is relatively high.

Using a similar method for the calculation, P for each station and for each of the sampling periods early March, 1975 to late February, 1976 and mid-February, 1976 to mid-February, 1977

Table 5.12 R. obtusa: The Computation of Somatic-Production (as ash-free dry weight), 1975-76 Data.

Sampling Date	Cohort	Time t (yrs)	Mean Weight (mg)	$N m^{-2}$	Biomass $\bar{N} \bar{w}$ ($mg m^{-2}$)	Over Period \bar{w}	- N	\bar{w}	P $(N \bar{w})$ ($mg m^{-2}$)	M $(\bar{w} N)$ ($mg m^{-2}$)	Cohort $N m^{-2}$	Mean Weight (mg)	P ($mg m^{-2}$)
Mar. '75	1974	0	0.050	28.6	1.430	-	-	-	-	-	1973	0.594	-
Apr. '75		0.085	0.045	85.7	3.860	57.15	0.047	-0.005	-0.286	-2.712		0.695	4.151
May '75		0.167	0.076	100.0	7.600	92.85	0.060	0.031	2.878	-0.865		1.062	13.634
June '75		0.252	0.167	171.4	28.620	135.70	0.121	0.091	12.349	-8.675		1.957	14.051
July '75		0.334	0.129	228.6	29.490	200.00	0.148	-0.038	-7.600	-8.466			
Aug. '75		0.419	0.230	236.4	54.370	232.50	0.179	0.101	23.482	-1.400			
Sep. '75		0.501	0.412	175.0	72.100	205.70	0.321	0.182	37.437	19.709			
Oct. '75		0.586	0.444	73.6	32.680	124.30	0.428	0.032	3.978	43.399	1975	0.039	-
Nov. '75		0.671	0.720	140.7	101.304	107.15	0.582	0.276	29.573	-39.052		0.064	0.429
Dec. '75		0.753	0.700	62.9	44.030	101.80	0.710	-0.020	-2.036	55.238		0.052	-0.343
Jan. '76		0.838	1.088	17.1	18.600	40.00	0.894	0.388	15.520	40.945		0.068	0.549
Feb. '76		0.923	1.474	7.9	11.640	12.50	1.281	0.386	4.825	11.785		0.203	5.062
May '76		1.167	1.675	5.0	8.375	6.45	1.575	0.201	1.296	4.567			

Population Annual Production, 1975-76:

1973 Cohort = 31.836 $mg m^{-2}$
 1974 Cohort = 120.120 $mg m^{-2}$
 1975 Cohort = 5.697 $mg m^{-2}$
 Total = 157.653 $mg m^{-2}$ afdw = 1.102 $g m^{-2} yr^{-1}$ tdw.

was calculated together with the mean biomass for each age cohort and the cohort and total station population P/\bar{B} values (Table 5.13a). The mean values for the area for each age cohort and for the combined population were then determined (Table 5.13b). The mean values for the production and the P/\bar{B} for the stations for 1975-76 are considerably lower than those obtained by the first estimate in which the population of the area was treated as being continuous. At some of the stations, some age cohorts that were represented in very low densities, such that animals of that cohort were not recovered in either the preceding or following samples, did not contribute anything to the production calculation although they were included in the biomass calculations. The P/\bar{B} for the area was therefore lower and corresponds to the values found in other estuarine macroinvertebrate production estimates.

The production and mean biomass estimates were lower for 1976-77 than 1975-76 although the productivity values were similar, suggesting that the difference in estimates were not wholly attributable to the longer sampling period during 1976-77. However, the production and biomass estimates for Station B3 on a monthly sampling basis for 1976-77 were higher than when calculated on a quarterly sampling basis. It is considered therefore, that production estimates calculated on the shortest possible sampling period are most accurate, a conclusion also reached by Golikov (1970).

The productivity of R. obtusa also showed an inverse relationship with cohort age. This was shown particularly by the data for 1975-76 in which the main cohort for that year had a P/\bar{B} value of 2.622 whereas the preceding and succeeding cohorts had values of 0.717 and 4.876 respectively (Table 5.13b).

Table 5.13 *Retusa obtusa*: The Areal Total and Station Production ($\text{mg Fdw m}^{-2} \text{ yr}^{-1}$), Mean Biomass (mg Fdw m^{-2}) and Annual P/\bar{B} .
1975-76(a)

Station	1974 Cohort		1973 Cohort		1975 Cohort		Total	
	P	\bar{B}	P	\bar{B}	P	\bar{B}	P	\bar{B}
A1	-12.81	41.445	0	1.132	0	0	-12.81	42.577
A2	172.00	39.148	0	2.002	-3.08	2.467	168.92	43.617
A3	302.09	58.939	8.14	16.681	28.96	3.759	339.19	79.379
A4	-37.73	9.654	0	2.610	0	0	-37.73	12.264
B1	0	0	0	0.110	0	0	0	0.110
B2	-11.99	53.180	0	8.330	0.32	0.933	-11.67	62.443
B3	625.19	164.066	101.55	13.004	47.33	7.804	774.07	184.874
B4	0	12.385	0	0	0	0	0	12.385
B5	-74.89	5.572	0	0	0	0	-74.89	5.572
C1	0	0.013	0	0	0	0	0	0.013
C2	20.77	10.367	0	0	0	0.707	20.77	11.074
C3	12.80	11.797	0	0	0	0	12.80	11.797
C4	14.23	11.171	0	0	0	0	14.23	11.171
C5	204.36	45.274	-0.01	109.115	1.40	0.880	205.75	155.269
\bar{x}	86.72	33.072	7.83	10.927	5.76	1.182	99.90	45.182
S.E.	50.07	11.449	7.23	7.690	3.97	0.592	6.68	15.609

1975-76(b)

Station	1975 Cohort		1974 Cohort		1976 Cohort		Total	
	P	\bar{B}	P	\bar{B}	P	\bar{B}	P	\bar{B}
A1	0	8.008	-6.03	2.413	0	0	-6.03	10.421
A2	-21.16	13.039	-24.36	9.746	2.12	0.848	-43.40	23.633
A3	-9.49	18.356	-22.14	13.624	0	3.328	-31.64	35.308
A4	0.40	1.040	0	1.344	0	0	0.40	1.040
B1	0	1.960	0	0	0	0	0	1.960
B2	29.12	14.720	-3.72	1.490	0	0	25.39	16.210
B3	413.86	112.106	0	0	0	1.744	413.86	113.850
B3*	595.57	120.625	0	0	11.44	5.733	607.01	126.358
B4	0	2.900	0	0	0	0	0	2.900
B5	0	0	0	0	0	0	0	0
C1	0	0.240	0	0	0	0	0	0.240
C2	167.04	30.848	0	0	0	1.232	167.04	32.080
C3	0	8.448	-5.42	2.170	0	0	-5.42	10.618
C4	0	0	-19.52	7.808	0	0	-19.52	7.808
C5	40.19	17.918	-13.57	14.428	0	0	26.62	32.346
\bar{x}	44.28	16.399	-6.77	3.787	0.15	0.511	37.66	20.697
S.E.	30.98	7.756	2.44	1.413	0.15	0.264	31.80	7.917

1976-77(b)

(B3* based on monthly sampling, all other stations 1976-77 data based on quarterly sampling).

5.3.5.3. Prey-size Taken by R. obtusa.

Over the sampling period several R. obtusa individuals were collected and fixed with whole or partly digested Hydrobiae in their pharynx. In such cases, the prey must have been taken prior to sampling and had not been digested sufficiently to be withdrawn into the shell (and stomach); this also prevented the foot of the Retusae being withdrawn into its shell (Plate 5.1). The R. obtusa photographed was 3.7mm in length and the Hydrobiid approximately 2.2mm long (the terminal whorl had been partly digested). This R. obtusa also had the foraminiferan Elphidium striato-punctatum within its pharynx. Hurst (1965) suggests that when carnivorous shelled opisthobranchs are sampled with large prey organisms within their pharynx, in an attempt to withdraw their foot the prey is often extruded through the mouth. These findings may suggest that although the Retusae have stomach plates for crushing shelled prey items, initial digestion of large prey is performed within the pharynx.

Analysis of the data obtained from the Retusae found containing Hydrobiids outside the predators' shell (Table 5.14) suggests that, although the sample size was small, the mean size of Hydrobiid taken increased with time throughout the year although there appears to be no correlation between the sizes of the predator and prey. There also appears to be a minimum size of Retusae (3.7mm) which will ingest Hydrobiae in this way. However one may suggest that smaller Hydrobiids than those found here will be withdrawn into the predators shell or taken by smaller predators. Smith (1967a) suggests that a R. obtusa individual 2.5mm long could ingest Hydrobiae 0.5mm in length.

The Hydrobiae taken by the predators were all within the



Plate 5.1 A Photograph of Hydrobia ulvae Within the Pharynx of R. obtusa. The Length of the R. obtusa was 3.7mm and the Hydrobiid 2.2mm. The Animals Were Taken at Station A1 in December, 1975.

Table 5.14 H. ulvae Taken by R. obtusa.

Date	Station	<u>Length Retusae (mm)</u>	<u>Length Hydrobiae (mm)</u>
September 1976	B3	4.2	1.8
		4.2	1.4
October 1975	A3	4.2	1.7
November 1976	B3	4.3	2.0
		4.2	1.6
December 1976	B3	4.8	1.5
		4.4	1.9
		4.7	2.2
		4.0	1.9
December 1975	A1	3.7	≈2.2
February 1976	A2	4.5	2.3
		4.2	2.0
	A3	4.5	2.0

0+ group cohort (Fig. 5.4). However there appears to be no relationship between the number of 0+ group Hydrobiae at a station and the presence of large Retusae. At Stations A3 and C5, ranked second and third in the amount of R. obtusa production at the stations, there was a very small 0+ group cohort (Fig. 5.4) although there was probably an influx of young to these stations later in the year as indicated by the decrease in the station Hydrobiae M.I.W. in October, 1975 (Fig. 5.5).

5.3.6. The Relationships Between the R. obtusa Production Summary Data and the Environmental Variables and the H. ulvae Production Data.

The R. obtusa P, \bar{B} and P/\bar{B} data for 1975-76 was included in a correlation matrix against the environmental variables and the H. ulvae summary data (Fig. 5.7). There were no significant linear correlations between the R. obtusa data and the environmental variables, however some relationships were significant when logarithmically transformed. The data was also incorporated into stepwise multiple linear regressions (Table 5.15).

(i) R. obtusa Mean Biomass.

The positive exponential relationship between this variable and tidal height was correlated to a very significant level when transformed. A negative logarithmic relationship (*) was also obtained between this variable and the water content of the sediment. Although a low biomass was found on all substrate types, high \bar{B} values were associated with both coarse and fine substrate at Stations C5 and B3 respectively.

However, the relationships between the H. ulvae and R. obtusa populations on Torry Bay are of greater relevance. R. obtusa \bar{B}

Table 5.15 R. obtusa : Spatial Data Analysis - Multiple Regression Equations of Production Summary Data With Environmental and H. ulvae Production Variables. (Legend as Fig. 5.7.)

Dependent Variable	Incorporated Variables and Significant Equation	Excl. Variables	Total Variance Accounted For	Main Variables
(1) R \bar{B}	TH., M.P.D., S.C., SK., %H ₂ O, %C, %N, %S. & C., Slope, C/N, Salinity, H \bar{B} , H \bar{N} , H P, H M.I.W., H P/ \bar{B} . $\begin{aligned} &^{***} 71.04_{SK} - 167.04_{TH} - 115.68_{H P/\bar{B}} - 5.425_{C/N} + 0.294_{M.P.D.} \\ &^{**} - 11.53_{Salinity} + 17.52_{H P} + 190.7_{H M.I.W.} + 96.61_{S.C.} \\ &+ 1644.66 \end{aligned}$	%H ₂ O, %C, %N, %S. & C.	99.8%	H P (41.3%), H M.I.W. (13.9%), C/N (10.6%).
(2) R \bar{B}	H \bar{N} , H P, H M.I.W., H P/ \bar{B} . $20.112_{H P} + 62.92$	-	51.2%	H P (41.3%).
(ii) (1) R P	TH., M.P.D., S.C., SK., %H ₂ O, %C, %N, %S. & C., Slope, C/N, Salinity, H \bar{B} , H \bar{N} , H P, H M.I.W., H P/ \bar{B} . $3646.6 - 576.1_{TH} - 7.41_{%S. \& C.} - 34.06_{C/N} + 1226.6_{S.C.}$ $- 717.26_{H P/\bar{B}} + 1573.0_{H M.I.W.}$	M.P.D., %H ₂ O, %N, H P.	99.7%	%S. & C. (18.1%), S.C. (17.4%), H P/ \bar{B} (15.1%), C/N (13.8%), Salinity (12.9%), S.K. (11.2%).
(2) R P	H \bar{N} ; H P, H M.I.W., H P/ \bar{B} . $All\ n.s. + 161.5$	-	15.9%	H P (11.8%).

Table 5.15 Continued

Dependent Variable	Incorporated Variables and Significant Equation	Excl. Variables	Total Variance Accounted For	Main Variables
(iii)(1) R P/̄B	TH., M.P.D., S.C., SK., %H ₂ O, %C, %N, %S. & C., Slope, C/N, Salinity, H̄B, H̄N, H P, H M.I.W. $^{**}27.185\%C - 3.341\%H_2O - 1.513C/N + 1.790\text{Salinity} - 94.671$	TH., %N, %S. & C.	97.8%	C/N (17.9%), S.C. (16.1%), H M.I.W. (11.6%), Salinity (11.4%).
(2) R P/̄B	H̄B, H̄N, H P, H M.I.W. All n.s. + 8.183	-	51.7%	H̄B (24.4%), H P (16.2%), H M.I.W. (8.7%).

was positively and curvilinearly related (***) to H. ulvae P and \bar{B} . R. obtusa \bar{B} was also positively and curvilinearly related to H. ulvae numbers producing a highly significant relationship when logarithmically transformed. Stations B3 and C4 did not strictly follow this pattern as the latter had high H. ulvae numbers with a low R. obtusa biomass and vice versa for Station B3. This may be an indication of the high meiofaunal content of fine muds providing additional prey for the opisthobranch (see below). In addition the higher R. obtusa biomasses were found on sites with the lower H. ulvae P/\bar{B} values. This is a reflection of the higher P and \bar{B} of H. ulvae and lower P/\bar{B} at the higher tidal levels leading to greater R. obtusa biomasses.

The multiple regression analysis shows that although many factors were significant in their relationships with R. obtusa biomass (Table 5.15(i)), the major part of the variance of this variable was accounted for by H. ulvae annual production. The H. ulvae mean individual weight may also have influenced the R. obtusa ^{biomass} ~~production~~ at any station.

(ii) R. obtusa Annual Production.

Very little information regarding the effect of environmental factors on this variable has been obtained as all levels of production were encountered within different environments. A curvilinear relationship was found between H. ulvae production and R. obtusa production, although Stations B3 and to a lesser extent C5 did not strictly follow this pattern (see below).

The multiple regression analysis shows that the variance of the dependent variable was attributed to many environmental factors and that the Hydrobiid population data only accounted for a small part of that variance (Table 5.15(ii)).

(iii) R. obtusa P/ \bar{B} .

This variable was found to be influenced by many variables including the sediment sorting coefficient, salinity, mean weight of H. ulvae and slope of shore (Table 5.15(iii)).

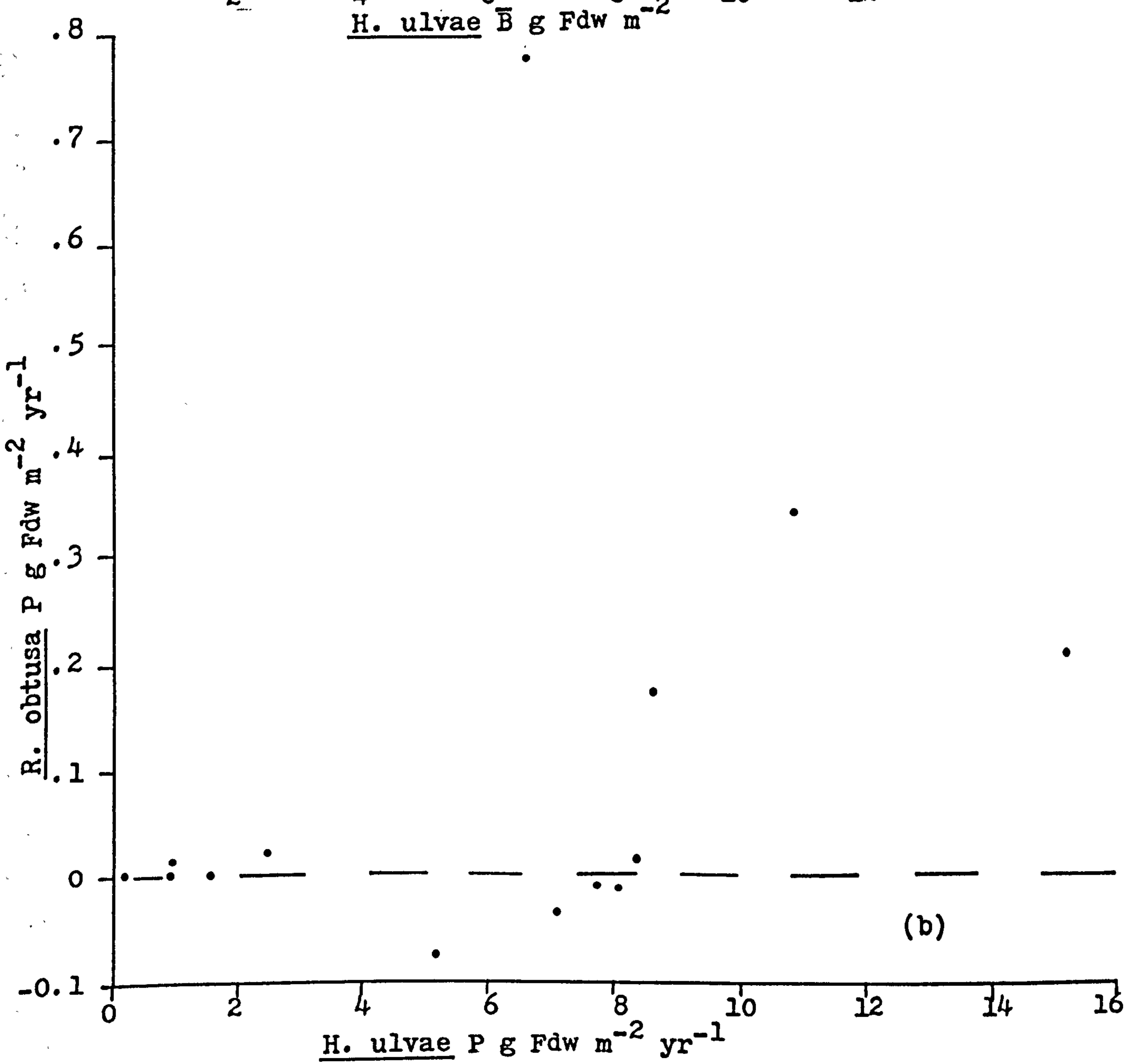
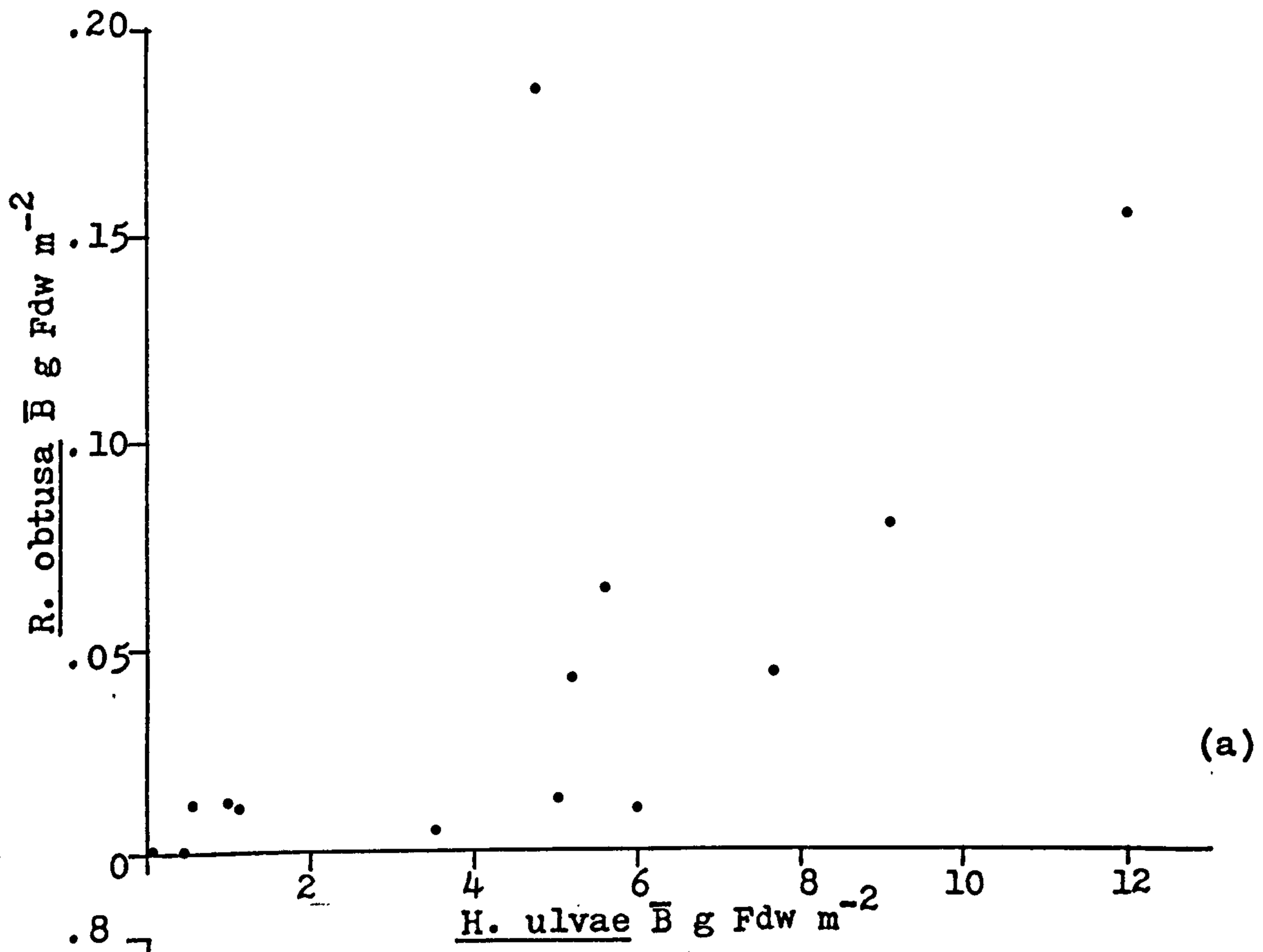
Interrelationships Between the R. obtusa Population Variables.

The biomass and production of R. obtusa described a linear relationship (***) demonstrating the relative constancy of the P/ \bar{B} values. The Station C5, however, had a population production too low for the biomass supported (possibly a reflection of the lack of meiofauna in clean sand for the young Retusae). As expected there were highly significant interrelationships between R. obtusa production, mean biomass and P/ \bar{B} .

R. obtusa and H. ulvae Interrelationships.

The interrelationships between the production and biomass estimates of H. ulvae and R. obtusa (Figs. 5.20a, b; 5.21) are to a greater or lesser extent curvilinear such that they are significant to low levels in the untransformed Pearson correlation matrix (Fig. 5.7). Of greatest significance is the relationship between the production of H. ulvae at a station and the R. obtusa biomass supported by that production (Fig. 5.21). In these figures, the data from all stations except B3 follow a well-defined curvilinear pattern. Station B3, however appears to have a R. obtusa biomass larger than that suggested by the H. ulvae production. It may therefore again be suggested that B3 has a large biomass of other prey utilized by R. obtusa such as bivalve spat, meiofauna and foraminiferans. Observations suggest that foraminifera are common in the fine muddy areas on Torry Bay; however, this conclusion was subjectively reached but although it

Figure 5.20 R. obtusa and H. ulvae ;
The Relationships Between (a) Mean
Annual Flesh Biomasses and
(b) Mean Annual Flesh Production
Values.
(1975-76 Data.)



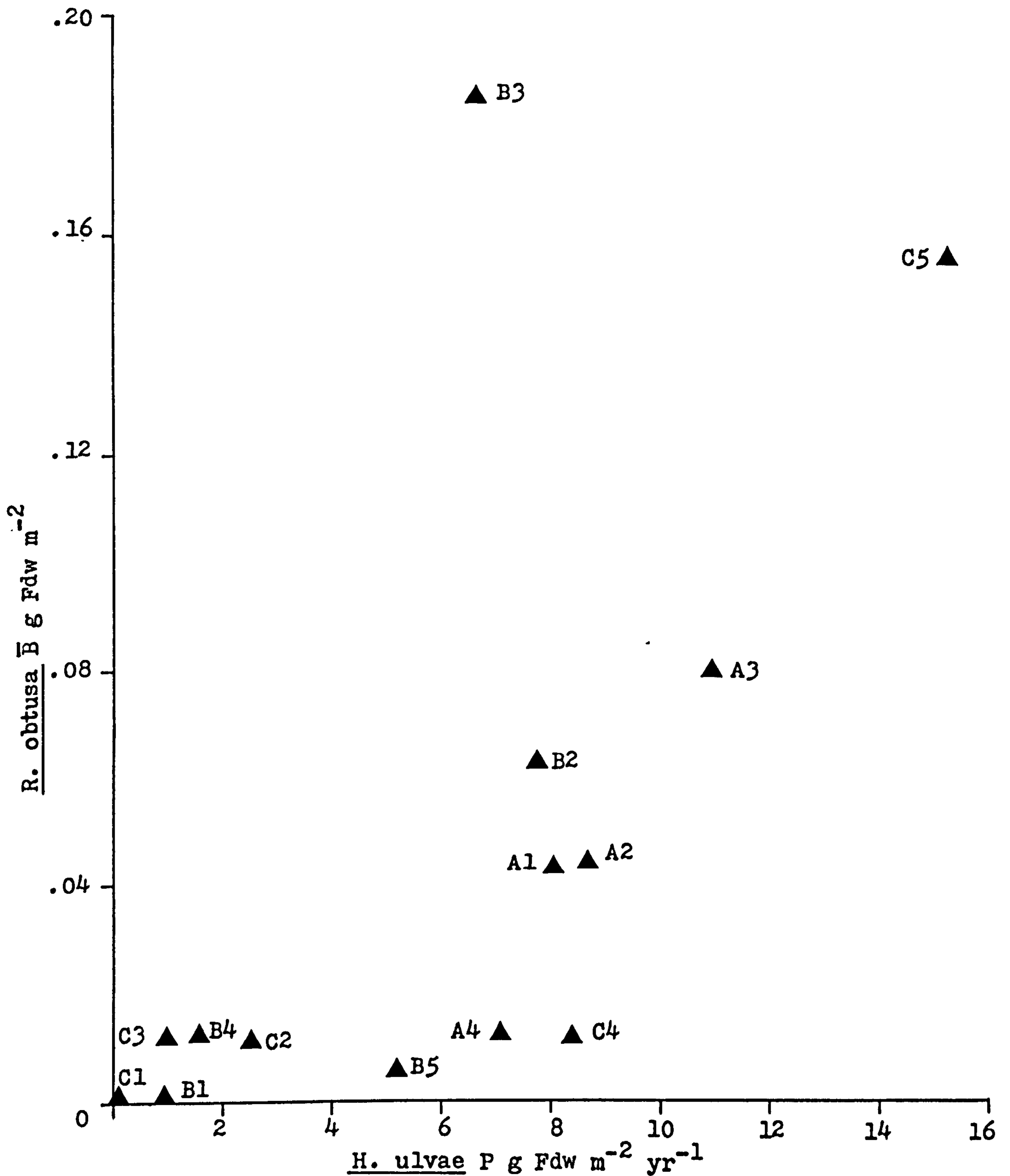


Figure 5.21 The Relationship Between H. ulvae Annual Flesh Production and the Mean Annual Flesh Biomass of R. obtusa (1975-76 Data).

is realized that many of these sarcodines were destroyed during sieving, Muus (1967) and Ankar (1976) report large foraminiferan populations on soft muddy bottoms. Estimations of the density of oligochaetes, nemertines and nematodes (see Section 7.3.1.; Table 7.2) show that the muddy substrate areas had the richest populations although the extent to which meiofaunal richness influenced the size of the R. obtusa populations is uncertain. It is considered that a large R. obtusa biomass at a station will only result from the presence of O+ group Hydrobiae on which adult Retusae feed and other smaller prey items such as foraminera which can be utilized by small Retusae.

5.4. Discussion.

The results show that the H. ulvae population on Torry Bay had its centre at an optimal tidal height and exposure period, in sediments which suggest that the species had a preference for greater wave action and in an area which had a supply of detritus as food provided by the Z. marina beds and associated epiphytes and microflora. At that population centre, most of the areal production occurred by the largest animals which, although constituting the greatest biomass, had the lowest productivity. Away from that centre, primary recruitment to the population occurred resulting in areas with high biomasses and population densities at only certain times of the year. These latter areas' populations consisted of high numbers of young animals with a correspondingly high productivity and with a high metabolism per unit weight; however, because of their high mortality and small biomass they made a small contribution to the population energy flow. The population was therefore dominated metabolically, but not necessarily numerically, by the large snails present in constant numbers with a low growth rate. These points will be discussed below.

It is considered that the spat preferentially settled at the lower levels because of one or more of the following reasons; firstly, passive settlement of larvae would occur in areas of fine mud where water currents were slowest; alternatively, settlement induced by chemical stimulation from fine mud would have the same effect. Secondly, this would avoid direct competition with the adults for food or space. Thirdly, the smaller animals may have different food particle, exposure, salinity or substrate preferences from the adults.

There is a paucity of literature regarding the settlement of intertidal gastropods (Crisp, 1974), although the study by Scheltema (1961) on Nassarius obsoleta warrants consideration here. N. obsoletus possibly occupies the corresponding ecological niche to H. ulvae on the Atlantic coast of North America as it occurs in large numbers on estuarine mud, is a deposit feeder and has a planktotrophic method of dispersal. The larvae settle on fine muds often away from the main distribution of the adult and may delay settlement until suitable substratum is found. Scheltema (1961) experimentally found that whilst the physical character of the deposit was important, the settlement inducing factor was a water-soluble substance possibly originating from microbial metabolites or the product of detritus degradation. The possibility that H. ulvae larvae may have receptive abilities similar to N. obsoletus cannot be disregarded.

However, although it may be suggested that the high numbers of deposit feeders found on fine substrate is the result of substrate selection, the same correlation would be caused by the passive settlement and sorting of both larvae and sediment by water movements. This hypothesis has been postulated for bivalve larvae (see Sections 3.5.1. & 4.4.1. and Pratt, 1953) but may also play a part in gastropod settlement. The structure and composition of the substrate are possibly the most essential factors influencing the composition of a bottom community (Thorson, 1957), but substrate induced settlement is likely to be the result of many determining factors including sediment type, water currents and density and type of microorganisms present (Crisp, 1965, 1974).

Research concerning the mobility of the larvae appears

confusing. The larvae may be passively distributed owing to its little developed velar cilia which are incapable of raising the larvae from the bottom (Pilkington, 1971), thus keeping the free-swimming phase short. Fish and Fish (1976) however, found that the larvae are planktotrophic, have a well developed velum and have a pelagic phase of about 4 weeks (cf. Muus, 1967). Conversely, Green (1968) and Anderson (1971) cite work where no or very little free-swimming activity by the larvae has been seen and suggest that the suppression of a larval stage is advantageous to estuarine animals where there is the danger of being carried out to sea. A limited mobility, however, would allow for distribution down the shore.

The larvae of H. ulvae may not be too discriminative of substrate type when settling. In 1975, the areas receiving the largest settlements consisted of fine mud towards the low-shore, e.g. B2 and A1 which had densities of up to 1.05×10^5 and 8.4×10^4 animals m^{-2} respectively; C4, however, also had a density of $8.4 \times 10^4 m^{-2}$ possibly suggesting that settling also occurred during slack water at high tide. These generalisations do not apply to all low- and high-shore stations respectively such that there appears to be few firm principles regarding settlement of H. ulvae larvae.

It should be realized that although the larvae may be able to delay metamorphosis until a suitable settling area is reached (Thorson, 1957; Scheltema, 1961) metamorphosis cannot be postponed indefinitely and periods of calm water may result in some spat settlement. The larvae may undergo a series of settling stages (Thorson, 1957) such that at a nearly-metamorphosing stage the larvae will be more willing to settle in any area than newly-

hatched larvae. The latter would have more time to search for a suitable substrate and will therefore be more critical. Whether the change from one phase to the other is accomplished in the period between high and low water is unknown, but if the planktonic phase of H. ulvae larvae is short (Muus, 1967) then it will have a correspondingly short critical period.

The settlement of spat in an area away from that of the adult population may indicate either different food and immersion period preferences or the avoidance of competition between young and adults. Following the work of Fenchel et al (loc. cit), it may be suggested that different sized animals in a population have different food size preferences although this phenomenon could not be verified here. It has been shown, however, that whereas some stations support mainly large or small animals in unimodal populations, others had bimodal populations. It has also been shown that the size of Hydrobiae increases with tidal height (and possibly also with particle size). From these points it may be suggested that different sized animals have different preferences and that some resource partitioning may occur.

Fenchel and his co-workers have demonstrated particle size selectivity during feeding by Hydrobiae (and Corophium) such that species may coexist because of resource partitioning (Fenchel, 1975b; Fenchel et al, 1975). Within the three Hydrobia species the modal size of ingested particles was proportional to the shell length; also, where two species coexist one will have individuals larger than the other. This work, however, did not describe the mechanism by which given sizes of particles were selected by snails, i.e. whether certain sizes of particles were preferentially selected or whether the frequency of sizes of ingested

particles reflected the availability of these particles in the sediment. Fenchel and Kofoed (1976) found that although the latter was more important it was used together with the former mechanism. They also found that there is a critical minimum size of particles which snails can ingest and the larger animals will leave particles below that size for exploitation by the smaller animals.

The mortality following spat settlement was found to decrease the population densities by up to 50%. Spat settlement was greater in 1975 than the following year but differential mortality resulted in the maintenance of a stable population. This greater settlement, however, had little influence on the overall P , \bar{B} , and P/\bar{B} values such that there were no significant differences between sampling years. The spat mortality (after September, 1975) was much greater in the Forth than recorded for a comparable population in the Grevelingen estuary (Wolff and De Wolf, 1977). At Stations A1, C2 and C4 the numbers decreased by more than 20% during the following month and by 50% at B2. However at those stations which did not initially receive a large number of spat, the population increased later in the year by a "secondary" spatfall, e.g. A2, A3, A4, B3 and C5, such that the decrease in numbers after September at the settling areas was not wholly due to mortality.

Spat mortality may be affected by the number of deposit- and suspension-feeding animals in an area (Thorson, 1966; Hancock, 1973; Meikilovsky, 1974), such that in fine mud areas, where deposit feeders predominantly occur over M. edulis beds excessive mortality may occur (see Section 4.4.1.). The spat primarily

settled in an area away from the adult population and then secondarily moved into the latter area after initial growth, thus spat mortality by adult predation was decreased. Verwey (1952) and Thiesen (1972) have suggested that this happens in M. edulis populations. However, as H. ulvae spat were found to settle primarily in muddy areas, predation by the large populations of M. balthica and C. edule might occur.

Gregarious settlement by larvae has been postulated as occurring in most marine invertebrates except gastropods (Newell, 1970; Crisp, 1974; Meikilovsky, 1974). The settlement in large numbers of H. ulvae spat found here is thought to be more a function of settlement being influenced by environmental factors than of the gregarious behaviour by larvae.

The secondary settlement of young H. ulvae to areas higher in the tidal range possibly occurred by a combination of the movement of young by water currents and deposition in areas with a particle size which may correspond to the size of the animals and by the floating behaviour of the animals (Newell, 1964, 1970; Anderson, 1971).

The largest animals were primarily influenced by tidal height and the presence of Z. marina such that the most productive areas occurred together with those environmental factors associated with the high tidal level. The animals were found to aggregate at the highest levels with shallow slopes, with possibly well-sorted sediment and in areas with the lower salinities and possibly the greatest salinity range. These findings are not wholly compatible with Newell (1965) who found a high correlation between the particle size, amount of organic

matter (and bacterial populations) and numbers of H. ulvae. He further suggested that in coarse, as opposed to fine, deposits the small bacterial populations lead to a slow breakdown of organic debris and hence support only a small detritivore population. However, as detritus will probably be biodegraded more quickly in more aerobic conditions (Fenchel, 1972) such as in coarse deposits and also more organic matter will be deposited by water currents in fine than in coarse sediments, the conclusions reached by Newell (1965) may be erroneous.

Newell (1965) sampled his population in November and encountered large numbers of small animals on the fine mud and few, larger ones on the coarse sediment. He suggested that the former population was of young animals not dwarfed adults. It is considered that had his findings been expressed in units of biomass and the mean yearly values of biomass and tidal height preferences of H. ulvae taken into consideration his conclusions may have been slightly different.

It is possible that on Torry Bay the microorganisms and epiphytes found on detritus and Z. marina at the upper part of the shore were preferred by H. ulvae to the microorganisms and microflora in the sediment lower down the shore. Also, the sediments at the high stations had a lower C/N, i.e. were possibly more nutritious, than at the lower stations. The shore studied by Newell (1965) had low C/N values further down the shore, a fact that may provide some explanation of the differing conclusions reached here.

It may be valid to suggest that in fine mud and bare sand H. ulvae will have to ingest particulate matter to utilize the

microflora on the particles' surface. This method of feeding has a low assimilation efficiency (Fenchel, 1972) and consequently requires high energy expenditure. It may be advantageous, therefore, for H. ulvae to browse microfloral epiphytes from the surface of Z. marina and its detritus where possible. The tidal height preference of H. ulvae must also be considered and it may be inferred that the animal will adopt the most suitable method of feeding at the preferred tidal height.

Wolff (1973) found maximum numbers in salt marshes, on the upper half of tidal flats and in dense Zostera beds; areas which coincided with areas of finest sediment. Stopford (1951) and Newell (1964, 1965) stated that H. ulvae has a preference for finer sediments owing to the larger microflora population and Wolff (1973) found an optimal substrate preference of 2.5-3.5 ϕ M.P.D. (88-178 μ m). The latter also suggested that the animals accumulated in this zone by passive wave transport during floating behaviour (Newell, 1964; Anderson, 1971), whereas Newell (1964) further suggested that the animals from the lower-shore accumulated on the highest available shallow slope by this means. Wolff (1973) suggests that this does not mean that fine grained sediments cannot be optimal for H. ulvae and that whilst the distribution of H. ulvae is chiefly determined by salinity and water movements, optimal development probably occurs in areas with muddy sediments. It may be suggested, therefore, that where the species distribution has been found to coincide with the finest sediments (Newell, 1965; Little and Boyden, 1976), then it is possible that those sediments coincide with the animals' optimal immersion and salinity requirements.

The fact that the H. ulvae population dynamics showed few

relationships with the sediment particle size possibly suggests that H. ulvae on Torry Bay should be regarded primarily as a herbivore or grazer than a selective (Fenchel, 1972) or indiscriminate (Newell, 1965) deposit feeder. It would be therefore unlikely to show that the deposit feeder/sediment particle size relationship found by many workers (Sanders, 1958; Newell, 1965; Longbottom, 1970; Rhoads and Young, 1970; Johnson, 1971, 1974; Young, 1971; Rhoads, 1973). It is suggested that the accepted view, that the Hydrobiae are mainly deposit feeders utilizing diatoms in the deposit, microflora attached to the sand grains and detrital particles but will also graze macrophyte and macroalgae surfaces for attached microorganisms (Newell, 1962, 1965; Muus, 1967; Fenchel et al, loc. cit.), should possibly be revised.

In previous studies on the ecology of H. ulvae, there is an apparant contradiction. It has been hypothesised that the distribution of H. ulvae is determined by the salinity and relatively high wave action (Muus, 1967; Wolff, 1973) and by the presence of fine particles (Newell, 1964, 1965, 1970). It is unlikely that these latter two can occur together as high wave action will result in the deposition of coarse particles. The study here indicates that the wave action preference is more important to the animal as the greatest biomass, etc., was found in areas of coarse sediment.

The presence of Z. marina may also have the effect of stabilising the coarse sediment and possibly decreasing the water current speed above the substrate. These factors would increase the attractiveness of the substrate for deposit feeders (Wildish, 1977) although the possibly decreased current speed is not

reflected in the size of particles found at the Z. marina covered higher part of the shore.

Although the size of particles at a station was not related to the size of H. ulvae, individuals of different sizes within that station may have utilized different particles. The positive relationship between \bar{B} , P and \bar{N}_{os} and the size classes of large particles, and the negative relationship with the small particles size classes, are possibly a reflection of the preference for areas with greater wave action (Muus, 1967).

The presence of Z. marina on Torry Bay is thought to have a large effect on the energy budget of H. ulvae, both as a producer of detritus and as an additional substrate for grazing. Thayer et al (1976) found that the standing crop of detritus in eelgrass beds was 150 times greater than the Z. marina biomass. The formation of detritus provides a stable food source for the major part of the year because of the slow decomposition of the detritus (Odum and Smalley, 1959). Fenchel (1972) found that Hydrobiae scrape the epiphytes and diatoms from the detrital particles rather than ingest the detritus and further estimated that up to 45% of the gut contents of H. ulvae may be diatoms (Fenchel et al, 1975). Thayer et al (1976) and Sand-Jensen (1975) suggest that the epiphyte biomass on Z. marina leaves may equal that of the aerial parts of Z. marina. It is therefore postulated that when a more nutriti^ous food source is available near its optimal tidal range, H. ulvae will utilize that source by either selective detrital-feeding or grazing as a herbivore. It may further be suggested that it is energetically beneficial to employ these methods of feeding rather than to deposit-feed indiscriminately.

The production estimates, of H. ulvae, of 5.991 and 4.034g fdw m⁻² yr⁻¹ for 1975-76 and 1976-77 respectively, are slightly higher than other studies on intertidal gastropods (Burke and Mann, 1974; Ankar, 1976), although they are within the range measured by Wolff and De Wolf (1976) for H. ulvae in the Netherlands. The population studied by the latter authors had a production of up to 12.8g fdw m⁻² yr⁻¹ from a mean biomass of up to 9.4g m⁻² in a muddy-sand flat area. On the south shore of the Firth of Forth, H. ulvae has a production of 6.4g fdw m⁻² yr⁻¹ from a biomass of 4.69g m⁻² (J.M. Warnes, pers. comm.), values which are in general agreement with the estimates obtained in the present study. However, whereas the production calculated by J.M. Warnes (pers. comm.) and Wolff and De Wolf (1976) is of somatic production only, i.e. the amount of organic material produced by the biomass as growth to the individuals of the population; the production calculated from the Log P/Log R relationship includes somatic growth, exuvia and reproductive products.

The P/ \bar{B} ratios obtained in the present study, 1.675 and 1.770 are again similar to others obtained on other Hydrobiid populations, e.g. 1.78, 1.24, 1.36 (Wolff and De Wolf, 1976) and 1.36 (J.M. Warnes, pers. comm.). These values agree with the general range of productivity values encountered for marine invertebrates with a 2+ year life span (Zaika, 1973; Burke and Mann, 1974; Warwick and Price, 1975; see Sections 3.5.5. and 4.4.5.).

The study here of the R. obtusa population has reaffirmed many of the findings by Smith (1967a), the only comparable study,

but has suggested that others should be reconsidered. The maximum size in the Barry Inlet, South Wales, population was 3.5mm, considerably lower than the Torry Bay population. These maximal sizes, however, were much lower than the maximal size of 15mm recorded for the species by Thompson (1976). The time of occurrence of maximal numbers of young Retusae was the same in each study although because of the differing sampling methods used it is impossible to directly compare those maximal numbers.

Smith (1967a) suggests that although the gonads mature as early as October and mature ova were always found in the ovatestis after that date, production of young in November to December occurred very rarely and only under ideal conditions such as warm weather. He also suggested that animals spawned at such times would reach maturity and themselves spawn the following spring with the adults in the population, i.e. these young only had half the normal life cycle. The young produced during late autumn each year by the Torry Bay population do not appear to follow this pattern and it is considered that young produced during the early winter period survive an annual cycle and possibly reproduce earlier than the majority of the population the following year. Smith (1967a) suggests that if conditions conducive to spawning occur early then a limited amount of spawning will occur by those adults which mature earlier than others.

A brief mention may also be made of an erroneous conclusion reached by Yonge and Thompson (1976) in suggesting that minute stalked egg capsules are attached to the shells of the adults after spawning. Examination has shown that these are stalked ciliate protozoans, a conclusion also reached by Thompson and

Brown (1976). In the present study egg capsules have been found on the mud surface.

The R. obtusa population summary data was related to very few environmental variables and, although the species was found on all substrate types, its mean biomass increased with tidal height and with decreasing sediment water content, %N, %C, %H₂O and slope of shore. Any study of the ecology of a predator, however, cannot be restricted to the environmental variables; some reference to the prey species, H. ulvae, foraminiferans, bivalve spat and microfauna, must be made.

The R. obtusa mean biomass was predominantly influenced by the H. ulvae production, although the relationship was distorted such that in some coarse sand areas the H. ulvae production was apparently high in relation to the low R. obtusa mean biomass present, and in some fine-mud areas it was too low for the high R. obtusa mean biomass present. This may be indicative of the availability and importance of foraminiferans, meiofauna and spat in the diet of R. obtusa (Hurst, 1965).

The production of R. obtusa was indirectly influenced by many dependent variables although the size of the production was directly determined by the population mean biomass. The P/\bar{B} ratio of R. obtusa was also found to decrease with an increase in age of each cohort.

The predator/prey relationship between H. ulvae and R. obtusa indicates that H. ulvae was not the sole prey of R. obtusa nor R. obtusa the sole predator of H. ulvae. The ecological efficiency, as the ratio of food intakes of each trophic level, is usually of the order of 0.1 to 0.2 (Slobodkin, 1960; Steele,

1974). If it is assumed, in this case, that the assimilation and respiration rates for each species are of the same order then :

$$\text{Ecological Efficiency} = \frac{P_{n+1}}{P_n} = \frac{\text{R. obtusa P}}{\text{H. ulvae P}} \quad (\text{Ricklefs, 1973})$$

where n, n+1 are successive trophic levels.

Therefore, for 1975-76 and 1976-77, the ecological efficiencies were 1.67% and 0.93% respectively. These values are an order of magnitude lower than for systems where the prey species is almost totally supporting the predator population and suggests that R. obtusa was a lesser predator of H. ulvae than other predators such as birds and fish (see Section 7.3.2.).

In considering the size of H. ulvae taken by R. obtusa, it has been found that the mean size of the prey increased with time through the predators life cycle. There was, however, no correlation between the sizes of prey taken and predator. A minimum size of R. obtusa was found to ingest H. ulvae and Hydrobiae up to 2.3mm in length were ingested, a size considerably larger than that found by Smith (1967a). Younger Retusae either would ingest relatively smaller Hydrobiae such that the whole animal was taken into the shell, or did not feed on H. ulvae but on foraminiferans etc. It is considered, from a knowledge of the sizes of individuals of the two species at various times of the year, that the latter of these two alternatives occurs.

Retusae were found to have only ingested 0+ group Hydrobiae although the R. obtusa production at a station could not be related to the abundance of 0+ group Hydrobiae at that station. The occurrence here and in the population sampled by Anderson

(1971), of H. ulvae egg capsules having been deposited on adult Retusae shells confirms the suggestion that large, mature H. ulvae are not preyed upon by R. obtusa.

R. obtusa had a sigmoid growth rate over the life cycle and the mean size of the cohort was affected by the inflow of young over the settling period and the mortality of senescent animals. The maximal growth rate for each area was associated to some extent with the occurrence and abundance of the O+ group H. ulvae and the presence of maximum numbers of other prey items of R. obtusa.

It is possible to suggest, therefore, that R. obtusa had a life cycle synchronised to that of its prey, such that at the time the predators were large enough to feed on H. ulvae, there were the maximum numbers of an appropriate size prey available. In addition, before and during this time the predators would also supplement their diet with foraminiferans, bivalve spat and meiofauna.

The present study indicates that an extended spawning period is a normal occurrence in R. obtusa and not only the result of unusual conditions as suggested by Smith (1967a). The extended spawning period from October to the following spring was the result of the presence of mature gonads from October onwards (Smith, 1967a, b; Thompson, 1976), although the spawning was probably not continuous throughout this period as indicated by the increase in mean cohort size from October to February and then a decrease as newly settled individuals were incorporated into the cohort. It is not known whether the early spawned animals have to utilize prey items other than H. ulvae due to the absence of Hydrobiae of a suitable size in the population.

In addition, the limited ability of R. obtusa for dispersal, attributable to the direct development of the species (Thompson, 1976), was demonstrated by the absence of R. obtusa from certain areas of Torry Bay. The main areas supporting adults of R. obtusa also receive the majority of the young as would be expected by this limited method of dispersal. Occasionally young Retusae were found transported by wave action, although this did not result in the colonisation of new areas.

Whether or not the presence of either H. ulvae, foraminiferans, or other prey items, induces spawning in R. obtusa is as yet unknown but considered feasible. The planktotrophic larvae of the carnivorous opisthobranch Adalaria proxima were found to be stimulated to settle by the presence of the adults' prey, the bryozoan Electra pilosa, and chemosensory larval discrimination in settlement by opisthobranchs has been found for other species with planktotrophic larvae (Thompson, 1958). However, a species with direct development that was spawned in an area which contained the prey items in large numbers does not necessarily require advanced powers of chemoreception.

The limited ability for dispersal and/or the salinity tolerance range of R. obtusa is reflected in its distribution in the Firth of Forth. The Torry Bay population has not colonised any other areas on the north shore even though Low Valleyfield Bay and Culross Bay to the west and Ironmills Bay to the east all support H. ulvae populations (McLusky et al, 1976). The latter two bays have predominantly sandy-mud substrate with the other bay being of fine soft mud, substrate types on which R. obtusa has been known to occur.

On the south shore, a self-maintaining R. obtusa population

occurs at Skinflats Bay in an area of the greatest biomass and density of H. ulvae. However, although the overall production, biomass and population densities of H. ulvae were greater on Skinflats Bay than Torry Bay (J.M. Warnes, pers. comm.), these trends were not reflected in the size of the R. obtusa population. The lower salinity here may have influenced the distribution of R. obtusa.

R. obtusa has not been positively recorded from any other south shore area. Retusae shells have been found in small areas of Kinneil Bay which support large H. ulvae populations but it is considered that the population was not self-maintaining. An unidentified bullmorph mollusc was found on Carriden Bay to the east (M. Teare, pers. comm.) which may possibly have been R. obtusa. Therefore, although H. ulvae has an extensive distribution on the estuarine Firth of Forth, this is not reflected by the distribution of R. obtusa. This pattern has also been found on the Severn estuary where R. obtusa has a very restricted distribution in the middle reaches of the estuary and is only found at the mouth-wards limit of H. ulvae distribution (Boyden and Little, 1973; Little and Boyden, 1976). R. obtusa was absent from some shores where it was expected to be found. Muus (1967) and Wolff (1973) also found H. ulvae in many areas and R. obtusa in very few and only then on fine and muddy sands in the marine reaches of the estuaries studied. The distribution of R. obtusa, therefore, can be attributable to both the non-pelagic development and the restricted salinity tolerance of the species as well as the animals' food and possible substrate preferences.

Chapter 6. Experimental and Pollution Studies on *M. balthica*.

6.1. Field (Mark and Recapture) and Laboratory Multivariate Experiments.

6.1.1. Introduction.

The conclusions reached in Section 3.5. regarding the variation in the production ecology of *M. balthica* were based on correlation and multiple regression analyses of the environmental and population data. As correlations between variables do not necessarily reflect direct "cause and effect" situations, conclusions reached from such an analysis should, if possible, be verified by controlled laboratory experiments. Such experiments also permit the study of certain habitats which did not occur within the field study area but which *Macoma* are known to inhabit. Long-term, multivariate experiments were therefore designed to answer the basic questions: what size of macrofaunal population can be supported by a given type of habitat; and will that habitat support the growth and production as well as the maintenance of that population? Two laboratory experiments were thus designed and performed to study the effects of changes of sediment type, tidal height and population density upon the survivorship, flesh condition, growth and productivity of *Macoma* :-

(a) A tidal-tank experiment (T.T. Expt.) in which treatments of two different substrates (coarse and fine) were prepared each containing a fixed population density and placed at three tidal levels: high, middle and low, under uniform temperature and salinity.

(b) A constant-temperature experiment (10°C C.T. Expt.) in which treatments containing varying population densities in two

different substrates were prepared and kept under constant immersion, temperature and salinity.

The laboratory experiments also provided the opportunity to observe and comment upon the feeding methods employed by Macoma which have previously been studied and discussed with some confusion (e.g. Pohlo, 1969; Reid and Reid, 1969)(Section 6.2.).

In addition, as the methods employed to measure the field growth rates of Macoma, i.e. by growth cessation ring analysis and by the modal analysis of size-frequency histograms, were indirect, it was desirable to check the accuracy of those methods by the direct measurement of field growth by the release and recovery of marked individuals (abbreviated Field M & R Expt.). Haskin (1954) first tabulated the errors involved in mollusc growth determination by the use of indirect methods and suggested that two independent growth-determination methods should be used together (see Section 3.2.2.). Mark and recapture experiments have often been performed on commercially important species (*¹), but only Gilbert (1973) has determined growth in M. balthica by such a method (and then only as the absence of growth cessation rings prevented the use of other methods). An initial "pilot" mark and recapture experiment was performed with the intent, depending on its success, of performing a second, more elaborate, experiment. Although the initial experiment was successful, the repeat experiment failed because of interference of the experimental pots. Therefore only the "pilot" experiment will be discussed.

*¹ M. edulis (e.g. Seed, 1969; Thiesen, 1975; Dare and Edwards, 1976); M. californianus (Coe and Fox, 1942); Venus mercenaria (Chestnut, 1952); C. edule (Orton, 1926); and M. arenaria (Swan, 1952).

6.1.2. Materials and Methods.

6.1.2.1. Field M & R Expt.

The experiment commenced on 1st. July, 1975 and, although a year period would have been preferable, the experiment was terminated on 6th. February, 1976 (220 days). A second set of field experiments was commenced during May, 1976 with two experimental areas, Stations B3 and C4, but was unsuccessful (the experimental pots had been removed by wave action and by human interference).

The experiment was performed at Station B3 from which ninety-nine animals were obtained by sieving the sediment through a 2mm mesh sieve. The animals were tissue-dried, marked with indelible ink and measured. The substrate, retained from sieving, was then poured into five pots (*¹), which were buried within a 1m² area until the top of each pot was level with the sediment surface and into which a number of marked bivalves were allowed to burrow. The initial density and size-frequency distribution of animals in each pot were comparable to those encountered at the station, i.e. the majority of experimental animals were within the range 4-8mm height.

The treatment given to each animal resulted in the formation of growth cessation rings attributable to disturbance. On recovery, therefore, it was possible to measure the initial size of the animals from such disturbance rings; that size was then verified by comparison with the size measurements taken when the animals were initially obtained. The initial total dry weight

*¹ The pots used in all experiments were Ward 5½" (14cm) I.D., depth 9cm and surface area 154cm² dwarf plastic pots.

(tdw) and flesh dry weight (fdw) were then computed from the appropriate relationships for Station B3, July, 1975 (Appendix 3.1).

The final length, height, tdw and fdw were noted for the recovered animals which enabled the calculation of the parameters: the final and initial shell weights (sw); the final and initial CF_H values; the change in CF_H , fdw and sw over the period; and the final flesh and shell weight as a percentage of the initial flesh and shell weights (see Appendix 6.1).

6.1.2.2. Tide-tank Experiment.

An experimental tidal tank was prepared (see Fig. 6.1) which was divided vertically into two blocks (for replicates) through three tidal levels; at the high (H) level, the top of the pots were covered for 3 hours 46 minutes (31% of the tidal cycle); at the middle (M) level for 4 hours 36 minutes (38%) and the low (L) level for 6 hours 54 minutes (57.5%) during each 12 hour tidal cycle. Three pots (numbered 1-3) containing coarse sediment (from Station C4) and three pots (numbered 4-6) containing fine sediment (from Station B3) were randomly placed at each level and in each block. Large stones and all bivalves were removed from the sediment by sieving through a 2mm mesh sieve. The bottom of each pot was lined with stones to prevent the loss of mud and to facilitate drainage.

The tidal tank was illuminated by 4 x 40w white strip-lighting tubes placed 19cm above the top of the tank and running the length of the tank and on a 12 hour light/12 hour dark sequence. De Wilde (1975) found that a similar light regime provided sufficient illumination to support an adequate primary

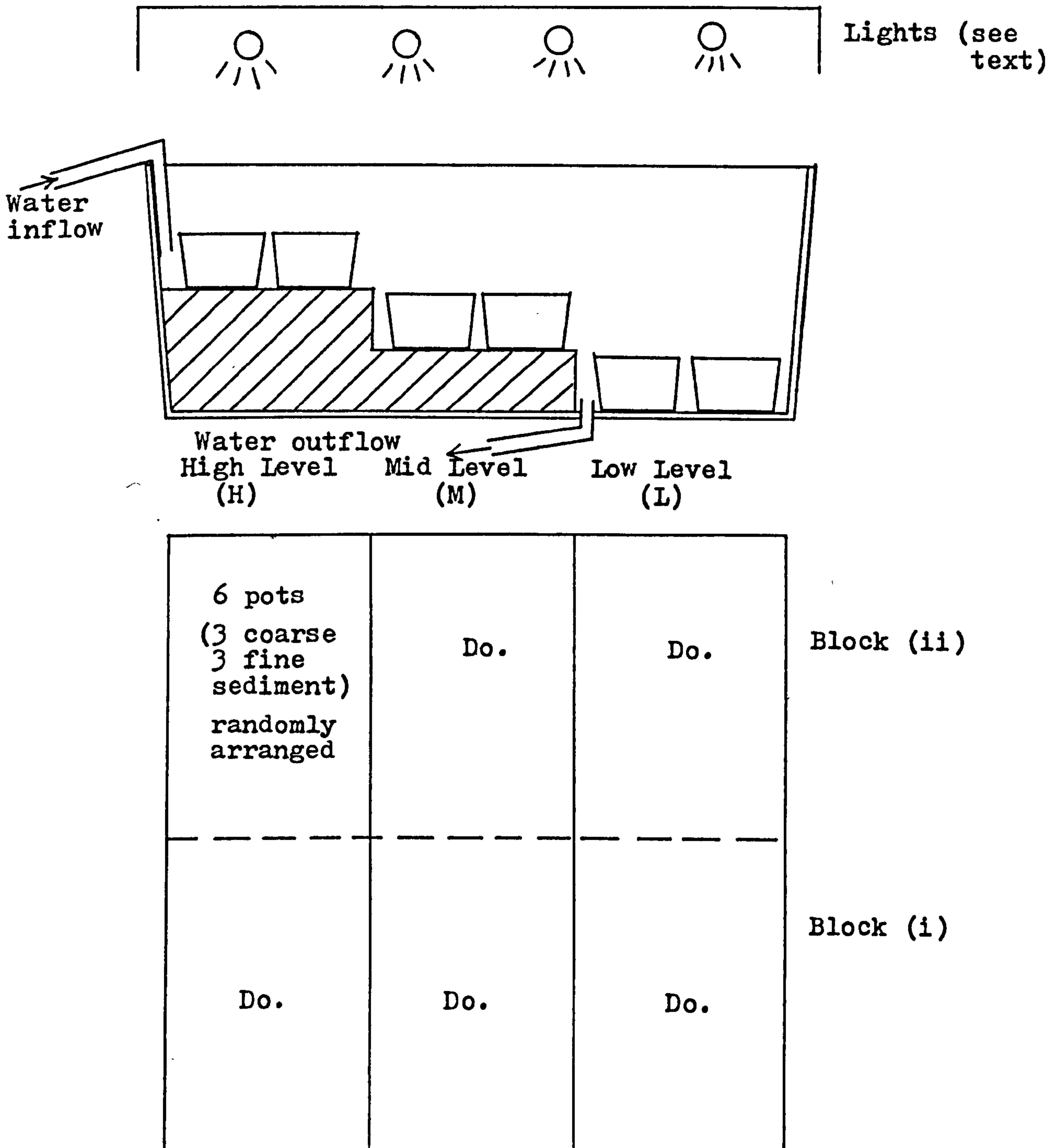


Figure 6.1 T.T. Expt. ; The Arrangement of the Experimental Pots at the Beginning of the Experiment.

production by the benthic microflora. He obtained fixation rates of 100-150gm C m⁻² day⁻¹ by ¹⁴C measurements, thought to provide ample food for M. balthica. On a light intensity meter using an arbitrary scale which recorded 12.5 for a bright, moderately cloudy (August) day and zero for total darkness, the illumination above the high and middle level pots was recorded as 12.2 and above the low level pots 10.5 units.

The tide-generating machine was essentially that devised by De Blok (1964) which controlled a continuous flow of water by a rotating siphon action. The water flow into the tank remained constant whilst the level of the outlet tube rotated vertically throughout a 12-hour cycle. This cycle produced a high water level 1cm below the top of the experimental tank and a low water level 10cm below the bottom of the tank. The continuous flow seawater was maintained at the temperature 10 ± 1.5°C and the experimental tank maintained at an ambient temperature of 15°C. The salinity of the seawater was approximately 34‰ and known to be constant.

The animals used in the experiment were obtained from Station B3, measured and marked either with indelible ink (in small animals, <8mm Ht.) or with a small notch cut into the ventral margin of the shell of the larger animals. Twenty individuals, covering the size range of 2-15mm height were placed onto the sediment surface of each pot when covered by water. The animals which failed to burrow into the sediment after one hour were replaced. A reference sample of 50 animals was retained for analysis. The pots were prepared on 1st. May, 1976 and the animals placed in them on 12th. May, 1976.

At intervals of 105, 204 and 320 days after commencement of

the experiment (i.e. 25.08.76; 02.12.76; 23.03.77 respectively), one pot from each block, sediment type and tidal level was removed. Two replicate surface sediment samples from each removed pot were taken and dried for carbon and nitrogen analysis. The content of each pot was then sieved through a 2mm mesh sieve and the animals recovered. At each recovery the animals were placed in filtered seawater for 4-5 hours and, based upon siphon and/or foot movement, the percentage of live animals was noted. The animals were then dried, weighed and measured. After each removal, the remaining experimental pots in each block were grouped together. During the experiment any macroalgae, including filamentous green algae, were removed in order to allow maximum production by the benthic microalgae in the pots.

The water content of the final removal surface sediment samples was also determined as was the sediment particle size distribution in each sediment type. The particle size analysis was performed (as in Section 2.2.3.1.) on pooled sub-samples of all coarse and fine sediment treatments.

6.1.2.3. 10°C Constant Temperature Experiment.

Experimental pots containing different sediment types and population densities were placed in four experimental tanks, 40 x 65 x 15mm deep within a constant temperature room at $10 \pm 1.5^{\circ}\text{C}$. Each tank was placed under 2 x 30w Atlas cool-white strip-lighting tubes and, as this illumination was less intense than that over the tidal experiment, an 18 hour light/6 hour dark regime was used. The top of each experimental pot was 24cm below the light source and received an illumination of 11.5 units (see previous section) although that level would decrease when the

pots were covered with water.

The tanks were arranged in adjacent pairs, each pair being a block containing four replicate treatments which allowed for a removal of two replicates of all treatments at 3-monthly intervals for one year. The treatments prepared were:

Sediment Type	Population Density	Initial Abundance (animals/pot)	Treatment Abbreviation
Fine	Low	10	10F(1-8)
"	Intermediate	20	20F(1-8)
"	High	30	30F(1-8)
Coarse	Low	5	5C(1-16)
"	Intermediate	10	10C(1-8)
"	High	15	15C(1-8)

In order to provide sufficient animals for analysis, the number of 5C treatment replicates were doubled. Each treatment (pot) was therefore designated a code indicating its initial population density, its substrate type and the number of that particular pot, e.g. 10F1. One block contained pots numbered 1-4 (and 9-12 in 5C) and the other pots 5-8 (and 13-16 in 5C). At the first removal pots numbered 1 and 5 were analysed (1, 5, 9, 13 in 5C); at the second removal 2 and 6 (+ 10, 14 in 5C); at the third removal 3 and 7 (+ 11, 15 in 5C) and at the fourth removal 4 and 8 (+ 12, 16 in 5C). The pots were randomly arranged within each block.

The fine and coarse sediments were obtained and prepared as in the tide-tank experiment. The animals were also obtained from Station B3 and measured before being placed in the experimental pots in the same manner as in the previous experiment; a

reference sample population was also taken. The pots were prepared 17.05.76 and the animals were placed in them 29.06.76.

The pots were kept under a continuous still water, seawater immersion with the water being aerated by air-lines and filters going to all parts of each tank. The seawater in each tank was changed at fortnightly intervals when macroalgal mats and filaments were removed from the mud surface of the pots. The water in the tanks was at a temperature of $10.0 \pm 1.0^{\circ}\text{C}$ and had a constant salinity of $34^{\circ}/\text{oo}$.

Each treatment (2 pots in the case of 5C) from each block was removed at intervals of 103, 205, 296 and 385 days after the beginning of the experiment (i.e. 10.10.76; 20.01.77; 21.04.77 and 10.07.77 respectively); each pot was treated as in the previous experiment. Surface sediment samples were taken at each removal for carbon/nitrogen analysis and, at the fourth removal, for water content and particle size analyses.

6.1.3. Results and Discussion of Field M & R Expt.

The initial and final densities of M. balthica within the experimental pots were comparable to the Station B3 densities over the period :

Table 6.1 The Density (Initial and Recovered) of Macoma/Pot.

Pot	Initial no./pot	Initial no./m ²	Recovered no./pot	Recovered no./m ²
B31	24	1560	17	1105
B32	24	1560	20	1300
B33	18	1170	18	1170
B34	22	1430	15	975
B35	14	910	7	455

The majority of the animals which disappeared over the period were first year animals (i.e. spawned during 1974) (see Appendix 6.1) and although it is not possible to give the cause of their removal, either size-selective predation or the greater inability of young animals to withstand the treatment are possible reasons for their disappearance. (The density of pot B33 remained the same as animals of 4.7 and 3.1mm height were recruited into the pot. As both of these animals had distinct disturbance rings then it is considered that they were overlooked during the initial sieving.)

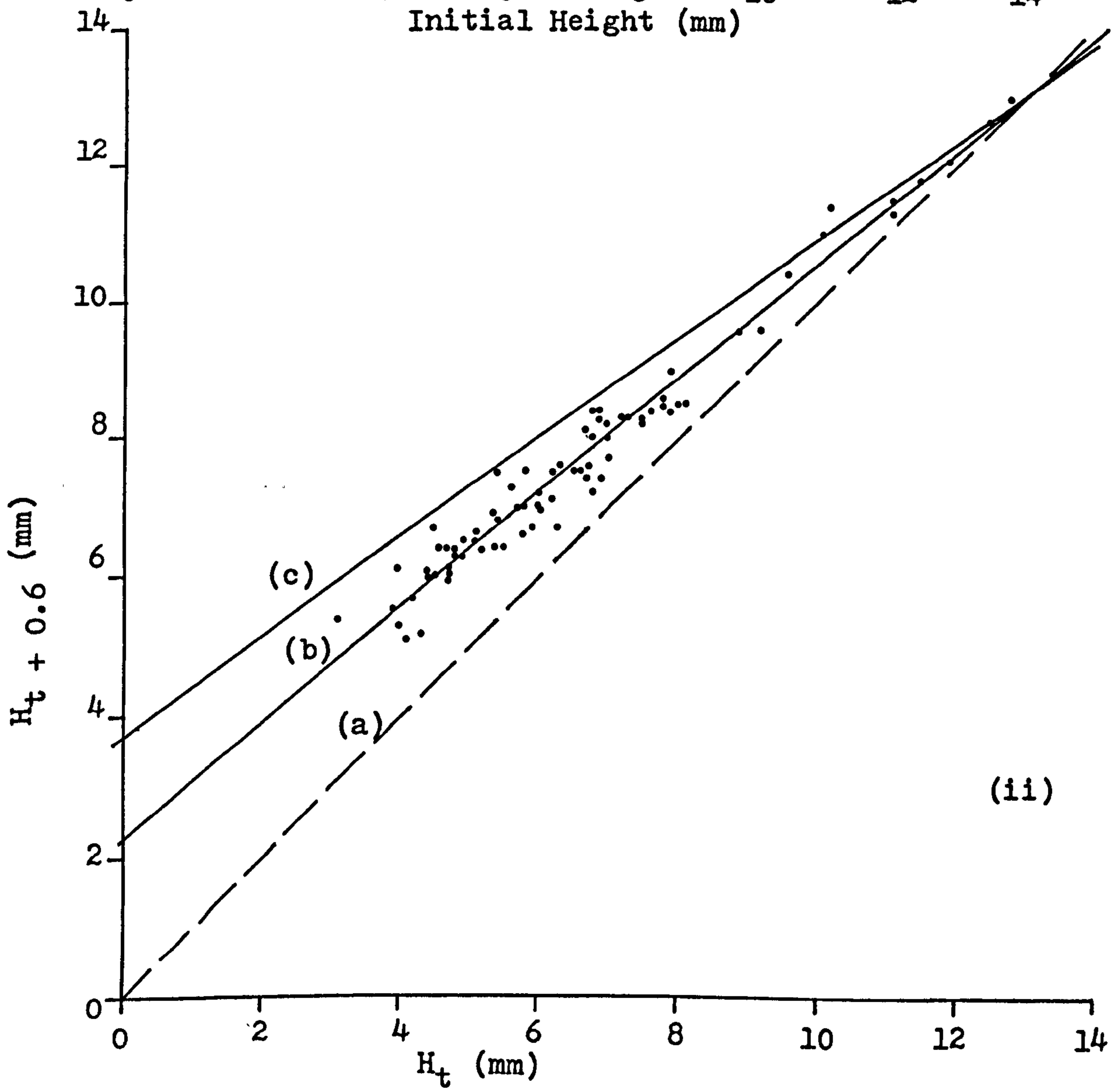
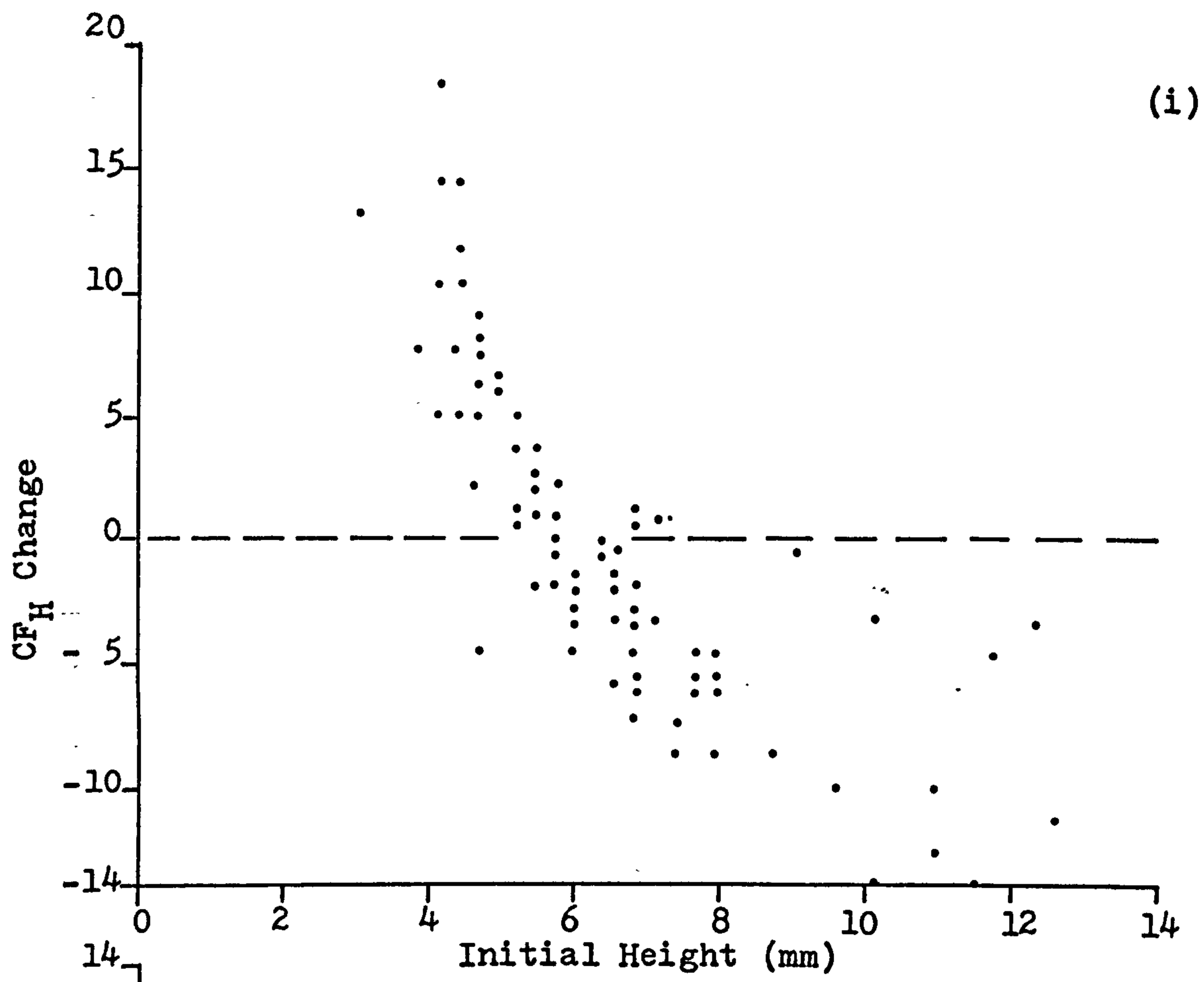
The change in flesh condition during the experiment showed a negative curvilinear relationship with the initial height of the animals (Fig. 6.2(i)). At heights less than 6mm the animals' flesh condition increased over the period to a maximum increase of 18CF_H units at 4mm. The condition of the larger animals (>6mm) decreased over the period, i.e. the extent of the net emaciation

Figure 6.2 M & R Expt. : (i) The Change in Flesh Condition Over the Experimental Period With Initial Height.

(ii) Ford-Walford Plot of Experimental Growth : (a) 45° Intercept.

(b) $H_t + 0.6 = 0.826 \pm 0.018 H_t + 2.25$
n = 77
r = 0.983
p < 0.001
 $H_\infty = 12.93\text{mm}$
K = 0.191

(c) Modified Line and B3 Station Animal Ford-Walford Plot Stage 1.



increased with size until at a height 10-12mm the animals' condition had decreased by 12 CF_H units. Similarly, as a proportion of the initial flesh and shell weights, the final flesh and shell weights also showed negative exponential relationships with increasing size of the animals (Fig. 6.3). The proportionate weight change of the smaller animals (<7.0mm) increased with decreasing size such that a 3mm animal increased its flesh and shell weight by an order of magnitude over the period. The animals larger than 8mm showed little decrease in the proportionate change with increasing size although even in the larger animals the shell weight had increased by one half, to 150%, of the original weight. At sizes greater than 7mm, however, the flesh weight of the majority of the animals exhibited net emaciation over the period and decreased by up to 40% of the initial weight.

The absolute changes in shell and flesh weight over the period further quantify these patterns (Fig. 6.4a & b). The flesh weight of the smaller animals (<7mm) increased by 0-7mg whereas that of the larger animals decreased by 0-20mg. At sizes greater than 9mm there was a large increase in the amount of flesh lost through emaciation. The change in the flesh content was the net result of the increase due to growth and the decrease due to emaciation over the period. Whereas that net result was positive in small animals and negative in the larger ones, in animals of size 7-8mm there was no net change. As all animals showed some linear growth over the period the shell weight of all animals increased; the smaller animals produced 35mg of shell material whereas the largest animal produced 140mg (Fig. 6.4b).

The increase in shell height over the period showed an

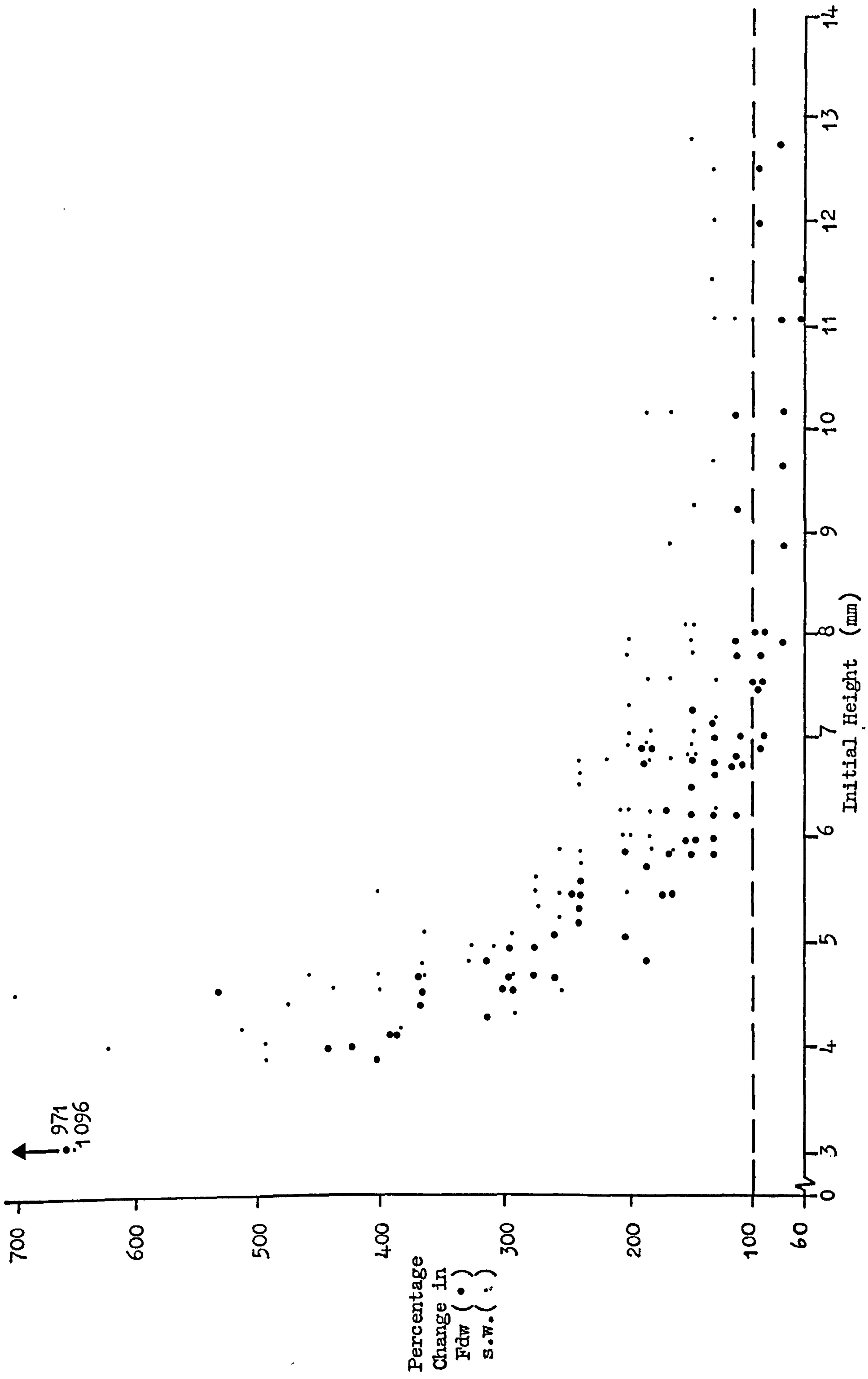
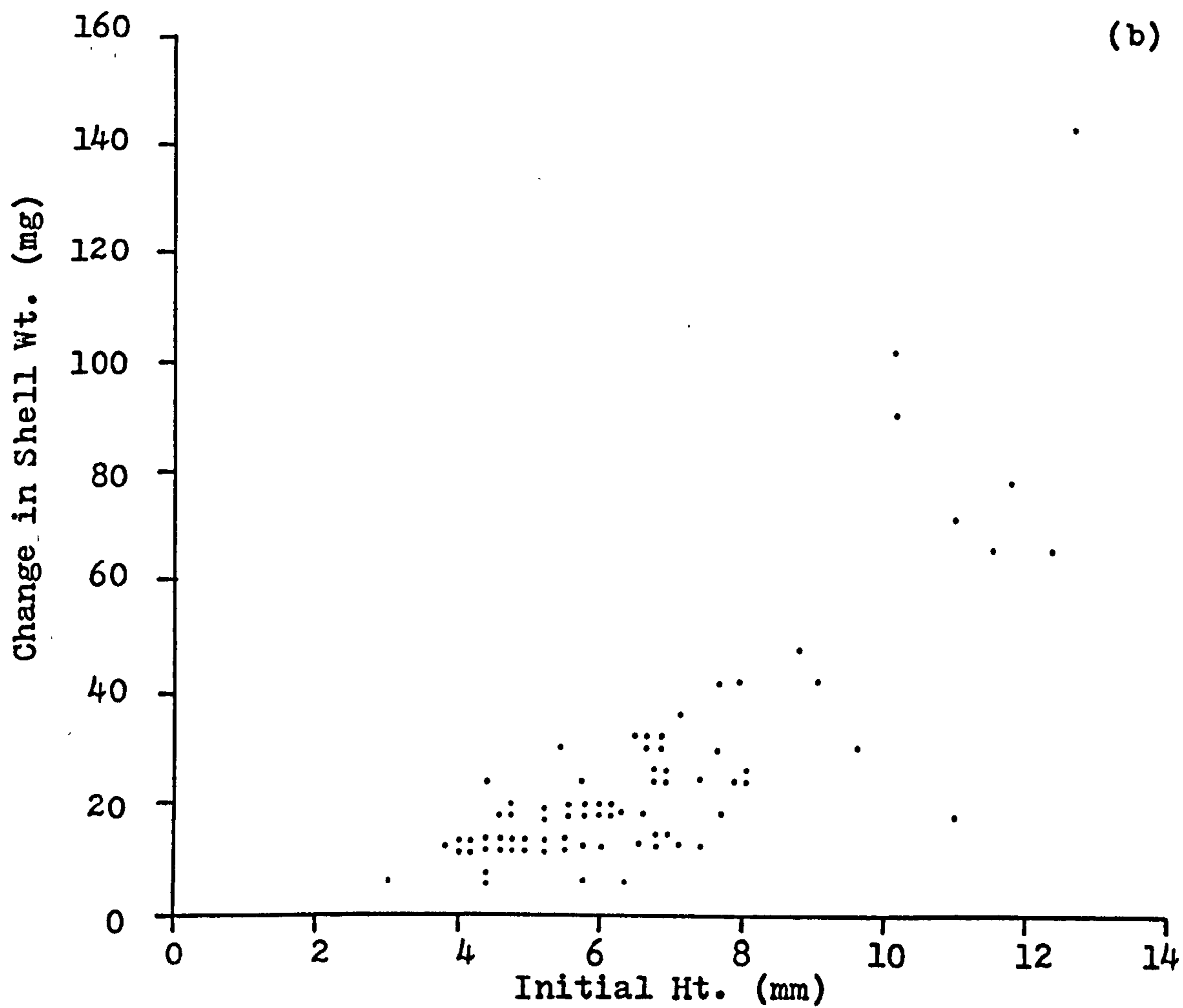
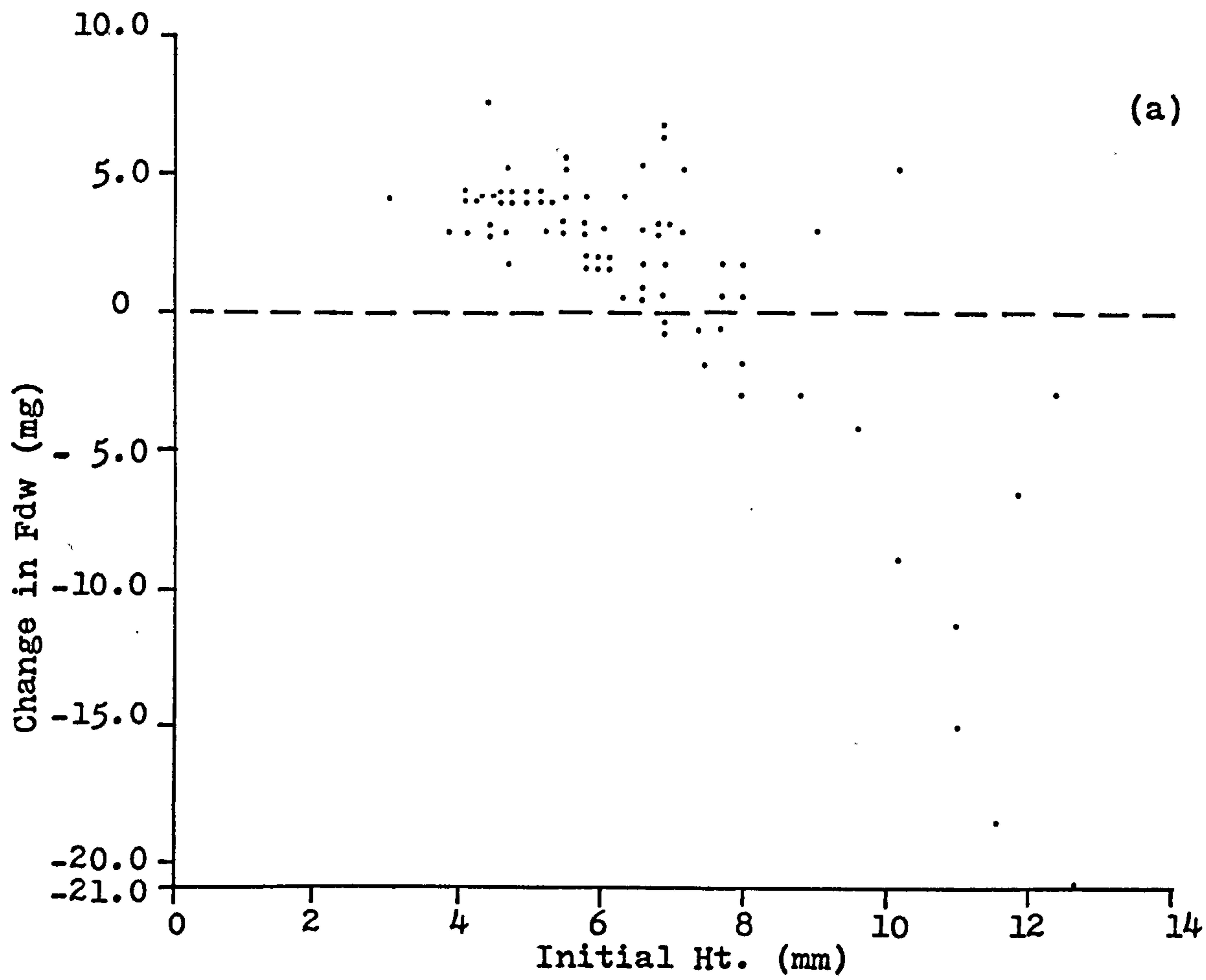


Figure 6.3 M. & R. Expt. : The Change in Flesh (•) and Shell (•) Dry Weight (as a Percentage of the Initial Weights) With Initial Height.

Figure 6.4 M & R Expt. : The Change in
(a) Flesh Dry Weight and (b) Shell
Weight Over the Experimental Period
With Initial Height.



almost linear decrease with increasing initial height although there was a large amount of variation within the relationship (Fig. 6.5). The extent of shell growth over the period was mathematically represented as a plot of height at release (H_t) against height at recapture ($H_t + 0.6$) (Fig. 6.2(ii)). This is not strictly a Ford-Walford plot as individual measurements rather than the mean data were used; it is, however, analagous to the Manzer-Taylor plot which is regarded as being comparable to the Ford-Walford plot (Hancock, 1965). Also the period between release and recapture was only 0.6yr and therefore also unlike the normal Ford-Walford analysis (see Section 3.2.2.2.). The resulting Manzer-Taylor plot gave the relationship :

$$H_t + 0.6 = 0.826 \pm 0.018 H_t + 2.250 \quad (\text{I})$$

with the Bertalanffy parameters (see Section 3.2.2.2.) $H_\infty = 12.93\text{mm}$ and $K = 0.191$. This may be compared with the Stage I Ford-Walford equation obtained for Station B3 animals from the growth ring analysis (Section 3.3.2. and Table 3.3) :

$$H_t + 1 = 0.714 \pm 0.031 H_t + 3.709 \quad (\text{II})$$

$$H_\infty = 12.98\text{mm} \text{ and } K = 0.336$$

Therefore while the maximum theoretical sizes (H_∞) obtained by the two methods were in good agreement, the rate of catabolism coefficient (K) was greatly reduced in the experimental population. This pattern is attributable to the reduced growth period in the experiment. A "corrected plot" was subsequently prepared which allowed for an annual growth by the animals as a factor of 1.67 greater than that shown for the experimental period (of 0.6yr). It was considered that although in some cases this would have underestimated the annual growth increment as the major part of

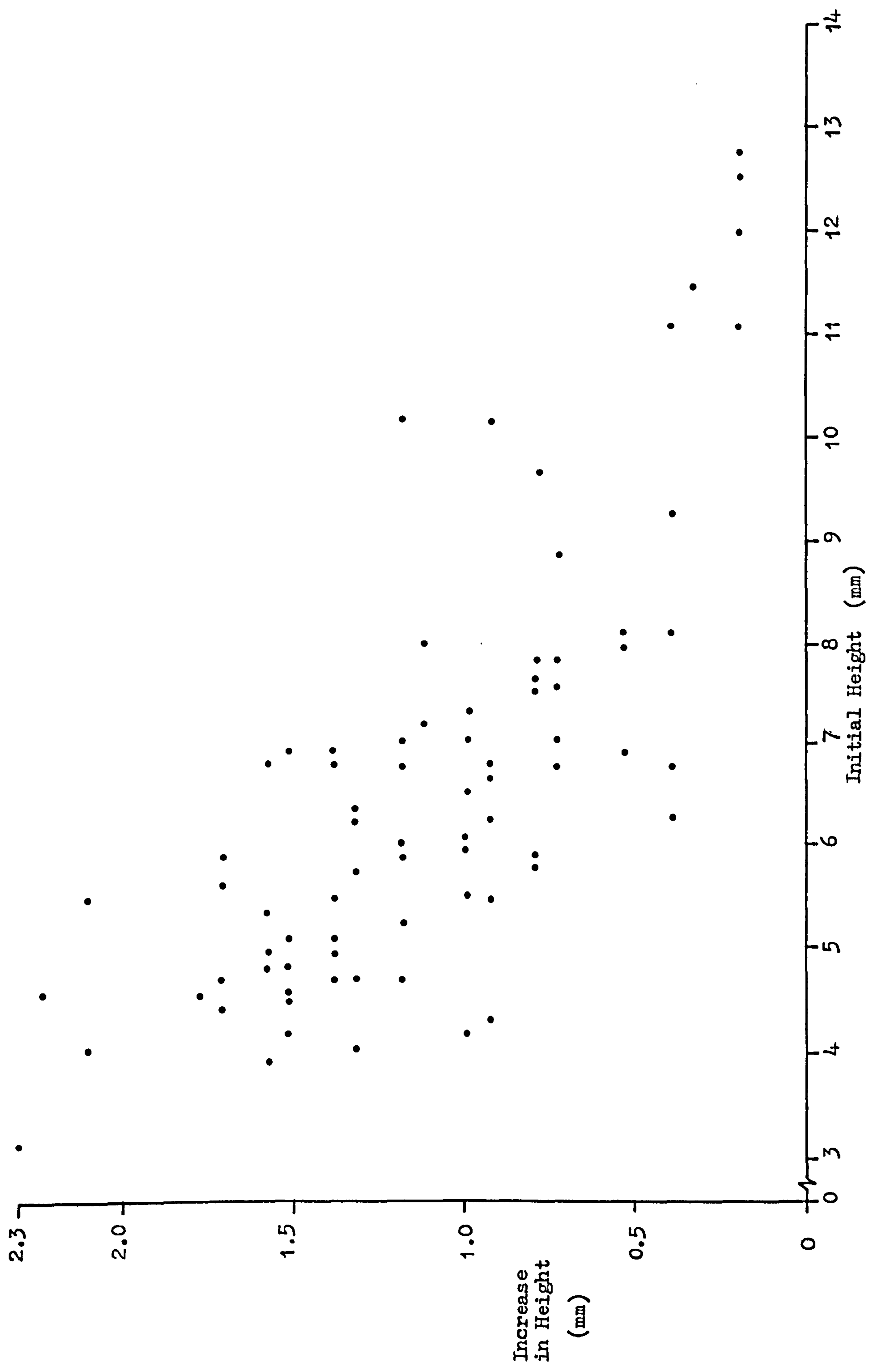


Figure 6.5 M. & R. Expt. : The Growth of the Marked Animals Over the Experimental Period.

the shell growth was found to occur in the period from April-May to July-August, in other cases, depending on the age of the animal, growth does not proceed until after the cessation of spawning and then occurs later into the year (see Fig. 3.36). The modified growth equation :

$$H_t + 1 = 0.710 \pm 0.030 H_t + 3.757 \quad (\text{III})$$

$$K = 0.342, H_{\infty} = 12.95\text{mm}$$

is an accurate estimation of growth as compared to the equation given by the growth ring analysis (cf. equations II and III above) (see Fig. 6.2(ii)).

Finally, the production by the experimental animals was calculated by the formula :

$$P_t = B_t - B_0 + B_e \quad (\text{Zaika, 1972})$$

where P_t = production in time t

B_t = biomass at t

B_0 = biomass at time zero

B_e = biomass eliminated

$$\text{i.e. } P = \Delta B + M = (B_t + 0.6 - B_t) + M \quad \text{following IBP notation.}$$

where M = mortality = $\bar{W} N$ where $\bar{W} = \frac{1}{2}(\bar{W}_t + \bar{W}_{t + \Delta t})$

(Crisp, 1971)

In the experiments, therefore, where the initial size of all animals is known, the mortality increment may be regarded as the sum of the mean weights of the animals which did not survive (Tables 6.2 & 6.3).

$$\therefore \text{For the five pots } P = 105.41\text{mg fdw}/0.108\text{m}^2/7 \text{ months.}$$

$$\bar{B} = 857.36\text{mg fdw } 0.108\text{m}^{-2}$$

$$P/\bar{B} = 0.123$$

Table 6.2 The Initial and Extrapolated Final Size and Weight of Animals Which did not Survive.

e.g. For Pot B31

Animals Lost				
Initial Ht. (mm)	Calc. Initial fdw (mg) *1	Extrapolated final		Mean wt. Over Period (mg)
		Ht. (mm) *2	fdw (mg) *3	
8.7	17.26	9.4	13.42	15.34
5.5	3.42	6.8	4.49	3.95
5.1	2.62	6.5	3.86	3.24
4.8	2.12	6.2	3.29	2.70
4.9	2.28	6.3	3.47	2.87
4.3	1.44	5.8	2.62	2.03
4.8	2.12	6.2	3.29	2.70
	31.26			M = 32.85

Obtained by:

$$*^1 \text{ fdw} = H^{3.527} \quad (\text{B3 July, 1975})$$

119.3

$$*^2 H_t + 0.6 = 0.826 H_t + 2.25 \quad (\text{see text})$$

$$*^3 \text{ fdw} = H^{3.381} \quad (\text{B3 February, 1976})$$

145.3

Total initial fdw and M were incorporated in computation of production for each pot (see Table 6.3).

Table 6.3 The Computation of Production for Field M. & R. Pots.

	Total Init.fdw mg	Final fdw mg	\bar{B} mg	B mg	(B+M) mg	P/ \bar{B}
B31	31.26+140.2 =171.46	181.70	176.58	9.98	42.83	0.242
B32	14.73+215.4 = 230.13	228.20	229.16	- 2.01	15.91-2.01 = 13.90	0.061
B33	0 + 152.3 = 152.3	176.90	164.60	24.43	24.43 + 0 = 24.43	0.148
B34	13.65+103.9 = 117.55	138.90	128.22	21.12	21.12+17.77 = 38.89	0.303
B35	11.41+162.4 = 173.81	143.80	158.80	-30.04	-30.04+15.40 = -14.64	-0.092

where Total initial fdw = Σ initial weight of
animals lost + Σ initial weight of surviving
animals (see Table 6.2).

Final fdw = Σ final weight of surviving
animals.

This is equivalent to :

$$P = 1.370g \text{ (fdw) } m^{-2} \text{ over period } \equiv 2.192g \text{ (fdw) } m^{-2} \text{ yr}^{-1}$$

$$\bar{B} = 11.146g \text{ (fdw) } m^{-2}$$

Hence, assuming a stable biomass, $P/\bar{B} = 0.197$

When compared with the 1975-76 production data of large animals (>2.5mm) for this station, where $P = 4.326g \text{ (fdw) } m^{-2} \text{ yr}^{-1}$, $\bar{B} = 8.994g \text{ (fdw) } m^{-2}$ and $P/\bar{B} = 0.481$, it is apparent that although the biomass in the experimental pots was greater than the mean annual biomass, the production by that biomass was substantially lower. It is considered, therefore, that the experimental period was later in the year than the most productive part of the annual cycle (see Fig. 3.36) and, also, that the limited findings by this experiment support those reached by the field survey, e.g. that flesh growth ceases earlier in the year than shell growth and that in the larger animals the net flesh change, as a balance between flesh growth and emaciation, is negative.

It may thus be concluded that the easiest and most direct method of assessing the individual growth, condition change and productivity of a benthic population is by the use of a mark and recapture experiment. Such an experiment has also proved valuable in supporting the indirect assessment of growth and production by growth ring and size-frequency techniques. The field experiment described, although supporting much of the field survey analysis (Chapter 3), would have been greatly improved if, firstly, it had been extended to a one year period; secondly, more experimental pots had been prepared such that some could have been removed at intervals throughout the period; and thirdly, it had been performed in different habitats.

6.1.4. Results of Laboratory Experiments.

6.1.4.1. The Sediment Characteristics and Changes.

Each coarse and fine sediment type showed good agreement between the different experiments; the coarse sediment being termed medium-sand and the fine sediment had a M.P.D. only slightly greater than the 'muddy-sand' category (Fig. 6.6; Table 6.4; Section 2.4.1.1.). The low degree of sorting in all sediments shows little alteration from the natural state. The proportion of silt and clay was negligible in the coarse sediment but over 20% in the fine sediment. The sediments' characteristics were in good agreement with the respective field types (B3 for fine and C4 for coarse sediment) except that some very fine particles were removed from the sediments during the initial sieving. The coarse sediment used in the tide-tank experiment had a greater proportion of large particles than in the field whilst large stones were removed from the fine sediments during the initial sieving.

10°C C.T. Expt. - %C, %N, %H₂O Levels (Fig. 6.7).

When compared to field levels, the coarse sediment %C and %N values were approximately normal; the measured levels in the fine sediments were slightly lower than average although they did correspond to autumn/winter months data. There was no consistent change in %N or %C in the fine sediments with time although in the coarse sediments these levels increased slightly with time. There was more variation in the %C and %N levels of the fine sediments than the coarse ones. There was no consistent pattern of change in %C and %N between the different population densities in either the coarse or fine deposits.

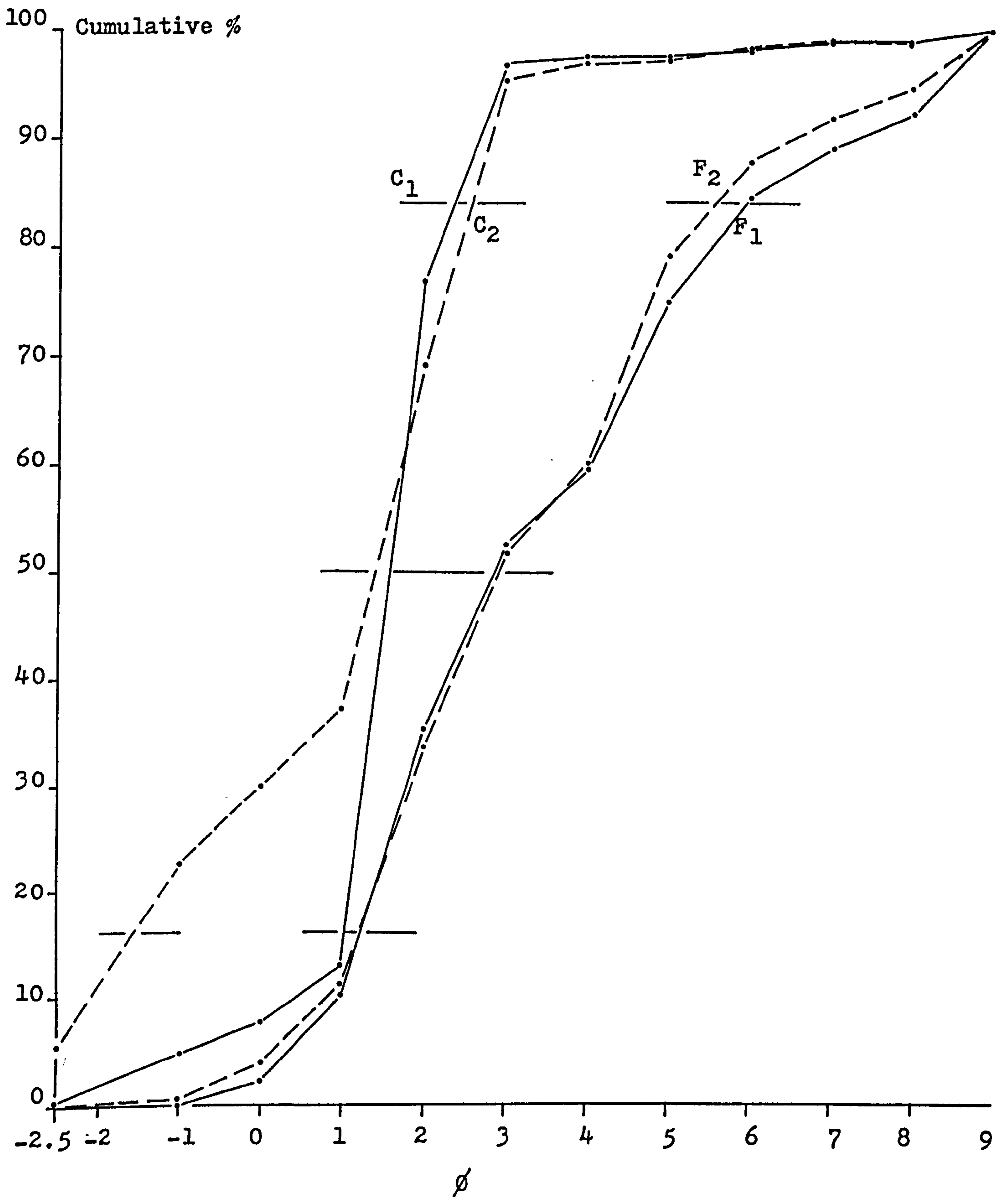


Figure 6.6 Particle Size Analysis of Experimental Sediments ;
 Cumulative Phi Curves (10°C C.T. Expt. ; F₁ = Fine,
 C₁ = Coarse Sediment ; T.T. Expt. ; F₂ = Fine,
 C₂ = Coarse Sediment).

Table 6.4 Characteristics of Experimental Sediments.

Name	M.P.D. (ϕ)	M.P.D. (μm)	Quartile Values (ϕ values)		Sorting Coef. (ϕ)	Skewness	%S.& C.
			84%	16%			
C1	1.587	333	2.367	1.033	1.70	0.169	2.39
F1	2.860	138	5.967	1.233	3.60	0.313	25.27
C2	1.400	379	2.567	-1.533	2.06	-0.433	2.79
F2	2.920	132	5.587	1.227	3.41	0.223	20.86

C1 - Poorly sorted, positively skewed medium-sand.

F1 - Very poorly sorted, positively skewed fine-sand/muddy-sand.

C2 - Very poorly sorted, definitely negatively skewed medium-sand.

F2 - Very poorly sorted, positively skewed fine-sand/muddy-sand.

Table 6.5 Reference Data of Experimental Animals.

(a) 10°C C.T. Expt. (n=36).

$$\text{T.d.w.} = \text{Ht} \frac{3.584}{30.37} \pm 0.080 \quad r = 0.992 \quad p \text{ ***}$$

$$\text{f.d.w.} = \text{Ht} \frac{3.008}{57.90} \pm 0.061 \quad r = 0.993 \quad p \text{ ***}$$

$$\text{s.w.} = \text{Ht} \frac{3.695}{45.80} \pm 0.093 \quad r = 0.989 \quad p \text{ ***}$$

$$\text{CF}_H = 18.220 - 0.081 \pm 0.175\text{Ht.} \quad r = -0.079 \quad \text{n.s.}$$

$$\text{CF}_H \bar{x} = 17.644, \text{ S.E.} = 0.341, \text{ S.D.} = 2.048$$

(b) T.T. Expt. (n=47).

$$\text{T.d.w.} = \text{Ht} \frac{4.105}{82.72} \pm 0.084 \quad r = 0.991 \quad p \text{ ***}$$

$$\text{f.d.w.} = \text{Ht} \frac{3.192}{118.7} \pm 0.155 \quad r = 0.951 \quad p \text{ ***}$$

$$\text{s.w.} = \text{Ht} \frac{4.215}{117.1} \pm 0.095 \quad r = 0.989 \quad p \text{ ***}$$

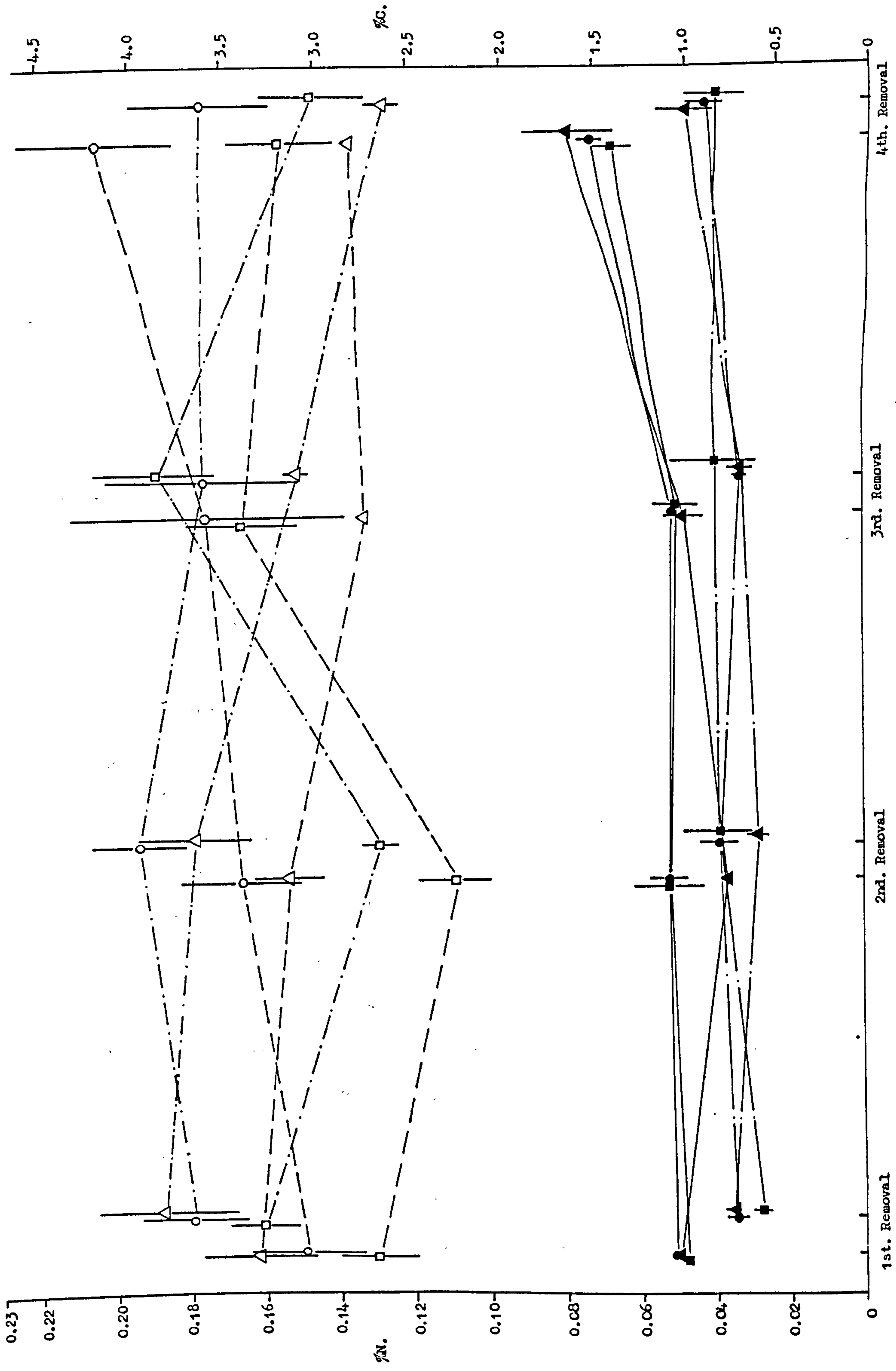
$$\text{CF}_H = 10.624 + 0.277 \pm 0.231\text{Ht.} \quad r = 0.176 \quad \text{n.s.}$$

$$\text{CF}_H \bar{x} = 12.748, \text{ S.E.} = 0.442, \text{ S.D.} = 3.027$$

Figure 6.7 10°C C.T. Expt. : The Surface Sediment Carbon and Nitrogen Contents in Each Treatment at Each Removal ($\bar{x} \pm 1$ S.E. given).

Legend

	%N.	%C.
10F	--○--	---○---
20F	--△--	---△---
30F	--□--	---□---
5C	—●—	.—●.—
10C	—▲—	.—▲.—
15C	—■—	.—■.—



The mean C/N values :

Treatment \ Removal	1	2	3	4
10F	24.09	23.27	20.08	17.34
20F	23.10	23.31	22.77	18.72
30F	24.67	23.75	27.76	18.99
5C	13.39	14.73	12.94	11.80
10C	14.08	15.27	13.58	12.27
15C	11.50	14.69	15.94	12.10

again demonstrate that the fine sediment treatments had higher C/N values than those of the coarse sediments (see Section 2.5.). The slight decrease in the C/N levels with time was more marked in the fine than coarse treatments. The only other trend was shown by the 30F treatment, which always had a higher C/N value than the others.

The water content levels :

Treatment	10F	20F	30F	5C	10C	15C
Mean %H ₂ O	56.35	43.56	47.84	26.75	26.76	25.01
1 S.E.	4.40	1.76	1.21	0.44	1.47	1.06

were in agreement with the field data for the coarse sediment but lower than those in the fine sediment and again reflect the slight loss of small particles from the fine sediment during the initial sieving (see Section 2.4.1.3.).

T.T. Expt. - %C, %N, %H₂O Levels (Fig. 6.8).

When compared to field data the coarse sediment had higher values of carbon whereas the fine sediment had low-to-normal values. The coarse sediment at the low tidal level had nitrogen

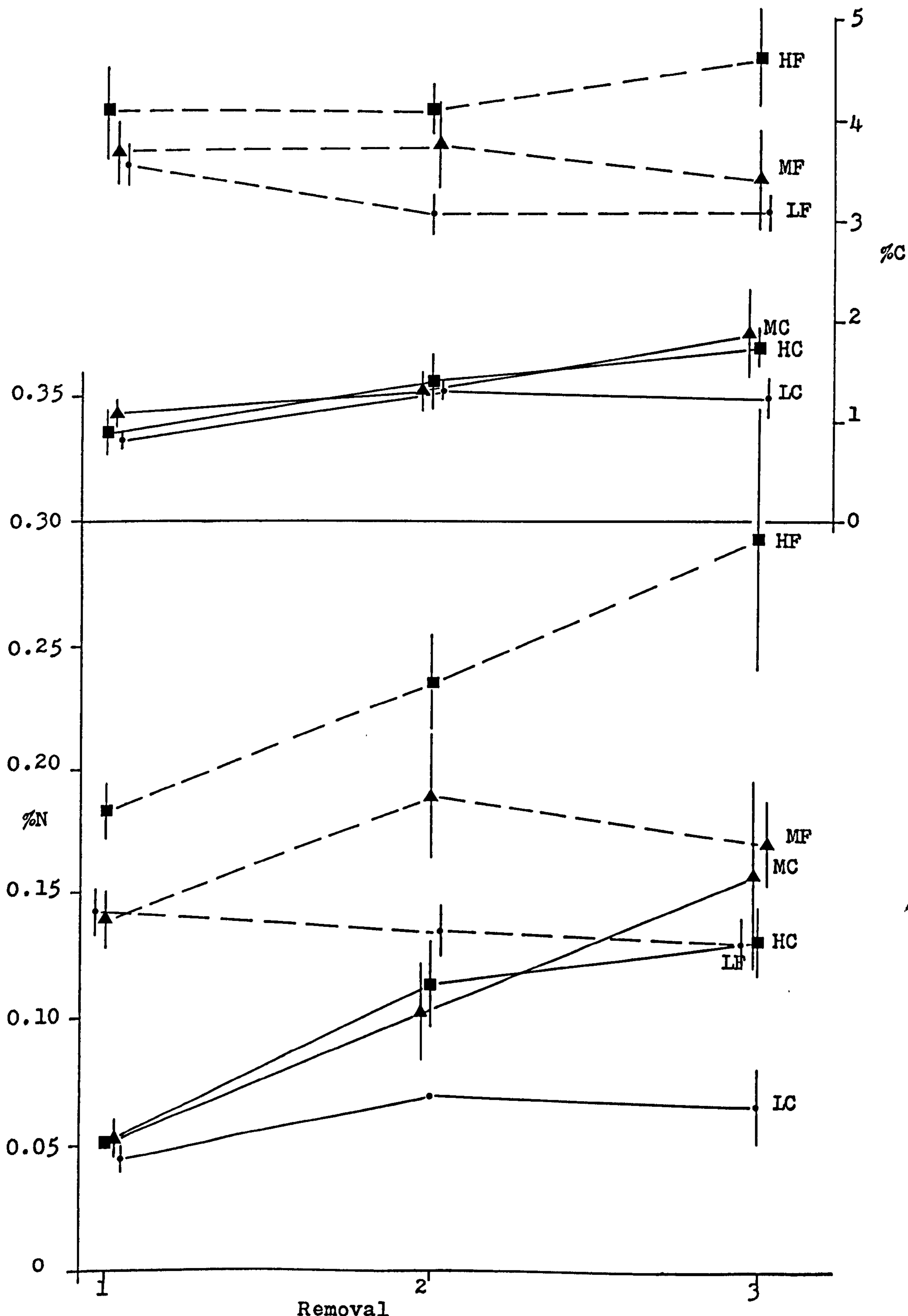


Figure 6.8 T.T. Expt. : Sediment Analysis - %C and %N in Surface Sediment at Each Removal. ($\bar{x} \pm 1 \text{ S.E.}$)

values remaining approximately normal whereas the HC and MC treatments had normal levels at the beginning of the experiment which then increased with time. The LF sediment was constantly low in nitrogen with respect to the field data, that of the MF treatment was low at the beginning but normal at the end and the HF treatment sediment increased with time from normal at the beginning. The carbon and nitrogen decreased with a progression down through the tide levels in the fine sediments and also, to a lesser extent, in the coarse treatments.

The HF treatment, and to a lesser extent HC, tended to dry out between tidal cover which caused an algal crust to be formed on the surface of the sediment which had to be broken-up periodically. Other patterns of change in carbon and nitrogen levels were as described for 10°C C.T. Expt. (cf. Figs. 6.7 & 6.8).

The mean C/N values :

Treatment \ Removal	1	2	3
HC	17.53	12.41	13.45
HF	22.27	17.39	15.81
MC	20.53	12.74	12.01
MF	26.30	19.79	20.11
LC	18.27	19.06	19.11
LF	24.84	22.72	24.01

were found to decrease at the high and mid tidal levels with time. The C/N value in treatment LC increased with time and in LF remained constant. This was the net result of several factors ; a large population may keep the sediment microbial population constant when there is no inflow of organic matter;

the primary production by the sediment microalgae, and the senescence and breakdown of those primary producers.

The water content levels (mean \pm 1 S.E.) :

	High	Mid	Low
Coarse	26.57	29.55	23.00
	1.02	1.46	1.75
Fine	39.33	48.04	47.91
	1.68	3.19	3.06

in all but treatment HF, were within the normal range experienced in the field. Treatment HF, however, because of increased exposure, had a lower water content. A fine sediment at a high tidal level therefore has a decreased water holding capacity due to the consolidation of the small particles following drainage (see Section 2.5), this would provide a harsh environment for the infauna (e.g. cf. Station A3 in Chapter 3). In addition, mechanical failure on a few occasions caused the 'high-level' treatments to be uncovered during successive 'tides'.

6.1.4.2. Survivorship Patterns.

In the 10°C C.T. Expt. (Fig. 6.9a) only treatments 20F and 30F showed a decline in population density over the whole period; the former showed a marginally greater decline, i.e. the losses over the period were 20% and 16.7% respectively, and whereas the 30F treatment density showed a lesser decline over the last period (3-4 removal), the 20F treatment density declined steadily over the whole period. There was no difference between the mortalities of the 10F and 10C treatments although at densities greater than those employed the coarse treatments may show greater mortalities.

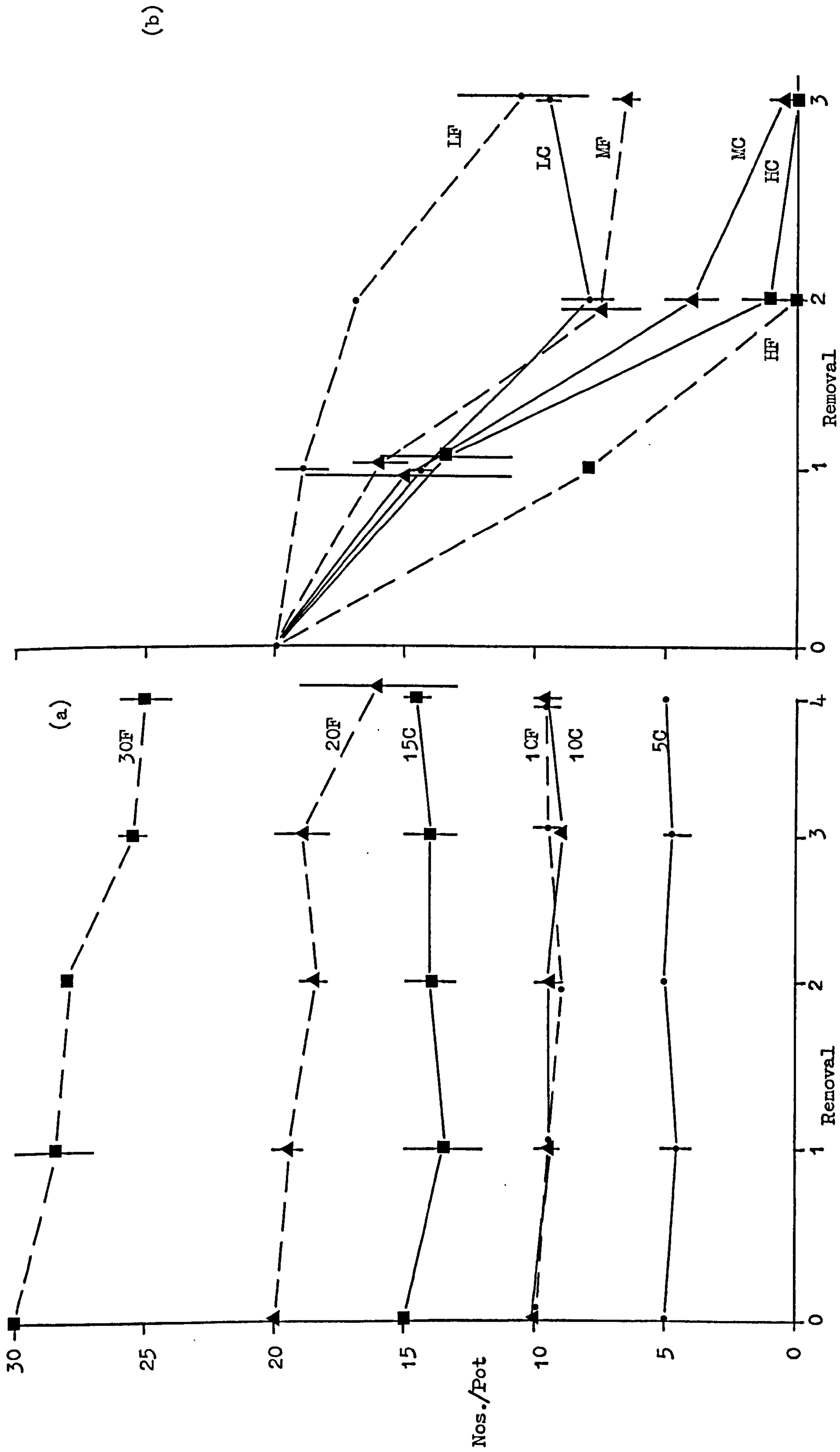


Figure 6.9 (a) 10°C C.T. Expt. and (b) T.T. Expt. : The Mean Survivorship in Each Treatment at Each Removal. (Vertical Bars = Range of Values.)

In the T.T. Expt. (Fig. 6.9b), mortality over the period resulted in only one animal surviving in the two replicates of treatment MC while at the high tidal level no animals survived. The HC treatment animals survived longer than those in the HF treatment suggesting a marginally better environment in the former. At the end of the experimental period there was no difference between the surviving densities of LC and LF treatments which were both greater than MF.

6.1.4.3. Flesh Condition.

As the flesh condition of the reference animals did not give a significant relationship with the animals' size, the mean flesh condition values are used throughout this section (Table 6.5). The T.T. Expt. reference flesh condition was lower (12.75) than that in the 10°C C.T. Expt. (17.64) reflecting the dates at which the animals for each experiment were obtained (9/5/1976 and 28/6/1976 respectively). It is considered that whilst the former were taken either during or following spawning, the latter were obtained when the flesh condition was increasing after spawning. In addition, the T.T. Expt. animals were obtained three days before being used in the experiment whereas the 10°C C.T. Expt. animals were obtained the day before the start of the experiment.

The major part of the data analysis in these experiments was performed on the pooled data of the replicates of each treatment. The Students' t-test was performed on the pairs of the replicates' condition factor values of each treatment and showed that, with only a few exceptions, the replicates of each treatment were not significantly different from each other (see Appendix 6.2).

In the 10°C C.T. Expt., the mean flesh condition over the experimental duration followed an annual pattern similar to the field situation in that the condition decreased with time from the start of the experiment in June until January; after this the condition increased to values either similar to or higher than the initial condition (Fig. 6.10). At the first removal 10C animals were significantly different from 20F, 15C and 30F. At the second removal 20F mean condition was significantly different from 10F, 30F and 15C; 10C was significantly greater than 15C; and 5C was as such from 10F and 15C. At the third removal, the treatments flesh condition were in three groups 20F and 30F, 15C and 10F, and 5C and 10C, the groups having a significantly increasing flesh condition. At the final removal, 5C treatment condition was higher than all others; that of 30F lower than all others; that of 20F was significantly different from all but 15C; and 15C different from only the highest and lowest treatment values. At the end of the experimental period the condition decreased in each substrate with increasing density.

The comparable density treatments 10C and 10F had identical condition values, i.e. no difference in condition could be attributable to sediment type changes. The fine sediment treatment mean condition values increased more during the April to July period than during January to April; those of 5C and 15C treatments increased linearly from January, but the period of greatest condition increase in the 10C treatment was January to April.

An analysis of the variance in the final condition values (on the pooled data from the replicates) (Table 6.6) suggested significant differences within sediment types, population

Figure 6.10 10°C C.T. Expt. : The Mean Condition
Factor (\pm S.E. Range) in Each
Treatment at Each Removal. (Legend
as Fig. 6.9(a).)

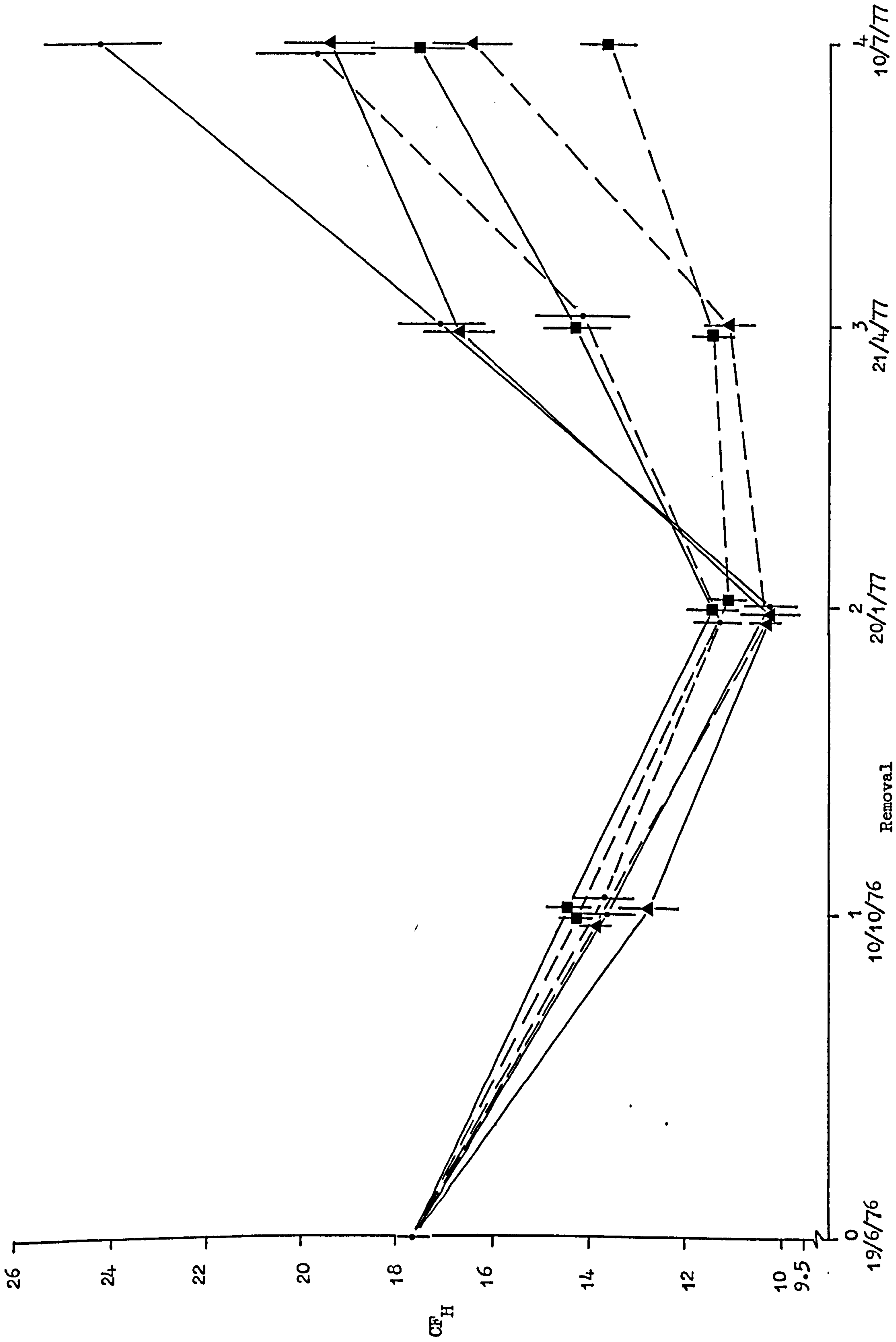


Table 6.6 10°C C.T. Expt. Final Flesh Condition: Analysis of Variance.

Source of Variation	df.	SS.	MSQ.	F Ratio	p
Total	11	152.888			
Treatment Combinations	5	128.628	25.726	6.363	*
Sediment Types	1	43.133	43.133	10.669	*
Pop ⁿ . Density Types	2	84.449	42.224	10.443	*
Sed. X P.D. Interactions	2	169.944	84.972	21.017	**
Residual	6	24.260	4.043		

Treatment Means:

	Coarse	Fine	\bar{x}
Low P.D.	24.290	19.880	22.085
Mid. P.D.	19.455	16.460	17.957
High P.D.	17.660	13.690	15.675
\bar{x}	20.468	16.677	

Least Significant Difference between sediments = 2.841 at $t_{0.5}$ level.

" " " " P.D.s = 3.479 " " "

" " " " Treatments = 4.920 " " "

Therefore for individual treatments:

	5C	10C	15C	10F	20F	30F
5C	-	n.s.	*	n.s.	*	*
10C		-	n.s.	n.s.	n.s.	*
15C			-	n.s.	n.s.	n.s.
10F				-	n.s.	*
20F					-	n.s.

densities and within the sediment/population density interactions. These findings were then confirmed by least significant difference (L.S.D.) analysis which showed, firstly, the sediment mean values to be significantly different and, secondly, within both sediments the low population densities were significantly different from the mid and high population densities but the mid population densities were not significantly different from the high ones. The treatment 5C was significantly different from 15C, 20F and 30F and both 10C and 10F treatments were different from the 30F treatment.

In the T.T. Expt., as a result of mortality no comment can be made on the condition change in the high level animals over the whole period. At the first removal the HF animals had a much lower condition than in all other treatments whereas the HC animals had the same condition as the mid and low level treatments (Fig. 6.11; Appendix 6.3). The environmental conditions, therefore, in the HF treatment were too harsh such that all animals died before the second removal. The HC animals' condition followed the same pattern as the other treatments until the last of the animals in that treatment died between the 2nd. and 3rd. removals; it is probable that their condition continued to decline after the second removal when the other treatments' mean condition values either stabilised or increased. As with the previous experiment, the flesh condition generally followed the field annual cycle although the animals' condition did not decline over the first period but only during the second period. While the treatments' LF, MF and MC flesh condition increased after the second removal that of the LC decreased slightly but not significantly. At the final removal the MF animals'

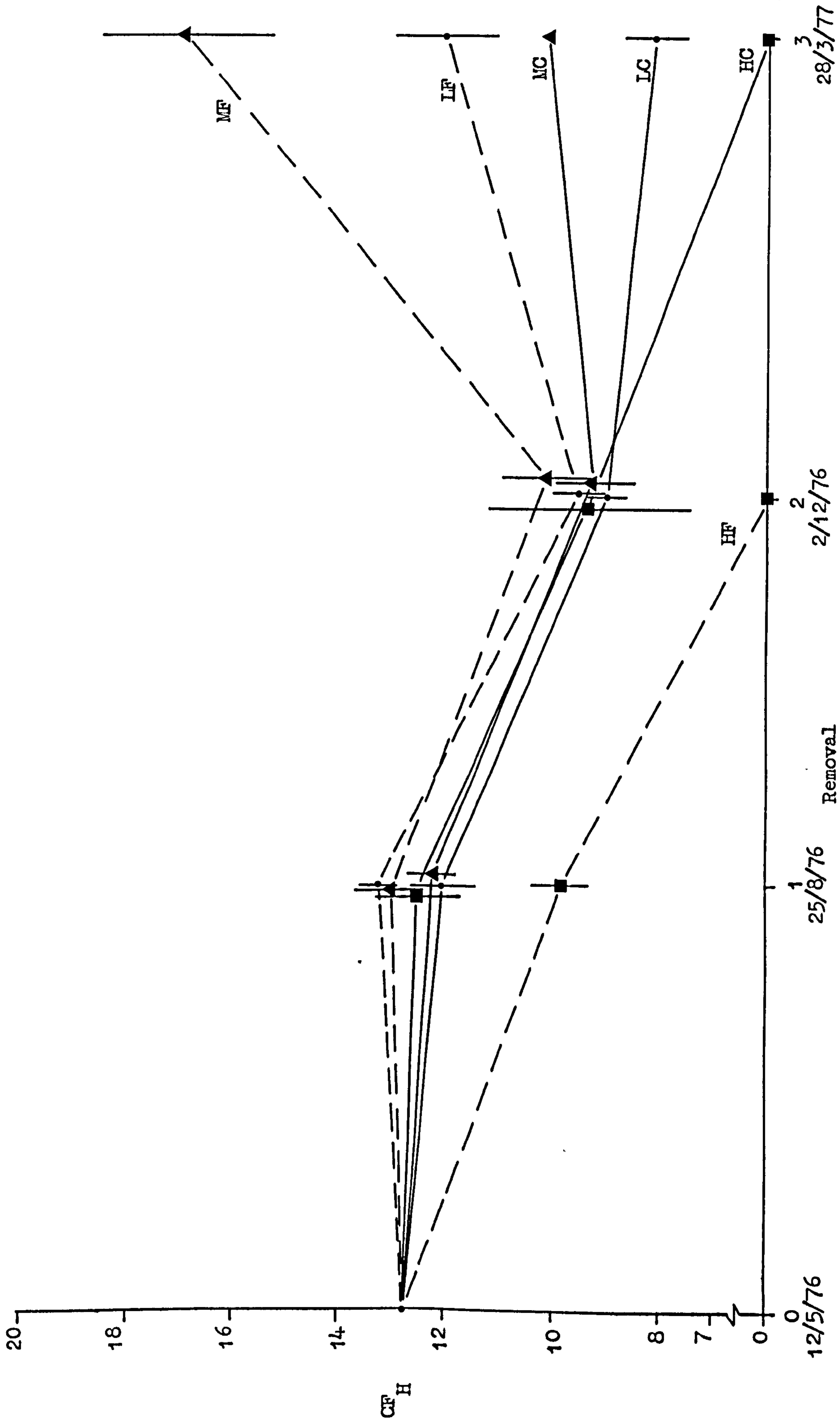


Figure 6.11 T.T. Expt. : The Mean Condition (\pm S.E. Range) at Each Removal (Legend as Fig. 6.9(b)).

condition was much greater than that of the LF animals and both of these treatments had a higher mean condition than MC and LC treatments.

6.1.4.4. Growth.

The growth over each experimental period in each treatment was analysed by three methods :

(i) a comparison of the regression equations produced of initial with final size, flesh weight and shell weight and the computation of the change in those parameters in initial 4 and 8mm animals;

(ii) a comparison of the changes in flesh and shell weights of standard 4mm and 8mm animals;

(iii) by Ford-Walford Stage I plots (Manzer-Taylor plots) of initial against final shell size.

Growth equations were produced of initial against final shell height, flesh weight and shell weight for both individual replicate and pooled treatments. As the replicates were shown to be not-significantly different from each other, only the pooled data are considered here (Appendices 6.4 (b), 6.6 - 6.8). (The replicate equations are given in Appendices 6.4 (a), 6.6 - 6.8.) The statistical significance of the change in these parameters was determined using a modified Students' t-test. A significant change in these parameters is reflected in the significance of the difference of the regression coefficient from a hypothetical value of 1.0 (i.e. $y = x$); the latter would be produced if no growth or change had occurred. That significance was determined by :

$$t = \frac{b - c}{\text{S.E.}} = \frac{b - \beta}{S/\sqrt{\sum(x - \bar{x})^2}} \quad (\text{Bailey, 1959; Zar, 1973})$$

where b = regression coefficient and
S.E. its standard error.

S = S.D. of b

β = c = hypothetical regression coefficient;

the significance of t was then determined with n-2 degrees of freedom. An increase in size or weight therefore produces a negative value whereas a positive value would be indicative of emaciation. These postulates are valid only if, firstly, growth decreases with age leading to similar theoretical maximum sizes, and secondly, the equation intercept is close to the axes origin. If the intercept was not close to the origin then the whole equation could be significantly different from $y = x$ but the slope not necessarily so, i.e. if the t-value is not significant then either growth had not occurred or all sizes had grown by the same amount producing a regression equation parallel to $y = x$, and in which case the magnitude of the intercept of the line on the y-axis is important.

6.1.4.4.1. 10°C C.T. Expt. Growth.

In the case of the height at removal against the initial height (Appendix 6.4 (b)), significant growth had occurred in treatment 5C by each removal except the first; 10C and 10F were the next treatments to have significant growth in the progression through the removals and then, at the final removal, all treatments showed significant growth. In comparing the flesh weights initially and at each removal, all regressions were significant except 5C at the final treatment (Appendix 6.4 (b)). This treatment, however, had a much larger regression intercept than

all other treatments, i.e. in this treatment the flesh weight of all sizes increased giving a final regression line parallel to $y = x$ (or $fdw_{n+1} = fdw_n$). Surprisingly all t-values were negative which did not support the conclusions from the condition changes where emaciation was seen. It is considered, therefore, that although the flesh weight increased over this period, the shell size also increased, but disproportionately so, thus leading to a decline in flesh condition during the ~~centre of the~~ centre of the experimental duration.

The change in shell weight over the experimental periods gave positively significant t-values (Appendix 6.4 (b)), this does not agree with the above theory but is a result of the fact that while a small amount of growth in the shell size of older animals produced a large change in the shell weight, the amount of shell weight produced by growth of the young animals was small, i.e. with an increasing age the regression lines therefore deviated from the line $y = x$ and their regression coefficients increased with time.

The regressions of initial against final size and weight were also used to study the growth of initially 4mm and 8mm animals over the period. The height of both sizes changed little up to the third removal (Fig. 6.12a & b) after which the major part of the growth occurred. The initially 4mm animals showed a maximum difference of 1.4mm between the different treatments whereas the initially 8mm animals showed only a 0.7mm difference, this reflects the decreasing growth rate with age. In each sediment type and initial size the amount of size growth over the total period decreased with increasing population density. There was no significant difference between the 10F and

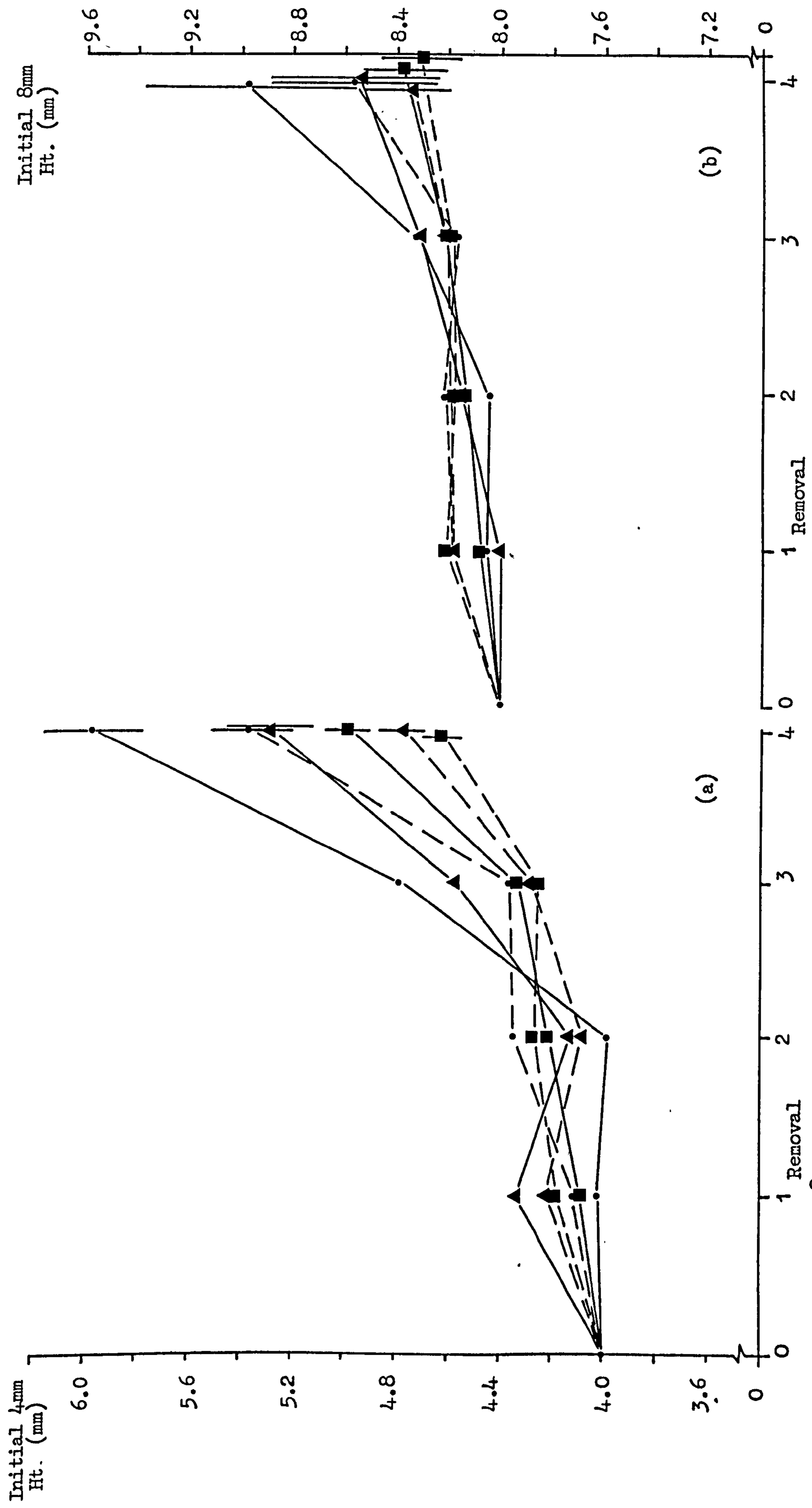


Figure 6.12 10°C C.T. Expt : The Change in Shell Size of (a) Initial 4mm and (b) 8mm Animals. (Legend as Fig. 6.9(a).)
 (Mean \pm S.E. Range For Last Points.)

10C treatments.

During the period of little size-growth (up to the third removal) the changes in flesh weight of the initially standard animals followed the condition factor change patterns; however after the third removal, there was a large amount of flesh growth (Fig. 6.13a & b). The growth of the initial 4mm animals was greatest in the 5C treatment, then in the 10C and 10F treatments which were of the same weight and then in the 15C treatment. In the 20F and 30F treatments the net growth was very low with the flesh weight changing little over the year. The flesh growth of the initial 8mm animal in the 5C treatment almost doubled its flesh weight over the total period; those of the 10C and 10F treatments were again similar although the removal period of greatest flesh increase was different in each of these treatments. The 15C and 20F treatments again showed a similar final flesh weight of the initially 8mm animal which in turn was much lower in the 30F treatment.

The shell weight of an initially 8mm animal gradually increased with time in all treatments (Fig. 6.14a); and although the coarse sediment treatments showed continued shell weight increase after the first removal, the fine treatments did not do so to such an extent. This increase was attributable to growth and not to significant shell thickening as is shown by the shell weight of a standard 8mm animal over the experimental period (Fig. 6.14b) which was calculated from log. height/log. weight regression equations for each removal and treatment (Appendix 6.5). However, the standard animal shell weights in the coarse sediment treatments increased more than those of the fine treatments although that difference was not significant; the latter is shown

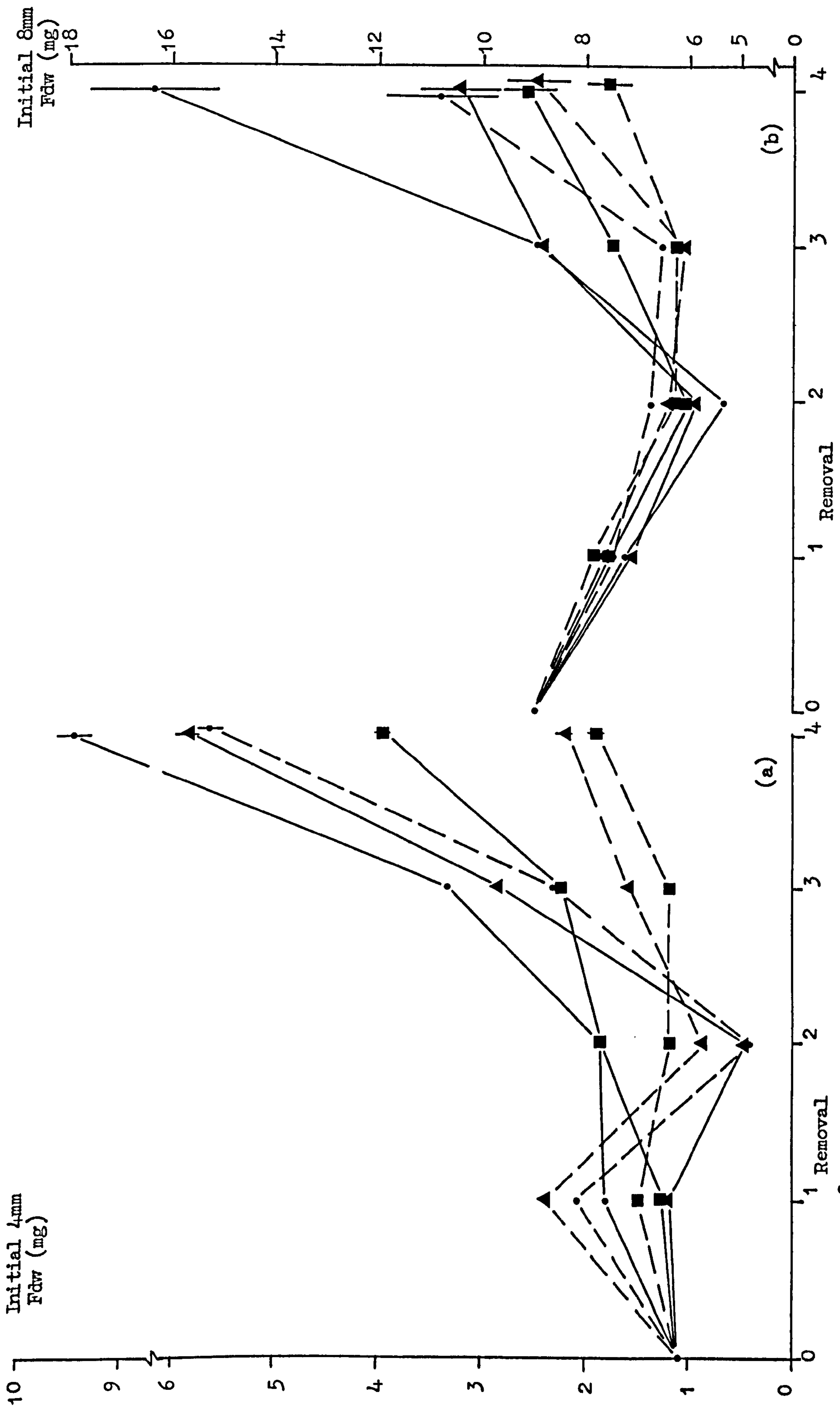
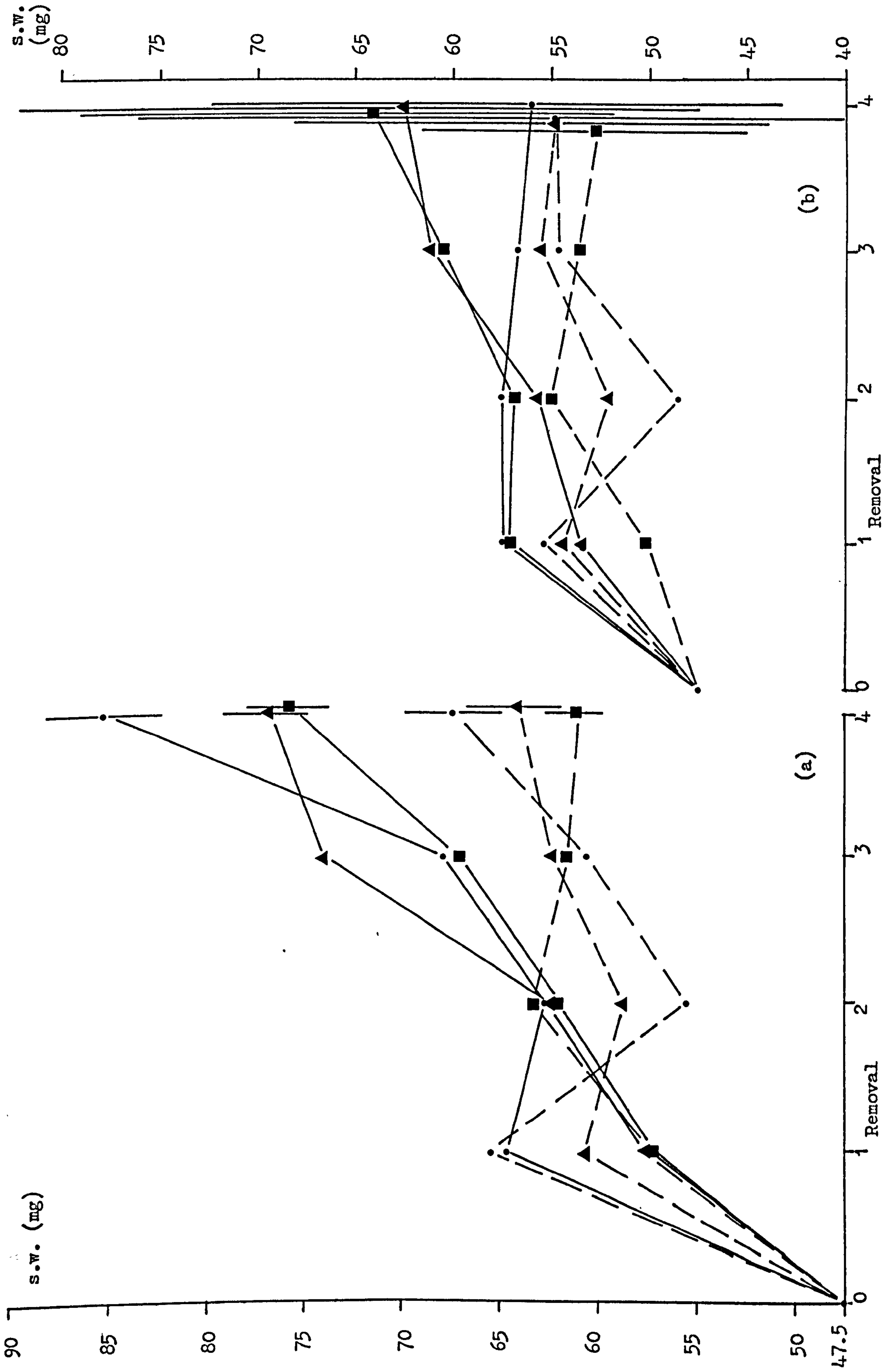


Figure 6.13 10°C C.T. Expt. : The Change in Flesh Dry Weight of (a) Initial 4mm and (b) 8mm Animals. (Legend as Fig 6.9(a).) (Mean \pm S.E. Range For Last Points.)

Figure 6.14 10°C C.T. Expt. : The Change in Shell Weight
of (a) Initial 8mm and (b) Standard 8mm
Animals. (Legend as Fig. 6.9(a).) (Mean \pm
S.E. Range For Last Points.)



by the large variation produced by the use of the standard errors of the exponential regression coefficients (Fig. 6.14b).

The flesh weights of standard 4mm and 8mm animals were similarly calculated (Fig. 6.15a, b; Appendix 6.5) and show the same progression through the treatments as the condition factor and flesh growth. The flesh weight decreased to a minimum at the second removal and then increased rapidly to the final removal. Again the large variation was the result of the method of calculation of the standard animal flesh weight.

In order to detect any change in shell shape with a change of sediment type the shell height of the animals recovered at the final removal was regressed against the shell length (Table 6.7a). The regression coefficients were not significantly different from each other in all cases (see Table 6.7b). When the total regression equation was considered by the calculation of the heights of standard length animals, again there was no difference between the treatments (Table 6.7c). Therefore, over the experimental period, the type of substrate did not affect the shape of the shell.

The final height/initial height equations are analagous with the Ford-Walford Stage I plot (see Section 6.1.3.1.) and enable the Bertalanffy parameters K and H_{∞} to be calculated (Table 6.8). Whereas within each sediment type the K values decreased with increasing population density, the H_{∞} values did not differ between treatments. The diagrams (Fig. 6.16a, b) show the uniformity of the final theoretical size and the effect of population density and sediment type on the catabolic rate. Overall, it is considered that the K value was inversely and curvilinearly related to population density.

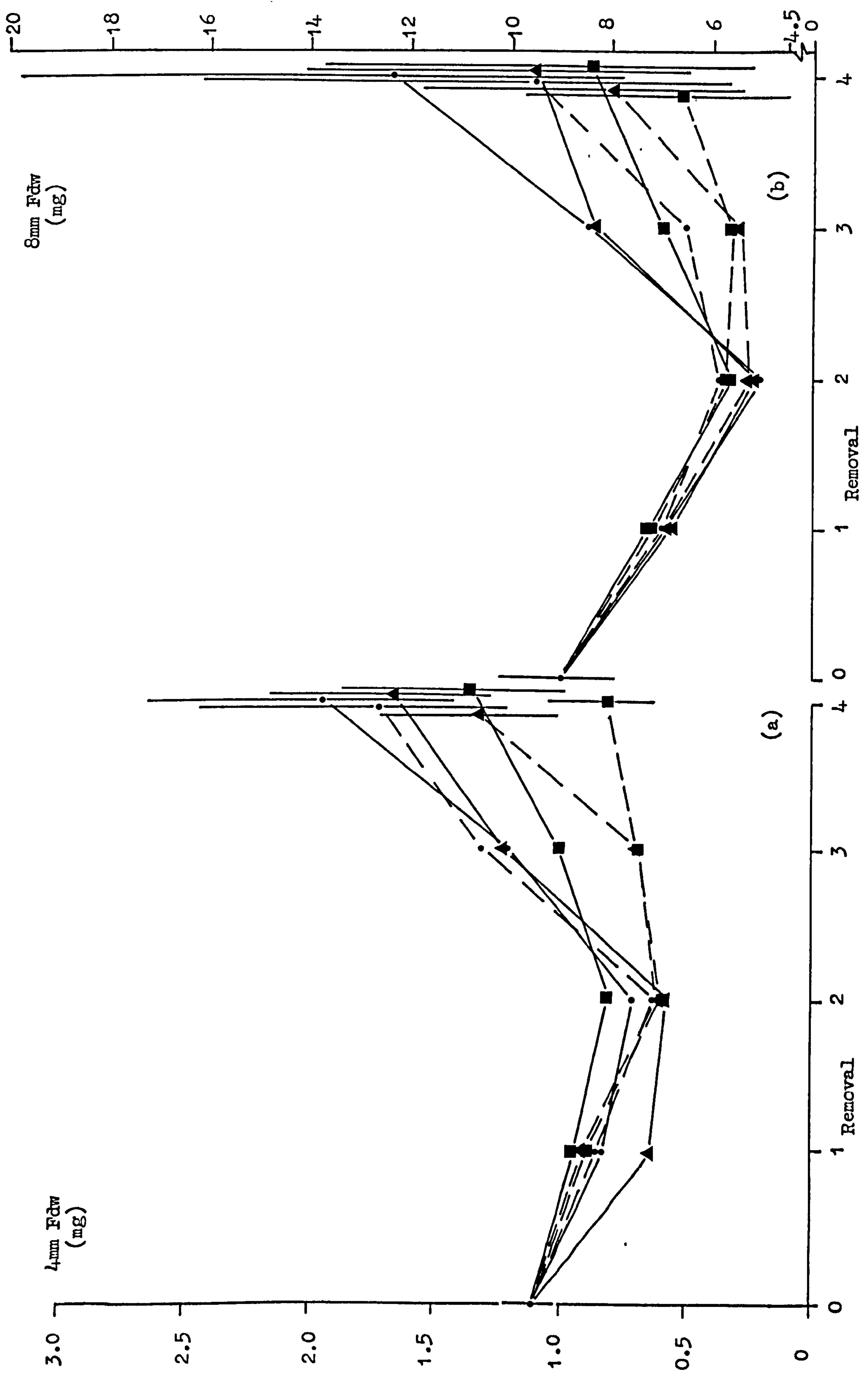


Figure 6.15 10°C C.T. Expt. : The Change in Flesh Dry Weight of (a) 4mm and (b) 8mm Standard Size Animals. (Legend as Fig. 6.9(a).) Mean \pm S.E. Range For Last Points.)

Table 6.7 10°C C.T. Expt. Shell Length/Height Relationships.

(a) Length/Height Equations :

Treatment	Equation	n	r	p
Reference	Ht. = 0.829 ± 0.016L - 0.260	36	0.994	***
5C	Ht. = 0.796 ± 0.026L + 0.153	20	0.990	***
10C	Ht. = 0.753 ± 0.019L + 0.485	19	0.995	***
15C	Ht. = 0.784 ± 0.017L + 0.193	29	0.994	***
10F	Ht. = 0.792 ± 0.024L + 0.189	19	0.992	***
20F	Ht. = 0.762 ± 0.013L + 0.360	32	0.995	***
30F	Ht. = 0.791 ± 0.016L + 0.068	50	0.990	***

(b) To Test for Significant Differences Between Regression Coefficients:

d-values of modified t-tests:-

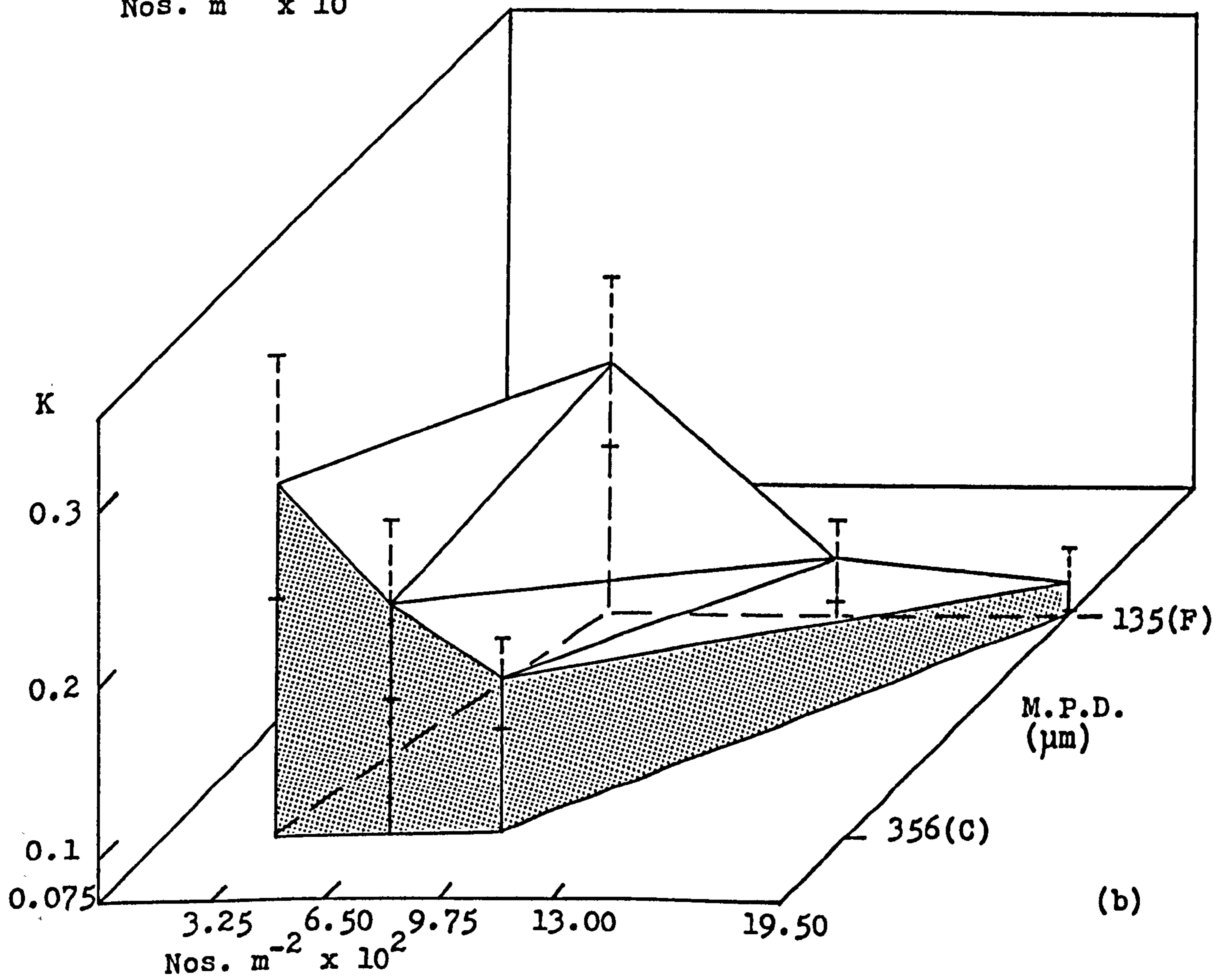
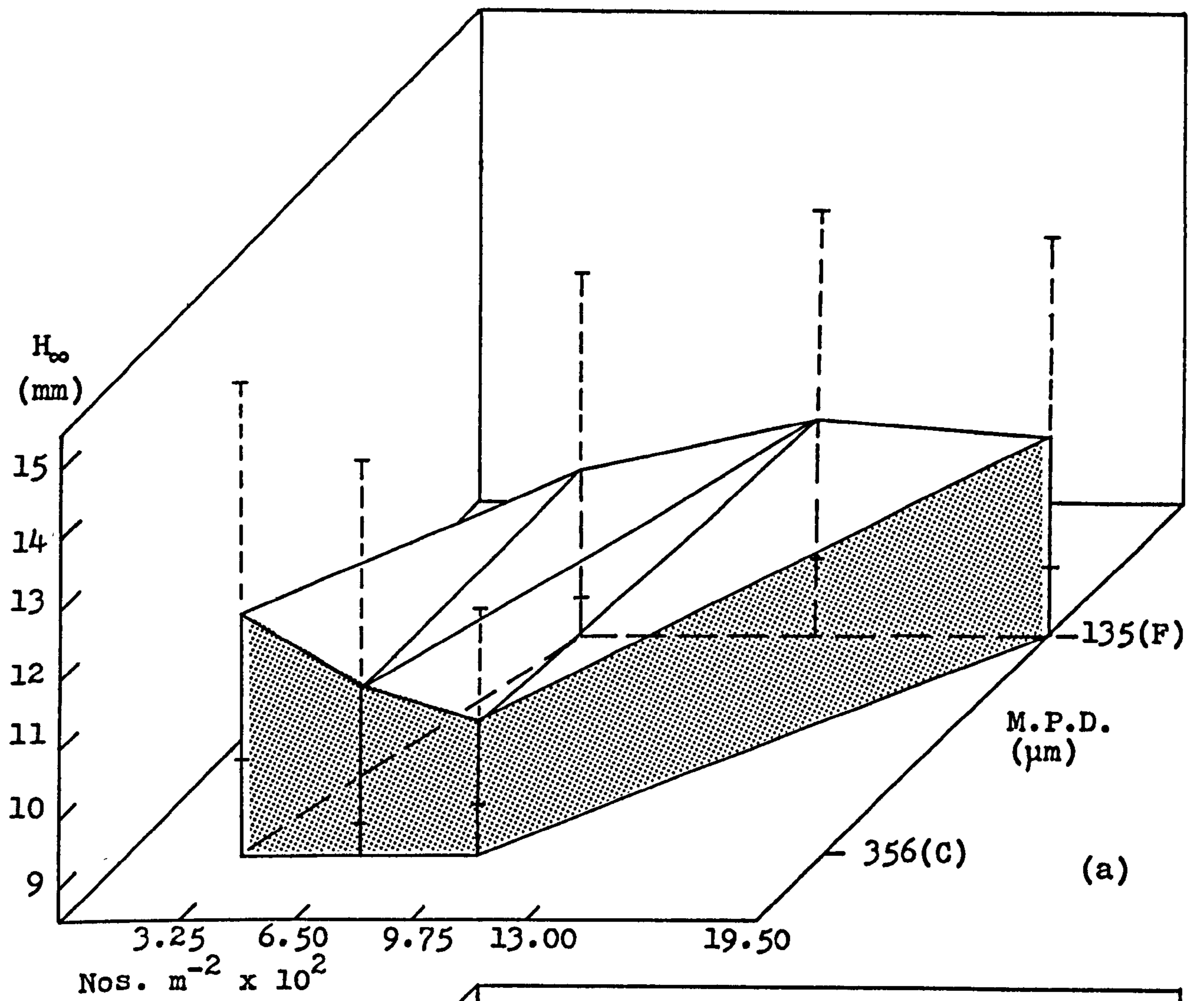
	5C	10C	15C	10F	20F	
10C	1.335					All values n.s.
15C	0.386	1.216				
10F	0.113	1.270	0.272			
20F	0.170	0.391	1.028	1.099		
30F	0.164	1.530	0.300	0.035	1.407	

(c) The Calculation of the Height of Standard Length Animals.

Treatment	Length	5mm.	10mm.	15mm.
Reference		3.88	8.03	12.17
5C		4.13	8.11	12.09
10C		4.25	8.01	11.78
15C		4.11	8.03	11.95
10F		4.15	8.11	12.07
20F		4.17	7.98	11.79
30F		4.02	7.98	11.93

Figure 6.16 10°C C.T. Expt. : Diagrammatical
Representations of the Bertalanffy
Parameters After One Years Growth :
(a) H_{∞} and (b) K with the Density
and Particle Size in the Experimental
Treatments.

(Mean Values \pm S.E. Range Given.)



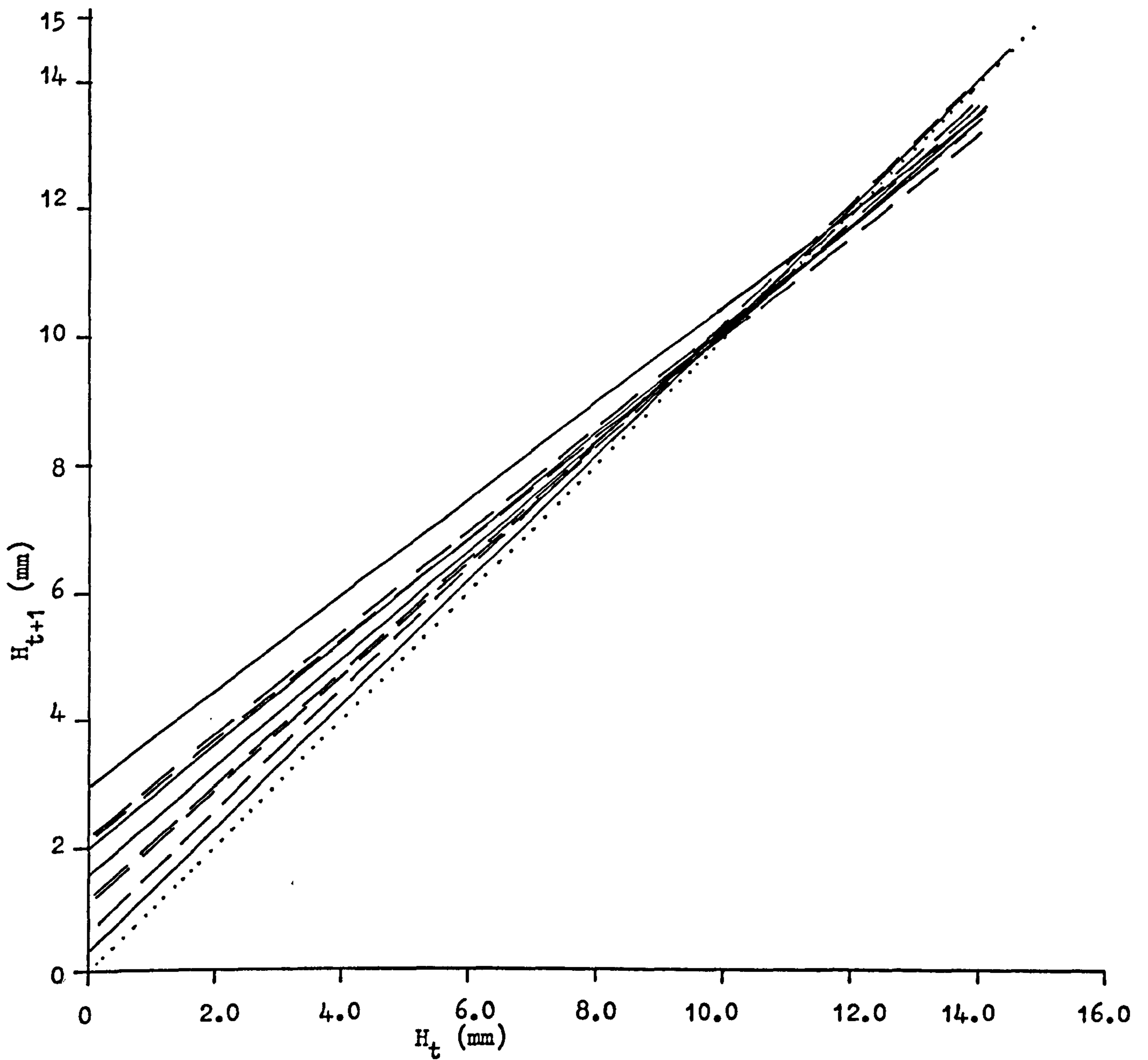


Figure 6.17 Ford-Walford Stage 1 (Manzer-Taylor) Plots for 10°C C.T. Expt. and T.T. Expt. (Extrapolated for one year). ...=45° Slope. Lines ascending on ordinate : LC, LF, 30F, 20F, 15C, 10C, MF, 10F, 5C.

Table 6.8 10°C C.T. Expt. : Ford-Walford Stage 1 Equations.

Treatment	Initial Density $n. m^{-2}$	Equation	Bertalanffy Parameters with S.E. Range	
			H_{∞}	K
5C	325	$H_{t+1} = 0.754 \pm 0.053H_t + 2.952$	12.00 (9.87-15.29)	0.282 (0.355-0.214)
10C	650	$H_{t+1} = 0.815 \pm 0.042H_t + 2.020$	10.92 (8.90-14.13)	0.205 (0.257-0.154)
15C	975	$H_{t+1} = 0.848 \pm 0.020H_t + 1.590$	10.46 (9.42-12.04)	0.165 (0.189-0.142)
10F	650	$H_{t+1} = 0.802 \pm 0.040H_t + 2.154$	10.88 (9.05-13.63)	0.221 (0.272-0.172)
20F	1300	$H_{t+1} = 0.898 \pm 0.021H_t + 1.180$	11.57 (9.59-14.57)	0.108 (0.131-0.084)
30F	1950	$H_{t+1} = 0.909 \pm 0.018H_t + 1.036$	11.38 (9.50-14.19)	0.095 (0.115-0.076)

An analysis of the variance of the H_{∞} values showed no significant difference within the sediment or population density types or in the sediment/population density interaction (Table 6.9). The analysis of the variance of K values suggested significant differences within the sediment/population density interaction but not within either variable on its own. The L.S.D. analysis showed a significant difference between the upper and lower population densities within each sediment type. In considering single treatments, the only significant difference was between the 5C and the 20F and 30F treatments. In the treatments 10F and 10C the former had a slightly, but not significantly, higher K value.

The full plots (Fig. 6.17) show the ascending order of growth lines as 30F, 20F, 15C, 10C, 10F and 5C and again demonstrate the importance of the population size rather than sediment type.

6.1.4.4.2. T.T. Expt. Growth.

All of the pooled data regressions of initial against final size, flesh weight and shell weight had significantly negative t-values (see Appendices 6.6 - 6.8) showing that where the animals had survived some growth had occurred. The size of initial 4mm and 8mm animals increased uniformly over all removal periods in the treatments 1C and 1F (Fig. 6.18a, b), but in MF the height of the initially 4mm animal increased by up to 1mm during the final removal period. Similarly the initial 8mm animal in the MF treatment also increased by the greatest amount over that period. The size growth of those treatments in which all animals died during the experimental period followed the same pattern as that of the other treatments until death. At the final removal the animals in the MF treatment had shown the greatest growth then

Table 6.9 10°C C.T. Expt. Bertalanffy Parameters: Analysis of Variance.

(a) K-values:

Source of Variation	df.	SS.	MSQ.	F Ratio	p
Total	11	0.093			
Treatment					
Combinations	5	0.066	0.0132	2.933	n.s.
Sediment Types	1	0.024	0.0240	5.333	n.s.
Pop ⁿ . Density Types	2	0.041	0.0205	4.556	n.s.
Sed. X P.D. Interactions	2	0.083	0.0415	9.222	*
Residual	6	0.027	0.0045		

Treatment Means:

	Coarse	Fine	\bar{x}
Low P.D.	0.2990	0.2275	0.2632
Mid. P.D.	0.2185	0.1035	0.1610
High P.D.	0.1670	0.0840	0.1255
\bar{x}	0.2282	0.1383	

Least Significant Difference between sediments = 0.095 at $t_{0.5}$ level.

" " " " P.D.s = 0.116 " " "

" " " " treatments = 0.164 " " "

Therefore for individual treatments:

	5C	10C	15C	10F	20F	30F
5C	-	n.s.	n.s.	n.s.	*	*
10C		-	n.s.	n.s.	n.s.	n.s.
15C			-	n.s.	n.s.	n.s.
10F				-	n.s.	n.s.
20F					-	n.s.

(b) H_∞-values:

Source of Variation	df.	SS.	MSQ.	F Ratio	p
Total	11	26.948			
Treatment					
Combinations	5	10.068	2.014	0.716	n.s.
Sediment Types	1	1.810	1.810	0.643	n.s.
Pop ⁿ . Density Types	2	2.238	1.119	0.398	n.s.
Sed. X P.D. Interactions	2	10.496	5.248	1.866	n.s.
Residual	6	16.880	2.813		

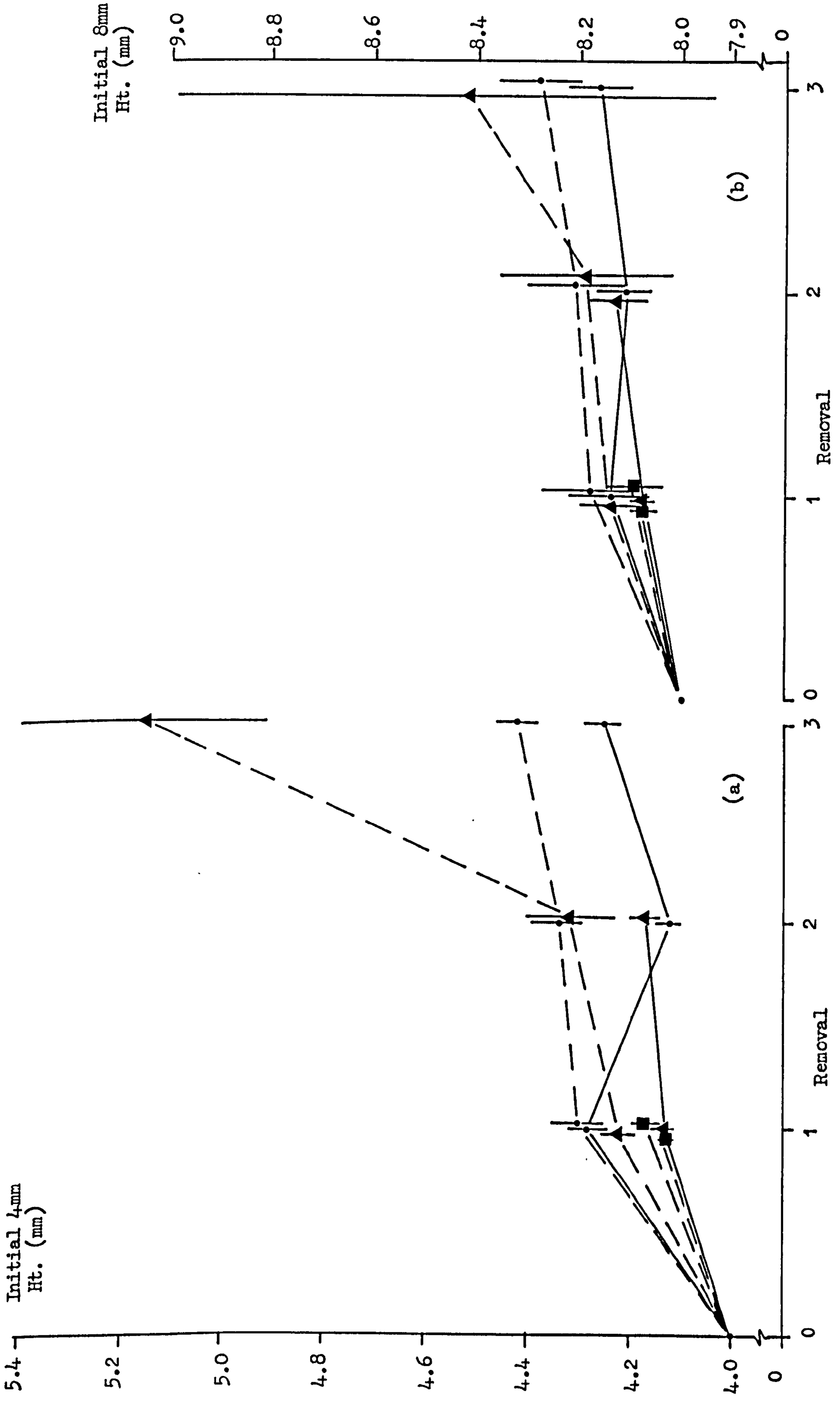


Figure 6.18 T.T. Expt. : The Growth Change in Shell Size of (a) Initial 4mm and (b) 8mm Animals Throughout the Experiment. (Legend as Fig. 6.9(b).) (Mean Values \pm S.E. Range Given.)

those of LF and then LC.

The flesh weight of the initial 4mm and 8mm animals generally showed the same trends as the flesh condition with only the HF animals markedly emaciating over the first period (Fig. 6.19a, b). The initially 4mm animals showed a small amount of emaciation over the "winter" period whereas the initially 8mm animals showed larger emaciation, with the LC treatment animals not recovering from that emaciation. The remaining treatments were in the same progression at the final removal as in the size growth figures.

The shell weight of the initially 8mm animals increased gradually but erratically with time; at the end of the experiment that in treatment LF was greater than LC which in turn was greater than MF although the variation within each treatment was large (Fig. 6.20a). The shell weight of a standard 8mm animal (Fig. 6.20b) remained constant over the experimental period, there was no evidence of shell thickening in different treatments.

The flesh weight of a standard 4mm animal (derived from logarithmic regressions in Appendix 6.9) increased over the first period, declined over the second period and then, in treatments MF and LF, increased by large amounts up to the final removal (Fig. 6.21a). The flesh weight of a standard 4mm animal at treatment LC did not increase during the last period; suggesting that although the animals could survive at the LC treatment there was insufficient food for growth. In addition, while the HC standard animals followed the same trends as the other treatments until death, those in HF did not; this again shows the harshness of that treatment. The final flesh weight of both standard animals showed the progression MF > LF > LC (Fig. 6.21a, b), i.e. within

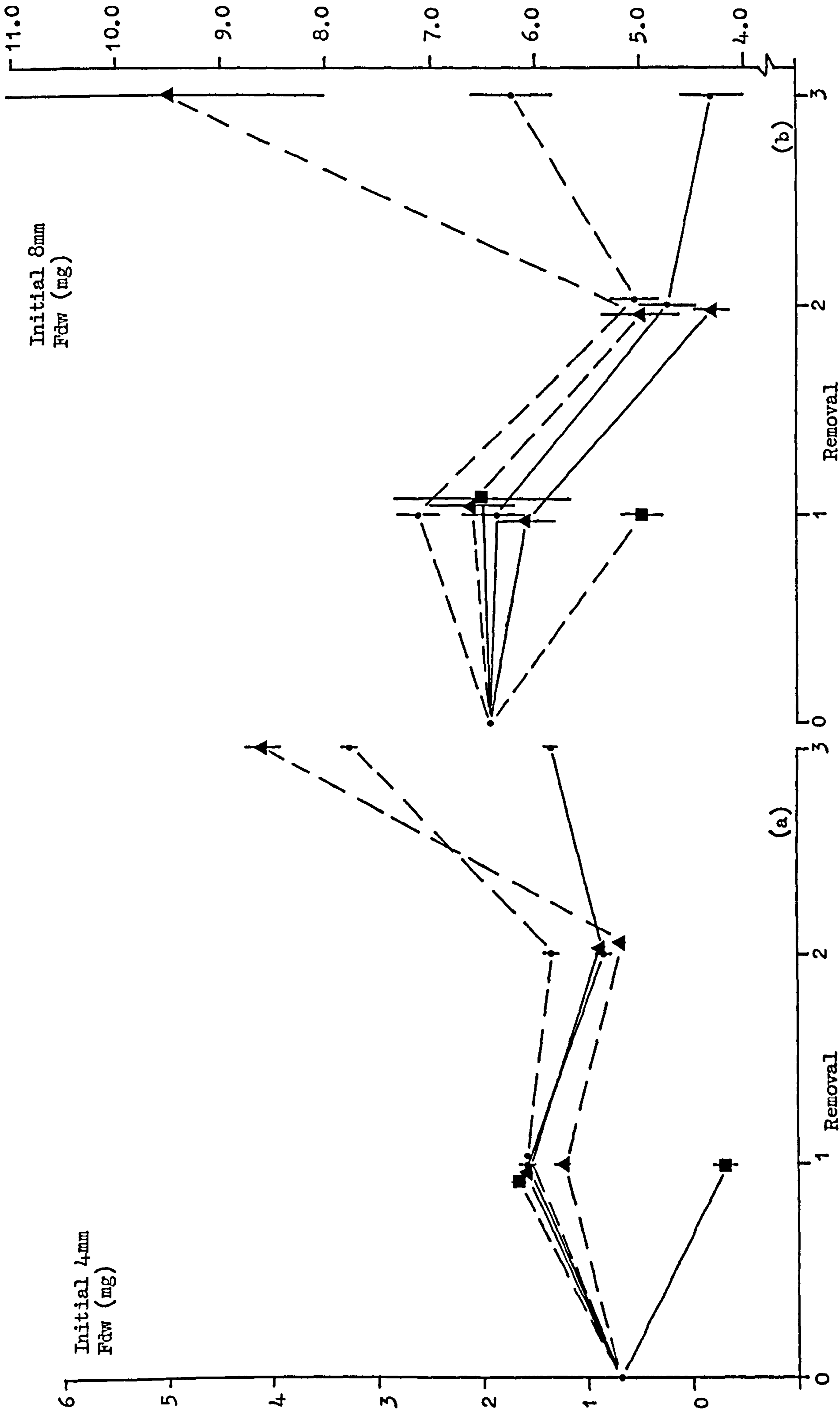


Figure 6.19 T.T. Expt. : The Growth Change in Flesh Dry Weight of (a) Initial 4mm and (b) 8mm Animals. (Legend as Fig. 6.9(b).) (Mean Value \pm S.E. Range Given.)

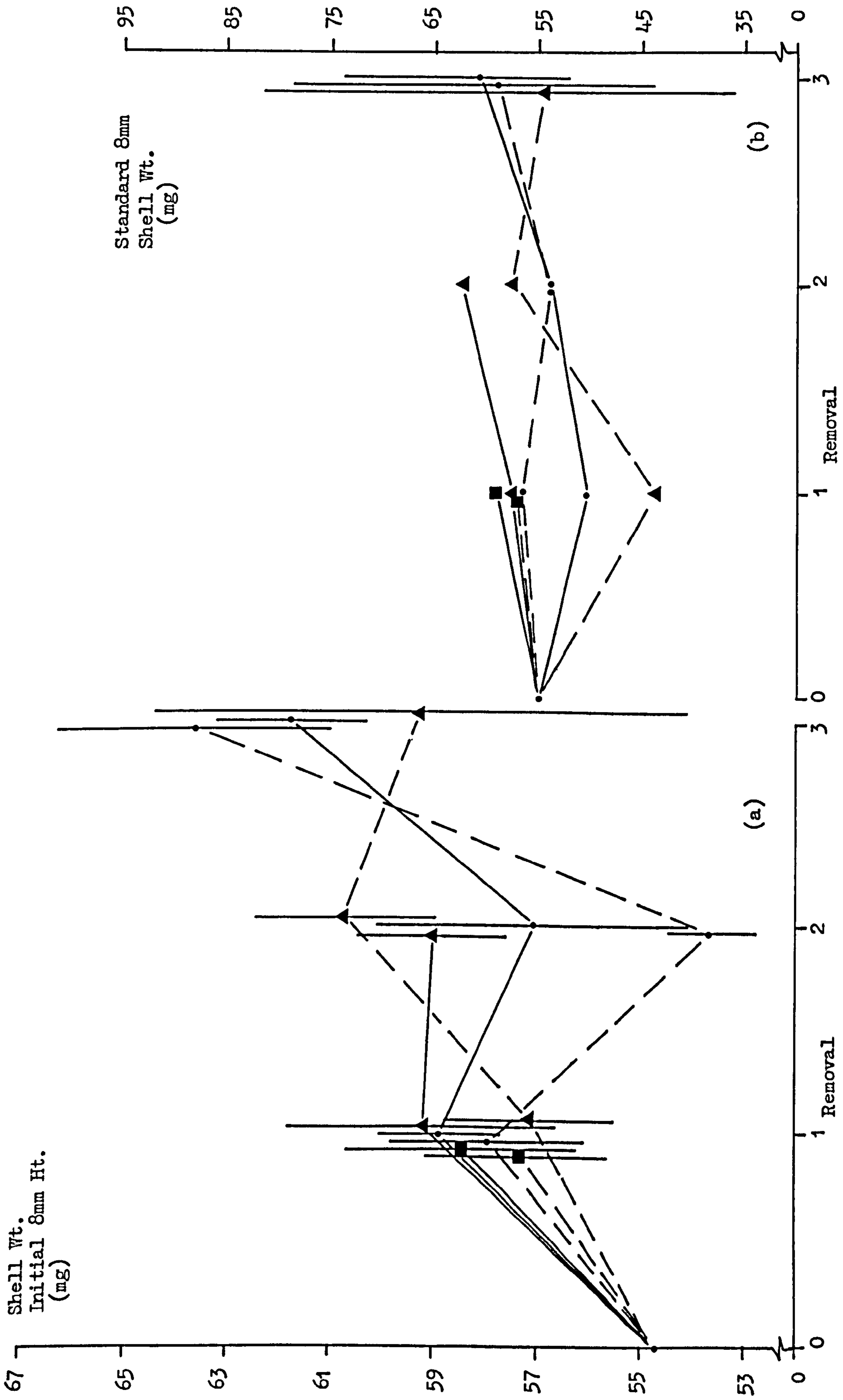


Figure 6.20 T.T. Expt. : The Change in the Shell Weight of (a) Standard and (b) Initial 8mm Height Animals Throughout the Experiment. (Legend as Fig. 6.9(b).) (Mean Value \pm S.E. Range Given.)

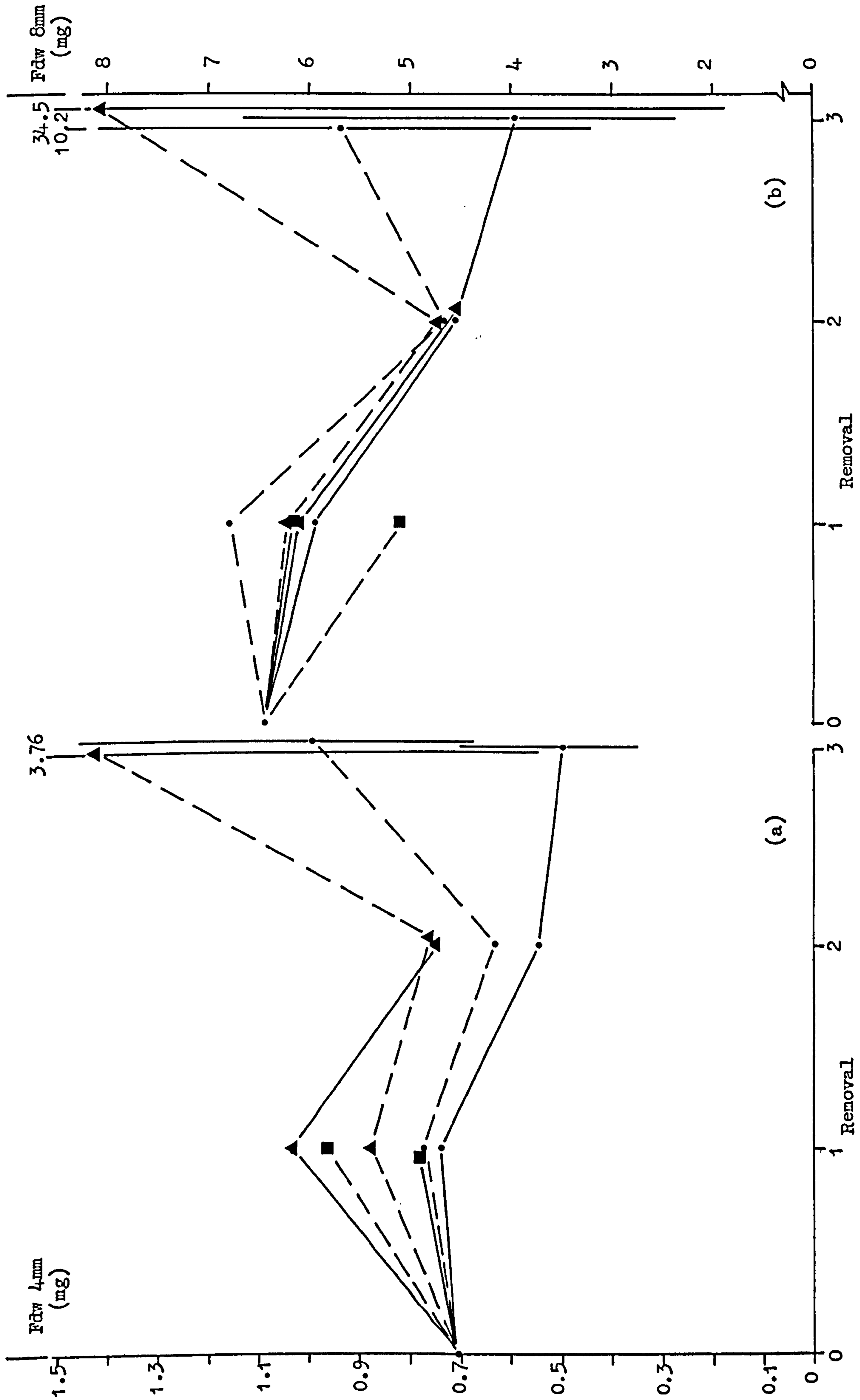


Figure 6.21 T.T. Expt. : The Flesh Dry Weight of (a) 4mm and (b) 8mm Standard Size Animals at Each Removal. (Legend as Fig. 6.9(b).) (Mean Value \pm S.E. Range For Last Point.)

the same tidal level the fine substrate animals had higher flesh values.

The Ford-Walford plots for this experiment were prepared by extrapolating from the growth shown at the end of the experiment (in 320 days) to one years' growth (Fig. 6.17; Table 6.10). As both good and poor growth were encountered during the experimental period, it has been assumed that one years' growth would have been proportionately greater than the growth measured. The low level treatments had similar equations although the growth in the LF treatment was slightly, but not significantly ($t = 1.0$, n.s.), greater. The MF treatment growth was greater than these treatments and comparable to the 10F and 10C treatments in the previous experiment. All of these growth plots were significantly different from the 45° intercept line. These trends are reflected in the magnitude of the Bertalanffy parameters H_∞ and K (Table 6.10).

Table 6.10 T.T. Expt. : Ford-Walford Growth Equations of Pooled Data Extrapolated to One Year.

$$H_{t+1} = b \pm \text{S.E. } H_t + a$$

T'ment	Ford-Walford Equation						Bertalanffy Parameters		t-test analysis	
	b	S.E.	a	n.	r	p	K (S.E. Range)	H_∞ (S.E. Range)	t	p
LC3	0.974	0.009	0.393	19	0.999	***	0.026 (0.017-0.036)	15.11 (11.23-23.12)	-2.89	*
LF6	0.959	0.012	0.648	21	0.999	***	0.042 (0.029-0.054)	15.80 (12.23-22.34)	-3.42	**
MC3	Insufficient Data									
MF6	0.792	0.069	2.146	13	0.961	***	0.233 (-0.150-0.324)	10.32 (7.75-15.44)	-3.01	*

where t = t-test value from analysis

p = significance of the regression coefficient from unity (see text).

6.1.4.5. Experimental Production, Biomass and P/\bar{B} Values.

The production in each treatment was calculated as the sum of the biomass change and the mortality loss over the period :

$$P = \Delta B + M \quad (\text{see Section 6.1.3.1.})$$

The mortality loss (M) from each treatment was calculated as the sum of the mean weights (i.e. of initial and projected fdw) of animals which had died during the experiments (see Appendix 6.10). The P/\bar{B} values were then estimated whereby the \bar{B} value was the average of the final surviving biomass and the initial total biomass (the biomass to survive plus that which did not).

In the 10°C C.T. Expt., the mean biomass supported in each treatment varied from 4.95 to 14.14g fdw m⁻² which gave an annual production ranging from 2.29 to -2.21g m⁻² and P/\bar{B} values from 0.462 to -0.156 (Tables 6.11, 6.12). The P/\bar{B} values describe a decreasing curvilinear relationship with increasing population density and flesh biomass (Fig. 6.22a, b). (For purposes of comparison the values are expressed over a m² basis.) An analysis of the variance in the P/\bar{B} values showed that significant variation was attributable to the resultant sediment/population density interaction but not to either of the single variables (Table 6.13). L.S.D. analysis showed significant differences between the highest and lowest population densities and between the highest and the middle population densities, but not between the middle and lowest population densities. The two overall sediment types with different population densities were also significantly different. On an individual treatment basis, the 5C treatment P/\bar{B} value was significantly different from that of the 15C, 20F and 30F treatments.

Table 6.11 10°C C.T. Expt. Calculation of Production at 4th. Removal. (All weights as mg.)

T'ment	I.F.d.w.	F.F.d.w.	C.F.d.w.	I.F.d.w. to disappear.	E.	Total I.F.d.w.	\bar{B}	ΔB	Total P.	P/\bar{B}
5C4	69.86	76.85	6.99			69.86	73.35	6.99	6.99	0.095
5C8	57.05	122.98	65.93			57.05	90.01	65.93	65.93	0.732
5C12	38.01	73.05	35.04			38.01	55.53	35.04	35.04	0.631
5C16	69.38	102.21	32.83			69.38	85.79	32.83	32.83	0.383
10C4	94.50	104.77	10.27			94.50	99.63	10.27	10.27	0.103
10C8	82.98	98.01	15.03	0.627	2.786	83.61	90.81	14.40	17.19	0.189
15C4	123.16	126.06	2.90	10.412	10.213	133.57	129.81	-7.51	2.70	0.021
15C8	153.00	148.22	-4.78			153.00	150.61	-4.78	-4.78	-0.032
10F4	118.82	106.48	-12.34			118.82	112.65	-12.34	-12.34	-0.109
10F8	70.63	111.05	40.42	32.791	39.423	103.42	107.23	7.63	47.05	0.439
20F4	132.97	123.96	-9.01	44.563	43.653	177.53	150.75	-53.57	-9.92	-0.066
20F8	186.63	189.19	2.56	3.075	3.722	189.70	189.44	-0.51	3.21	0.017
30F4	215.25	206.08	-9.17	48.741	48.345	263.99	235.03	-57.91	-9.57	-0.041
30F8	208.74	155.11	-53.63	36.228	31.479	244.97	200.04	-89.86	-58.38	-0.292

Where I.F.d.w. = initial flesh dry weight; E = mortality per treatment (see Appendix 6.10);
 F.F.d.w. = final " " ; P = production per treatment per year;
 C.F.d.w. = change " " ; B = biomass per treatment.

Table 6.12 10°C C.T. Expt. Calculation of Mean Production of Each Treatment.

T'ment	\bar{N} over period /t'ment	\bar{m}^2	Total \bar{B} (mg)	Total P (mg)	P/\bar{B}	\bar{B}/Pot (mg)	P/Pot (mg)	\bar{B}^{-2} ($g\ m^{-2}$)	P^{-2} ($g\ m^{-2}\ yr^{-1}$)	P/\bar{B}
5C	5.00	325	304.69	140.79	0.462	76.17	35.20	4.951	2.288	0.462
10C	9.75	634	190.44	27.46	0.144	95.22	13.73	6.189	0.892	0.144
15C	14.75	959	280.42	-2.08	-0.007	140.21	-1.04	9.114	-0.067	-0.007
10F	9.75	634	219.88	34.71	0.158	109.94	17.36	7.146	1.128	0.159
20F	18.00	1170	340.19	-6.71	-0.020	170.09	-3.36	11.056	-0.218	-0.020
30F	27.50	1787	435.07	-67.94	-0.156	217.54	-33.97	14.140	-2.028	-0.156

Figure 6.22 10°C C.T. Expt. ; The Relationships
Between Annual P/\bar{B} and (a) the Biomass
and (b) Density in Each Treatment.
(Mean \pm Range of Values.)
Lowermost Line Gives Conversion of
Abundance and Biomass From Per Pot to
Per m^2 .

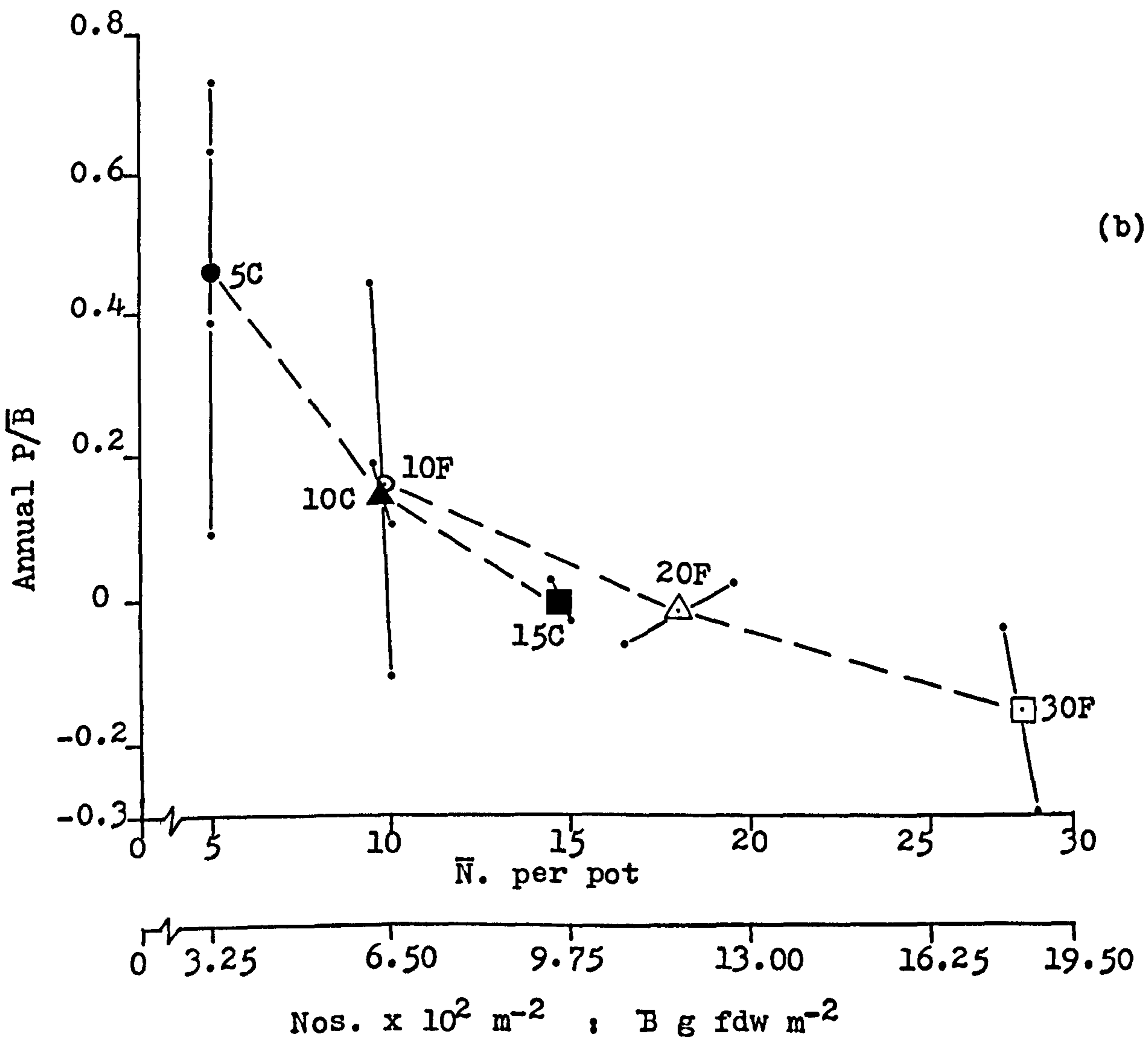
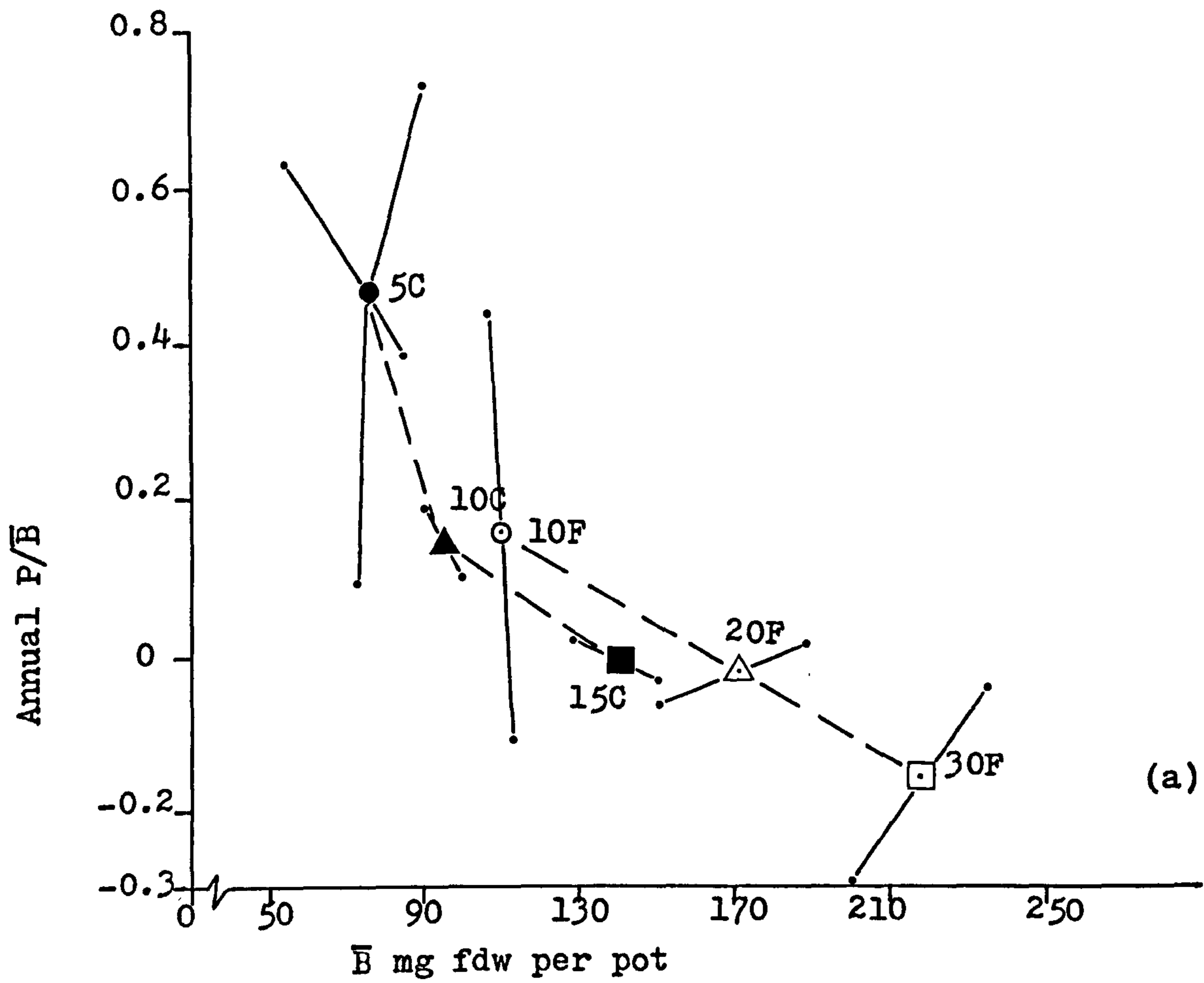


Table 6.13 10°C C.T. Expt. P/B Values: Analysis of Variance.

Source of Variation	df.	SS.	MSQ.	F Ratio	p
Total	11	0.662			
Treatment Combinations	5	0.467	0.093	2.861	n.s.
Sediment Types	1	0.131	0.131	4.031	n.s.
Pop ⁿ . Density Types	2	0.325	0.162	4.985	n.s.
Sed. X P.D. Interactions	2	0.661	0.330	10.154	*
Residual	6	0.195	0.032		

Treatment Means:

	Coarse	Fine	\bar{x}
Low P.D.	0.4600	0.1650	0.6250
Mid. P.D.	0.1460	-0.0245	0.1215
High P.D.	-0.0055	-0.1665	-0.1720
\bar{x}	0.6005	-0.0260	

Least Significant Difference between sediments = 0.255 at $t_{0.5}$ level.

" " " " P.D.s = 0.312 " " "

" " " " treatments = 0.441 " " "

Therefore for individual treatments:

	5C	10C	15C	10F	20F	30F
5C	-	n.s.	*	n.s.	*	*
10C		-	n.s.	n.s.	n.s.	n.s.
15C			-	n.s.	n.s.	n.s.
10F				-	n.s.	n.s.
20F					-	n.s.

In the T.T. Expt., as it was not possible to calculate the projected flesh weights in treatments in which the animals did not survive, the production was only calculated for the treatments MF, LF, LC. The annual production was then extrapolated in the same way as the annual growth. The treatments supported mean biomasses equivalent to 6.9 to 7.4g fdw m⁻² which produced from -3.32 to 4.07g fdw m⁻² yr⁻¹ giving P/B values from -0.48 to 0.57 (see Table 6.14; Appendix 6.10). The production estimates show that at the same (low) tidal level the fine substrate animals were more productive than those in the coarse substrate, although net emaciation occurred in both treatments over the period. That the MF animals were the most productive may reflect the fact that this treatment environment was most similar to that from which they were taken.

Table 6.14 T.T. Expt. Calculation of Production at Final Removal.

Treatment	I.F.d.w.		C.F.d.w.		I.F.d.w. to disappear		Total I.F.d.w. (mg)	ΔB (mg/pot)	Period P		Annual P	\bar{B} ($g\ m^{-2}$)	Annual P/\bar{B}
	(mg)	(mg)	(mg)	(mg)	(mg)	(mg/pot)			(mg/pot)	($g\ m^{-2}$)			
LC3'	77.38	43.82	-33.57	86.07	67.74	163.45	-119.63	-51.89	103.63	-3.847	6.736	-0.571	
LC3''	94.15	63.63	-30.53	59.41	52.37	153.56	-89.93	-37.56	108.59	-2.785	7.059	-0.394	
LF6'	94.98	61.94	-33.05	57.99	52.36	152.97	-91.03	-38.67	107.45	-2.867	6.985	-0.410	
LF6''	84.23	91.54	7.61	64.33	62.36	148.56	-57.02	5.34	120.05	0.396	7.803	0.051	
MC3'	Insufficient Data												
MC3''	"												
MF6'	50.14	71.95	21.84	101.95	146.25	152.09	-80.14	66.11	112.02	4.901	7.281	0.673	
MF6''	58.48	75.08	16.61	83.84	110.88	142.32	-67.24	43.64	108.70	3.235	7.065	0.458	
HC3'	Insufficient Data												
HC3''	"												
HF6'	"												
HF6''	"												

Treatment Means:	P		Annual P/\bar{B}
	($g\ m^{-2}\ yr^{-1}$)	($g\ m^{-2}$)	
LC3	-3.316	6.897	-0.481
LF6	-1.235	7.394	-0.167
MF6	4.068	7.173	0.567

See Table 6.11 for further explanation of column titles. Annual figures obtained as $1.14 \times \text{Exp'tal period}$.

6.1.5. Discussion (Experimental Findings).

In order to comment both on the experimental findings and on their relevance to the field populations of M. balthica, a comparison between the field and laboratory environmental characteristics is necessary. However, although the laboratory growth rates, condition and production can be compared with their field counterparts, they could not be used directly in analysing field populations (Crisp, 1971).

The sediment types in the two experiments were comparable to each other and to the field substrates. Similarly, in the 10°C C.T. Expt., the sediment carbon, nitrogen and water contents were similar to the field values and there was no obvious effect of greater sediment reworking by the higher population densities. However, although the %C and %N levels in the fine sediment did not change with time, those in the coarse sediments slightly increased which suggests that high populations may have some beneficial effects in this sediment. As in the field, the coarse sediment organic matter was nutritionally better than in the fine sediment although there was less organic matter available in the former sediment. The high densities of animals in the fine sediments may have removed microorganisms from the sediment at a greater rate than that at which the microorganisms utilize organic matter (see below).

The exposure of different sediments in the tidal tank led to increases in sediment organic matter with time; this was attributable to an increase in organic matter derived from both primary producing and decomposing benthic microorganisms although all values were still within the range experienced by the same field sediments. Also, the decrease in the high and mid

level sediment C/N values with time suggests that the utilisation of organic matter by microorganisms was greater than its fixation, although at these levels organic matter would be added to the sediment following the death of the experimental animals. It is possible that as the C/N value increased with time, the large population in treatment 1C also had a beneficial effect on the benthic microflora and removed microorganisms faster than their rate of production.

With respect to the field populations, only treatments 5C, 10F, MF and LF supported populations similar to coarse (in the case of 5C) and fine substrate populations in the field. Under favourable conditions of constant immersion in the laboratory, the coarse sediment supported populations larger than in the field, e.g. treatment 15C supported 9g fdw m^{-2} , although while maintaining that high population the animals showed little growth and no production. It may be concluded, from both experiments, that increased immersion increases both survivorship and the size of the biomass that a coarse sediment can support. The largest biomass supported in the experiments, over 14g fdw m^{-2} , was much larger than that supported on any part of the mud flats although, similarly, that high biomass also showed little growth and no production.

In the 10°C C.T. Expt. treatments where the only variable parameter was the sediment type (i.e. 10C cf. 10F), the mean flesh condition, flesh and size growth, mortality and production were not significantly different from each other. In addition, the treatment 10F Bertalanffy parameter K value was slightly but not significantly greater than that of the 10C treatment. All aspects of the analysis - condition, growth and productivity -

decreased with an increase in population size with the factors K and P/\bar{B} showing inverse curvilinear relationships with density and flesh biomass. All treatments produced similar H_{∞} values, the range of which encompass the Station B3 value (from where the experimental animals were obtained), although the mean H_{∞} values were also similar to the high shore, coarse sediment populations. Mortality only occurred in the highest population densities where only 20% mortality occurred over the period. Within certain limits therefore, although significant sediment/population density interactions were found, changes in population density effected a greater influence on the production biology of the species than did the changes in substrate type. The use of further treatments 5F, 20C and 30C, would show whether this general rule held for all cases; it is likely that higher densities in the coarse sediment would show increasing mortality.

At the end of the T.T. Expt. the flesh and size growth, condition and production were in the progression : treatment MF > LF > LC. Within the same (low) tidal level, the growth and productivity in the fine sediment were slightly greater than those of the coarse one; at the final removal, the flesh condition was greater in the fine sediment than in the coarse one at both the mid and lower tidal levels. In addition, in comparing the treatments LC and LF it is seen that although the former treatment provided sufficient food to maintain the population, there was, unlike in the latter treatment, insufficient food to allow for growth following the winter emaciation. It is therefore considered that the species has an optimal immersion period but it is secondarily influenced at such a tidal level by the substrate. By comparison, the experimental

lower-level immersion period was closer to the optimal level shown by the field data at around Stations B2 and B3, although the other rich, productive area A1 had a tidal level between that of levels L and M in the tide tank. The field optimal level was also influenced by the sediment type, and with a suitable substrate the more productive areas could have extended further upshore. At the experimental high tidal level the coarse sediment afforded a better environment for survival; that level presented the same problems to the benthos as in similar field situations. Sediment at a high tidal level is in danger of drying out and, whereas animals in coarse sediment could withstand that drainage (although in the experiment the coarse sediment dried out relatively less than did the fine sediment), the fine sediment aggregated upon drying out which resulted in making infaunal movement more difficult. The drying and compaction of high level substrates therefore contributed to the mortality in those areas. In the field, the water table would probably still be within reach of the animals even at the highest tidal level. By comparison, the Stations A4 and C5, which were closest to the experimental high level, supported the low mean biomasses of ≈ 1.3 and 0.6 g fdw m^{-2} respectively, and as such showed agreement with the above conclusions.

The field and laboratory growth may be compared (Table 6.15). The 4mm initial size animals in the 10F and 10C treatments showed flesh growth comparable to Station B3 although they showed poor size growth. Their size growth in treatment 5C was greater than that of Station C4 but less than that at B3 while the flesh growth in this treatment was much greater than at the latter station. The 20F treatment and Station C4 animals showed a

Table 6.15 The Final Size and Flesh Weight of Standard Animals
(Actual or Extrapolated to One Year) of Experimental
and Field Animals.

(a) 10°C C.T. Expt.

Initial Size and Weight	4mm	≈1mg	8mm	≈9.0mg
Treatment	(mm)	(mg)	(mm)	(mg)
5C	6.0	9.5	9.0	16.5
10C	5.3	5.5-6.0	8.6	10.0-11.0
15C	5.0	4.0	8.3-8.4	9.0
10F	5.3	5.5-6.0	8.6	10.0-11.0
20F	4.8	2.2	8.3-8.4	9.0
30F	4.6	1.7	8.3-8.4	7.5

(b) T.T. Expt.

Initial Size and Weight	4mm	0.75mg	8mm	6.5mg
Treatment	(mm)	(mg)	(mm)	(mg)
MF	5.3	4.6	8.5	9.9
LF	4.5	3.7	8.3	6.2
LC	4.3	1.5	8.2	4.0

(c) Field Change Over One Year.

Station	Initial Size at n yrs (mm)	Age at n yrs (yrs)	Fdw at n yrs (mg)	Size at (n+1)yrs (mm)	Age at (n+1)yrs (yrs)	Fdw at (n+1)yrs (mg)
B3	4	1.35	≈1.0	6.5	2.35	5.0
C4	4	≈1.35	≈1.0	5.8	2.35	2.4
B3	8	3.1	10.0	9.4	4.1	16.8
C4	8	4.2	8.1	8.9	5.2	11.6

similar flesh weight increase. In the T.T. Expt., none of the remaining treatments showed size or flesh growth as large as that at Station B3 although the flesh growth in treatments MF and LF was greater than at Station C4.

The direct comparison of initial 8mm animal laboratory growth with growth at Stations B3 or C4 is more difficult as the age of such an initial size varied with station. The treatment 5C animals in the 10°C C.T. Expt. showed similar flesh growth to Station B3 but the size growth was lower in the former. The size growth of initial 8mm animals in treatments 5C, 10C and 10F, was greater than or similar to that at Station C4. In the T.T. Expt. only the growth in treatment MF approached field growth rates and then it was less than that of Station C4. As the experimental water temperature was lower than the air temperature, the mid level animals were therefore exposed to higher temperatures for longer periods which could have contributed to the animals' better growth and flesh condition.

The lower growth rates are also observed when the experimental Bertalanffy parameters are compared with those obtained for the field populations (cf. Tables 3.5, 6.10 and 6.18); the K values of all treatments except 5C, 10C, 10F and MF were comparatively low. The H_{∞} values obtained in the 10°C C.T. Expt. and in treatment MF were slightly lower than in the field while those obtained in the treatments LF and LC in the T.T. Expt. were in agreement with the field estimates. In addition, the relationship between the experimental K and H_{∞} values is lower than the predicted patterns from the field populations (see Fig. 3.35).

All of the coarse sediment tidal treatments either suffered

total mortality or, in the case of treatment LC, had animals which, although surviving, showed continuing decline in condition. Furthermore, the lower initial condition in the T.T. Expt. treatments may have possibly contributed to the higher mortalities in that experiment than in the 10°C C.T. Expt. A condition factor minimum of 7.5 was found in the former experiment after which the animals died; such a low condition was recorded neither in the field sampling nor in the 10°C C.T. Expt. and suggests that, even after a period of natural emaciation in the field, the animals had body reserves which possibly could be utilized if environmental conditions further deteriorate.

The condition increase and period of greatest growth occurred at the same time in both experiments, i.e. the period before the final removal, although in the 10°C C.T. Expt. a disproportionate increase in shell size and flesh weight had occurred between other removals resulting in a lowering of condition that was not therefore attributable to emaciation. These patterns again support the field analyses. However, unlike the field study, there was little evidence of shell thickening in the experimental animals. In the 10°C C.T. Expt., shell weight growth was greater in the coarse sediment but the animals in those treatments did not have significantly thicker shells although the trends showed this to be possible. A change in shell shape with differing substrate, as found in the field survey, was not found in this experiment.

Whereas the sediment carbon and nitrogen levels in the 10°C C.T. Expt. did not account for the differences in the flesh condition, the particular tidal levels in the T.T. Expt. quantitatively and qualitatively affected the sediment organic

matter which in turn affected the animals' flesh condition. The sediment carbon and nitrogen and the condition factor for treatment MF were greater than for LF and similarly for MC than LC. At the final removal, the carbon values were in the same progression as the flesh condition values. However, although the C/N values of MF and LC were similar, this was not reflected in their animals' condition.

In the majority of treatments and removals, the condition values were either below or at the bottom of the range encountered in the field (cf. Figs. 3.5, 6.10, 6.11) although the final condition values in treatments 5C and MF were within that range. The animals' condition in both experiments followed the field annual cycle of flesh condition with the minimal condition over the winter months attributable to emaciation. However, whereas in the field emaciation was caused by seasonal differences or differential growth of flesh and shell, in the experiments the causes of those seasonal differences; changes in daylength, temperature and food availability remained constant. It is possible that emaciation may be regulated by endogenous rhythms that were not suppressed by constant laboratory conditions. Other possible explanations of this phenomenon are, firstly, that the animals may have been unduly stressed by transference to the laboratory, which resulted in the cessation of feeding and the production of a disturbance ring; or secondly, that it may have taken a while for the microbial and diatom populations to be reestablished in the sieved sediment. The data do not support either of these suggestions as firstly, the animals' growth was no less between the start and the first removal than between the first and second removal and, secondly,

the carbon and nitrogen levels did not markedly change with time. However, in most cases a disturbance ring was produced suggesting at least a short size-growth cessation period.

The production in the 10°C C.T. Expt. of 2.99 to -2.21g fdw m⁻² yr⁻¹ from a mean biomass of 4.95 to 14.14g fdw m⁻² resulted in P/ \bar{B} values of from 0.462 to -0.156. The respective values in the T.T. Expt. of -3.32 to 4.07 and 6.9 to 7.4 resulted in P/ \bar{B} values from -0.481 to 0.567. Although these values show the magnitude of the biomass and production of this species that could be supported by an area under certain conditions, a comparison of the productivity (i.e. P/ \bar{B}) of a species under certain conditions is of greater interest (cf. Tables 3.13, 6.12, 6.14). The productivity of the 5C treatment was similar to that of the low/mid-shore, fine mud field Stations A1, B2, B3 whilst that of 10F and 10C was similar to the mid/high-shore coarse sediment Stations B4, B5, C3, C4. In the T.T. Expt. the MF treatment P/ \bar{B} , P and \bar{B} values were similar to those of the low/mid-shore fine mud Stations A1, B2 and B3. This shows both the importance of a mid tide distribution, with the species being less successful above and below that level, and also that under conditions of low densities and long immersion periods coarse sediments could be as productive (in terms of P/ \bar{B} values) as fine, mid-shore field areas; the former habitat type however would not support such high biomasses as the latter have been found to in the field (see Table 3.13).

That the mid level, fine sediment treatment animals were the most productive is a reflection of the fact that this treatment was closest to that environment from which the experimental

animals were taken, i.e. the animals were under the least stress caused by adapting to, or being confronted by, differing conditions when transferred to the laboratory treatments as in the other treatments. It is probable that this condition of least stress contributed to the better growth, flesh condition and production shown by these animals. In addition, the mean of the \bar{B} and P/\bar{B} values of the treatments IC, LF and MF (7.155g fdw m^{-2} and -0.022 respectively) produces a point close to the inverse relationship curve given by the 10°C C.T. Expt. of the change in the productivity of a population with increasing population size (Fig. 6.22a, b). Such a density dependency by productivity as this was not encountered in the field although the highest experimental biomasses rarely occurred in the field populations studied.

The treatments 5C, 10C, 10F and MF were found to have P/\bar{B} values which were similar to the mean value for Torry Bay (see Table 3.27) i.e. values that were low for M. balthica intertidal populations but similar to sublittoral populations. This may be expected as the 10°C C.T. Expt. simulated shallow sublittoral conditions and again emphasises the importance of the periodic exposure in the species' productivity.

The experimental findings may therefore be summarised :-

(i) Increasing immersion increased survival whereas growth and production only increased to a certain level with increasing immersion and then decreased.

(ii) The type of sediment was important in terms of water retention, which increased survivorship and which may enable feeding during low tide, and the absolute amount of food rather

than the quality of that organic matter (see Section 6.2).

(iii) The population density, over the range used, had the greatest effect on all aspects of the animals' production ecology.

(iv) The experiments also supported the estimate of a low, sublittoral value of productivity for these animals, although they did not explain the reason for such a low productivity. It remains possible, therefore, that the population under study was affected by other factors not considered in these experiments, e.g. pollution (see Section 6.3.).

In conclusion, it is considered that these experiments reaffirmed many of the inferences from the field study and give some indication of the value of controlled, multivariate experiments in production ecology studies. However, although the necessity of using the whole size-range of animals resulted in the accumulation of further information, it made the data analysis and interpretation of results more complicated. It is considered that further experiments would benefit from the use of animals of the same size and age and, ideally, from a genetically homogeneous stock.

6.2. The Mode of Feeding by *M. balthica*.

It is necessary, in any ecological study, to understand the mode of feeding of an animal; in *M. balthica* this is considered to be complex. This species has been described as :

an unselective, indiscriminative deposit feeder (Yonge, 1949b; Newell, 1965);

a selective deposit feeder (Fenchel, 1972; Hulscher, 1973; Wolff, 1973);

an active deposit feeder (Segestråle, 1960; Vassallo, 1969);

a detritus feeder (Lammens, 1967);

usually a deposit feeder but occasionally suspension-feeding (De Wilde, 1975);

a detritivorous deposit and suspension feeder (Ankar, 1977);

either feeding on bottom detritus or suspended material (Brafield and Newell, 1961; Standley, 1970; Bubnova, 1972; Myren and Pella, 1977);

only a filter (suspension) feeder (Morton, 1970);

descriptions which cover the major feeding categories employed by infaunal macroinvertebrates and contribute to the fact that feeding in the family Tellinacea, and genus *Macoma* in particular, is more complex than first thought (e.g. Yonge, 1949b; Pohlo, 1969; Reid and Reid, 1969).

The mode of feeding may be described according to the inhalent siphon length and activity, the material intake size and selectivity and the stomach contents (Brafield and Newell, 1961; Reid, 1971). The inhalent siphonal activity by *M. balthica* has been variously recorded as : lying on the mud surface drawing in

food and water (Yonge, 1949b; Vassallo, 1969); groping over the surface leaving star-shaped patterns on the mud surface depending on the mud stability (Segestråle, 1960; Hulscher, 1973); exhibiting a rotating movement with the curled end of the siphon (Hulscher, 1973; and personal observations); and protruding vertically from the mud surface (also personal observations). In the present study, animals were observed under experimental conditions (Section 6.1.) and found to exhibit the latter two types of siphonal activity when covered by water. The rotating siphonal movements were identical to those shown by S. plana (Hughes, 1969b); Abra tenuis, A. alba and A. nitida (Hughes, 1973, 1975); and Macoma nasuta (Hylleberg and Gallucci, 1975); and were found to stir up the surface silt, detritus and diatomaceous layer which was then inhaled at the sediment/water interface, thus providing a crude suspension-feeding sorting process.

The animals were observed to suspension feed only after the water in the experimental tanks (see Section 6.1.2.1.) had been changed, a process which stirred-up detritus, etc. from the mud surface. Once this material had settled no suspension-feeding was observed. Bubnova (1972) also found that Macoma would filter feed when suspended material was present in the water layer above the bottom but that it would not stir-up the bottom mud if suspended material was absent. De Wilde (1975) found no suspension-feeding by his experimental animals but did not attribute this to the fact that his animals were in filtered seawater. Morton (1970) found that the formation of digestive tubules in Macoma followed a tidal rhythm preventing the animals from feeding during periods of low tide; he subsequently suggested that the processes of feeding and digestion are correlated with

the tidal rhythm and that (following Brafield and Newell, 1961) Macoma is therefore a suspension feeder with deposit-feeding playing a small, if any, part in the animals' nutrition.

The star-shaped patterns observed by Hughes (1969b) and Hulscher (1973) were not evident in the experimental tanks of either this study or that of De Wilde (1975); the latter attributes this to the occurrence of interstitial feeding by the bivalves (as Hughes, 1969b) although it is possible that feeding marks would not remain in many types of fine and coarse sediment.

When the experimental tanks were uncovered by water, siphonal activity was observed only in fine sediment which had a high water content. The animals inhalent siphons lay over the mud surface (as described by Yonge, 1949b for Tellina tenuis and M. balthica; and by Green, 1957 for S. plana) and sediment was both inhaled with the water film on the sediment and occasionally ejected as pseudofaeces through the inhalent siphon. In all cases the shorter exhalent siphon was observed to be within the substrate. It is unlikely, however, that the inhalent siphon would be exposed in the natural habitat during phases of the tidal cycle when predation may occur (Hughes, 1969b).

Therefore, M. balthica may either deposit or suspension feed depending on the tidal cycle and type of sediment. It may change its mode of feeding when other food sources increase in quantity or quality (Newell, 1965; Standley, 1970), an adaptation possibly ensuring a more continuous food availability and contributing to the success of the species (Myren and Pella, 1977). Deposit feeders have the advantage of longer feeding (over the tidal cycle and the year) (Lammens, 1967) whereas suspension feeders have a constantly renewed food supply thus

overcoming the need for locomotion, as in M. balthica (Braithwaite and Newell, 1961), to exploit new areas. Tunnicliffe and Risk (1977) found that M. balthica can fulfil its whole carbon requirement but only one fifth of its protein requirements by deposit-feeding and suggest that the species must suspension feed to some extent. However, these authors appear to confuse the sediment nitrogen and protein contents and the recalculation of their data indicates that the animals can obtain sufficient protein from the sediment (see below). It is possible therefore, but not known, whether M. balthica, as the related Tellina salmonea, will function as a suspension feeder in coarse sediment and a deposit feeder in fine sediment (Maurer, 1967). When compared to more conventional suspension-feeding tellinids, M. balthica has large palps in relation to the gill area and a modified stomach, both adaptations enabling the species to ingest large amounts of material (Yonge, 1949b; see also Hughes, 1975). It may be hypothesised that, if the mode of feeding does vary with substrate type (as does shell shape, flesh condition, shell weight, growth, etc.) then the internal anatomy (as palp and gill ratio) may also vary; this subject would benefit from further study.

M. balthica may therefore fall within many feeding categories suggesting that it is not possible, or in some cases desirable, to assign such a species to single or definite trophic levels within the food web. It may be repeated that it is this life-style which contributes to the success of the species within the estuarine environment.

The food of M. balthica has been identified as microphyto-benthos, diatoms, microfloral-rich detritus, plankton, bacteria,

dinoflagellates and even dissolved organic material (see above authors together with Hunt, 1925; Wernstedt, 1943; and Beukema et al, 1977). Fenchel (1972) found a reduction of 95% in bacteria, 100% in protozoa and 50-70% in diatoms after sediment had passed through the animals alimentary systems, and also that while the main food item particle size was <50µm, particles up to 300µm could be taken. M. nasuta was found to reject up to 97% of intaken sediment before it reached the stomach by discarding large particles and small particles not rich in organic matter (Hylleberg and Gallucci, 1975). Hughes (1973, 1975) showed that Abra spp. can discriminate against clean (uncolonised) particles and that whilst the particle size range taken by deposit-feeding tellinids is critical some modification of the sediment by grinding is possible (see also Yonge, 1949b).

The importance of bacteria in converting low-value plant and animal carbonhydrates (lignin, cellulose, chitin) to high protein microfloral biomass suitable for feeding by M. balthica has been demonstrated (e.g. Newell, 1965; Tunnicliffe and Risk, 1977; see also Section 2.5.). Tunnicliffe and Risk (1977) suggest that deposit feeders may be supported to a lesser or greater extent by bacteria in the sediment and that the abundance of M. balthica in particular may be predicted by the bacterial abundance. It is generally considered therefore that the microfloral component of the sediment together with the detrital component will have a greater or lesser influence on the feeding of this species; the feeding biology of the species can therefore be associated with the sediment carbon and nitrogen content (see Section 3.5.5.).

Using the following data regarding the assimilation and food requirements of M. balthica : a 12-14mm long animal processes

0.6g dry sediment per day, assimilates 70% of the organic matter and 62% of the protein and requires 2.44mg organic matter and 0.78mg protein per day (Bubnova, 1972; Tunnicliffe and Risk, 1977); together with the conversions : organic matter \equiv 1.8 x organic carbon (Tunnicliffe and Risk, 1977) and protein \equiv 6.25 x nitrogen (Crisp, 1971), the levels of food availability on Torry Bay may be calculated :-

Using average, summer sediment values (assuming all carbon and nitrogen is organic) :

Low-shore fine mud station 6.5%C \equiv 11.7% org. matter.

0.4%N \equiv 2.5% protein.

High-shore coarse sand station 1.0%C \equiv 1.8% org. matter.

0.05%N \equiv 0.31% protein.

Therefore, at the former stations, such an animal (12-14mm long) could obtain 49.14mg organic matter and 9.3mg protein per day, whereas at the latter stations only 7.56mg and 1.15mg respectively, all values are in excess of the requirements. Similarly, in order to provide insufficient food a sediment would have to contain 0.32% carbon and 0.034% nitrogen. Only at Stations C3, C4 and B4 were these values encountered and while at the latter two stations the animals growth rates and condition reflected the poor nutritive conditions (see Sections 3.4.2. and 3.4.3.), at Station C3, where there was a much greater immersion period, the animals were not greatly affected and may have supplemented their diet by suspension-feeding.

It is also considered that the amount of sediment processed will vary with both station, depending on the fine particle content, and age of the animals, as young animals can process

small organically rich particles more efficiently than older animals (Bubnova, 1972). The basic assumption used above regarding the sediment processed daily by a standard animal will therefore not be valid for some areas of Torry Bay. In addition, the bulky, well fed low-shore animals (of higher condition - see Section 3.5.4.1.) would have a higher food requirement for maintenance (Needham, 1964) as well as for growth (see Section 3.5.2.1.) when compared to the high-shore animals. These conclusions do not incorporate consideration of population density which because of the individuals' mobility will be important, e.g. a large area with low food availability may support a small mobile population. It is evident that the feeding requirements of this species warrant further study.

6.3. Pollution Studies.

6.3.1. Introduction.

Much of the work in Chapter 3 indicates that, when compared to other areas, the Forth estuary M. balthica population had an inferior growth, condition and production which was not wholly attributable to the differences in the major environmental factors experienced in the area. In the industrialised Forth estuary, it is possible that pollutants acting either independently or synergistically, may be a cause of that retarded productivity. A short study was therefore made on the heavy metal content of the animals and sediments in Torry Bay.

The choice of heavy metals as an indication of the severity of pollution was based on the ease of their analysis and on the knowledge that such pollutants occur in the estuary and were the subject of a comparable study on the filter-feeding M. edulis (Davies and Pirie, 1978).

The study had the aims :

(i) to obtain animal and sediment heavy metal concentrations and to make comparisons with other data both intertidally and geographically;

(ii) to obtain animal flesh metal contents such that estimates of uptake rates by predators may be made; and

(iii) to obtain some information regarding the accumulation of metals by the animals with increasing size and weight.

Previous work (e.g. Pringle et al, 1968) has shown that as the aquatic fauna is usually exposed to small amounts of pollutants over very long periods, it is the accumulation of these and the

effects of that accumulation that are more important than acute toxicity testing. This is especially important as molluscs, and bivalves in particular, can concentrate materials by up to several orders of magnitude of those found in the environment (e.g. Pringle et al, 1968; Bryan, 1976; Boyden, 1977).

An element may be regarded as being toxic when it impairs the growth, reproduction or metabolism of an organism when supplied or accumulated above a certain concentration. In the present study five elements (Fe., Zn., Cu., Pb., Cd.) were measured in animals and sediments. The first three, as micro-elements, are necessary in animals as enzyme activators. Copper is found in haemocyanin in the haemolymph of certain molluscs, zinc is essential for growth and iron is found in cytochrome systems as porphrin-based iron as well as in haemoglobin (Pringle et al, 1968; Naidu and Seymour, 1969; Newell, 1970). The blood pigment in Macoma, if any, is unknown; haemoglobin may be present in the haemocoel and/or the muscles and nervous system (Read, 1966) and although haemocyanin is present in a few bivalves it is not known whether M. balthica is one of those (Ghiretti, 1966; Morton, 1967; Newell, 1970). The latter two metals, although occurring naturally at high levels, are toxic at very high levels; and copper, although necessary at low levels, is toxic at only slightly higher levels. The metals lead and cadmium have an obscure biochemical role, if any, but both are probably enzyme inhibitors and are considered to be toxic at all levels (Jones, 1973; Darracott and Watling, 1975; Bryan, 1976). It is unclear what levels of heavy metals are normally present and the role and effect of high levels within the species. In addition, several of the metals may synergistically produce greater toxicity with

other metals, and extreme temperatures and salinities (Pringle et al, 1968; Romeril, 1974; Jones et al, 1976). Pringle et al (1968) placed heavy metals in four groups depending on their pollution potential; the metals Cd., Cu., Pb., and Zn. were assigned to the first group (a very high pollution potential) while iron was considered to have a high pollution potential (group 2).

6.3.2. Materials and Methods.

Seven animals were obtained from each of the Stations B3 and C4 in March, 1976 and kept in filtered seawater for six hours to evacuate their guts. The animals, covering the species size range at those stations, were measured and their flesh dissected from its shell. Both shell and flesh were then washed in deionised water, oven dried, weighed and then digested under reflux in 10ml boiling, Analar reagent concentrated nitric acid. After complete digestion the samples were cooled, diluted to 25ml with deionised water and aspirated through a Perkin-Elmer model 103 atomic-absorption spectrophotometer. The metal levels of two 1.0g air-dried sediment samples from each station were also obtained after ionic-exchange extraction using neutral ammonium acetate. The extraction could have been more accurately performed using ammonium acetate which had been buffered to the pH of the animals alimentary system if the latter pH had been known.

6.3.3. Results.

The sediment metal levels suggest that only small amounts of the metals are present in a readily exchangeable ionic form on the active surface sites of clay and organic colloidal particles under neutral pH conditions (see also Halcrow et al, 1973). The larger values of zinc and cadmium in the B3 sediment may reflect the larger number of fine particles with a larger surface area/volume ratio in that sediment although this is not shown with the other metal levels, (Table 6.16).

Table 6.16 The Sediment Metal Levels (as ppm dry weight).

Station \ Metal	Fe.	Zn.	Cu.	Pb.	Cd.
C4	1.2	0.7	1.5	ND	ND
	1.1	0.7	1.7	ND	ND
B3	1.1	1.1	1.5	ND	TRACE
	0.9	1.8	1.7	ND	TRACE

ND = non-detectable

The amount of a heavy metal within an organism can be expressed either as a concentration, i.e. as a relative amount per unit weight, or as the content, the total amount within the organism. The relationship between each of these and the size of the animal gives an indication of the rate of accumulation of the metal (Fig. 6.23 (a)-(j), data given in Appendix 6.11). Only statistically significant relationships are discussed (from the regression equations in Appendix 6.12).

A major criticism of heavy metal analysis using the atomic absorption spectrophotometer is the measurement of very low levels of some metals which may be outwith the sensitivity of the

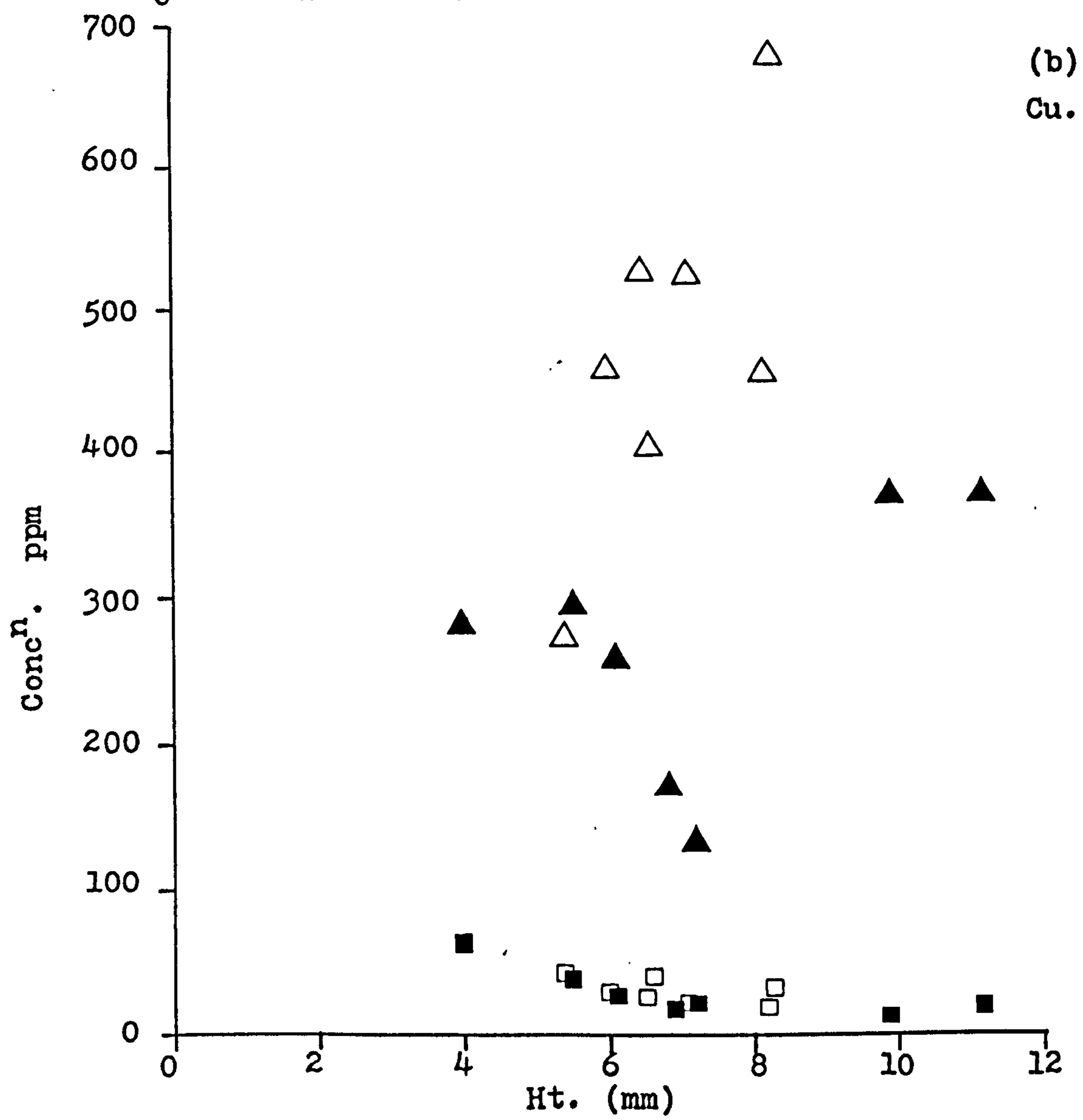
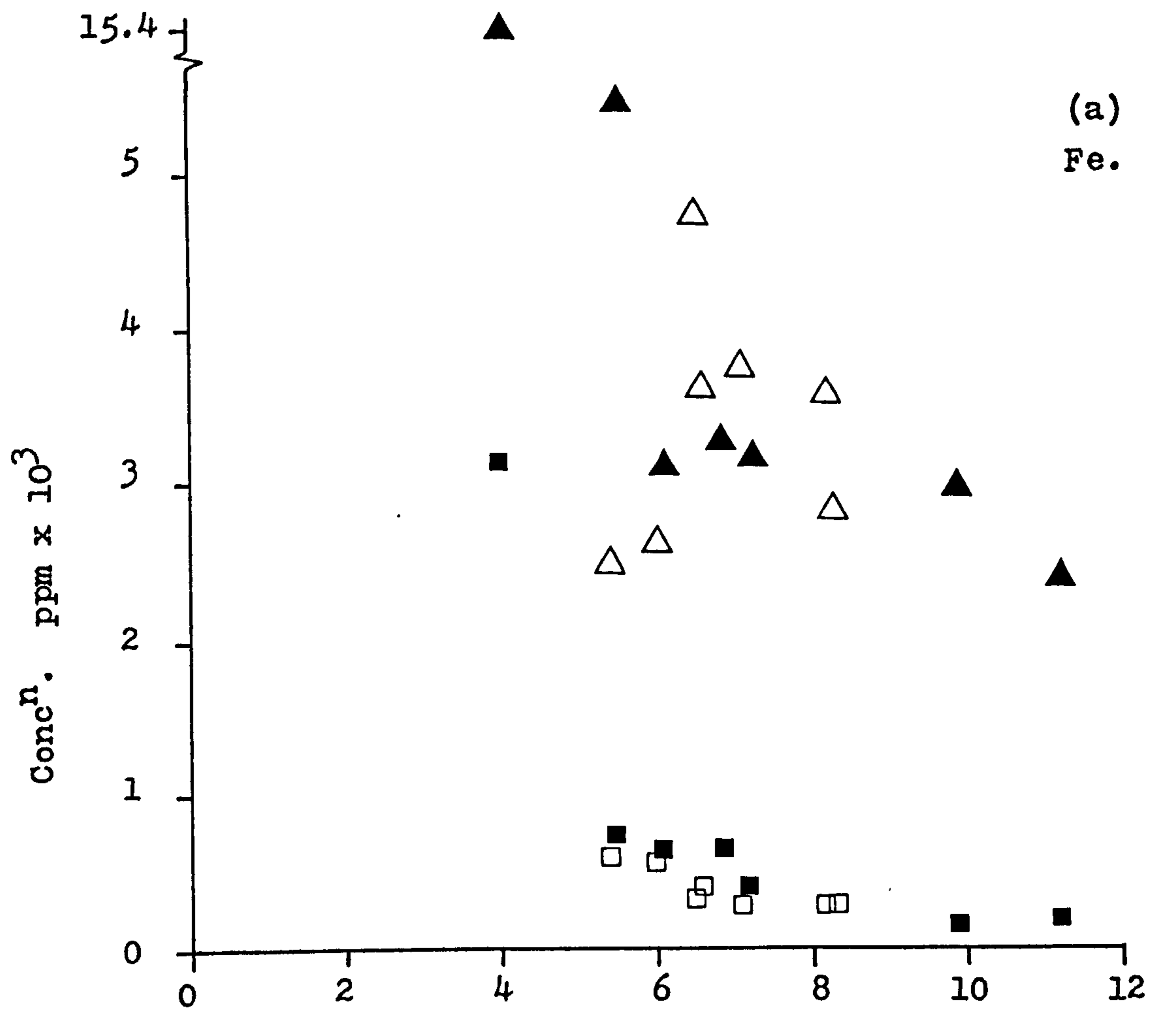
Figure 6.23 Heavy Metal Analyses :

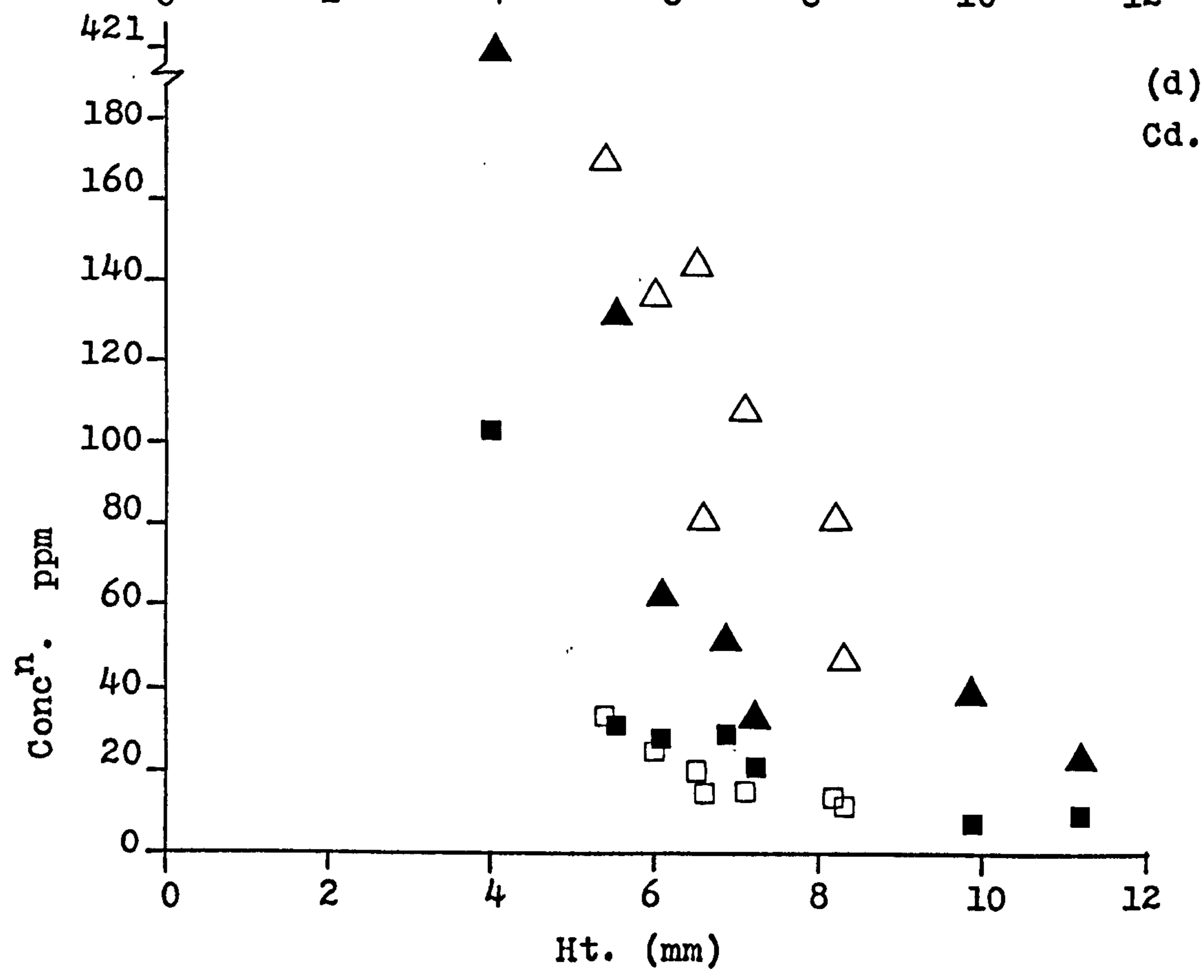
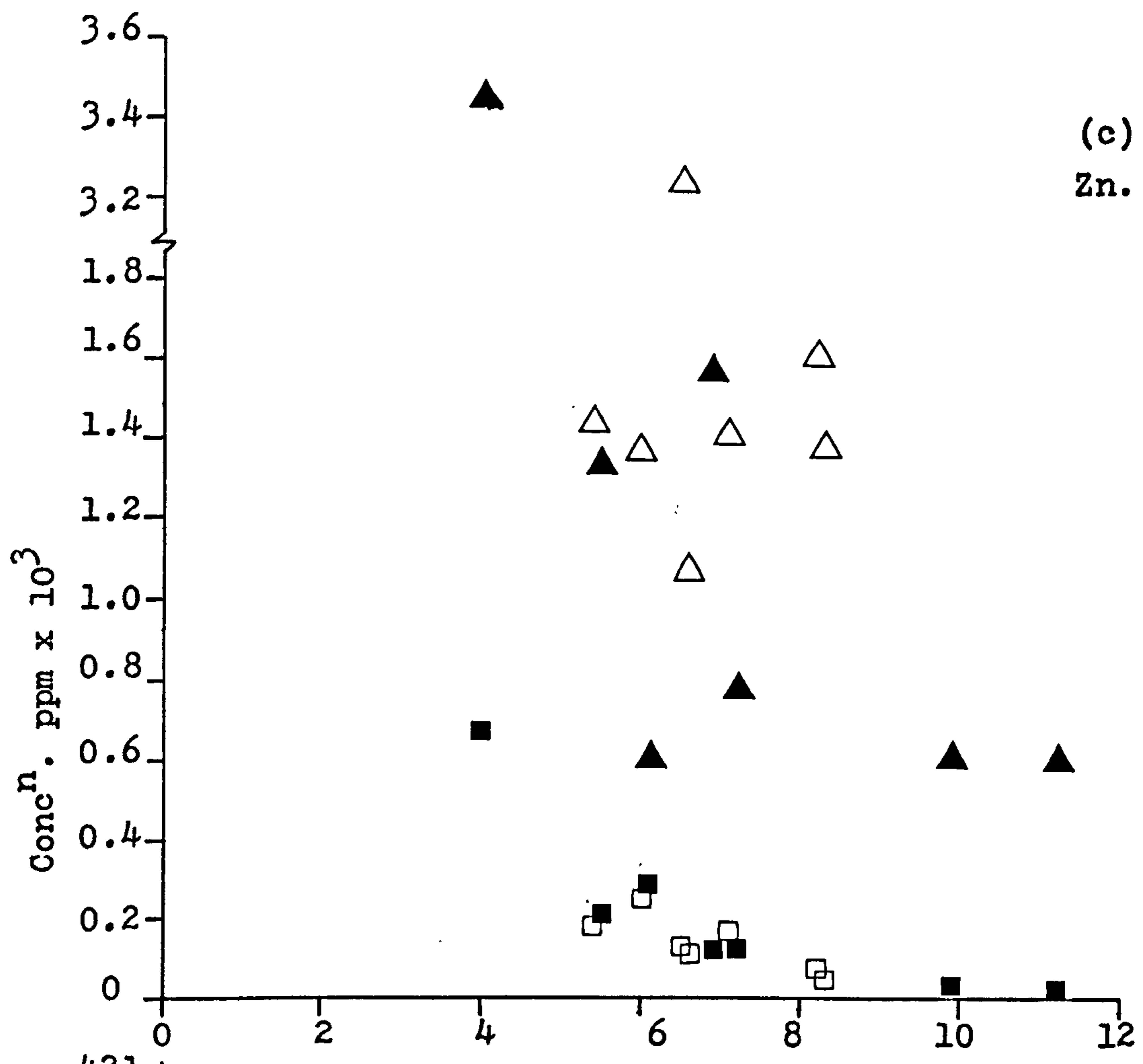
(a - e) The Change in Flesh and Shell
Metal Concentration With Shell Height.

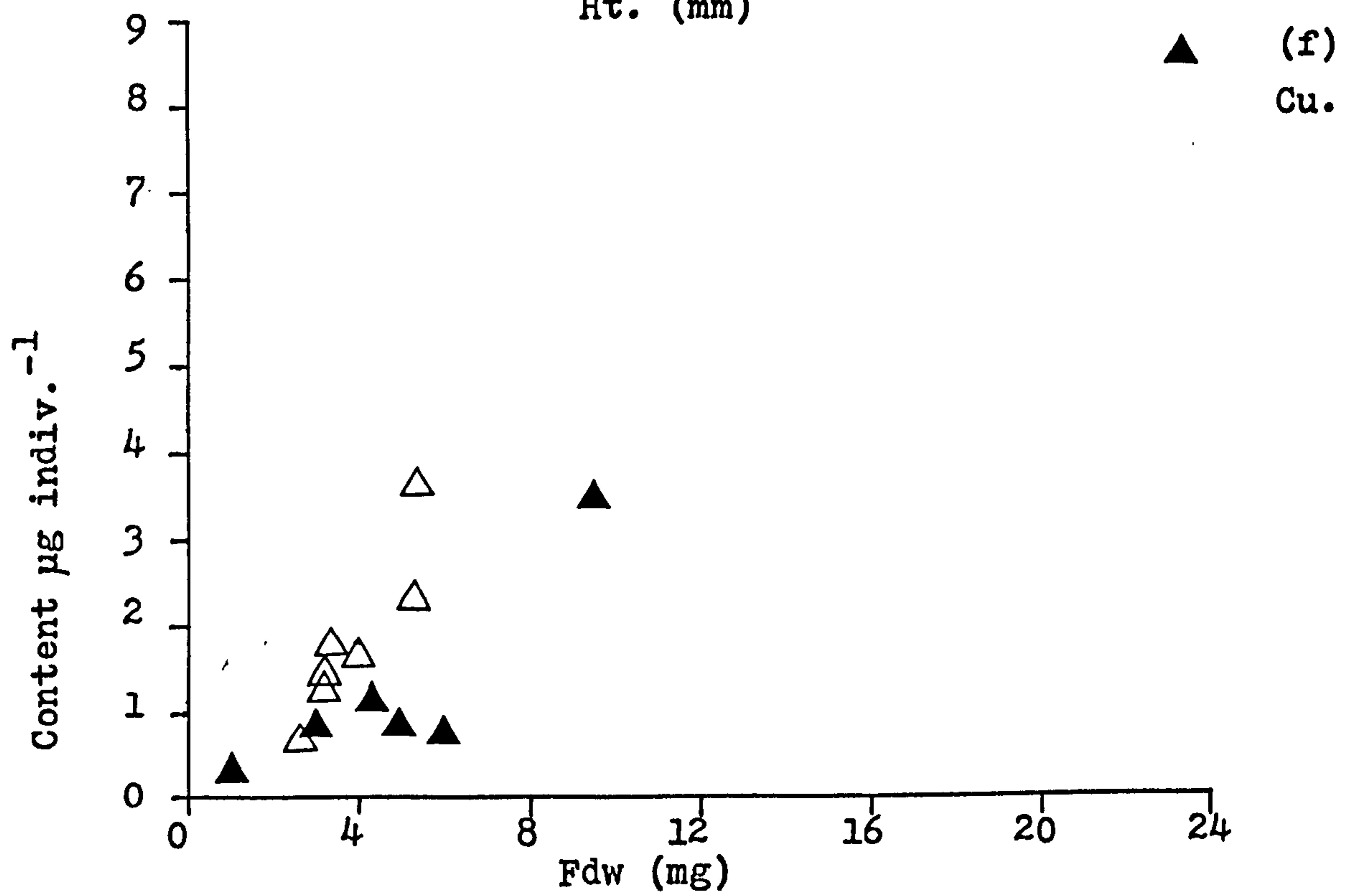
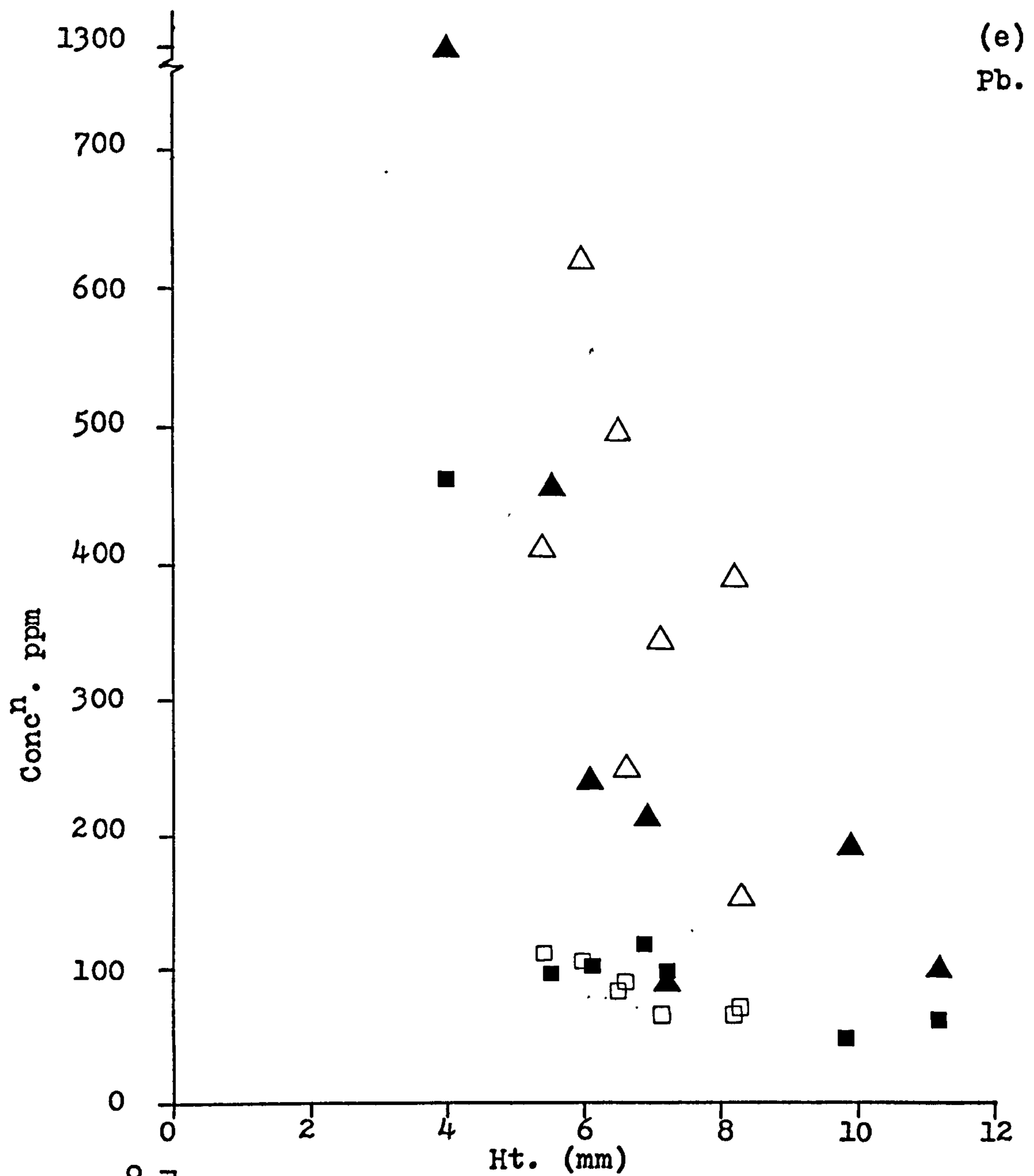
(f - j) The Change in Flesh Content
With Flesh Dry Weight.

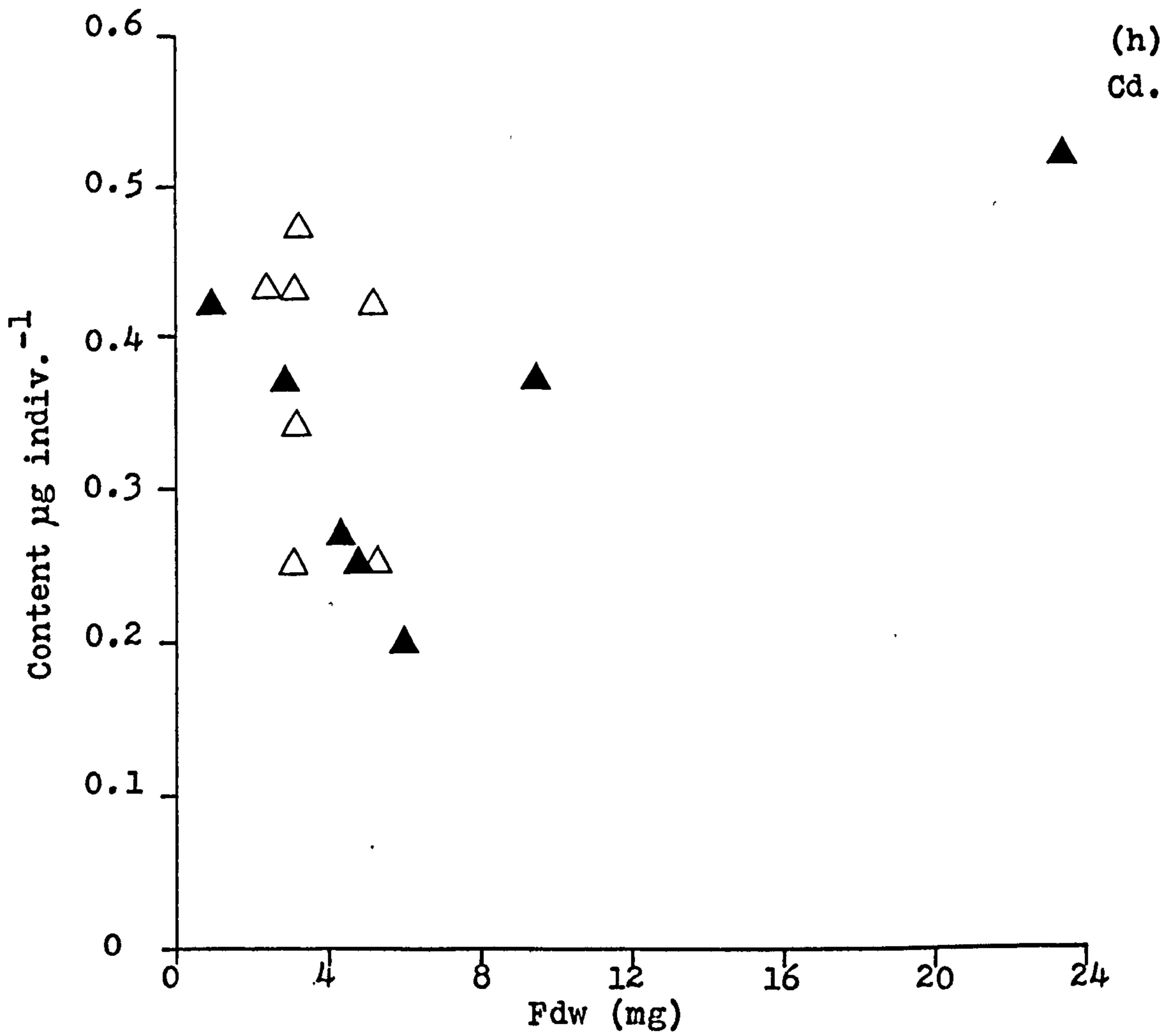
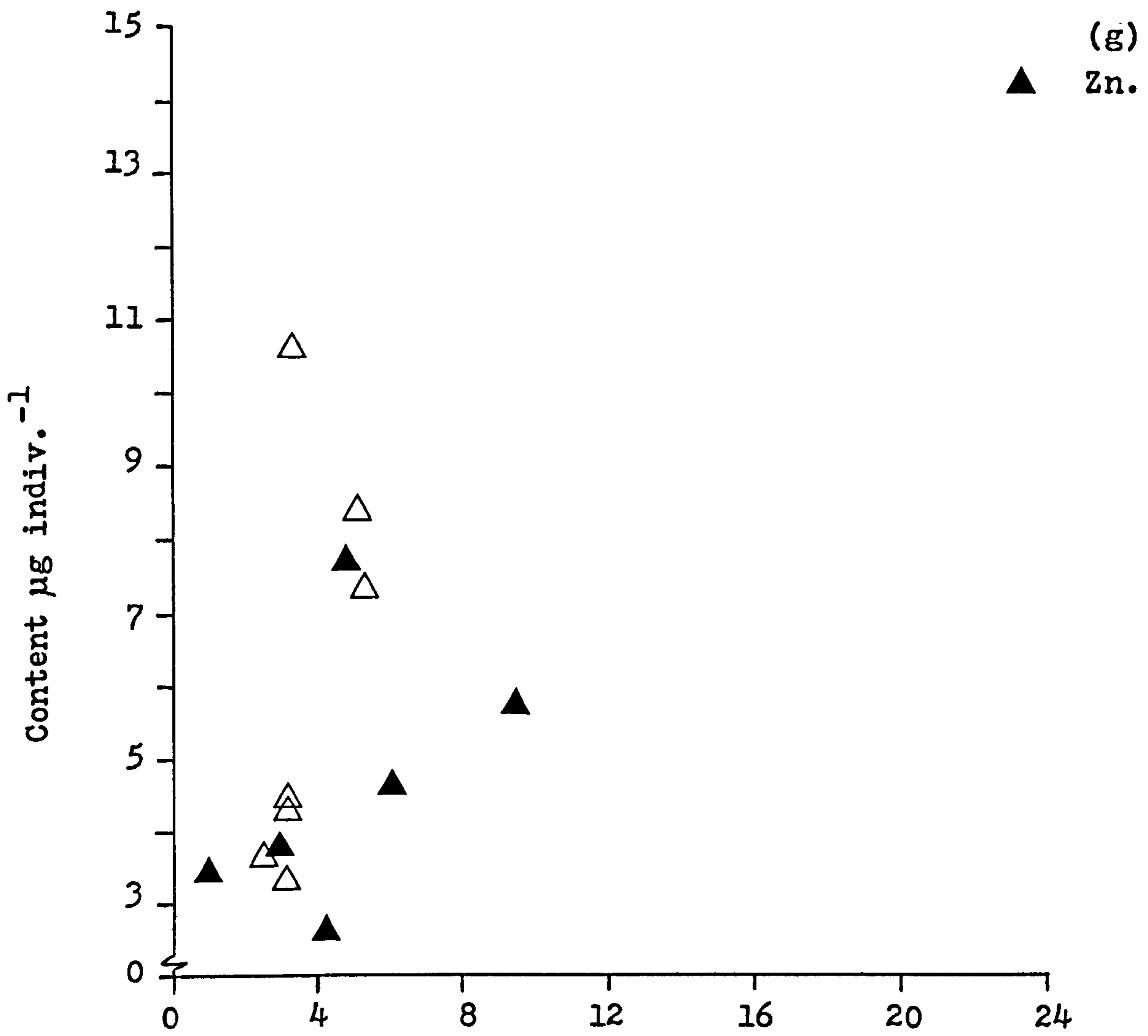
Legend.

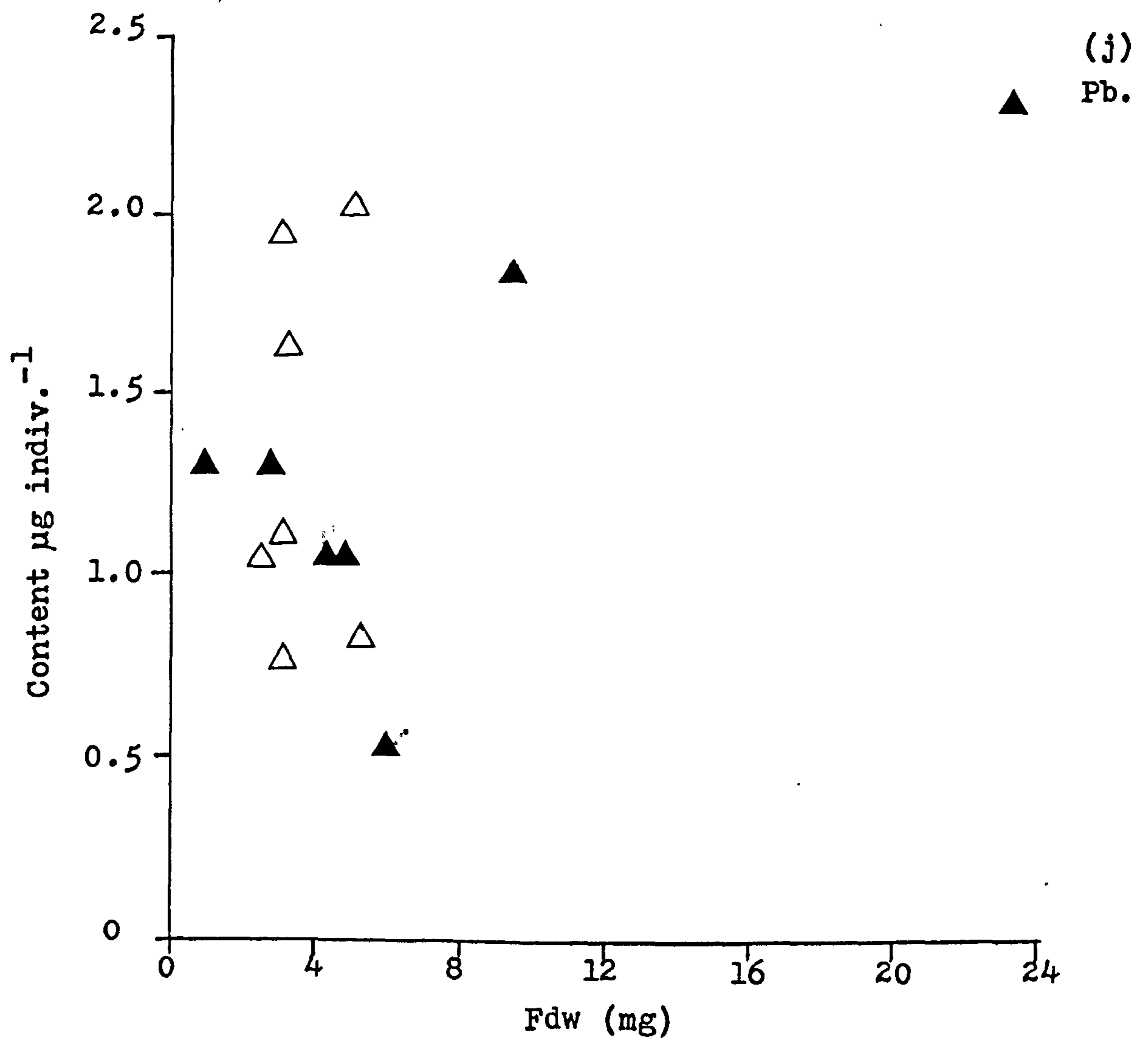
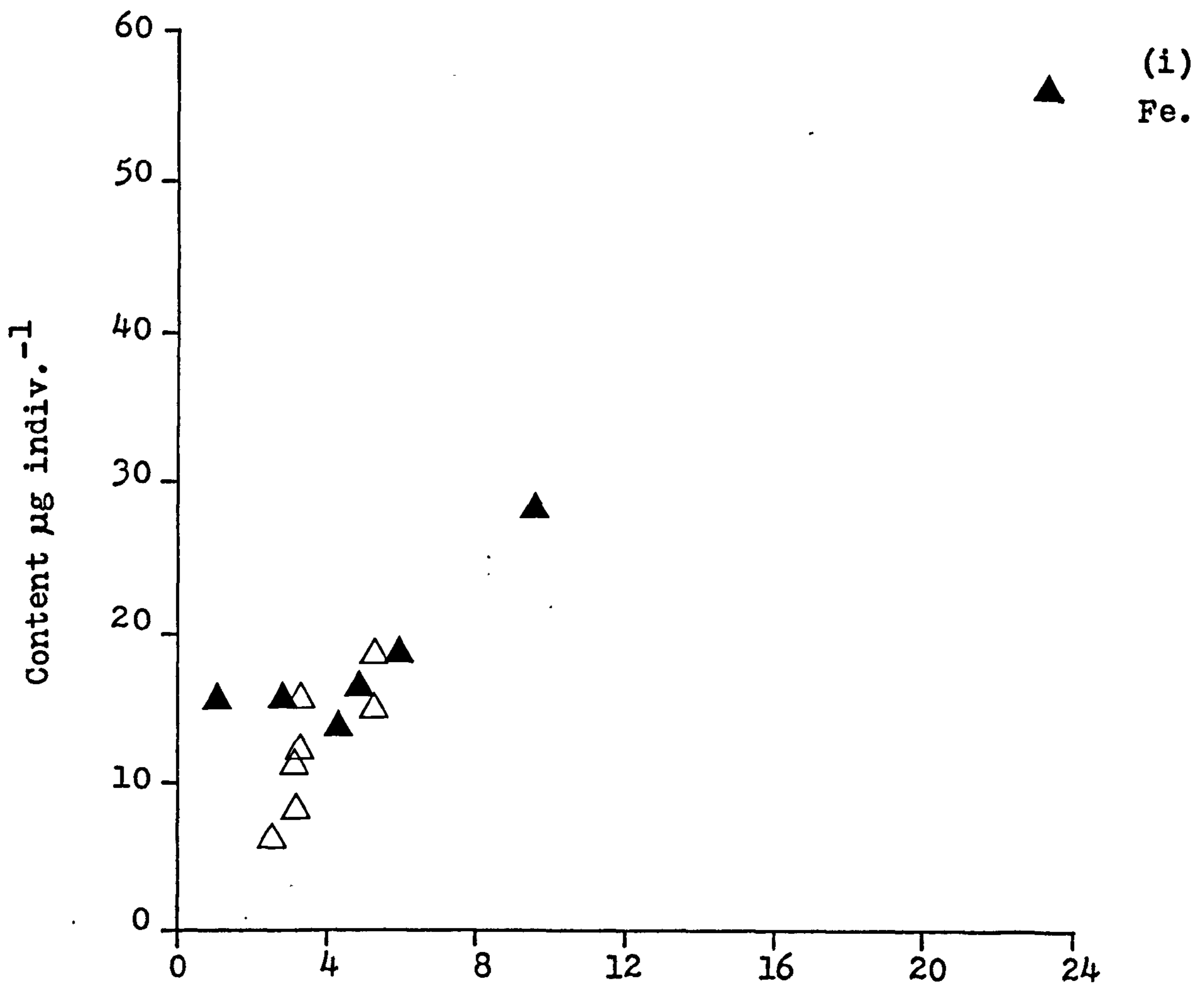
- ▲ Station B3 Animals Flesh
Concentration and Content.
- △ Station C4 Ditto.
- Station B3 Animals Shell
Concentration.
- Station C4 Ditto.











machine used for the analyses (I.M. Davies, pers. comm.). Pringle et al (1968) and Davies and Pirie (1978) give machine detection limits for the metals under consideration (Table 6.17). The detection limit of 0.1ppm is regarded as normal for the Perkin-Emler 103 machine although for certain metals this limit may be lower (W.R. Johnston, pers. comm., and cf. the sensitivities given in Table 6.17). The levels recorded for the metals copper and cadmium therefore may be near to the detection limit for the machine and should be regarded with caution.

On a linear basis, the shell concentrations of Zn., Cu., and Cd. at Station B3 decreased only with an increase in shell height whereas at Station C4 the shell concentration of Fe., Zn., Pb., and Cd. decreased with an increase in shell weight and height. There was also an inverse relationship between the flesh cadmium concentration and the height and flesh weight at Station C4.

On a double-logarithmic basis, the flesh concentration of Cd. at C4 and Fe., Zn., Pb., and Cd. at B3 decreased with increasing flesh weight. There was also an inverse relationship between the shell weight and the shell concentration of Fe., Zn., Pb., and Cd. at C4 and all metals at Station B3. The flesh Fe. and Cu. content increased with increasing flesh weight at C4 and the flesh Fe., Cu., and Zn. content similarly increased at B3. The logarithmic regression coefficients (b-values) (Appendix 6.12) may be compared for the two stations ; the flesh iron content b-values were 1.063 at C4 and 0.420 at B3; this suggests that the content increased uniformly with flesh weight at the former whereas at the latter station the uptake decreased with time. Similarly the flesh copper content b-values were 1.683 at C4 and

Table 6.17 Heavy Metal Analyses : (a) The Sensitivity and Detection Limits of the Atomic Absorption Spectrophotometer Used in This Study in Comparison with Data Given by Other Workers; (b) The Range of Detection Levels Recorded in the Present Study.

Metal	Sensitivity		Detection Limits (ppm)		Range of Detection Levels		No. of Specimens Analysed Below Detection Limit	
	* ₁	* ₂	* ₃	* ₄	Flesh	Shell	Flesh	Shell
Cd.	0.25	0.04	0.01	0.03	0.02 - 0.05	0.03 - 0.14	14	11
Cu.	0.10	0.20	0.005	0.02	0.03 - 0.86	0.03 - 0.26	4	8
Fe.	0.10	0.30	0.05	-	0.64 - 5.64	0.82 - 2.82	0	0
Pb.	0.50	0.50	0.15	0.3	0.05 - 0.23	0.10 - 0.89	3	0
Zn.	0.50	0.04	0.005	0.4	0.33 - 1.42	0.22 - 0.85	0	0

*₁ ppm per 1% absorption on Perkin-Elmer 103 used in Present Study.

*₂ " " " " Pringle et al (1968).

*₃ data from " " " "

*₄ " " " " Davies and Pirie (1978).

1.009 at B3, i.e. whereas at the latter station the uptake rate was constant, at C4 there was a greater uptake at the larger sizes. At Station B3 the flesh zinc content b-value was 0.438, i.e. the uptake decreased with time, but at Station C4 there was no significant relationship.

The figures show little difference between the two stations for the majority of metals, contents and concentrations (Fig. 6.23 (a)-(j)). However, for a certain size the C4 animals had elevated zinc and cadmium flesh concentrations (cf. those of B3), this may be an indication of the differential growth and state of emaciation between the sites (Fig. 6.23 (c),(d)).

In considering all data, the shell concentration of all metals and the flesh concentration of all metals except copper decreased linearly with increasing height. The significance of these relationships was increased when the data were logarithmically transformed. The direct logarithmic relationships between flesh iron, zinc and copper contents and the flesh weight gave b-values of 0.541, 0.441, 1.009 respectively; these values suggest a decreasing uptake with size in the former two metals and a constant uptake of copper with time.

In comparing the mean heavy metal values of the two stations, the B3 animals had higher values of mean shell concentrations of iron, zinc and cadmium, mean flesh concentrations of iron and mean flesh contents of iron and copper than those of C4 (Table 6.18a & b). However, many of these differences may be attributable to the larger size range of animals analysed from the former station as shown by the large coefficients of variation of the mean values. It may also be invalid to compare

Table 6.18 M. balthica Heavy-metal Analysis: (a) The Mean Flesh and Shell Concentrations (ppm dry weight);

(b) The Mean Flesh Contents (μg) of Each Metal, with the Mean Condition Factor.

Parameter	Station C4 Animals			Station B3 Animals			Total Animals		
	\bar{x}	S.E. of Variation	Coefficient	\bar{x}	S.E. of Variation	Coeff.	\bar{x}	S.E. of Variation	Coeff.
(a) Shell concentration	390.9	52.8	35.71	848.6	393.4	122.65	619.7	200.9	121.33
Flesh	3372.3	299.0	23.46	5145.4	1774.2	91.23	4258.9	898.6	78.95
Shell	140.6	26.4	49.68	211.3	86.1	107.77	175.9	44.3	94.31
Flesh	1647.0	272.8	43.83	1281.9	391.2	80.75	1464.4	234.7	59.95
Shell	30.9	3.3	28.65	28.4	6.4	60.07	29.6	3.5	44.27
Flesh	472.4	47.1	26.40	266.0	34.3	34.14	369.2	40.0	40.58
Shell	74.7	13.2	46.78	141.3	54.4	101.88	108.0	28.4	98.51
Flesh	380.3	57.7	40.17	370.6	162.0	115.65	375.4	82.6	82.34
Shell	18.7	2.9	41.09	32.6	12.2	99.03	25.7	6.3	92.35
Flesh	109.0	16.2	39.33	108.4	53.7	131.21	108.7	27.0	92.84
Flesh Condition Factor	11.606	1.067		15.604	1.098		13.605	0.921	
(b) Flesh content	12.42	1.62	34.46	23.49	5.78	65.13	17.96	3.27	68.10
"	6.03	1.05	46.27	6.04	1.50	65.89	6.03	0.88	54.73
"	1.82	0.35	51.65	2.27	1.13	131.28	2.05	0.57	104.39
"	1.34	0.20	38.81	1.34	0.22	43.28	1.34	0.14	39.55
"	0.37	0.03	24.32	0.34	0.04	32.35	0.36	0.03	27.78

such mean values as in none of the corresponding pairs of data were the $\text{Log}_{10} \text{conc}^n / \text{Log}_{10} \text{fdw}$ or $\text{Log}_{10} \text{content} / \text{Log}_{10} \text{fdw}$ regressions non-significant (Appendix 6.12).

The mean shell copper concentrations, lead and cadmium flesh concentrations and zinc flesh contents were similar in the animals of both stations, and the mean flesh zinc concentration in C4 animals was greater than in B3 animals although in each case the pairs of data gave significant double-logarithmic regressions. The mean flesh copper concentration in C4 animals was greater than in B3 animals and the mean flesh cadmium and lead contents were similar in both stations' animals. Each of these relationships had both double-logarithmic regressions that were non-significant suggesting that the conclusions reached regarding the mean values from such relationships are valid.

6.3.4. Discussion.

The methods of uptake of heavy metals are : particulate ingestion by suspension- or deposit-feeding; ingestion following pre-concentration in food material; the association of heavy metals with organic molecules and the incorporation of metals into physiological systems; and the uptake by exchange and mucous membranes (Pringle et al, 1968; Bryan, 1976). As many of the activities by the molluscs may decrease with age then the rate of uptake may also decrease. However, heavy metals have been found to impair or destroy the gills' capacity to perform gaseous exchange; this would lead to an increase in respiratory action which may in time increase the rate of uptake (Pringle et al, 1968).

The animals flesh metal levels did not reflect the small change in available sedimentary metals between the stations but they did, to some extent, reflect the differential growth and condition between Stations C4 and B3. The higher flesh levels of zinc and cadmium in C4 animals than B3 animals for a given size was a reflection of the lower condition and slower growth at the former station. Seasonal differences, in flesh condition and the annual reproductive cycle, and spatial differences in growth have been shown to influence heavy metal concentrations; the highest concentrations occurring at times of greatest emaciation irrespective of whether that emaciation was due to low temperatures and food availability or to spawning (Romeril, 1974; Frazier, 1975; Boyden, 1977). It is likely, however, that the content will increase over the year with the occurrence of flesh growth unless, as suggested by Frazier (1975), metal loss occurs during spawning. Pringle et al (1968) suggested that the rate of

uptake is related to temperature, salinity, dissolved oxygen, filtration rates and the physiological condition of the animals as well as the environmental level to which they are exposed. The intake rate may therefore decrease over the life cycle as the older animals have a lower metabolic rate.

The overall situation is further complicated by the facts that, firstly, the C4 animals were possibly exposed to less metals as they were tidally uncovered for a longer period and, secondly, B3 was a fine-sediment, depositing environment which increased the availability of certain metals to the infauna. (Halcrow et al (1973) also found that sedimentary heavy metal levels were directly proportional to the amount of small particles within those sediments.) Both of these factors were counteracted by the differential growth, etc., between the areas.

The uniformity of lead and cadmium contents with increasing size, i.e. a decreasing concentration with age, was possibly the result of either metal level regulation or a negligible uptake with increasing age. Boyden (1977) similarly found that the cadmium content in oysters was independent of size even over a large range of environmental concentrations and Leatherland and Burton (1974) found some decrease in flesh cadmium concentration with increasing age in Mercenaria mercenaria. In the present study, the copper, iron and zinc content increased with size while the respective concentrations also decreased with increasing size, i.e. the uptake continued throughout life but not, in the case of iron and zinc, at the same rate as the flesh growth. Romeril (1974) also found that the copper and iron concentrations in M. mercenaria decreased with increasing age whereas the zinc concentration was possibly greater in older

clams; the Cu., Fe. and Zn. contents also increased with increasing age. Bryan and Hummerstone (1977) found that the lead concentration in Mytilus, Cerastoderma and Patella decreased with increasing age but it increased with age in Scrobicularia where the metal was stored in the digestive gland. Boyden (1977) however, does not consider non-significant content/size regressions and so it is difficult to comment on those species where there was no change in metal content with increasing size. In addition, unlike the present study and that of the above authors, Boyden (1977) found that all the 'deduced' regression coefficients of concentration on body weight were not significant, i.e. he found no change in concentration with a size increase, although he does not comment on the relevance of such. The pattern of accumulation of metals by molluscs is therefore considered to vary with the metal, the species and the age of an individual and the type of habitat.

The high, mean flesh concentration values obtained in this study may be compared with other available data (Table 6.19). Specimens of Nereis divericolor from Kinneil Bay (Forth, south shore) were independently analysed for heavy metals by B.P. (Chemicals) Ltd. laboratory, Grangemouth. The mean values calculated are in agreement with those obtained in the present survey and suggest uniformly high heavy metal values within the estuarine Firth of Forth. Other workers have found values which encompass the Forth estuary values. The data obtained by Boyden and Romeril (1974), Bryan and Hummerstone (1977) and Boyden (1977), in comparing both clean and polluted areas, suggests that the Forth values are comparable with other areas which are either

Table 6.19 Comparable Studies of Macrofaunal Heavy-Metal Concentrations, (All levels in ppm dry flesh weight).

Location	Species	Iron	Zinc	Copper	Lead	Cadmium	Mercury	Author
Forth Est. N. Shore	<u>Macoma</u>	4259 ± 898	1464 ± 235	369 ± 40	375 ± 83	108.7 ± 27	-	This Study
" S. Shore	<u>Nereis</u>	-	1193 ± 212	215 ± 31	203 ± 31	102 ± 20	101	B.P. Ltd. Data
Severn Est.	<u>Littorina</u>	-	-	-	-	178	-	Jones et al (1972)
Devon and Cornwall Estuaries	<u>Nereis</u>	-	130 - 350	-	-	0.08 - 3.6	-	Bryan and Hummerstone (1973)
Clyde Est.	Macro-epifauna	-	75 - 8530	20 - 190	2 - 50	0.6 - 18	-	Halcrow et al (1973)
Humber Est.	<u>Macoma</u> Macrofauna	796 - 950 300 - 1850	90 - 125 52.6 - 308	7.0 - 22.0 2.3 - 174	5 - 12 3 - 312	0.46 - 3.8 0.32 - 6.0	-	Jones (1973) "
Severn Est. (Poll.)	<u>Crassostrea</u>	214 - 422	9860 - 35120	1760 - 6480	15 - 17	17 - 43	-	Boyden and Romeril (1974)
Menai Straits (Unpolluted)	"	158 - 800	1830 - 2750	200 - 340	7 - 12	4 - 6	-	"
Southampton Water	<u>Mercenaria</u>	0 - 400	0 - 140	0 - 45	-	-	-	Romeril (1974)
"	<u>Cerastoderma</u>	150 - 1500	50 - 170	-	-	-	-	"
Humber Est.	<u>Nereis</u>	-	-	40 - 109	-	-	-	Jones et al (1976)
Northumberland Coast	Crustaceans	-	96.25 - 284.2	37.8 - 115	-	0 - 39.2	-	Calculated from Wright (1976)
Tyne Est. Mouth	<u>Mytilus</u>	4487	3850	119	1204	35	-	"
Cornwall, Dorset and N. Wales	Molluscs	65.2 - 2594.2	92.2 - 4358.1	6.9 - 642.2	6 - 44.5	1.6 - 716.9	-	Boyden (1977)
Looe Est.	<u>Macoma</u>	502 - 1540	510 - 1160	90 - 615	15 - 61	0.21 - 0.085	-	Bryan and Hummerstone (1977)
Medway Est.	Macrofauna	-	93.8 - 411.6	3.5 - 287.0	0.7 - 33.6	1.4 - 21.0	0.21 - 3.2	Calc. from Wharfe and Broek (1977)
Dorset and Cornwall	<u>Mytilus</u>	91.1 - 228.1	96.8 - 264.5	6.9 - 12.7	14 - 19.0	1.6 - 94.2	-	Boyden (1977)
Inner Forth Est.	"	-	238	17.15	16.94	3.78	1.61	Calc. from Davies and Pirie (1978)

heavily industrialised (with power stations and petrochemical industries) or subject to mining area effluent. Boyden (1977), in studying marine molluscs from polluted areas (in Cornwall; the Severn estuary; Poole, Dorset) and clean areas (in Cornwall; Menai Straits), found zinc, copper and cadmium levels that were much higher in the worst polluted areas than in the Forth estuary, but the levels in the clean areas were very low in comparison to those found in the present study. In addition, while the Forth cadmium levels were comparable to those from a cadmium-enriched area in Dorset, the former were only 15% of those recorded for another cadmium-rich area in the Severn estuary. The maximum values of iron and lead recorded by Boyden (1977), however, were much lower than those in the present study. Davies and Pirie (1978), in analysing M. edulis from around the Scottish coastline, have shown that the inner Forth had the highest levels of pollutants of all areas studied. However, the values measured were considerably lower than in the present survey but, with the exception of cadmium, were comparable to the values found for M. edulis by Boyden (1977) in polluted areas (see Table 6.19). Wright (1976) cites considerably higher levels for M. edulis from a severely polluted area which shows the high variability of metal content within one species.

In all of these studies there is a paucity of data regarding base (clean) levels of metals in marine invertebrates generally and a lack of data regarding deposit-feeding animals. It is considered that, with the exception of oysters, the highest metal concentrations have not usually been encountered in suspension-feeding bivalves despite their remarkable powers of filtration. This may reflect the fact that sediments, especially those in

estuaries, may be regarded as trace element 'traps' (Jones, 1973; Chester and Stoner, 1975); although this is not shown by the sediment metal levels obtained in this study, it is shown by those values obtained for Kinneil Bay as total concentrations following acid digestion (see Table 6.20). Those total values were comparable to other total values from polluted areas while the extractable values obtained in the present study were also in agreement with those found by Halcrow et al (1973).

Halcrow et al (1973) found that the epifaunal metal levels were unrelated to either the total or readily extractable sediment trace metals. However, Bryan and Hummerstone (1973) found that the cadmium and zinc levels in Nereis diversicolor increased directly with the respective sediment levels, and Romeril (1974) found a high correlation between the sediment and Mercenaria mercenaria zinc levels although other metal levels were correlated with the clam levels to a lesser degree. The relative importance of extractable or total sediment metal levels in relation to the uptake by sediment feeders is unknown and therefore warrants further study, especially as metals within the water column adsorb to particulate matter and may settle out of suspension within a day or so of liberation into an estuary (I.M. Davies, pers. comm.).

The presence of high levels of metals within organisms from polluted areas in causing mortality is possibly not as important as the rate of uptake of those metals or the levels to which the animals are exposed (McLusky and Phillips, 1975; Jones et al, 1976). Exposure to high levels over long periods of time may result in either the non-function or death in molluscs although

Table 6.20 Comparable Studies of Sediment Heavy Metal Concentrations, (All Levels Corrected to ppm Dry Weight) Where

T = Total Extractable Levels and E = Ammonium Acetate Extraction Levels.

Location	Iron	Zinc	Copper	Lead	Cadmium	Mercury	Author
Forth - Torry (E)	1.07	1.11	1.60	N.D.	Trace	-	This Study.
Forth - Kinneil (T)	-	271	95	97	16	6.4	B.P. Data.
S.W. Estuaries (T)	-	27-2980	-	-	0.2-9.3	-	Bryan and Hummerstone (1973).
Clyde (T)	-	40-300	5-39	19-87	0-4.0	-	Halcrow et al (1973).
Clyde (E)	-	0.2-1.0	0.1-0.3	0.4-1.1	-	-	Halcrow et al (1973).
Humber (T)	10000-35000	100-550	0-140	0-300	0-7	-	Jones (1973).
Solent (T)	-	115-225	-	-	0.55-0.69	-	Leatherland and Burton (1974).
Solent (T)	6.3-29.8	63.3-222.5	20.8-88.2	-	-	-	Romeril (1974).
Severn (Polluted) (T)	45,000	280	38	119	-	-	Chester and Stoner (1975).
Severn (Unpolluted) (T) Near Shore Sediments	60,000	95	48	20	-	-	Chester and Stoner (1975).

they do to some extent have the ability to regulate or detoxify the metals. The rapidity at which they can do this, survival permitting, is dependent on the concentration to which they are exposed and on their metabolic rate (Pringle et al, 1968).

Pringle et al (1968) found a direct relationship between the rates of uptake and depletion of metals in estuarine suspension-feeding molluscs while Boyden (1977) suggested that the zinc concentration at least may be partly controlled and is not entirely dependent upon environmental concentrations.

Detoxification, as an explanation for the occurrence of the high metal levels encountered in organisms, has recently been shown to be widespread (Coombes and George, 1978) with many organisms possessing the ability to store metals in granular form in membrane-bound vesicles within the cell; this detoxifies the metal until elimination. Bryan (1976) cites widespread evidence for the excretion of metals as particles and granules by marine bivalves. A possible regulation of metal levels has been indicated in the present study by the decreasing concentration with increasing size.

Although not shown by the present limited survey, the regulation of 'normal' heavy metals, i.e. those metals of importance to an organism (e.g. Cu., Fe. and Zn.) may be widespread in marine organisms as the animals would have established mechanisms for utilizing, tolerating or excreting such metals. The levels of non-essential metals, e.g. lead and cadmium, may be less-well regulated as they are totally foreign to the organism (Bryan, 1976) and may therefore affect the animals' physiology to a greater extent. The effect of high concentrations of such metals on the growth, production and condition

has not been demonstrated although those high levels may be responsible, together with other pollutants, for the reduced growth and poorer productivity of deposit-feeding estuarine bivalves.

Chapter 7. General Discussion.

7.1. Population Characteristics.

Although the five species of molluscs studied occupied different ecological niches within the intertidal environment, many characteristics were common to all of the populations. Whilst having short, definite reproductive phases, all of the species showed gamete leakage over the remainder of the year, i.e. spat were present, to a lesser or greater extent, at all times of the year. However, the time of spawning influenced the survival of an individual; spat which settled either before or during the growing season were larger by the following winter than those which settled later in the year and therefore more able to survive the winter. The winter size, of M. balthica especially, may influence the success in avoiding predators, which are largely abundant throughout the winter, by enabling the animals either to burrow deeply or to be outwith the size range taken by certain predators (see Section 7.3.2.).

The successful settlement of marine infauna involves the successful completion of three phases : firstly, the spawning phase with an adequate production and release of gametes; secondly, the planktonic phase where the larvae grow and disperse; and thirdly, a settlement phase resulting in the establishment of high spat densities in a suitable area (McIntyre, 1970). The ultimate population of young, settled animals is determined and influenced by hazards in each of these phases.

The present study has indicated that the first of these varies with the habitat. Those animals in poor flesh condition, because of their habitat, can only divert a small proportion of

energy into reproduction, i.e. the production of gametes by an area will be in direct proportion to the animals' condition, and those sub-areas in which the animals are in good condition will contribute most of the areal production of gametes. Consideration of the planktonic phase was not included in the present study.

The settlement phase may include the settlement of spat either in the optimal area for population growth or in other areas and a later movement to the adult-populated areas. The ecological preferences of two size groups, spat and larger animals, were found to differ in both H. ulvae and C. edule. The spat of these species settled at areas away from the adult population; a phenomenon possibly attributable to one or more of the factors ; that the spat settled where possible because of current, shore slope, etc.; that the spat had different sediment and tidal preferences; or that the spat suffered increased mortality if they settled in areas of high adult density. The spat of the other bivalves settled with (M. balthica) or close to (M. arenaria) the main adult populations. The fact that the majority of all species' spat settled in the same area, an area subjected to low tidal current, suggests that they either all had similar preferences or were passively settling. The former is unlikely as the species have different methods of feeding although the mode of feeding may differ with age (see also Savilov, 1953). It is therefore suggested that all of these four species, which have weakly swimming planktonic larvae, have little control over their initial settlement. Such a settlement could be erroneously considered as gregarious; only further experimentation could elucidate this problem.

Following settlement, both selective spatial mortality and secondary spat transport resulted in the maintenance of populations in favourable areas of mudflat. As settlement need only fulfil the immediate requirements of the young (Quayle, 1952a), secondary settlement may have to occur in order for the optimal conditions required by the adults to be reached. Spat mortality may occur by ingestion by suspension feeders before settlement and by smothering by fine sediment in certain areas and ingestion by deposit feeders after settlement. Secondary spat settlement of first year animals, while maintaining the main population (as in C. edule) also led to the deposition of young animals on unfavourable areas, e.g. M. balthica on high-shore, coarse sediment areas.

The spat and first year animals played a small part in the production of all species. Despite their large numbers, the spat contributed less to the population production than did the immediately following cohorts. Within all species, however, the spat had the greatest productivity ^{which} ~~when~~ then declined with increasing age. These factors are characteristic of mollusc populations and are, to some extent, a reflection of the sigmoid growth pattern shown by the species over the life span.

The life-cycles growth patterns shown by the bivalve species were all suited to the Ford-Walford analysis and produced Bertalanffy equations after a small correction for the initial slow growth phase of the sigmoid growth curve has been made. Within the species M. balthica and C. edule, there was an inverse relationship, both geographically and intertidally, between the maximum size attained by an individual and the rate of catabolism undergone by that individual.

The molluscs also showed an annual sigmoid growth pattern and the bivalve growth throughout the year was linked with temperature or temperature-induced effects such as the quantity or quality of available food. While the cessation of growth during the winter by suspension feeders dependent on phytoplankton blooms is expected (Ansell and Trevallion, 1967), this also occurred in deposit feeders which had available a relatively constant and abundant food supply. These factors may therefore be regarded as characteristic of this class of molluscs (see also Lammens, 1967).

The annual periods of emaciation exhibited by the bivalves and associated with periods of spawning, disproportionate shell and flesh growth, and flesh deterioration caused by reduced food and temperature levels are considered to apply to most bivalves and will have implications for predator feeding studies (see Section 7.3.2.). However, it is probable that such emaciation does not totally deplete body reserves and the bivalves have sufficient flesh reserves to withstand further adverse conditions (see Section 7.2.).

In addition, physiological antagonism occurred between growth and spawning in each of the bivalve species studied. This suggests that food and/or temperature levels were insufficient to meet the needs of both activities. That energy is diverted into reproduction at the expense of growth is analagous to the diversion of energy by tellinids into siphon regeneration, after siphon loss by flatfish, at the expense of reproduction and growth (Steele et al, 1970). It is considered therefore that the utilization of available energy is dependent upon the relative importance of each activity.

The bivalves' spawning was found to be basically temperature regulated by the occurrence of either minimum threshold temperatures or thermal shocks (see also Caddy, 1967; De Wilde and Berghuis, 1978). However, above that temperature-control was the effect of food availability such that the suspension feeders, dependent on a more seasonal food supply, only spawned once whilst M. balthica, which had a constant food supply, had a smaller, secondary spawning later in the year following the growing season.

The suggested phenomenon of disproportionate growth of shell and flesh, found to produce emaciation effects in M. balthica during the latter part of the growing season, is of possible significance in ensuring survival from predation by increasing the depth at which animals could burrow during the winter. This further type of physiological antagonism, i.e. the diversion of energy from flesh growth into shell growth, was therefore also of survival value whilst still leaving the flesh with sufficient food reserves for the winter period. It is unknown whether this phenomenon was characteristic of other bivalves.

Over the study period, the mollusc species had relatively stable populations. While this may be usual in detritus or deposit-feeding populations which have a relatively constant food supply, the levels of marine suspension-feeding populations are dictated by the annual cycles of phytoplankton and macroflora blooms and as such are more variable (Levinton, 1972). However, in estuaries, detritus is abundant in the water column during the times of the year when the floral cycles are at a minimum; this results in a more stable food supply for the suspension-

feeding populations.

7.2. Conclusions Regarding the Laboratory and Field Studies on
M. balthica.

The factors immersion period, sediment type and population density were found to act together to explain the animals' distribution and production ecology. Whereas the immersion period was a primary factor in regulating the species' production ecology, its' effect was closely associated with the type of sediment which influences the optimal tidal height. The importance of partial immersion was shown experimentally, for example, where the productivity for comparable biomasses was 0.567 with exposure and 0.159 under constant immersion.

The type of sediment is considered to influence the length of the feeding time and is important in terms of food quantity rather than quality. The animals in coarse sediments may move more to exploit the lower food availability, this would result in higher energy expenditure and contribute towards the lower flesh condition and growth. Some areas of the bay, i.e. those with clean sand at the mid- to upper-shore, had insufficient food levels to meet the bivalves' requirements. In the experiments, the population density had a predominant effect on the production ecology as food, and space, was limiting at very high densities.

In addition to showing the importance of the immersion period and indicating the population that a sediment type can support, the experiments indicated the necessity for suspended food material. Coarse sediment areas, which are normally relatively unproductive, could support the same growth and

productivity as fine substrate, mid-shore areas if under a suitable immersion period and with a low population density. Such an environment was not studied on Torry Bay but is known to be inhabited by the species (Beukema pers. comm.). Experimental habitats were created which, although supporting much larger populations than in the field, did not allow for growth or production. The maximum population supported by an area in which growth occurred was dependent on food availability; that maximum population would be greater if suspended food was also available.

In the experimental sediment, which had a comparable food quantity and quality to those in the field, the occurrence of low growth and production was attributable to the necessity for suspended food, the difference in population density and the possible inherent poor growth, etc., in the animals. The latter factor is suggested as the growth of the experimental animals was not greater than in the field even under superior conditions in the experiments.

The experiments further demonstrated the annual cycle of growth and condition previously found in the field and suggested that the flesh condition is endogenously controlled. It is considered that the animals in the field had body reserves even after winter emaciation. This is probably a reflection on their mode of feeding which is less dependent on annual "blooms" of food availability.

The low growth, productivity etc., of the bivalves on certain areas of the intertidal zone may be attributable to stress caused by limitations in the immersion period, food

levels, substrate characteristics, temperature and salinity. The change in the size at maturity, the growth rate and the degree of emaciation may change the reproductive output and dictate the partitioning of the available energy. The term stress may therefore be used as the cumulative result of adverse conditions. The small population in those coarse, high-shore areas was the result of increased physiological stress, selective larval settlement and low spat input, and possibly higher predation by shore birds in areas exposed for the longest periods.

The control of the upper limits of intertidal species by physical factors has also been suggested by several other authors (Connell, 1971a, b; Beukema et al, 1977; Holland and Dean, 1977b). Those authors, however, suggest that the lower limits of such species are controlled by biotic interactions such as competition and increased predation. It is not possible to suggest that this is evident in the present study area although environmental stress did not explain the small populations at the extreme low-shore areas where the animals had relatively high growth rates, productivity and flesh condition.

In conclusion, therefore, the Torry Bay M. balthica population was found to be comparable to other intertidal populations in terms of biomass, production, spatfall and density but not in productivity, growth and condition where the population was comparable to a sublittoral one. At the high-shore areas, the low values were the result of living under harsh environmental conditions where insufficient food, for deposit-feeding, and immersion period, for suspension-feeding,

resulted in growth and condition retardation. However, at other areas and in the experimental studies the environmental parameters of food availability in both sediment and water, substrate and shore type, and the temperature and salinity variation did not wholly explain the anomalous slow growth and low productivity when compared to other intertidal environments.

It is considered that the high levels of heavy metal pollutants encountered in the area contribute to the depressed production ecology of this species. The fact that the other, non-deposit-feeding, species were less affected emphasises the relationships between the metals, sediment and the mode of feeding of M. balthica. It is therefore considered that M. balthica would be suitable as a pollution indicator in estuaries. M. edulis has been suggested as a suitable organism for bioassay techniques as: it is both geographically and locally abundant in estuarine areas, it provides suitably large quantities of analytical material, it is relatively easy to maintain and culture in the laboratory, and it is in direct contact with the water column (see also Bayne, 1976). However, M. balthica also has these qualities which, together with its association with the sediment which may concentrate pollutants, shows its importance as a monitor of the environment. Shaw et al (1976) and Bryan (1978) respectively suggest the suitability of M. balthica as an indicator of oil and metal pollution.

However, as indicated in the present study, the spatial and temporal variability in the growth, age, condition and productivity of any organism used in bioassay techniques should be considered in detail and taken into account.

In addition to aspects previously suggested as fields of further research, it is considered that two other areas of study would be particularly rewarding: firstly, the variation in physiological stress in estuarine bivalves and, secondly, the use of mathematical modelling to predict the state of both an individual and a population in a given type of habitat. It would be of interest to determine whether the respiration of M. balthica, like its production ecology, varies with the type of habitat and if so does the pattern further explain the variation in the production ecology. The preparation of a mathematical model, based upon data such as those given here, would enable M. balthica to be used in monitoring an environment and in predicting the effect of change in that environment.

7.3. The Role of the Intertidal Macrofauna in an Estuarine Food Web.

7.3.1. A Summary of the Invertebrate Biomasses and Production.

Over the bay, the five species of molluscs had a combined flesh biomass ranging from 2.3 to 16.7g m⁻² which annually produced 1.5 to 19.3g flesh m⁻² (1975-76 data), a variation within the area of an order of magnitude (Table 7.1). The most productive areas were the mid- to low-shore of Transect B; the upper-shore of Transect A and the top-shore of Transect C (Fig. 7.1a); this suggests that predators on the molluscs would have abundant prey available at all stages of the tidal cycle. However, the contribution of each species to that total production and biomass varied with area (Fig. 7.1b). Although H. ulvae dominated the biomass at some stations (A2-4, C4, C5), M. balthica was dominant at many others (A1, B1-3, B5, C1, C2) and C. edule was the dominant mollusc at B4. However, while M. balthica, C. edule and M. arenaria were each the largest producers at only one station (C1, B4, B1 respectively), H. ulvae was the dominant producer at all others. Similarly, whereas H. ulvae was dominant overall on Transect A, with an upshore progression on Transects B and C the importance of M. balthica declined while that of H. ulvae increased.

When considering the different feeding types of bivalves, the biomass of the suspension-feeding bivalves C. edule and M. arenaria was greater than that of M. balthica at only Stations A3, B4, C5, whereas their combined annual production was greater than that of M. balthica at all stations except A1, A4 and C1 (Fig. 7.1b). This reflects the relative success of the coarse sand, upper-shore areas in supporting the suspension feeders, the

Table 7.1 The Mean Biomass and Annual Production of the Mollusc Species Under Study at Each Station (1975-76 Data). All Figures in g fdw m⁻².

Station	Mean Biomass					Annual Production				
	<u>Macoma</u>	<u>Cerastoderma</u>	<u>Mya</u>	<u>Hydrobia</u>	<u>Retusa</u>	<u>Macoma</u>	<u>Cerastoderma</u>	<u>Mya</u>	<u>Hydrobia</u>	<u>Retusa</u>
A1	7.571	0.860	0.366	5.210	0.043	3.429	1.136	1.271	8.046	-0.013
A2	1.415	0.539	0.025	7.711	0.044	0.564	0.705	0.087	8.667	0.169
A3	2.101	1.128	1.327	9.091	0.079	0.812	1.476	4.807	10.945	0.339
A4	1.870	0.113	0.061	5.039	0.012	0.669	0.148	0.206	7.056	-0.038
B1	1.258	0.339	0.266	0.456	0.000	0.614	0.454	0.924	0.911	0
B2	5.242	0.535	1.339	5.628	0.062	2.554	0.701	4.830	7.764	-0.012
B3	9.095	1.371	1.237	4.810	0.185	4.395	1.814	4.444	6.623	0.774
B4	3.127	3.534	0.054	0.991	0.012	0.521	4.624	0.195	1.546	0
B5	4.084	1.075	0.130	3.520	0.006	0.655	1.407	0.474	5.133	-0.075
C1	1.834	0.473	0.002	0.020	0.000	0.795	0.618	0.008	0.076	0
C2	1.076	0.236	0.030	1.099	0.011	0.219	0.323	0.096	2.497	0.021
C3	1.961	0.438	0.028	0.562	0.012	0.350	0.579	0.082	0.979	0.013
C4	3.212	0.961	0.009	6.011	0.011	0.531	1.258	0.032	8.397	0.014
C5	0.820	2.013	0.416	11.978	0.155	-0.290	2.639	1.507	15.239	0.206

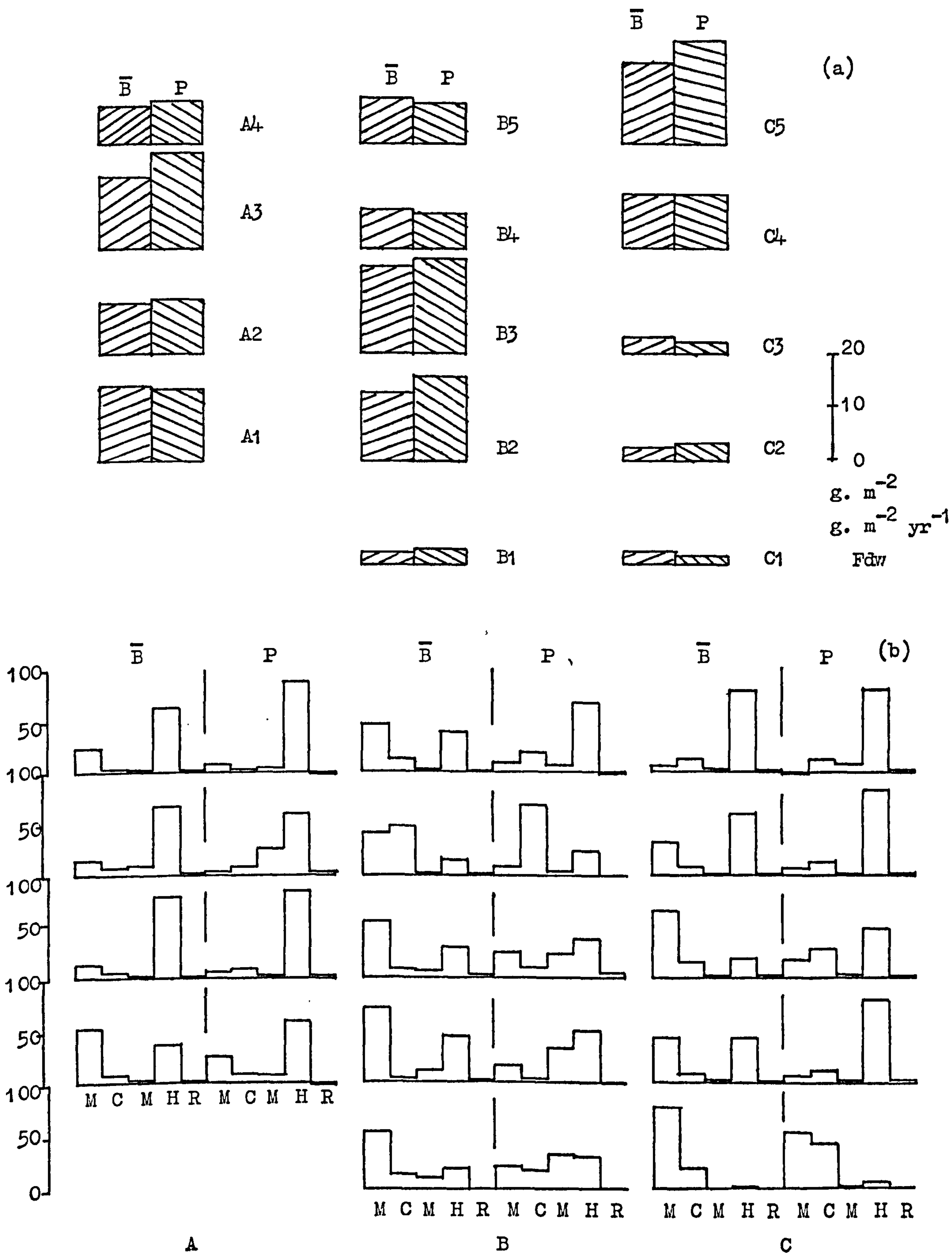


Figure 7.1 Torrey Bay Mollusc Production and Biomass Summary :

(a) Annual Production and Mean Biomass at Each Station (Σ all Species).

(b) Percentage of That Production and Mean Biomass Attributable to Each Species. Order :- Macoma, Cerastoderma, Mya, Hydrobia, Retusa.

success of the bay in maintaining M. balthica populations, and the relatively low productivity of those populations. A difference either in the species of predator or in the prey-preference of those predators may therefore be expected and related to the prey availability (see Section 7.3.2.).

The flesh biomass and abundance of the other species of macrofauna at Torry Bay were obtained during the period March-August, 1975, and their mean values calculated (Table 7.2). (The species encountered during the sampling are given in Appendix 7.1). The possible production of those species or groups (e.g. other tellinids, oligochaetes) was determined by using P/\bar{B} values obtained by other workers (see Table 7.3).

Several species, e.g. Nereis diversicolor, Corophium volutater and M. edulis were only found in small areas over the mud. Although this resulted in low values of mean P and \bar{B} for the former two species, the dense mussel beds on Torry Bay gave very high values of P and \bar{B} even when mean values for the whole area were calculated. The lugworm, Arenicola marina, occurred in low densities of large animals over the mudflat while the catworm, Nephtys hombergi, occurred at the majority of areas. Oligochaetes were found in high densities but low biomasses over most of the bay.

While M. balthica was the dominant bivalve, other species of tellinids were found in low densities (usually $<3m^{-2}$ mean density) at several stations (Table 7.4). Geographically, over British estuarine intertidal areas, there is an inverse relationship between the relative abundances of M. balthica and Scrobicularia plana, an estuarine deposit-feeding tellinid

Table 7.2 The Abundance, Mean Biomass and Annual Production of the Other Members of the Macrofauna.

Station	<u>Mytilus edulis</u>		<u>Nephtys hombergi</u>		<u>Nereis diversicolor</u>		<u>Arenicola marina</u>		<u>Corophium volutator</u>		Other Tellinids		Oligochaetes							
	\bar{N}/m^2	\bar{B}_{Fdw}	\bar{N}	\bar{B}	P	\bar{N}	\bar{B}	P	\bar{N}	\bar{B}	P	\bar{N}	\bar{B}	P						
A1	0	0	300	3.381	6.424	20	0.202	0.606	14	2.972	3.596	1400	0.643	4.951	12	0.006	0.002	2800	0.280	1.120
A2	0	0	0	0	0	5	0.050	0.150	36	7.641	9.246	3730	1.714	13.198	0	0	0	5800	0.580	2.320
A3	0	0	5	0.056	0.106	0	0	0	42	8.915	10.787	5000	2.298	17.695	0	0	0	2200	0.220	0.880
A4	0	0	0	0	0	0	0	0	21	4.457	5.393	650	0.299	2.302	1	0.095	0.025	4200	0.420	1.680
B1	253	142.8	300	3.381	6.424	100	1.010	3.030	2	0.424	0.513	0	0	0	6	0.024	0.006	4000	0.400	1.600
B2	927	339.9	400	4.508	8.565	0	0	0	2	0.424	0.513	0	0	0	4	0.005	0.001	17000	1.700	6.800
B3	0	0	100	1.127	2.141	0	0	0	11	2.335	2.825	0	0	0	26	0.025	0.007	2200	0.220	0.880
B4	0	0	210	2.367	4.497	5	0.050	0.150	32	6.792	8.218	0	0	0	1	0.001	0.000	400	0.040	0.160
B5	0	0	250	2.817	5.352	100	1.010	3.030	25	5.306	6.420	20	0.009	0.069	1	0.001	0.000	1000	0.100	0.400
C1	900	656.9	60	0.676	1.284	0	0	0	0	0	0	0	0	0	6	0.001	0.000	3000	0.300	1.200
C2	0	0	25	0.282	0.536	30	0.303	0.909	4	0.849	1.027	0	0	0	1	0.001	0.000	8000	0.800	3.200
C3	0	0	70	0.789	1.499	0	0	0	22	4.670	5.651	0	0	0	1	0.001	0.000	2200	0.220	0.880
C4	0	0	10	0.113	0.215	0	0	0	34	7.271	8.733	0	0	0	0	0	0	16000	1.600	6.400
C5	0	0	10	0.113	0.215	0	0	0	19	4.033	4.880	0	0	0	0	0	0	2600	0.260	1.040

Table 7.3 Conversion Factors for Productivity and Calorific Values.

Species	P/ \bar{B}	Calorific Value (K.cal/g flesh wt)	Author
<u>M. edulis</u>	1.2	4.8	Milne and Dunnet (1972); Burke and Mann (1974).
<u>Nephtys</u>	1.9		Warwick and Price (1975).
<u>Nereis</u>	3.0	4.36	Chambers and Milne (1975a).
<u>Arenicola</u>	1.2		Wolff and De Wolf (1977).
<u>Corophium</u>	7.7	4.65	Mossman (1977).
<u>Scrobicularia</u>	0.3	4.5	Hughes (1970); Warwick and Price (1975).
<u>Oligochaetes</u>	4.0	5.3	Waters (1969); Johnson and Brinkhurst (1971).
<u>Tellina</u> and <u>Polychaetes</u>		5.2	Steele <u>et al</u> (1970).

Table 7.4 The Occurrence of the Tellinacea on Torry Bay.

Species	Station	B1	B2	C1	A1	A3	C2	B3	A2	A4	B5	B4	C3	C4	C5
<u>M. balthica</u>		X	X	X	X	X	X	X	X	X	X	X	X	X	X
<u>S. plana</u>		X	X	X	X			X		X					
<u>A. nitida</u>		X		X	X			X							
<u>A. alba</u>			X				X	X							
<u>A. prismatica</u>								X							
<u>T. fabula</u>											X	X	X		
<u>T. tenuis</u>										X	X				

Habitat Type (Tebble, 1966) :

- M. balthica : see Chapter 3.
- S. plana : soft bottom, much detritus; intertidal.
- A. nitida : mud, sandy-mud, silty-sand, muddy gravel; sublittoral.
- A. alba : mud, silty-sand, soft muddy gravel; sublittoral.
- A. prismatica : clean sand, fine sand, muddy sand; sublittoral.
- T. fabula : clean sand, silty sand, muddy sand; mid-shore to sublittoral.
- T. tenuis : fine sand; mid tide to shallow sublittoral.

(J. Green, pers. comm.), the latter being more dominant in the south and the former of greater importance in northern areas. The relative abundances in the Forth estuary conform to this pattern. It is unlikely that the S. plana populations were accurately monitored as this species usually occurs at deeper levels in the sediment. However, small individuals would have been encountered with a greater frequency if the population had been larger.

The low densities and irregular occurrences of the tellinids, with the exception of M. balthica and possibly S. plana, suggests that they are not self maintaining populations. Individuals of some of the other species were probably washed inshore from the shallow sublittoral area although they were encountered in their preferred habitats (see Tebble, 1966). It is unlikely that, because of their low densities, these other tellinids actively compete either with M. balthica or, because of their different feeding methods and preferences, with any of the other bivalves C. edule, M. arenaria or M. edulis.

The annual production and mean biomass for the species and groups (excluding M. edulis) over the study area varied from 4 to 50g flesh m^{-2} and 3 to 25g flesh m^{-2} , respectively (Table 7.5). The mussels, although only occurring in three areas, had a flesh biomass of up to 660g m^{-2} which would possibly produce 790g m^{-2} annually. The mean annual production and biomass for the study area were therefore estimates as 22.7 and 15.5g flesh wt. m^{-2} respectively (Table 7.6). However, although the annual production for each species has been calculated, it is not possible to state the proportion of that which is passed onto the higher trophic

Table 7.5 Station Values of Biomass and Production.

Area	\bar{B} g flesh m^{-2}				P g m^{-2} yr $^{-1}$			
	⁵ Species	Others	<u>Mytilus</u>	Σ^*	⁵ Species	Others	<u>Mytilus</u>	Σ^*
A1	14.23	7.48		21.71	13.87	16.70		30.57
A2	9.73	9.98		19.72	10.19	24.91		35.11
A3	13.73	11.49		25.21	18.38	29.47		47.85
A4	7.09	5.27		12.37	8.04	9.40		17.44
B1	2.32	5.24	142.8	7.56	2.90	11.57	171.4	14.48
B2	12.81	6.64	339.9	19.44	15.84	15.88	407.9	31.72
B3	16.70	3.71		20.40	18.05	5.85		23.90
B4	7.72	9.25		16.97	6.89	13.02		19.91
B5	8.81	9.24		18.06	7.59	15.27		22.86
C1	2.33	1.00	656.9	3.31	1.50	2.48	788.3	3.98
C2	2.45	2.23		4.69	3.16	5.67		8.83
C3	3.00	5.68		8.68	2.00	8.03		10.03
C4	10.20	8.93		19.14	10.23	15.35		25.58
C5	15.38	4.41		19.79	19.30	6.13		25.44

where Σ^* = Total excluding Mytilus

Table 7.6 Macrofaunal Production Summary (Mean Values for Torry Bay). (\bar{B} g flesh m^{-2} ; P g m^{-2} yr $^{-1}$.)

Species	Nos.	S.E.	\bar{B}	S.E.	P	S.E.
<u>M. balthica</u>	See Chapter 3	3	3.190	0.672	1.130	0.358
<u>C. edule</u>	See Chapter 4	4	0.972	0.239	1.277	0.313
<u>M. arenaria</u>	See Chapter 4	4	0.378	0.138	1.354	0.500
<u>H. ulvae</u>	See Chapter 5	5	4.438	0.962	5.991	1.173
<u>R. obtusa</u>	See Chapter 5	5	0.045	0.016	0.100	0.060
Total 5 spp.			9.036	1.366	9.853	1.695
<u>M. edulis</u>	148.6	88.5	81.4	51.1	97.7	61.3
<u>N. hombergi</u>	124.3	37.0	1.401	0.417	2.661	0.793
<u>N. diversicolor</u>	18.6	9.5	0.187	0.096	0.562	0.289
<u>A. marina</u>	18.9	3.7	4.002	0.789	4.843	0.954
<u>C. volutator</u>	771.4	425.6	0.354	0.196	2.730	1.506
Other tellinids	4.2	1.9	0.011	0.006	0.003	0.000
Oligochaetes	5100.0	1389.6	0.510	0.139	2.040	0.556
Total 6 spp. + gps. excl. <u>Mytilus</u>			6.467	0.824	12.839	2.027
Total macrofauna excl. <u>Mytilus</u>			15.503	1.839	22.692	3.104
Total including <u>Mytilus</u>			96.903	52.939	120.39	64.404

levels. That proportion may vary between 50 and 90% of the annual production (e.g. Hughes, 1970; Chambers and Milne, 1975a, b).

In the present study, the extent of the variation in the production and biomass values within a small area gives some indication of the validity of comparing production values from different geographical areas. In many studies, where only a single P or \bar{B} value had been calculated for a large area, both the range of values within that area and the position of the given values within that range are unknown. However, in the absence of such further information, only simple comparisons may be made.

The total macrofaunal biomass and production supported on Torry Bay are comparable to other estuarine or brackish areas for the benthic macrofauna; the values encountered within the bay encompass most of those found by other workers on both intertidal and sublittoral estuarine areas (see Table 7.7). The production and biomass values of estuarine areas, which are an order of magnitude greater than marine intertidal and sublittoral areas and fresh water areas, reflect the high nutrient status of estuaries. An estuary acts as a "nutrient-sink" which results in the support of large deposit- and suspension-feeding populations and which is the basis of the high productivity of estuarine areas. The combined tidal and fresh water inflow activity renders the secondary-producer populations of invertebrates more or less independent of local primary production and allows for the maintenance of greater biomasses and production (see also McIntyre, 1970; Milne and Dunnet, 1972). The large presence of detritivores and deposit feeders in the estuarine food web is

Table 7.7 Comparable Studies on the Production and Biomass of Benthic Communities.

Area	Location	Fauna	Biomass		Production		Author, Remarks
			g Fdw m ⁻²	g Fdw m ⁻²	g Fdw m ⁻² yr ⁻¹	g Fdw m ⁻² yr ⁻¹	
Estuarine, intertidal	Forth Est.	Macrobenthos	3.3 - 25.2	4.0 - 47.8	22.7	This Study, range of values mean excluding <i>M. edulis</i>	
"	Grevelingen Est.	"	15.5 96.9	120.4	120.4	" including "	
"	Lynher Est.	"	13.2	0.1 - 119.9	50 - 58	Wolff and de Wolf, (1977), range mean values for estuary	
"	Southampton Water	Polychaetes Bivalves Total	60 - 70 31 - 123 190	114 - 133 38 - 92 220	13.3	" " for main spp. Warwick and Price (1975) Hibbert (1976)	
"	Tees Est.	Meiofauna	0.04-225.9			Gray (1976)	
Brackish Shallow Sublittoral	Baltic	Macrofaunal detritivores	6.45	7.97		Ankar and Elmgren (1976)	
"	"	Soft-bottom macroinfauna	12.95	69.74		Ankar (1977)	
"	"	Macrobenthos	4.5	6.8		Cederwall (1977)	
Estuarine, sublittoral	Long Is., U.S.A.	"	0.3 - 22.6	8.0 - 64.5		Sanders (1956)	
Marine, intertidal	W. Scotland	"	0.6			McIntyre (1970), range of values mean, exposed areas	
"	Loch Ewe	"	1.13			mean, moderately exp. areas	
"	Nova Scotia	Epifauna	9.2			mean, sheltered areas	
"	Wadden Sea	Macrofauna	1.3	17.5		McIntyre and Eleftheriou (1968)	
"	N.E. England	Meiofauna	24.7			Miller et al (1971)	
Marine, intertidal and shallow sublittoral	Venezuela	Macrofauna	2 - 28			Beukema (1974)	
Marine, sublittoral	N.E. England	Meiofauna	0.12-10.33			Gray (1976)	
"	Loch Ewe	Macrofauna	2.98-3.25	12.4		Edwards (1973, a, b) polluted area	
"	Kiel Bight	Meio- and macrofauna	1.08-5.84	2.4		unpolluted area	
Marine, shallow sublittoral	"	Macrofauna	3.98	1.74		Buchanan and Warwick (1974)	
"	"	Macrofauna	3.7	17.9		McIntyre and Eleftheriou (1968)	
Highest recorded fresh-water values	"	Benthos	26.3	49.5		Arntz and Brunswig (1975)	
		"		42.4		Johnson and Brinkhurst (1971)	
		"				Maitland and Hudspith (1974)	

especially important in utilizing the large amounts of material previously lost to the decomposer part of the food chain (Ricklefs, 1973). This in turn indicates the importance of the decomposer microbiota in transferring energy to the meiofauna and to the detritivorous macrofauna (see also Ankar, 1977).

The large macroinfaunal populations also increase sediment reworking (bioturbation), oxygen penetration into the substrate and organic matter turnover (Rhoads and Young, 1970; Ankar, 1977). The grazing by the deposit-feeding macrofauna stimulates microbial production and also leads to the release of nutrients from the sediment by the bacterial mineralisation of organic matter (Ankar, 1977). Furthermore, the interdependence of the pelagic and benthic systems is also of importance and may be summarised:

"... the pelagic system acting as a donor of chemical potential energy to the benthic system which in turn acts as a releaser of nutrients fertilising the pelagic system ..."

(Ankar, 1977)

Additionally, the benthic macroinfauna bioturbation and sediment agitation which may be followed by resuspension and sediment transport, will influence the sediment geochemistry.

An adverse affect of large macrofaunal populations may be the excessive production of faeces. This would render large amounts of organic matter unavailable to the macrofauna and may in turn lead to conditions of food-limitation (Milne and Dunnet, 1972; Ankar, 1977; Tunnicliffe and Risk, 1977). However, this is unlikely under normal-sized populations such as those encountered in the present study.

7.3.2. Predation on the Macrofauna.

As a whole, the Forth estuary supports internationally

important overwintering populations of wading birds and ducks (Bryant and McLusky, 1975-78). Within the estuary Torry Bay is the third most important site and supports populations of mallard, Anas platyrhynchos (300-500); Wigeon, A. penelope (up to 510); Redbreasted mergansers, Mergus serrator, with winter maximal numbers of 600. Oystercatchers, Haemotopus ostralagus; turnstone, Arenaria interpres; curlew, Numenius arquata; bar-tailed godwit, Lumosa lapponica; redshank, Tringa totanus; knot, Calidris canutus; dunlin, C. alpina; and shelduck, Tadorna tadorna, all occur in large populations. In addition, plovers, Pluvialis spp. and lapwing, Vanellus vanellus occur in smaller numbers.

The presence and feeding distribution of these birds on the study area was studied during the winter 1975-76 (see Bryant, 1976, for maps of the birds' feeding distributions). With respect to the stations used in the present study, the mudflat utilization by the main bird species may be summarised :

Species	Stations	'Feeding hours'/12.5 hour tide
Shelduck	A1-3	50 - 99
	B1-3	10 - 49
	A4, B4-5, C1-5	0
Wigeon	Observed at all stations	
Redshank	A1-4, B2-3, C1-5	20 - 49
	B1, B4-5	10 - 19
Knot	A1-4, B1, C2-5	1 - 99
	B2-5, C1	0
Dunlin	A1-4, B1-3, C3-5 B4-5, C1-2	10 - 99

where 'Feeding hours' = no. of birds
x time spent feeding at an area.

The usual role of these birds in the estuarine intertidal food web is summarised in Fig. 7.2 using information given by Goss-Custard (1970, 1977); Davidson (1971); Prater (1972); Burton (1974); Buxton (1975); Bryant and Leng (1976); Goss-Custard and Jones (1976); Goss-Custard et al (1977) and by D.M. Bryant and J.M. Warnes (pers. comm.). The flow diagram is based on generalisations which may vary with area. The mean biomass and annual production by each species of macrofauna are given on the diagram; however, the relative proportions of the production that are passed onto the predators or lost to the decomposers are unknown. The above authors agree that the number and species of prey taken by a predator is dependent on the availability of the prey, which in turn is influenced by the shore type and the behaviour of the invertebrates, and varies with the tidal, diurnal and annual cycles.

The distribution of feeding by the predators may be compared with the presence and production of the macroinvertebrates; it is, however, necessary to incorporate the physical characteristics of the area into the considerations. Shelduck were found to utilize all areas except the top of Transect B and the whole of Transect C; they therefore missed the areas of highest production by H. ulvae, considered to be the preferred prey of this predator. However, as coarse substrate is unsuitable for this predators' mode of feeding, then its absence from the uppermost areas of the shore would be expected (Bryant and Leng, 1976). The apparent contradiction, that shelduck prefer large H. ulvae (of size 3-4mm, Buxton, 1975) which mainly occur in sediments in which the predator cannot feed, suggests that on Torry Bay shelduck are more dependent on other prey species abundant at the

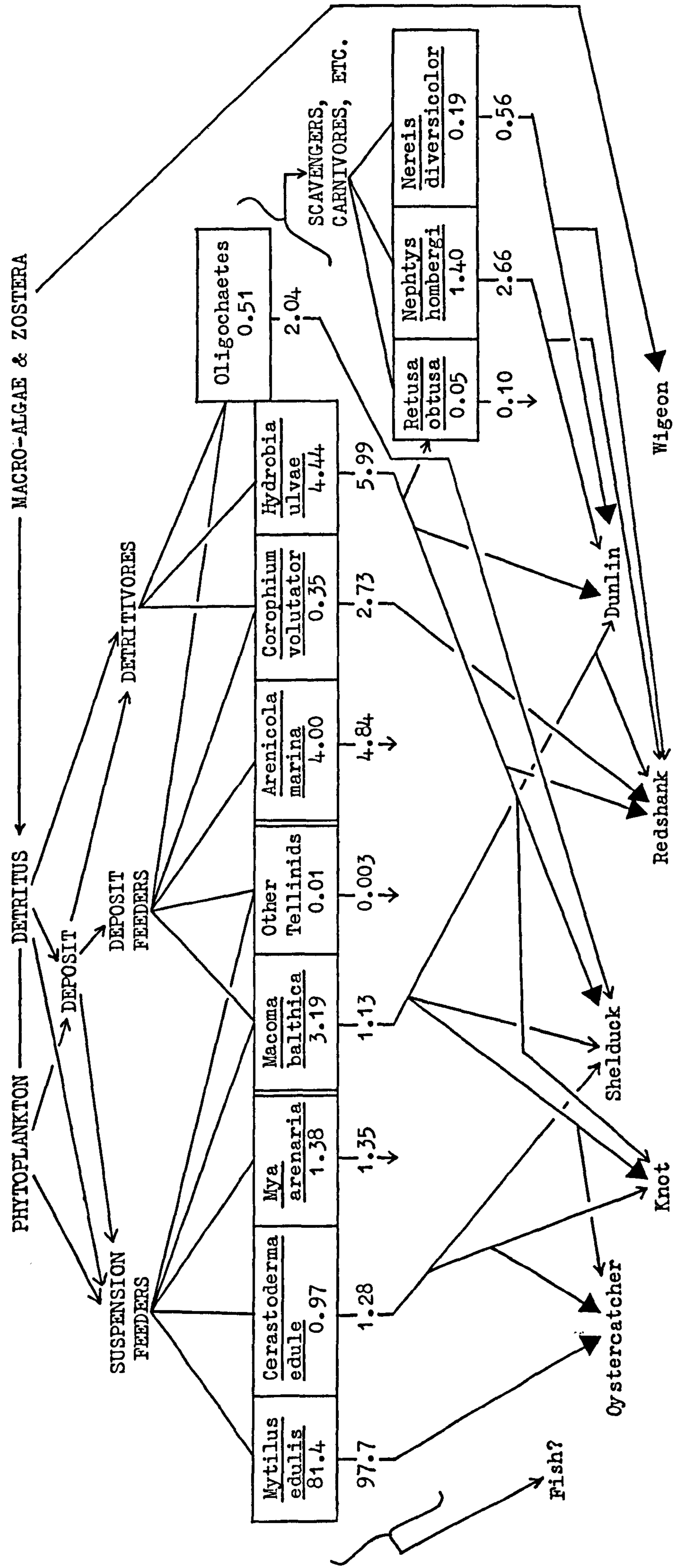


Figure 7.2 The Role of the Intertidal Macrofauna Within a Simplified Estuarine (Torry Bay) Food-web.

Key:

Species
 \bar{B}
 P ↓

where \bar{B} = mean biomass ($g\ m^{-2}$);
 P = production ($g\ m^{-2}\ yr^{-1}$);
 → indicates main prey of predators.

lower areas, e.g. polychaetes and oligochaetes.

Redshank and dunlin have both been observed feeding on the most productive H. ulvae areas although both species apparently avoid the top-shore area of Transect B. This latter area supports both H. ulvae and Corophium volutator but is close to the Torryburn village and therefore subject to disturbance. Dunlin, redshank and shelduck take significantly different sizes of H. ulvae (2.08, 2.5 and 3-4mm in length respectively, Burton, 1974; Buxton, 1975). It may be suggested that as the size of H. ulvae present on the intertidal area varies both temporally and spatially, then the feeding areas used by these predators may similarly vary.

A similar resource-partitioning may occur in predation on M. balthica. Redshank and dunlin have been found to feed only on small individuals (<7mm long) whilst knot select those 6 to 15mm in length despite a greater abundance, but not biomass, of the former size group (Davidson, 1971; Prater, 1972; Burton, 1974). On Torry Bay, large feeding populations of redshank and dunlin occur in favourable M. balthica areas whereas the knot populations, in avoiding the mid-shore Transect B area, do not utilize those optimal areas. The recorded dependence of knot on M. balthica suggests that this situation is unusual (Prater, 1972).

The areas used by feeding oystercatchers on Torry Bay have not been recorded; however, its main prey, M. edulis and C. edule, occur at different areas and could therefore provide the predator with a food source over the major part of the tidal cycle. This is also possible for the other species, knot, redshank and dunlin, in which the prey species taken may vary with area of mudflat, e.g. knot could utilize the optimal areas for

M. balthica, C. edule and H. ulvae as they moved inshore with the flow tide (see Fig. 7.2).

The mussels and lugworms on Torry Bay were among the most productive members of the macrofauna (see Table 7.6; Fig. 7.2); however, neither are known to support large populations of predators. The mussel beds, especially at Station C1, consisted of large, old mussels; this suggests that predation by wading birds and ducks, which usually taken only smaller animals, was small. In contrast to the Forth estuary, the Ythan estuary mussel beds support large populations of eider ducks, these take 21% of the mussel production (Milne and Dunnet, 1972). The density of the large mussel production on Torry Bay is therefore unknown although that production may not be used to support populations of predators. Similarly, the production by A. marina was also relatively large but was utilized by an unknown number of predators. The low densities, but high biomasses, of the polychaete may have been taken by curlews and godwits, both of which were present in low densities, but were outwith the reach of other predators (Green, 1968).

The above considerations are based firstly upon bird feeding observations which, as they were made from the shore, may not be accurate to the stations in this study, and secondly on the flesh production and biomasses of the prey species within an area. The density, rather than the flesh biomass, may be of greater value when considering predator/prey relationships (D.M. Bryant, pers. comm.). However, Goss-Custard et al (1977), found that the utilization of prey (polychaetes) by a predator (redshank) was related to their biomass in the sediment rather than to their density.

A final consideration on the feeding by wading birds is the spatial and temporal variation in the flesh condition of the prey species, such as that found in M. balthica, C. edule and M. arenaria in this study. Within each species and during each winter, the condition had decreased by 40-50% from its maximum in the spring; winter predators would therefore have to consume 2-3x as many bivalves of a certain size to obtain a certain energy intake in comparison with summer condition levels. This could have the effect of increasing the foraging energy expenditure of the predators. With respect to Macoma, this difficulty for predators was further increased as fewer bivalves were available during the winter; this situation was also encountered in the Wadden Sea but not on the Ythan estuary where increased winter densities of M. balthica compensated for the condition decrease (Chambers and Milne, 1975b; Beukema and De Bruin, 1977).

The spatial variation in flesh condition and abundance of M. balthica and C. edule on Torry Bay indicated that the most favourable areas for feeding by waders were uncovered by the tide for shorter periods when compared to less favourable areas. This, however, particularly with respect to Macoma, would have been a greater problem to summer predators than to winter ones. This difference may also have been counterbalanced by the greater time available for feeding on the upper-shore.

It is possible, therefore, that the predators' feeding strategies were modified with the tidal cover to accommodate any variation in prey condition and abundance (see also Milne and Dunnet, 1972). Dare and Edwards (1975) questioned as to whether or not predators could compensate for seasonal fluctuations in

prey quality, and Goss-Custard and Jones (1976) found that the prey species taken by predators may differ with the time of year; it is suggested that compensation by the predators for spatial differences in the prey quality should also be questioned and studied. Further consideration of these problems is outwith the present study.

Only brief mention may be made of the other major predators, the estuarine fish, which are known to take all of the species studied. Summers (1974) found that flounders in the Ythan estuary removed 97% and 50% of the production of Corophium and Nereis respectively although both species' production was much greater than on Torry Bay (9.4 and $3.8 \text{ g m}^{-2} \text{ yr}^{-1}$ respectively cf. Fig. 7.2). He also found a seasonal change in the diet of flounders with C. volutator being important in the summer, but Nereis, Macoma and Hydrobia were important in the autumn and winter. However, the food of these predators may not necessarily be correlated with the abundance of their prey as many attacks by the predators may be unsuccessful (e.g. as with plaice and amphipods, Steele et al, 1970).

In addition to taking whole prey items, the cropping of parts of prey, e.g. siphons of bivalves and palps of polychaetes, by flatfish may also remove large amounts of material depending on the size of the populations (McIntyre and Eleftheriou, 1968; Steele et al, 1970). Although not necessarily increasing mortality, the siphon cropping necessitates the diversion of energy into regeneration at the expense of reproduction and growth by the bivalves. This in turn may result in decreased recruitment to the population which ultimately causes the

predator to change its prey. While this phenomenon is important on a flatfish nursery ground, its role in other intertidal areas is unknown.

However, the role of estuarine fish in the Torry Bay food web, described above, cannot be evaluated because of the paucity of data regarding their presence, species composition and feeding on the intertidal areas of the Forth estuary. It is likely that some fish feed within the bay as cormorants have been observed feeding in the area (Bryant, 1976).

In conclusion, therefore, the diversity of predators within an estuarine, intertidal system such as that studied here may be regarded as a result of, firstly, the variety and productivity of the detritus, deposit and suspension feeders within each habitat, and secondly, the complexity and number of habitats within the intertidal area or, indeed, within the whole estuary.

The present study has given an indication of the complexity of the estuarine ecosystem and of the relationships not only between the environment, the macrofauna and their predators, but also within a single species. After considering such an ecosystem, many estuarine biologists would agree with Eltringham (1971) :

"The ecology of sandy shores and mudflats is at a threshold, over which lie unlimited opportunities for research, which should yield results of the greatest ecological significance."

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Appendix 2.1 Sediment Pipette Analysis : Recalculated Settling Velocities (S.V.) and Time Taken to Settle 20cm (in case of 62.5 μ m) or 10cm (in case of Other Sizes).

Temp.	Particle Size (μ m)									
	62.5		31.2		15.6		7.8		3.9	
	S.V.	* ₁	S.V.	* ₁	S.V.	* ₁	S.V.	* ₁	S.V.	* ₂
20	0.35	0:57	0.0876	1:54	0.0218	7:39	0.00545	30:35	0.00136	2:02:33
21	0.36	0:56	0.0898	1:51	0.0224	7:26	0.00559	29:49	0.00140	1:59:03
22	0.37	0:54	0.0920	1:49	0.0229	7:17	0.00573	29:05	0.00143	1:56:33
23	0.38	0:53	0.0942	1:46	0.0235	7:06	0.00586	28:27	0.00147	1:53:23
24	0.39	0:51	0.0963	1:44	0.0240	6:57	0.00600	27:47	0.00150	1:51:07
25	0.40	0:50	0.0986	1:41	0.0246	6:47	0.00614	27:09	0.00154	1:48:14

where S.V. = cm/sec

*₁ = time to settle (min : sec)

*₂ = time to settle (hr : min : sec)

Addendix 2.2 Sediment Analysis : A Comparison of Acid-treated and Untreated Sediment Samples for C/N Analysis (February 1975 Samples).

Station	UNTREATED			ACID-TREATED		
	%N	%C	C/N	%N	%C	C/N
A1	0.34	8.23	24.21	0.31	8.03	25.90
2	0.07	1.09	15.57	0.06	1.20	20.00
3	0.10	1.23	12.30	0.08	1.27	15.88
4	0.09	2.12	23.56	0.09	2.77	30.78
5	0.16	1.73	10.81	0.11	1.69	15.36
6	0.12	1.69	14.08	0.06	1.24	20.67
7	0.05	0.71	14.20	0.04	0.66	16.50
B1	0.08	1.87	23.37	0.09	1.73	19.22
2	0.16	4.94	30.87	0.17	4.72	27.76
3	0.04	1.51	37.75	0.07	1.85	26.43
4	0.08	2.36	29.50	0.06	2.48	41.33
5	0.04	0.93	23.25	0.04	1.13	28.25
6	0.02	0.35	17.50	0.04	0.87	21.75
7	0.04	1.13	28.25	0.08	0.92	11.50
8	0.06	1.87	31.17	0.10	2.45	24.50
C1	0.22	7.05	32.04	0.32	7.43	23.22
2	0.17	4.63	27.23	0.25	4.36	17.44
3	0.15	4.10	27.33	0.17	4.67	27.47
4	0.04	0.29	7.25	0.05	0.23	4.60
5	0.02	0.70	35.00	0.02	0.59	29.50
6	0.09	0.46	5.11	0.10	0.46	4.60
7	0.05	0.55	11.00	0.13	0.54	4.15
8	0.07	0.75	10.71	0.02	0.67	33.50

Appendix 2.3 Cumulative Percentages of Grain Sizes From Sediment Particle-size Analysis (Means of Replicates \pm S.D.).

Grain Size (mm) (ϕ units)	A1	A2	A3	A4	B1	B2	B3	B4	B5	C1	C2	C3	C4	C5
>5.6 (-2.5)	0	0	0	1.056 0.719	0	5.863 1.492	1.935 0.142	0.660 0.099	0	1.801 0.084	1.675 2.369	0.174 0.246	4.365 1.350	10.953 7.301
2.0-5.6 (-1)	0.206 0.053	0.033 0.020	0	1.705 0.534	0.045 0.064	7.411 1.121	2.785 0.178	1.338 0.097	0.115 0.022	2.986 0.010	2.642 2.466	0.639 0.199	10.609 1.182	14.551 8.168
1.0-2.0 (0)	0.459 0.096	0.340 0.167	0.284 0.057	5.104 3.110	0.062 0.088	7.728 1.257	5.200 0.175	2.924 0.017	0.676 0.033	6.313 0.208	4.623 2.729	1.132 0.207	13.704 1.104	19.150 7.393
0.5-1.0 (1)	1.414 0.040	2.900 0.887	3.165 0.235	14.311 2.841	0.162 0.111	8.431 1.365	14.912 0.431	7.633 0.231	3.765 0.334	9.621 0.308	8.867 2.655	2.803 0.206	22.504 1.277	34.751 5.692
0.25-0.5 (2)	4.922 0.595	14.898 2.780	16.911 0.613	41.473 1.388	0.564 0.223	10.920 1.415	37.232 0.593	33.672 0.701	26.450 0.778	15.524 0.064	25.773 1.957	45.614 0.525	74.802 1.227	76.251 1.848
0.125-0.25 (3)	12.015 2.135	49.817 4.482	38.772 0.671	81.257 0.449	2.685 0.971	15.655 1.363	61.462 0.885	95.391 0.456	74.312 0.298	29.693 0.390	74.765 2.454	94.335 0.367	97.833 0.403	96.646 0.057
0.063-0.125 (4)	20.713 5.769	68.112 3.120	45.238 0.463	86.029 0.591	15.650 6.483	23.627 1.929	70.218 0.867	97.044 0.421	97.314 0.062	45.881 0.699	78.858 2.376	96.066 0.297	98.825 0.237	98.117 0.049
0.031-0.063 (5)	68.548 4.520	87.211 0.795	72.669 0.654	92.146 0.081	66.129 6.467	76.992 0.643	89.807 6.518	97.659 0.000	97.909 0.044	75.429 2.262	85.838 2.222	97.442 0.339	98.947 0.180	98.673 0.146
0.016-0.031 (6)	83.178 2.368	91.271 0.337	81.542 0.247	95.006 0.058	78.918 2.812	85.143 0.567	93.169 2.538	98.412 0.175	98.537 0.140	91.282 0.512	91.946 1.830	98.439 0.200	99.278 0.308	99.262 0.195
0.008-0.016 (7)	90.351 0.022	93.786 0.204	87.375 0.916	96.639 0.062	85.874 1.672	90.345 0.817	95.671 1.380	98.885 0.174	98.866 0.032	94.022 0.028	95.107 1.300	98.936 0.278	99.424 0.258	99.496 0.113

Appendix 2.4 Suspended Particulate Water Analysis, (Mean \pm 95% Conf. Limits).

Date	Organic Carbon (mg l ⁻¹)		Carbohydrate (mg l ⁻¹)	
	\bar{x}	Range	\bar{x}	Range
20/01/75	0.558	0.664-0.481	0.458	0.658-0.352
14/02/75	0.421	0.501-0.363	0.987	1.416-0.757
26/02/75	0.089	0.106-0.077	0.355	0.507-0.272
19/03/75	0.345	0.411-0.298	0.448	0.643-0.344
18/04/75	0.573	0.682-0.494	0.293	0.420-0.224
21/05/75	1.039	1.237-0.896	0.501	0.719-0.384
13/06/75	0.506	0.602-0.436	2.110	3.028-1.619
11/07/75	0.927	1.104-0.799	1.211	1.738-0.929
11/08/75	1.088	1.295-0.938	1.305	1.873-1.002
11/09/75	0.451	0.537-0.389	1.590	2.281-1.220
08/10/75	0.476	0.566-0.410	1.771	2.541-1.359
07/11/75	1.073	1.277-0.925	0.872	1.252-0.669
10/12/75	0.558	0.644-0.481	1.368	1.964-1.050
23/01/76	0.751	0.894-0.648	1.165	1.672-0.894
10/02/76	0.985	1.172-0.849	0.895	1.285-0.687
21/05/76	0.876	1.042-0.755	1.124	1.614-0.863
15/08/76	0.891	1.060-0.768	1.379	1.978-1.058
14/11/76	0.567	0.674-0.489	1.926	2.764-1.478
15/02/77	1.139	0.982-1.356	0.694	0.532-0.995

Appendix 3.1 Macoma balthica: The Exponential and Linear Regression

Equations and Mean Condition Factors Derived from the Field
Data for Each Station and Sampling Occasion.

Tdw = Animal total dry weight (mg);

Fdw = " flesh " " " ;

sw = " shell " " " ;

L, H = Shell length, height (mm) respectively;

CF_L , CF_H = Flesh condition factor in relation to length,
height respectively;

b = Regression coefficient;

S.E. = Standard error of b-values and mean CF_L , CF_H values;

a = Regression constant;

p = " significance, all relationships significant at
p *** level unless stated;

n.s. = non-significant relationship;

N.C. = Equation not computed as significance of relationship
too low;

I.D. = Insufficient Data , relationships not computed.

Appendix 3.1 continued. March, 1975 Data.

Relationship	Station	A1	A2	A3	A4	B1	B2	B3	B4	B5	C1	C2	C3	C4	C5
$Td_w = \frac{L^b + S.E.}{a}$		3.305	I.D.	3.536	3.228	3.349	2.961	3.827	3.714	4.442	I.D.	3.692	5.376	3.601	4.130
		S.E.		0.092	0.096	0.247	0.333	0.118	0.148	0.393		0.112	0.184	0.094	0.159
		a		43.18	23.02	35.87	15.59	93.54	57.37	32.40		54.16	2628.0	41.46	133.0
													*		*
$Td_w = \frac{H^b + S.E.}{a}$		3.326		3.637	3.438	3.433	3.278	3.807	3.659	4.339		3.475	4.075	3.594	3.250
		S.E.		0.095	0.108	0.237	0.368	0.111	0.132	0.491		0.176	0.529	0.082	0.381
		a		23.70	17.00	19.14	16.48	39.66	24.45	111.3		16.88	54.62	20.78	13.82
													n.s.		n.s.
$Fd_w = \frac{L^b + S.E.}{a}$		3.185		3.073	2.823	2.812	2.556	2.985	3.530	3.475		3.241	3.760	3.392	3.202
		S.E.		0.125	0.080	0.042	0.616	0.286	0.067	0.517		0.190	0.605	0.106	0.260
		a		123.0	69.65	80.39	54.66	79.80	350.9	301.7		148.2	580.9	213.1	130.6
													n.s.		n.s.
$Fd_w = \frac{H^b + S.E.}{a}$		3.199		3.151	2.983	2.867	2.748	2.975	3.464	3.304		3.056	2.909	3.376	2.537
		S.E.		0.140	0.120	0.079	0.705	0.344	0.089	0.662		0.188	0.011	0.111	0.187
		a		71.86	51.31	46.49	49.04	37.22	151.9	107.0		53.75	43.64	109.1	23.30
													n.s.		*
$sw = \frac{L^b + S.E.}{a}$		3.324		3.602	3.303	3.465	3.003	4.034	3.738	4.543		3.776	5.578	3.625	4.302
		S.E.		0.105	0.113	0.307	0.336	0.174	0.168	0.428		0.098	0.140	0.107	0.129
		a		57.51	31.45	53.98	19.97	185.2	68.19	462.7		75.73	4709.0	50.15	223.9
													*		*
$sw = \frac{H^b + S.E.}{a}$		3.346		3.706	3.520	3.555	3.338	4.022	3.686	4.447		3.553	4.221	3.619	3.381
		S.E.		0.105	0.121	0.296	0.363	0.133	0.148	0.506		0.176	0.588	0.093	0.424
		a		31.30	23.20	28.29	21.70	76.40	29.07	158.5		22.96	83.51	25.09	20.99
													n.s.		n.s.
$CF_L = \frac{b + S.E.L + a}{a}$		0.353		0.071	-0.249	-0.308	0.054	0.040	0.563	0.438		0.486	0.696	0.469	0.331
		S.E.		0.178	0.119	0.057	0.239	0.439	0.089	0.567		0.252	0.603	0.168	0.372
		a		8.884	12.09	10.85	8.840	12.11	3.947	5.701		7.257	2.949	6.922	9.003
					*			n.s.		n.s.		n.s.	n.s.	*	n.s.
$CF_H = \frac{b + S.E.H + a}{a}$		0.837		0.433	N.C.	-0.590	0.522	-0.168	1.100	0.497		0.416	-0.223	0.850	-1.186
		S.E.		0.485		0.313	0.616	1.211	0.209	1.359		0.577	0.040	0.373	0.403
		a		15.95		20.44	12.99	25.48	8.355	14.28		18.27	20.77	13.35	25.94
								n.s.		n.s.		n.s.	n.s.	*	n.s.
CF_L		9.331	12.119	9.616	10.324	9.309	9.332	12.518	9.152	10.615	-	10.730	9.720	11.472	11.575
		S.E.		0.465	0.265	0.197	0.916	1.143	0.554	0.995		1.306	0.725	0.640	0.403
		a		17.073	24.810	18.073	16.891	24.099	16.690	18.892		20.698	19.030	20.182	17.919
												1.867	0.183	1.143	1.144
CF_H		0.785	7.766	0.996	0.642	0.491	1.838	2.586	0.947	1.961		1.867	0.183	1.143	1.144

Appendix 3.1 continued. April, 1975 Data.

Relationship	Station	A1	A2	A3	A4	B1	B2	B3	B4	B5	C1	C2	C3	C4	C5
$T_{dw} = \frac{L^b \pm S.E.}{a}$	b	3.725	3.969	3.812	3.162	3.719	3.674	3.889	3.686	3.721	I.D.	I.D.	3.603	3.857	3.725
	S.E.	0.080	0.194	0.084	0.087	0.355	0.127	0.070	0.068	0.097			0.124	0.225	0.119
	a	82.08	113.4	86.72	23.36	69.44	61.34	96.23	56.61	63.02			39.61	74.74	56.97
$T_{dw} = \frac{H^b \pm S.E.}{a}$	P														
	b	3.849	4.091	3.792	3.360	3.988	3.707	3.774	3.762	3.868			3.778	3.806	3.967
	S.E.	0.109	0.230	0.072	0.103	0.254	0.137	0.106	0.080	0.107			0.122	0.145	0.143
$F_{dw} = \frac{L^b \pm S.E.}{a}$	a	47.39	63.16	38.22	16.90	59.47	33.17	33.18	31.21	42.98			28.02	30.92	42.54
	P														
	b	3.425	3.969	3.938	2.612	2.882	3.127	2.832	2.974	2.894			3.013	2.604	3.380
$F_{dw} = \frac{H^b \pm S.E.}{a}$	S.E.	0.086	0.194	0.160	0.095	0.136	0.097	0.078	0.053	0.092			0.078	0.259	0.131
	a	176.2	700.3	833.7	48.40	63.24	128.7	54.09	108.1	73.14			72.64	34.53	186.5
	P														
$F_{dw} = \frac{H^b \pm S.E.}{a}$	b	3.546	4.091	3.922	2.765	3.071	3.165	2.729	3.033	2.959			3.152	2.595	3.605
	S.E.	0.102	0.230	0.144	0.061	0.119	0.082	0.115	0.037	0.104			0.094	0.141	0.146
	a	107.6	389.9	361.7	36.38	53.68	78.00	23.97	66.67	49.45			53.74	20.07	144.3
$SW = \frac{L^b \pm S.E.}{a}$	P														
	b	3.810	3.969	3.787	3.287	3.910	3.760	4.119	3.790	3.882			3.724	4.035	3.775
	S.E.	0.094	0.194	0.084	0.105	0.403	0.152	0.084	0.079	0.114			0.141	0.226	0.136
$SW = \frac{H^b \pm S.E.}{a}$	a	131.3	135.3	95.52	35.94	131.7	87.32	200.2	80.60	106.1			61.34	129.1	74.99
	P														
	b	3.935	4.091	3.766	3.494	4.195	3.791	4.001	3.869	4.045			3.907	3.976	4.019
$CF_L = b \pm S.E.L + a$	S.E.	0.124	0.230	0.076	0.119	0.298	0.164	0.114	0.090	0.113			0.136	0.171	0.162
	a	74.49	75.36	42.41	25.73	112.4	46.35	65.36	43.73	72.47			43.01	50.74	55.63
	P														
$CF_H = b \pm S.E.H + a$	b	0.660	1.321	0.994	-0.599	-0.161	0.087	-0.220	-0.030	-0.149			0.043	-0.437	0.645
	S.E.	0.161	0.330	0.190	0.033	0.008	0.133	0.111	0.001	0.007			0.156	0.307	0.254
	a	8.494	0.176	0.685	14.20	13.87	9.622	15.14	9.019	12.26			13.85	16.28	6.812
$CF_H = b \pm S.E.H + a$	P		**				n.s.	n.s.	n.s.	n.s.			n.s.	n.s.	*
	b	1.947	3.298	2.255	-0.819	0.205	0.281	-0.550	0.089	-0.180			0.619	-0.975	2.084
	S.E.	0.463	0.852	0.415	0.204	0.348	0.231	0.233	0.095	0.219			0.396	0.360	0.587
$CF_H = b \pm S.E.H + a$	a	13.37	-1.32	1.224	23.24	19.82	15.87	28.38	15.40	20.36			20.66	29.62	8.176
	P		**				n.s.	*	n.s.	n.s.			n.s.	n.s.	**
	\bar{x}	14.459	13.447	7.862	9.740	11.936	10.596	13.061	8.795	10.972			14.230	11.634	11.260
CF_L	S.E.	0.501	1.116	0.571	0.261	0.383	0.454	0.485	0.018	0.087			0.479	0.807	0.599
	\bar{x}	27.558	25.470	14.498	18.340	21.824	18.492	25.944	15.944	19.069			25.045	21.142	20.013
	S.E.	1.137	2.233	1.038	0.412	0.978	0.675	2.217	0.246	0.549			1.069	1.121	1.199

Appendix 3.1 continued. June, 1975 Data.

Relationship	Station A1	A2	A3	A4	B1	B2	B3	B4	B5	C1	C2	C3	C4	C5
$T_{dw} = L \frac{b}{a} \pm S.E.$	b	3.834	3.832	3.529	3.448	3.773	3.716	3.885	3.794	I.D.	3.685	4.194	4.710	3.393
	S.E.	0.098	0.122	0.065	0.192	0.130	0.112	0.061	0.131		0.145	0.213	0.408	0.335
	a	102.2	84.48	45.90	53.70	87.84	78.93	84.68	74.47		71.32	182.4	490.5	27.36
$T_{dw} = H \frac{b}{a} \pm S.E.$	p	3.657	3.896	3.558	3.489	3.946	3.743	3.830	3.800		3.864	3.984	4.265	3.036
	b	0.100	0.107	0.075	0.199	0.132	0.103	0.075	0.112		0.289	0.255	0.178	0.252
	a	32.52	45.25	23.98	29.45	61.84	39.26	35.74	35.47		47.67	52.84	80.63	8.978
$F_{dw} = L \frac{b}{a} \pm S.E.$	p	3.232	2.594	2.612	2.882	2.758	2.727	2.974	2.991		3.297	2.995	2.920	2.113
	b	0.084	0.113	0.041	0.052	0.035	0.095	0.040	0.174		0.107	0.173	0.299	0.229
	a	105.0	27.88	48.40	63.28	44.51	31.08	108.1	69.77		113.1	63.48	60.61	10.92
$F_{dw} = H \frac{b}{a} \pm S.E.$	p	3.076	2.644	2.631	2.907	2.869	2.752	2.928	3.007		3.444	2.849	2.631	1.911
	b	0.098	0.096	0.033	0.067	0.046	0.084	0.047	0.142		0.259	0.188	0.223	0.144
	a	40.01	18.54	29.80	37.73	33.39	18.82	55.46	39.77		77.02	26.45	19.25	5.654
$sw = L \frac{b}{a} \pm S.E.$	p	4.058	4.186	3.707	3.732	4.061	4.119	4.002	3.969		3.828	4.493	4.971	3.780
	b	0.090	0.139	0.076	0.283	0.165	0.117	0.070	0.154		0.190	0.229	0.436	0.377
	a	222.8	234.4	78.27	132.5	217.3	278.8	123.4	135.8		134.0	450.0	1033.0	75.39
$sw = H \frac{b}{a} \pm S.E.$	p	3.864	4.259	3.739	3.781	4.252	4.148	3.946	3.972		4.020	4.268	4.504	3.385
	b	0.108	0.119	0.084	0.287	0.165	0.108	0.081	0.145		0.319	0.274	0.181	0.279
	a	66.59	119.2	39.66	69.71	150.2	128.3	50.79	62.15		89.21	119.3	154.6	21.92
$CF_L = b \pm S.E.L + a$	p	0.443	-0.722	-0.499	-0.251	-0.359	-0.461	-0.026	-0.030		0.574	N.C.	-0.106	-2.015
	b	0.142	0.199	0.017	0.012	0.018	0.185	0.001	0.277		0.218		0.367	0.583
	a	11.80	21.59	13.51	14.37	16.66	22.35	8.980	14.59		11.79		14.83	31.87
$CF_H = b \pm S.E.H + a$	p	0.394	-1.410	-1.067	-0.508	-0.424	-0.961	-0.147	-0.026		1.941	n.s.	n.s.	-4.822
	b	0.380	0.366	0.112	0.316	0.142	0.393	0.105	0.488		1.220	-0.528	-1.008	0.805
	a	26.29	37.47	24.30	25.55	26.46	40.33	16.82	25.98		17.39	32.19	32.28	57.57
CF_L	p	n.s.	**	**	n.s.	**	*	n.s.	n.s.		n.s.	n.s.	n.s.	
	\bar{x}	16.198	15.459	9.448	12.760	13.336	17.591	8.765	14.262		16.410	15.659	13.738	17.362
	S.E.	0.453	0.586	0.228	0.098	0.196	0.641	0.016	0.795		0.341	0.603	0.429	1.908
CF_H	p	29.506	27.619	17.197	22.867	23.214	32.238	15.823	25.751		30.177	27.598	23.636	27.079
	\bar{x}	0.603	0.876	0.446	0.442	0.388	1.105	0.263	1.152		1.274	1.310	0.785	3.721
	S.E.	0.877	0.876	0.446	0.442	0.388	1.105	0.263	1.152		1.274	1.310	0.785	3.721

Appendix 3.1 continued. July, 1975 Data.

Relationship	Station A1	A2	A3	A4	B1	B2	B3	B4	B5	C1	C2	C3	C4	C5
$Td_w = \frac{L^b + S.E.}{a}$	b 3.765 S.E. 0.095 a 85.70	3.518 0.099 42.47	3.642 0.115 55.85	3.379 0.115 32.18	3.967 0.146 126.9	4.049 0.156 174.2	4.080 0.117 193.0	3.982 0.084 105.1	3.755 0.089 59.41	3.695 0.165 55.73	3.733 0.181 64.97	4.288 0.191 199.4	3.612 0.171 41.64	3.827 0.329 68.08
$Td_w = \frac{H^b + S.E.}{a}$	P 3.724 b S.E. 0.080 a 36.92	3.548 0.097 20.27	3.665 0.098 29.39	3.526 0.098 20.87	3.923 0.179 54.92	4.101 0.108 81.81	4.013 0.091 70.04	4.031 0.072 50.83	3.809 0.075 31.51	3.771 0.143 33.83	3.780 0.203 34.01	3.960 0.109 44.07	3.322 0.206 11.17	3.678 0.249 25.03
$Fd_w = \frac{L^b + S.E.}{a}$	P 3.409 b S.E. 0.106 a 180.5	2.374 0.035 30.88	3.012 0.128 86.18	2.597 0.070 53.92	3.271 0.079 138.4	3.482 0.100 244.0	3.603 0.122 301.1	2.999 0.065 102.4	2.988 0.147 61.38	2.996 0.348 56.13	3.532 0.141 154.6	2.952 0.114 74.13	2.888 0.162 58.19	3.541 0.436 270.2
$Fd_w = \frac{H^b + S.E.}{a}$	P 3.371 b S.E. 0.097 a 84.03	2.390 0.033 18.59	3.026 0.123 50.23	2.688 0.053 37.21	3.230 0.126 68.92	3.488 0.094 117.8	3.527 0.127 119.3	3.019 0.052 57.50	3.043 0.129 37.99	3.045 0.370 36.33	3.564 0.210 81.96	2.717 0.088 25.71	2.647 0.208 19.93	3.427 0.343 111.3
$sw = \frac{L^b + S.E.}{a}$	P 3.873 b S.E. 0.103 a 139.3	3.748 0.123 80.44	3.799 0.126 94.45	3.517 0.139 49.04	4.146 0.185 238.5	4.171 0.194 291.9	4.212 0.130 334.9	4.156 0.102 176.4	3.919 0.095 105.5	3.872 0.152 106.7	3.806 0.239 104.8	4.513 0.198 390.7	3.733 0.184 63.83	3.874 0.324 87.28
$sw = \frac{H^b + S.E.}{a}$	P 3.831 b S.E. 0.088 a 58.59	3.782 0.117 36.71	3.822 0.110 48.34	3.674 0.119 31.53	4.099 0.215 99.40	4.235 0.137 136.7	4.147 0.097 118.8	4.211 0.084 83.28	3.973 0.086 54.13	3.953 0.114 63.48	3.859 0.241 54.74	4.166 0.115 79.58	3.435 0.213 16.44	3.719 0.249 31.52
$CF_L = b + \frac{S.E.L}{a}$	P 0.680 b S.E. 0.156 a 7.466	-0.824 0.054 16.20	0.102 0.253 11.35	-0.536 0.024 12.61	0.424 0.139 9.214	0.616 0.017 6.061	0.833 0.172 5.038	-0.001 0.000 9.755	-0.131 0.249 17.64	0.102 0.595 17.37	1.260 0.338 9.397	-0.060 0.149 12.83	-0.140 0.218 14.74	0.957 0.768 4.197
$CF_H = b + \frac{S.E.H}{a}$	P 1.383 b S.E. 0.306 a 14.67	-2.015 0.169 31.72	0.303 0.486 19.30	-0.950 0.154 21.58	0.752 0.456 17.44	1.205 0.321 13.56	1.631 0.421 12.14	0.076 0.129 17.58	N.C. 0.868 29.411	0.386 1.355 28.35	3.054 1.038 15.21	-0.780 0.250 28.62	-1.066 0.601 33.03	1.671 1.272 9.685
CF_L	P 13.627 S.E. 0.639 a 24.923	9.555 0.610 18.780	12.149 0.584 21.270	8.463 0.300 15.620	12.515 0.452 22.285	12.097 0.576 23.113	12.902 0.748 24.574	9.750 0.550 18.077	16.339 0.868 29.411	18.650 2.323 32.372	19.445 1.017 35.193	12.203 0.520 21.911	13.247 0.391 23.619	10.225 0.908 18.337
CF_H	S.E. 1.060	1.193	0.928	0.512	1.018	1.334	1.372	0.308	1.390	4.416	2.132	1.147	1.169	1.305

Appendix 3.1 continued. August, 1975 Data.

Relationship	Station	A1	A2	A3	A4	B1	B2	B3	B4	B5	C1	C2	C3	C4	C5
$T_{dw} = \frac{L^b \pm S.E.}{a}$	b	3.948	3.953	3.600	3.633	4.043	3.806	3.917	3.752	3.872	3.771	3.915	3.966	3.160	4.317
	S.E.	0.085	0.131	0.091	0.113	0.355	0.113	0.089	0.100	0.113	0.310	0.121	0.185	0.460	0.650
	a	123.9	109.8	45.43	57.79	18.81	79.87	125.1	63.83	82.58	82.04	99.40	87.28	13.48	149.3
	P										**				
$T_{dw} = \frac{H^b \pm S.E.}{a}$	b	3.717	4.163	3.718	3.658	3.845	3.814	3.835	3.903	3.972	3.967	3.852	3.718	3.196	4.744
	S.E.	0.090	0.124	0.079	0.093	0.367	0.102	0.086	0.086	0.106	0.363	0.148	0.199	0.335	0.630
	a	34.21	69.81	28.39	28.10	60.99	37.47	42.63	38.34	46.07	62.44	39.19	26.91	8.026	144.5
	P										**				
$F_{dw} = \frac{L^b \pm S.E.}{a}$	b	3.818	3.026	2.569	3.496	3.824	2.871	3.259	3.157	3.142	2.806	3.006	2.954	2.147	3.836
	S.E.	0.071	0.142	0.143	0.120	0.353	0.090	0.123	0.125	0.111	0.305	0.099	0.111	0.253	0.624
	a	539.6	91.83	31.41	245.9	452.2	56.01	140.5	91.35	91.89	48.45	69.52	61.09	11.31	367.9
	P										*				
$F_{dw} = \frac{H^b \pm S.E.}{a}$	b	3.592	3.187	2.640	3.514	3.637	2.875	3.190	3.278	3.229	2.974	2.969	2.761	2.097	4.216
	S.E.	0.083	0.142	0.156	0.114	0.362	0.086	0.121	0.127	0.098	0.231	0.095	0.147	0.244	0.614
	a	154.6	64.98	21.91	121.3	156.3	31.53	57.27	58.82	57.81	41.50	34.72	25.03	6.725	358.0
	P										**				
$sw = \frac{L^b \pm S.E.}{a}$	b	3.970	4.177	3.833	3.663	4.131	4.072	4.167	3.894	4.048	3.955	4.207	4.208	3.280	4.417
	S.E.	0.099	0.131	0.103	0.114	0.356	0.131	0.106	0.114	0.126	0.325	0.127	0.201	0.507	0.657
	a	157.6	214.4	90.03	74.87	307.2	184.4	281.5	108.6	150.3	153.8	235.9	177.7	20.14	215.7
	P										**				
$sw = \frac{H^b \pm S.E.}{a}$	b	3.738	4.400	3.961	3.690	3.927	4.082	4.080	4.052	4.153	4.156	4.136	3.948	3.326	4.853
	S.E.	0.101	0.122	0.086	0.092	0.371	0.118	0.103	0.099	0.122	0.408	0.163	0.211	0.376	0.635
	a	43.24	132.9	54.76	36.29	97.03	82.28	89.52	64.16	81.45	114.1	86.36	51.17	12.00	208.6
	P										**				
$CF_L = b \pm S.E.L + a$	b	1.008	0.041	-0.677	0.670	1.525	-0.189	0.427	0.304	0.266	-0.209	0.085	-0.052	-0.739	1.424
	S.E.	0.087	0.217	0.202	0.176	0.292	0.139	0.170	0.229	0.198	0.339	0.192	0.224	0.239	1.430
	a	2.085	11.27	18.90	6.070	1.267	15.69	8.806	12.88	12.58	15.35	13.97	15.45	19.70	3.848
	P		n.s.	**	**		n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.
$CF_H = b \pm S.E.H + a$	b	1.545	0.677	-1.171	1.625	2.578	-0.392	0.732	1.145	0.862	-0.076	0.036	-0.900	-1.815	4.317
	S.E.	0.247	0.506	0.494	0.413	0.636	0.307	0.422	0.548	0.400	0.511	0.427	0.607	0.506	2.798
	a	9.635	17.53	31.64	11.02	6.340	28.54	20.40	21.40	21.01	23.51	27.14	32.13	37.06	-1.34
	P		n.s.	*		**	n.s.	n.s.	*	*	n.s.	n.s.	n.s.	**	n.s.
CF_L	\bar{x}	11.768	11.639	13.376	11.452	10.803	13.718	13.014	15.543	14.917	12.971	14.632	15.074	11.263	13.107
	S.E.	0.695	0.437	0.562	0.565	1.368	0.660	0.640	0.604	0.567	0.675	0.418	0.507	0.492	1.453
CF_H	\bar{x}	21.762	22.318	23.772	21.582	19.607	25.186	26.124	29.487	27.198	22.786	27.366	26.803	19.906	22.189
	S.E.	1.083	0.826	0.987	1.086	2.209	1.177	1.223	1.199	0.984	0.741	0.758	1.378	0.924	2.635

Appendix 3.1 continued. October, 1975 Data.

Relationship	Station	A1	A2	A3	A4	B1	B2	B3	B4	B5	C1	C2	C3	C4	C5
$Td_w = \frac{L^b + S.E.}{a}$	b	3.754	3.569	3.655	3.477	3.773	3.805	3.714	3.901	3.938	I.D.	3.669	3.848	3.938	3.620
	S.E.	0.073	0.097	0.108	0.091	0.098	0.085	0.087	0.090	0.136		0.118	0.103	0.085	0.160
	a	93.07	51.34	57.88	41.47	79.91	96.16	81.47	89.52	99.04		66.74	84.82	79.68	48.17
$Td_w = \frac{H^b + S.E.}{a}$	p														
	b	3.693	3.466	3.724	3.598	3.685	3.675	3.678	3.921	3.946		3.857	3.843	3.865	3.560
	S.E.	0.071	0.105	0.105	0.093	0.114	0.076	0.079	0.085	0.124		0.120	0.084	0.067	0.222
$Fd_w = \frac{L^b + S.E.}{a}$	a	36.39	19.92	32.97	24.34	30.68	31.88	32.22	40.60	47.37		41.45	39.62	32.10	24.18
	p														
	b	3.300	3.437	3.174	3.231	3.284	3.697	3.420	3.435	3.564		3.733	3.355	3.300	3.401
$Fd_w = \frac{H^b + S.E.}{a}$	S.E.	0.125	0.225	0.164	0.154	0.172	0.108	0.062	0.104	0.097		0.141	0.093	0.156	0.252
	a	238.0	263.6	133.1	156.4	154.5	428.4	260.5	247.1	319.0		333.9	170.9	183.0	241.6
	p														
$Fd_w = \frac{H^b + S.E.}{a}$	b	3.277	3.342	3.229	3.338	3.210	3.572	3.380	3.442	3.568		3.933	3.346	3.212	3.393
	S.E.	0.122	0.219	0.168	0.164	0.173	0.098	0.067	0.112	0.088		0.127	0.085	0.183	0.246
	a	103.6	106.7	80.95	94.32	67.61	146.9	109.5	121.0	162.9		208.4	87.20	80.52	137.4
$sw = \frac{L^b + S.E.}{a}$	p														
	b	3.842	3.601	3.743	3.524	3.874	3.834	3.770	3.973	3.998		3.655	3.950	4.014	3.661
	S.E.	0.074	0.098	0.120	0.094	0.105	0.133	0.097	0.099	0.148		0.134	0.116	0.093	0.174
$sw = \frac{H^b + S.E.}{a}$	a	134.2	64.83	83.18	54.74	123.1	127.5	111.8	121.1	131.7		84.16	128.5	106.0	60.24
	p														
	b	3.780	3.496	3.814	3.649	3.782	3.711	3.734	3.995	4.006		3.839	3.946	3.943	3.594
$CF_L = b + S.E.L + a$	S.E.	0.072	0.108	0.116	0.093	0.122	0.125	0.089	0.093	0.136		0.142	0.097	0.065	0.239
	a	51.31	24.90	46.84	32.00	46.02	41.84	43.22	54.26	62.30		52.13	58.93	42.23	29.72
	p														
$CF_H = b + S.E.H + a$	b	0.389	0.459	0.299	0.248	0.455	0.816	0.535	0.605	0.841		1.239	0.677	0.213	0.518
	S.E.	0.114	0.215	0.218	0.211	0.191	0.170	0.064	0.120	0.114		0.248	0.143	0.191	0.312
	a	5.300	6.002	8.602	8.541	8.253	3.649	4.808	5.183	3.413		3.749	6.883	8.907	5.644
$CF_H = b + S.E.H + a$	p	**	n.s.	n.s.	n.s.	*								n.s.	n.s.
	b	0.794	0.768	0.856	1.030	0.766	1.629	1.149	1.464	1.778		3.779	1.321	0.141	1.012
	S.E.	0.263	0.524	0.491	0.539	0.458	0.372	0.205	0.301	0.221		0.496	0.283	0.452	0.565
$CF_H = b + S.E.H + a$	a	11.20	13.34	13.75	13.68	17.45	9.509	11.00	9.521	6.171		2.748	13.33	18.69	9.014
	p	**	n.s.	n.s.	n.s.	n.s.								n.s.	n.s.
	\bar{x}	8.594	9.959	10.934	10.344	11.379	11.367	9.324	10.011	9.883	9.883	10.934	11.211	12.111	11.145
$CF_H = b + S.E.H + a$	S.E.	0.374	0.670	0.420	0.471	0.709	0.880	0.369	0.434	0.662		0.861	0.456	0.489	0.661
	\bar{x}	11.599	18.727	19.267	19.698	21.709	21.902	18.700	18.961	17.472	17.222	21.132	21.729	19.914	14.857
	S.E.	0.682	1.283	0.776	0.956	1.335	1.533	0.749	0.858	1.136	1.782	1.782	0.752	0.955	1.033

Appendix 3.1 continued. November, 1975 Data.

Relationship	Station	A1	A2	A3	A4	B1	B2	B3	B4	B5	C1	C2	C3	C4	C5
$T_{dw} = \frac{L^b \pm S.E.}{a}$	b	3.790	3.479	3.720	3.529	3.469	3.578	3.914	3.834	3.973	4.244	3.701	3.873	3.896	3.905
	S.E.	0.070	0.091	0.073	0.096	0.108	0.086	0.084	0.087	0.086	0.127	0.231	0.145	0.064	0.133
	a	87.77	40.91	69.98	47.84	46.52	54.64	129.7	78.70	110.5	262.0	66.00	85.17	78.84	90.84
$T_{dw} = \frac{H^b \pm S.E.}{a}$	P	3.758	3.556	3.941	3.680	3.443	3.516	3.856	3.792	4.010	4.209	3.714	3.807	3.780	3.850
	b	0.072	0.101	0.078	0.094	0.089	0.081	0.070	0.082	0.099	0.124	0.196	0.122	0.055	0.131
	a	37.69	23.01	49.62	30.11	20.46	21.92	47.22	33.52	52.52	105.4	29.69	33.44	28.02	37.72
$F_{dw} = \frac{L^b \pm S.E.}{a}$	P	3.521	3.160	3.391	3.733	3.309	3.332	3.645	3.494	3.837	3.025	3.369	3.153	3.352	3.838
	b	0.079	0.060	0.107	0.218	0.198	0.068	0.081	0.076	0.102	0.330	0.217	0.156	0.094	0.262
	a	293.8	121.3	220.6	566.1	148.7	178.8	497.5	276.7	627.3	103.0	193.9	118.3	228.9	646.5
$F_{dw} = \frac{H^b \pm S.E.}{a}$	P	3.489	3.229	3.585	3.901	3.301	3.268	3.587	3.452	3.877	2.966	3.376	3.091	3.248	3.795
	b	0.086	0.074	0.124	0.219	0.169	0.074	0.078	0.077	0.106	0.360	0.197	0.147	0.093	0.250
	a	130.3	71.76	159.0	352.0	69.77	75.58	192.3	126.3	308.4	49.42	93.07	54.55	93.07	278.3
$sw = \frac{L^b \pm S.E.}{a}$	P	3.852	3.544	3.788	3.501	3.525	3.628	3.953	3.891	3.995	4.390	3.772	4.014	3.957	3.928
	b	0.076	0.113	0.082	0.098	0.099	0.095	0.091	0.096	0.090	0.150	0.237	0.149	0.071	0.148
	a	124.2	57.19	96.47	52.23	67.70	74.49	166.2	103.5	133.6	434.8	92.58	137.1	101.0	109.0
$sw = \frac{H^b \pm S.E.}{a}$	P	3.821	3.623	4.015	3.650	3.493	3.566	3.896	3.849	4.031	4.357	3.786	3.945	3.840	3.872
	b	0.077	0.124	0.085	0.098	0.091	0.089	0.077	0.090	0.104	0.138	0.198	0.125	0.060	0.147
	a	51.46	31.86	68.13	32.91	29.12	29.57	59.98	43.56	63.14	170.8	41.07	52.07	35.39	44.91
$CF_L = b \pm S.E.L + a$	P	0.722	0.260	0.661	0.790	0.730	0.512	0.638	0.676	0.978	0.023	0.792	0.245	0.257	0.775
	b	0.089	0.095	0.147	0.174	0.332	0.089	0.082	0.098	0.100	0.247	0.296	0.267	0.101	0.273
	a	4.234	9.378	4.957	2.140	7.484	6.926	2.565	4.648	1.316	10.44	4.952	9.908	7.322	2.875
$CF_H = b \pm S.E.H + a$	P	1.620	0.905	2.125	2.367	1.588	0.939	1.366	1.424	2.305	n.s.	1.874	0.244	0.375	1.759
	b	0.228	0.254	0.406	0.394	0.671	0.247	0.183	0.210	0.265	-0.028	0.644	0.544	0.218	0.629
	a	8.565	15.50	5.101	0.728	15.54	15.63	6.623	9.138	1.917	19.77	9.863	20.57	15.15	4.901
CF_L	P	10.128	11.140	10.282	7.867	12.373	11.301	7.877	9.886	9.253	10.792	10.929	11.714	10.054	9.176
	S.E.	0.503	0.326	0.396	0.470	0.852	0.481	0.513	0.402	0.577	0.918	1.055	0.604	0.276	0.483
	\bar{x}	19.253	20.488	19.029	14.654	24.054	22.076	15.668	18.184	17.156	19.412	21.203	22.026	18.416	16.634
CF_H	S.E.	0.953	0.748	0.909	0.937	1.441	0.922	0.911	0.715	1.130	1.647	1.946	1.041	0.471	0.905
	\bar{x}	0.953	0.748	0.909	0.937	1.441	0.922	0.911	0.715	1.130	1.647	1.946	1.041	0.471	0.905

Appendix 3.1 continued. December, 1975 Data.

Relationship	Station	A1	A2	A3	A4	B1	B2	B3	B4	B5	C1	C2	C3	C4	C5
$T_{dw} = \frac{L^b + S.E.}{a}$	b	3.649	3.429	3.568	3.365	3.400	3.855	3.789	3.728	3.816	I.D.	2.882	3.753	3.767	3.689
	S.E.	0.089	0.184	0.100	0.056	0.093	0.085	0.112	0.072	0.204		0.067	0.086	0.097	0.074
	a	61.63	36.87	49.61	35.04	40.18	108.5	92.74	65.03	81.93		17.94	59.09	58.96	58.21
$T_{dw} = \frac{H^b + S.E.}{a}$	P	3.665	3.581	3.653	3.493	3.474	3.716	3.789	3.782	3.923		3.070	3.740	3.737	3.638
	b	0.078	0.162	0.099	0.043	0.099	0.077	0.100	0.083	0.221		0.064	0.075	0.107	0.101
	a	30.15	22.79	27.85	21.86	21.06	33.72	41.92	34.22	44.72		12.32	28.16	25.94	26.96
$F_{dw} = \frac{L^b + S.E.}{a}$	P	3.308	2.907	3.357	3.247	3.177	3.757	3.889	3.378	3.505		2.905	3.296	3.267	3.662
	b	0.114	0.257	0.140	0.113	0.075	0.112	0.136	0.087	0.211		0.163	0.049	0.119	0.204
	a	174.7	94.82	219.0	164.3	135.4	507.9	774.5	240.6	331.4		103.1	183.1	195.4	458.1
$F_{dw} = \frac{H^b + S.E.}{a}$	P	3.321	3.045	3.426	3.381	3.252	3.626	3.880	3.434	3.560		3.093	3.282	3.237	3.617
	b	0.108	0.225	0.152	0.101	0.072	0.097	0.135	0.087	0.228		0.172	0.045	0.129	0.209
	a	91.31	64.25	124.7	105.9	74.59	164.2	336.7	136.1	188.8		70.44	95.95	95.23	215.4
$sw = \frac{L^b + S.E.}{a}$	P	3.723	3.520	3.613	3.393	3.450	3.866	3.780	3.779	3.859		2.876	3.818	3.823	3.701
	b	0.096	0.180	0.107	0.055	0.103	0.098	0.117	0.081	0.208		0.069	0.097	0.110	0.078
	a	87.70	51.56	64.04	44.77	54.96	135.5	107.3	83.68	103.4		21.72	78.07	74.56	68.08
$sw = \frac{H^b + S.E.}{a}$	P	3.739	3.674	3.700	3.521	3.523	3.725	3.782	3.833	3.968		3.064	3.806	3.793	3.650
	b	0.086	0.159	0.103	0.045	0.110	0.091	0.103	0.094	0.224		0.065	0.086	0.119	0.105
	a	42.32	31.39	35.80	27.73	28.48	41.91	48.72	43.56	56.14		14.94	36.77	32.41	31.44
$CF_L = \frac{b + S.E.L + a}{a}$	P	0.410	-0.058	0.476	0.297	0.357	0.810	1.047	0.387	0.484		-0.168	0.403	0.194	0.612
	b	0.126	0.275	0.158	0.152	0.085	0.123	0.128	0.099	0.239		0.261	0.070	0.136	0.182
	a	7.666	9.401	5.858	7.908	7.975	3.159	0.044	6.008	5.237		9.274	6.694	7.543	3.778
$CF_H = \frac{b + S.E.H + a}{a}$	P	**	n.s.	**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.		n.s.	n.s.	n.s.	**
	b	0.962	0.293	1.365	1.148	1.032	1.679	2.332	1.024	1.405		0.251	0.781	0.349	1.214
	a	0.279	0.706	0.390	0.310	0.202	0.270	0.296	0.215	0.573		0.677	0.143	0.338	0.436
CF_L	P	13.85	15.22	9.092	11.85	14.85	8.800	0.659	9.851	8.160		15.28	12.42	14.54	7.027
	b	**	n.s.	**	n.s.	n.s.	n.s.	n.s.	n.s.	*		n.s.	n.s.	n.s.	*
	a	11.090	8.817	9.899	10.100	10.227	10.082	8.834	9.098	9.094		8.394	9.920	9.401	7.974
CF_H	P	0.490	0.520	0.445	0.414	0.293	0.678	0.724	0.348	0.727		0.284	0.424	0.345	0.488
	b	20.402	17.547	18.488	18.705	20.044	20.199	16.543	16.535	17.198		16.332	17.591	17.279	13.948
	a	0.901	1.039	0.910	0.752	0.602	1.186	1.334	0.655	1.403		0.553	0.702	0.692	0.922

Appendix 3.1 continued. January, 1976 Data.

Relationship	Station	A1	A2	A3	A4	B1	B2	B3	B4	B5	C1	C2	C3	C4	C5
$TdW = \frac{L^b + S.E.}{a}$	b	3.568	3.488	3.579	3.450	3.581	4.141	3.751	3.583	3.964	4.122	3.243	3.961	3.824	3.495
	S.E.	0.079	0.103	0.076	0.079	0.154	0.083	0.098	0.075	0.090	0.490	0.225	0.126	0.082	0.120
	a	62.47	46.25	54.29	44.57	46.62	211.5	83.18	52.29	104.2	153.4	25.89	102.1	69.00	40.42
$TdW = \frac{H^b + S.E.}{a}$	P	3.524	3.609	3.659	3.580	3.603	4.027	3.822	3.628	3.890	3.977	3.339	3.855	3.761	3.441
	b	0.097	0.152	0.078	0.080	0.128	0.083	0.092	0.086	0.090	0.228	0.199	0.123	0.063	0.106
	a	24.81	27.05	29.79	26.64	22.95	68.95	39.78	25.79	40.38	51.22	16.44	37.27	28.92	18.11
$FdW = \frac{L^b + S.E.}{a}$	P	3.078	2.970	3.132	3.454	2.949	3.894	3.604	3.268	3.474	2.969	3.123	3.314	3.240	3.169
	b	0.115	0.115	0.140	0.117	0.154	0.141	0.106	0.082	0.118	1.239	0.239	0.147	0.106	0.296
	a	132.8	115.5	165.8	294.1	81.87	1052.0	458.6	223.3	270.1	80.83	136.6	207.3	197.4	162.4
$FdW = \frac{H^b + S.E.}{a}$	P	3.042	3.085	3.209	3.574	2.970	3.783	3.671	3.299	3.402	2.957	3.211	3.220	3.192	3.137
	b	0.122	0.126	0.138	0.132	0.124	0.143	0.104	0.104	0.127	1.058	0.235	0.150	0.088	0.268
	a	60.12	75.02	99.17	172.2	45.85	363.6	225.0	115.0	115.8	46.49	87.26	88.49	95.54	80.78
$SW = \frac{L^b + S.E.}{a}$	P	3.675	3.571	3.625	3.445	3.687	4.161	3.768	3.623	4.038	4.229	3.263	4.050	3.898	3.561
	b	0.083	0.109	0.074	0.097	0.157	0.100	0.105	0.085	0.105	0.440	0.233	0.137	0.087	0.139
	a	94.93	63.90	73.02	52.24	69.55	252.9	99.97	65.01	142.1	224.6	31.77	141.8	90.29	53.23
$SW = \frac{H^b + S.E.}{a}$	P	3.629	3.693	3.733	3.576	3.709	4.048	3.840	3.670	3.964	4.070	3.362	3.942	3.833	3.504
	b	0.103	0.161	0.077	0.097	0.132	0.099	0.099	0.093	0.102	0.168	0.205	0.133	0.070	0.130
	a	36.64	36.81	39.52	31.33	33.50	82.06	47.68	31.92	54.28	71.03	20.16	50.72	37.13	23.45
$CF_L = b + S.E.L + a$	P	0.137	-0.049	0.100	0.449	-0.018	0.539	0.596	0.267	0.615	-0.130	0.278	0.487	0.220	0.079
	b	0.100	0.122	0.154	0.144	0.174	0.119	0.115	0.085	0.183	1.098	0.343	0.151	0.110	0.291
	a	7.876	8.646	7.342	5.199	11.38	2.252	2.903	5.683	5.045	14.03	7.455	5.448	6.670	8.196
$CF_H = b + S.E.H + a$	P	n.s.	n.s.	n.s.	**	n.s.	1.106	1.643	**	**	n.s.	n.s.	**	n.s.	n.s.
	b	0.306	0.212	0.481	1.340	N.C.	1.106	0.798	0.271	1.191	-0.144	0.626	0.810	0.400	0.146
	a	0.302	0.340	0.342	0.385	0.289	0.263	0.263	0.271	0.431	1.851	0.729	0.346	0.200	0.639
CF_L	P	16.41	14.34	12.09	8.488	5.582	4.967	10.172	**	*	21.946	13.093	12.005	12.48	15.17
	x	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.
	S.E.	9.015	8.177	8.125	9.269	11.208	7.669	8.083	7.680	10.557	11.961	9.468	9.389	8.698	8.771
	x	0.370	0.329	0.372	0.356	0.808	0.563	0.558	0.250	0.596	2.100	0.746	0.529	0.323	0.481
CF_H	P	18.411	15.961	15.145	18.180	20.892	14.565	16.252	14.947	19.413	20.033	16.832	17.358	15.525	16.049
	x	0.867	0.704	0.665	0.766	1.270	1.064	1.105	0.614	1.104	3.064	1.338	0.925	0.490	0.870

Appendix 3.1 continued. May, 1976 Data.

Relationship	Station	A1	A2	A3	A4	B1	B2	B3	B4	B5	C1	C2	C3	C4	C5
$Td_w = \frac{L^b + S.E.}{a}$	P	3.623	I.D.	3.500	3.181	3.928	4.001	3.649	3.841	3.914	4.179	3.554	3.700	3.782	3.492
	S.E.	0.090		0.099	0.100	0.146	0.130	0.102	0.083	0.079	0.027	0.101	0.112	0.081	0.106
	a	71.81		45.01	23.97	119.9	153.1	70.43	86.18	95.04	196.6	48.66	62.38	64.59	38.39
$Td_w = \frac{H^b + S.E.}{a}$	P	3.722		3.613	3.419	3.924	3.951	3.785	3.895	3.939	4.308	3.651	3.733	3.814	3.516
	S.E.	0.105		0.084	0.120	0.105	0.158	0.082	0.076	0.070	0.195	0.067	0.098	0.080	0.095
	a	40.11		26.01	18.70	53.46	60.13	40.39	39.79	44.98	118.4	29.29	31.15	32.06	20.02
$Fd_w = \frac{L^b + S.E.}{a}$	P	3.160		2.733	2.612	2.821	2.754	2.700	2.974	2.886	2.680	2.968	2.750	2.703	2.554
	S.E.	0.100		0.108	0.126	0.097	0.174	0.068	0.134	0.077	0.113	0.078	0.108	0.136	0.211
	a	117.5		63.69	48.41	52.90	44.17	51.99	108.1	71.68	35.23	79.47	65.33	13.69	53.14
$Fd_w = \frac{H^b + S.E.}{a}$	P	3.261		2.827	2.803	2.804	2.725	2.782	3.022	2.895	2.759	3.035	2.778	2.732	2.562
	S.E.	0.095		0.087	0.148	0.099	0.179	0.083	0.128	0.085	0.224	0.077	0.097	0.131	0.218
	a	72.49		41.89	39.16	28.73	23.46	33.26	60.22	40.54	25.23	50.87	39.16	44.98	32.21
$sw = \frac{L^b + S.E.}{a}$	P	3.745		3.661	3.294	4.158	4.382	3.852	3.968	4.078	4.486	3.688	3.845	3.902	3.641
	S.E.	0.117		0.102	0.115	0.169	0.168	0.116	0.090	0.090	0.049	0.123	0.121	0.081	0.105
	a	122.7		74.30	35.99	255.0	470.7	135.4	130.8	160.6	508.4	79.82	98.68	92.34	59.73
$sw = \frac{H^b + S.E.}{a}$	P	3.841		3.777	3.541	4.154	4.322	3.997	4.022	4.106	4.623	3.791	3.878	3.935	3.668
	S.E.	0.137		0.090	0.136	0.128	0.201	0.094	0.086	0.081	0.230	0.089	0.108	0.080	0.090
	a	66.49		41.72	27.84	108.7	167.2	75.51	58.57	73.79	294.5	47.37	47.85	44.84	29.93
$CF_L = b + S.E.L + a$	P	0.122		-0.369	-0.483	-0.227	-0.342	-0.372	-0.133	-0.172	-0.372	-0.072	-0.313	-0.284	-0.619
	S.E.	0.135		0.148	0.151	0.106	0.220	0.080	0.109	0.093	0.079	0.136	0.134	0.114	0.254
	a	10.81		12.37	13.45	15.16	16.59	13.70	10.21	12.59	17.81	12.47	11.92	9.973	12.82
	P	n.s.		*	**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	*	*
	b	0.619		-0.552	-0.535	-0.598	-0.851	-0.683	-0.193	-0.413	-0.600	-0.011	-0.647	-0.586	-1.365
	S.E.	0.300		0.280	0.393	0.256	0.499	0.222	0.267	0.229	0.450	0.269	0.277	0.260	0.596
	a	18.18		21.31	21.52	28.83	31.49	25.10	19.20	23.43	29.44	21.06	21.53	17.85	23.37
	P	*		n.s.	n.s.	*	n.s.	**	n.s.	n.s.	n.s.	n.s.	*	*	*
$CF_H = b + S.E.L + a$	P	11.653		10.016	9.097	12.245	12.758	10.341	8.933	10.977	12.811	12.006	9.595	7.269	8.470
	S.E.	0.294		0.499	0.428	0.487	0.527	0.366	0.314	0.285	1.265	0.355	0.346	0.360	0.671
	a	21.657		18.465	17.685	22.541	23.735	20.184	17.720	20.277	22.819	21.004	17.605	13.294	15.545
	S.E.	0.545		0.697	0.693	1.005	1.007	0.685	0.598	0.578	2.019	0.579	0.584	0.650	1.258

Appendix 3.1 continued. August, 1976 Data.

Relationship	Station	A1	A2	A3	A4	B1	B2	B3	B4	B5	C1	C2	C3	C4	C5
$Td_w = \frac{L^b \pm S.E.}{a}$	b	3.722	3.212	3.240	2.829	3.684	3.915	3.753	3.821	3.597	I.D.	3.631	3.584	3.728	3.512
	S.E.	0.070	0.150	0.098	0.385	0.073	0.070	0.078	0.083	0.093		0.248	0.090	0.138	0.098
	a	86.28	24.05	26.28	11.49	75.36	123.4	91.47	80.44	48.53		63.17	53.94	60.29	41.43
$Td_w = \frac{H^b \pm S.E.}{a}$	P	3.753	3.292	3.407	3.074	3.713	3.799	3.922	3.864	3.627		3.731	3.613	3.607	3.527
	b	0.077	0.123	0.126	0.422	0.068	0.071	0.090	0.098	0.093		0.162	0.097	0.122	0.100
	a	38.04	14.09	18.32	10.09	34.52	43.40	54.08	37.57	25.03		32.53	26.93	20.75	19.25
$Fd_w = \frac{L^b \pm S.E.}{a}$	P	3.126	2.596	2.471	2.604	3.391	3.481	2.957	2.978	3.119		3.095	2.403	2.793	3.113
	b	0.066	0.158	0.084	0.516	0.069	0.065	0.061	0.063	0.077		0.205	0.134	0.136	0.104
	a	114.9	50.93	43.15	54.83	171.2	243.6	85.57	97.92	126.9		112.0	32.31	89.17	171.8
$Fd_w = \frac{H^b \pm S.E.}{a}$	P	3.151	2.668	2.605	2.756	3.420	3.381	3.086	3.014	3.148		3.171	2.414	2.701	3.120
	b	0.074	0.124	0.089	0.595	0.059	0.061	0.078	0.071	0.072		0.151	0.149	0.127	0.125
	a	57.97	33.56	33.17	41.51	83.73	96.68	56.07	56.58	71.93		62.46	20.03	39.98	86.10
$sw = \frac{L^b \pm S.E.}{a}$	P	3.877	3.319	3.367	2.880	3.777	4.021	3.956	3.964	3.676		3.756	3.841	3.826	3.565
	b	0.084	0.158	0.110	0.405	0.081	0.077	0.089	0.090	0.104		0.265	0.097	0.146	0.111
	a	154.8	34.81	39.39	14.91	120.8	195.5	177.5	127.4	67.17		100.9	108.6	82.49	51.86
$sw = \frac{H^b \pm S.E.}{a}$	P	3.910	3.400	3.540	3.140	3.806	3.902	4.134	4.008	3.705		3.863	3.871	3.702	3.581
	b	0.088	0.134	0.139	0.437	0.078	0.078	0.102	0.107	0.105		0.176	0.106	0.130	0.109
	a	66.18	19.98	29.04	13.28	54.19	66.79	102.0	60.87	34.12		51.01	51.58	27.60	23.86
$CF_L = b \pm S.E.L + a$	P	0.166	-0.626	-0.687	-0.378	0.682	0.636	-0.080	N.C.	0.178		0.227	-0.891	-0.156	0.096
	b	0.102	0.216	0.081	0.406	0.124	0.104	0.081		0.104		0.282	0.181	0.107	0.125
	a	9.935	14.01	13.74	11.33	7.532	5.965	11.43	n.s.	8.742		9.176	16.38	8.679	6.579
$CF_H = b \pm S.E.H + a$	P	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.		n.s.	n.s.	n.s.	n.s.
	b	0.523	-1.152	-1.141	-0.759	1.772	1.228	0.190	0.108	0.499		0.735	-1.946	-0.574	0.231
	a	0.300	0.423	0.207	1.118	0.275	0.212	0.263	0.202	0.208		0.529	0.453	0.249	0.368
CF _L	P	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.		n.s.	n.s.	*	n.s.
	\bar{x}	11.202	9.129	8.084	7.431	13.013	12.201	10.758	9.826	10.189		10.937	10.305	7.066	7.216
	S.E.	0.351	0.777	0.532	0.489	0.671	0.607	0.204	0.186	0.345		0.481	0.597	0.274	0.295
CF _H	P	22.685	16.935	14.852	14.817	25.613	22.618	21.083	18.267	18.462		21.878	19.198	13.658	14.229
	\bar{x}	22.685	16.935	14.852	14.817	25.613	22.618	21.083	18.267	18.462		21.878	19.198	13.658	14.229
	S.E.	0.808	1.154	0.742	0.982	1.320	0.991	0.510	0.395	0.581		0.759	1.119	0.572	0.682

Appendix 3.1 continued. November, 1976 Data.

Relationship	Station	A1	A2	A3	A4	B1	B2	B3	B4	B5	C1	C2	C3	C4	C5
$T_{dw} = \frac{L^b -}{a}$	b	3.297	6.213	3.235	3.238	3.779	3.721	3.602	3.956	3.829	3.772	3.363	3.644	3.876	3.344
	S.E.	0.061	2.108	0.053	0.091	0.172	0.066	0.059	0.085	0.092	0.181	0.094	0.191	0.121	0.107
	a	39.77	24100	28.21	29.97	81.47	72.44	65.01	97.09	78.38	68.61	39.00	54.79	90.59	30.60
$T_{dw} = \frac{H^b -}{a}$	P		n.s.												
	b	3.376	5.542	3.339	3.378	3.620	3.694	3.695	3.858	3.657	4.049	3.291	3.654	3.803	3.407
	S.E.	0.068	1.279	0.073	0.100	0.146	0.069	0.056	0.093	0.104	0.246	0.097	0.206	0.102	0.099
$F_{dw} = \frac{L^b -}{a}$	a	20.06	1414.0	16.14	19.23	27.71	29.55	33.62	35.53	25.19	63.98	16.36	25.71	35.61	16.85
	P		*												
	b	3.126	4.825	2.444	2.562	3.263	3.459	3.413	3.065	3.334	2.118	3.087	3.064	2.528	2.849
$F_{dw} = \frac{H^b -}{a}$	S.E.	0.069	1.223	0.157	0.110	0.124	0.081	0.060	0.083	0.090	0.565	0.063	0.086	0.179	0.115
	a	169.1	8818.0	41.92	66.31	183.4	267.9	289.3	121.4	219.0	8.908	137.7	116.7	57.35	103.5
	P		*								*				
$F_{dw} = \frac{H^b -}{a}$	b	3.202	4.018	2.528	2.673	3.122	3.436	3.499	3.006	3.192	2.368	3.002	3.076	2.499	2.901
	S.E.	0.073	0.984	0.158	0.116	0.109	0.079	0.062	0.057	0.089	0.518	0.110	0.092	0.158	0.114
	a	88.63	529.4	27.75	46.69	71.91	116.9	154.4	57.62	82.69	10.87	60.23	62.13	32.37	62.19
$sw = \frac{L^b -}{a}$	P		*												
	b	3.336	6.382	3.376	3.351	3.873	3.768	3.634	4.067	3.899	3.936	3.408	3.729	3.997	3.408
	S.E.	0.068	2.258	0.059	0.104	0.189	0.070	0.064	0.093	0.097	0.215	0.112	0.222	0.124	0.117
$sw = \frac{H^b -}{a}$	a	51.64	40070	44.28	43.18	118.1	95.26	32.12	140.6	104.5	118.4	51.22	77.11	129.6	39.28
	P		n.s.												
	b	3.416	5.727	3.482	3.496	3.711	3.741	3.728	3.965	3.723	4.216	3.339	3.738	3.921	3.472
$CF_L = b \pm S.E.L + a$	S.E.	0.074	1.370	0.090	0.110	0.163	0.074	0.061	0.103	0.111	0.313	0.106	0.237	0.107	0.110
	a	25.86	2342.0	24.61	27.29	39.12	38.38	42.25	49.87	32.82	107.4	21.34	35.53	49.32	21.38
	P		*												
$CF_H = b \pm S.E.H + a$	b	0.149	1.366	-0.731	-0.467	0.464	0.563	0.450	0.014	0.390	-0.630	0.103	0.048	-0.324	-0.207
	S.E.	0.079	0.947	0.258	0.102	0.128	0.097	0.069	0.089	0.108	0.398	0.089	0.119	0.113	0.145
	a	6.521	-5.99	14.13	10.46	5.917	5.109	4.491	9.445	6.041	20.37	7.871	9.395	9.345	8.835
CF_L	P		n.s.		*	**			n.s.	**	n.s.	n.s.	n.s.	**	n.s.
	b	0.657	1.931	-1.521	-0.805	0.557	1.322	1.331	-0.048	0.551	-1.046	N.C.	0.143	-0.761	-0.310
	S.E.	0.221	2.017	0.580	0.265	0.245	0.240	0.160	0.147	0.251	0.797	0.302	0.302	0.218	0.328
CF_H	a	12.31	0.347	25.95	17.65	14.16	10.60	7.701	18.01	13.84	32.40	n.s.	17.58	17.38	15.58
	P		n.s.	*	*	*			n.s.	*	n.s.	n.s.	n.s.	**	n.s.
	b	7.554	8.486	9.353	6.039	8.725	9.324	8.020	9.579	9.308	10.380	8.495	9.741	6.025	7.468
CF_L	S.E.	0.201	0.540	0.949	0.712	0.541	0.518	0.312	0.227	0.384	1.351	0.150	0.327	0.270	0.370
	a	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
	S.E.	0.460	0.966	1.596	1.029	0.734	0.998	0.661	0.308	0.670	1.874	0.497	0.667	0.464	0.640

Appendix 3.1 continued. February, 1977 Data.

Relationship	Station	A1	A2	A3	A4	B1	B2	B3	B4	B5	C1	C2	C3	C4	C5
$T_{dw} = \frac{L^b}{a}$	b	3.618	3.426	3.438	3.784	3.667	4.129	3.620	3.583	3.872	I.D.	3.247	3.298	3.519	3.397
	S.E.	0.115	0.385	0.082	0.392	0.116	0.175	0.088	0.102	0.125		0.152	0.202	0.123	0.113
	a	70.44	30.89	42.58	100.3	68.17	222.9	67.35	50.19	86.52		32.10	29.57	36.84	33.85
$T_{dw} = \frac{H^b}{a}$	p	n.s.													
	b	3.492	3.544	3.351	4.633	3.702	3.832	3.527	3.486	3.696		3.304	3.328	3.384	3.210
	S.E.	0.086	0.311	0.076	0.622	0.085	0.166	0.072	0.096	0.086		0.155	0.134	0.104	0.081
$F_{dw} = \frac{L^b}{a}$	a	25.13	19.72	17.66	258.4	33.62	51.99	25.65	19.51	26.28		16.66	15.19	13.35	11.91
	p	*	*	*	*										
	b	2.813	2.850	2.838	1.635	3.269	3.448	3.066	2.914	3.243		2.853	2.842	2.910	2.797
$F_{dw} = \frac{H^b}{a}$	S.E.	0.147	0.116	0.177	0.497	0.144	0.152	0.073	0.102	0.155		0.289	0.195	0.133	0.171
	a	88.86	119.2	92.47	6.212	183.1	334.8	149.9	109.7	192.7		103.0	88.76	129.1	90.59
	p	*	*	*	*						**	**			
$sw = \frac{L^b}{a}$	b	2.708	2.937	2.770	2.125	3.304	3.181	2.982	2.830	3.096		2.925	2.877	2.795	2.655
	S.E.	0.136	0.192	0.166	0.532	0.108	0.162	0.067	0.104	0.130		0.211	0.086	0.141	0.135
	a	39.45	80.42	45.01	12.11	98.06	95.13	65.49	50.55	71.03		59.98	50.77	55.31	39.19
$sw = \frac{H^b}{a}$	p	*	*	*	*										
	b	3.746	3.474	3.557	3.988	3.742	4.229	3.708	3.683	3.970		3.323	3.378	3.582	3.484
	S.E.	0.127	0.422	0.094	0.440	0.118	0.186	0.092	0.107	0.122		0.136	0.212	0.126	0.114
$sw = \frac{H^b}{a}$	a	110.0	37.43	63.43	182.1	95.96	327.9	94.95	70.04	121.4		43.59	40.22	45.83	45.62
	p	n.s.	n.s.	n.s.	*	*	*	*	*	*		*	*	*	*
	b	3.616	3.595	3.467	4.867	3.778	3.928	3.613	3.583	3.789		3.377	3.407	3.444	3.290
$CF_L = b \pm S.E.L + a$	S.E.	0.099	0.347	0.086	0.710	0.091	0.173	0.074	0.100	0.081		0.165	0.157	0.106	0.088
	a	37.81	23.76	25.54	476.8	46.61	74.29	35.36	26.55	35.73		22.15	20.26	16.30	15.57
	p	*	*	*	*	*	*	*	*	*		*	*	*	*
$CF_H = b \pm S.E.H + a$	b	-0.196	-0.147	-0.196	-0.760	0.312	0.398	0.100	-0.093	0.381		-0.119	-0.262	-0.076	-0.324
	S.E.	0.136	0.080	0.192	0.318	0.138	0.131	0.066	0.119	0.160		0.365	0.305	0.120	0.200
	a	9.503	7.512	9.625	14.68	6.913	4.465	6.900	8.508	5.505		8.273	10.25	7.120	10.00
$CF_H = b \pm S.E.H + a$	p	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.		n.s.	n.s.	n.s.	n.s.
	b	-0.671	-0.160	-0.697	-1.276	0.844	0.407	-0.028	-0.485	0.441		-0.097	-0.450	-0.477	-1.059
	S.E.	0.288	0.358	0.459	0.806	0.220	0.309	0.151	0.287	0.324		0.672	0.301	0.304	0.357
CF_L	a	19.81	12.30	19.70	23.72	12.12	12.26	15.13	17.97	13.97		15.35	18.58	15.84	20.66
	p	*	*	*	*	*	*	*	*	*		*	*	*	*
	b	8.039	6.245	8.129	6.788	9.290	8.792	7.742	7.795	8.957		7.459	8.588	6.409	7.459
CF_H	S.E.	0.384	0.472	0.517	0.553	0.845	0.424	0.223	0.303	0.471		0.583	0.592	0.299	0.382
	a	15.792	11.173	15.366	13.147	17.328	15.914	14.934	14.953	17.198		14.819	16.289	12.199	13.881
	S.E.	0.736	0.893	1.077	0.726	1.499	0.768	0.420	0.650	0.734		0.840	0.539	0.773	0.682

Appendix 3.1 continued. Station B3 Monthly Sampling Data, 1976-77.

Relationship	Mar. '76	Apr. '76	June '76	July '76	Sep. '76	Oct. '76	Dec. '76	Jan. '77
$T_{dw} = L^b \pm \frac{S.E.}{a}$	b 3.856 S.E. 0.106 a 112.7	3.872 0.120 122.4	3.793 0.080 92.58	3.786 0.056 94.58	3.680 0.076 68.68	3.662 0.070 74.96	3.726 0.067 75.68	3.797 0.062 87.92
$T_{dw} = H^b \pm S.E.$	P b 3.783 S.E. 0.080 a 38.99	3.666 0.096 31.37	3.833 0.067 43.87	3.864 0.053 47.51	3.668 0.066 29.47	3.628 0.067 28.62	3.648 0.053 28.43	3.664 0.050 29.24
$F_{dw} = L^b \pm \frac{S.E.}{a}$	P b 3.292 S.E. 0.086 a 287.1	3.072 0.092 186.1	3.034 0.059 106.0	3.005 0.043 97.05	3.107 0.041 124.8	3.221 0.041 222.0	3.522 0.074 348.7	3.450 0.060 314.9
$F_{dw} = H^b \pm \frac{S.E.}{a}$	P b 3.206 S.E. 0.097 a 110.8	2.902 0.085 62.34	3.059 0.062 57.55	3.059 0.048 55.45	3.087 0.052 60.05	3.188 0.047 94.61	3.448 0.063 138.1	3.327 0.054 115.4
$sw = L^b \pm \frac{S.E.}{a}$	P b 3.917 S.E. 0.118 a 146.7	3.971 0.128 172.8	3.939 0.095 156.4	3.953 0.066 168.4	3.783 0.089 103.2	3.724 0.080 99.15	3.757 0.070 94.50	3.847 0.069 113.4
$sw = H^b \pm \frac{S.E.}{a}$	P b 3.845 S.E. 0.089 a 70.06	3.759 0.103 42.80	3.982 0.082 72.14	4.034 0.063 82.10	3.771 0.078 43.38	3.690 0.076 37.27	3.678 0.057 35.21	3.713 0.057 37.22
$CF_L = b \pm S.E.L + a$	P b 0.171 S.E. 0.061 a 5.087	0.059 0.065 5.833	N.C.	-0.032 0.055 10.78	0.120 0.052 9.002	0.182 0.041 5.608	0.576 0.074 3.806	0.404 0.063 4.769
$CF_H = b \pm S.E.H + a$	P b 0.244 S.E. 0.177 a 11.91	-0.184 0.153 14.83	n.s. 0.052 19.28	n.s. 0.045 20.04	0.180 0.163 18.41	0.393 0.121 12.35	1.162 0.155 8.942	0.718 0.142 11.12
CF_L	P x 6.671 S.E. 0.235 x 13.697	6.410 0.205 13.418	10.248 0.305 19.666	n.s. 10.499 20.363	n.s. 9.963 19.559	** 7.015 14.721	8.342 0.486 16.273	8.213 0.360 16.034
CF_H	S.E. 0.513	0.420	0.567	0.390	0.454	0.340	0.818	0.592

Appendix 3.2 Macoma balthica: The Density and Total- and Flesh-dry-weight Biomass₂ of the Large- and Small-animal Parts of the Population at Each Station and Sampling Occasion, (as nos./m² and g/m² respectively).

Sampling Date	Station A1						Station A2						Station A3					
	L _N	L _{Tdw}	L _{Fdw}	S _N	S _{Tdw}	S _{Fdw}	L _N	L _{Tdw}	L _{Fdw}	S _N	S _{Tdw}	S _{Fdw}	L _N	L _{Tdw}	L _{Fdw}	S _N	S _{Tdw}	S _{Fdw}
Mar. '75	350	17.580	2.435	600	0.4800	0.0960	20	1.001	0.192	200	0.1800	0.0360	210	11.919	1.396	0	0	0
Apr. '75	700	28.028	6.343	600	0.5200	0.1040	90	9.146	1.480	200	0.0400	0.0080	270	8.629	1.205	400	0.1600	0.0320
May '75	900	41.651	10.812	1800	0.1400	0.0280	260	14.312	2.217	400	0.1600	0.0320	370	16.641	2.900	0	0	0
June '75	1510	72.656	17.278	1000	0.1400	0.0280	280	20.659	1.711	600	0.0600	0.0120	410	20.800	3.854	400	0.1800	0.0360
July '75	1170	44.784	9.217	2640	0.7184	0.1437	260	16.515	1.573	240	0.0080	0.0016	260	12.286	1.974	320	0.0480	0.0096
Aug. '75	1340	66.676	9.021	1360	0.5800	0.1160	160	10.439	1.492	160	0.0069	0.0014	320	13.412	2.112	240	0.0352	0.0070
Sep. '75	1350	58.091	8.940	1920	1.2828	0.2566	140	8.530	1.345	800	0.2692	0.0538	390	15.534	2.949	320	0.1192	0.0238
Oct. '75	1060	34.413	4.864	1600	1.1776	0.2355	160	10.048	1.415	320	0.3280	0.0656	310	13.221	1.977	240	0.1452	0.0290
Nov. '75	1130	52.962	8.798	1440	0.8164	0.1633	240	10.031	1.515	240	0.1236	0.0247	260	11.676	1.811	240	0.0768	0.0154
Dec. '75	1060	52.867	8.209	1360	0.7216	0.1443	150	12.740	1.458	320	0.0432	0.0086	240	13.831	1.916	480	0.3376	0.0675
Jan. '76	230	16.660	2.172	400	0.1256	0.0251	130	10.230	1.139	320	0.1158	0.0232	330	14.226	1.686	80	0.0840	0.0168
Feb. '76	230	14.017	1.414	80	0.0023	0.0005	250	9.972	1.179	80	0.0154	0.0031	230	9.677	1.190	80	0.0394	0.0079
S.D.	919	41.699	7.459	1233	0.5587	0.1118	178	11.135	1.393	323	0.1125	0.0225	300	13.488	2.081	233	0.1021	0.0204
S.E.	445	19.833	4.426	730	0.4136	0.0825	80	4.775	0.467	200	0.1054	0.0200	65	3.214	0.791	162	0.0954	0.0200
May '76	460	9.968	1.929	2320	0.2201	0.0440	30	0.976	0.156	0	0	0	170	5.693	0.707	320	0.0800	0.0160
Aug. '76	900	20.205	3.378	1920	0.7544	0.1509	130	5.507	0.639	480	0.0972	0.0194	160	7.045	0.735	80	0.0064	0.0013
Nov. '76	1000	11.958	1.901	1360	0.8591	0.1718	50	5.093	0.514	720	0.0404	0.0081	130	3.757	0.409	80	0.0003	0.0001
Feb. '77	700	11.946	1.365	800	0.2733	0.0547	30	3.191	0.174	480	0.1860	0.0372	150	5.878	0.705	800	0.2014	0.0403
S.D.	706	13.778	2.149	1510	0.4929	0.0986	87	4.539	0.496	370	0.0596	0.0119	162	6.068	0.700	230	0.0518	0.0104
S.E.	315	4.503	0.856	841	0.3747	0.0748	84	3.141	0.375	326	0.0686	0.0141	34	2.079	0.262	275	0.0748	0.0141
	158	2.251	0.428	420	0.1870	0.0370	42	1.570	0.187	163	0.0343	0.0070	17	1.039	0.131	137	0.0374	0.0070

Appendix 3.2 continued.

Sampling Date	Station A4						Station B1						Station B2					
	L _N	L _{TdW}	L _{FdW}	S _N	S _{TdW}	S _{FdW}	L _N	L _{TdW}	L _{FdW}	S _N	S _{TdW}	S _{FdW}	L _N	L _{TdW}	L _{FdW}	S _N	S _{TdW}	S _{FdW}
Mar. '75	250	7.976	1.119	0	0	0	220	2.296	0.341	400	0.1000	0.0200	420	34.940	4.279	0	0	0
Apr. '75	260	8.088	1.180	0	0	0	40	9.184	1.055	0	0	0	160	28.930	3.058	600	0.6600	0.1320
May '75	350	14.466	2.850	200	0.0200	0.0040	110	2.618	0.804	1800	0.2600	0.0520	250	13.528	3.386	200	0.0200	0.0040
June '75	340	17.596	2.027	600	0.1000	0.0200	190	2.811	0.748	1200	0.2600	0.0520	350	32.143	4.655	600	0.3200	0.0640
July '75	390	11.554	1.256	640	0.1296	0.0259	130	6.169	1.068	1360	0.3960	0.0792	170	23.472	3.284	2800	0.8080	0.1616
Aug. '75	220	10.627	1.831	400	0.2016	0.0403	150	4.677	1.107	560	0.2624	0.0525	220	46.817	5.304	1280	0.3072	0.0614
Sep. '75	180	9.713	1.660	80	0.0188	0.0038	490	6.936	2.068	400	0.1948	0.0390	390	27.669	4.820	800	0.6324	0.1265
Oct. '75	450	14.560	2.200	240	0.0416	0.0083	370	15.999	2.086	720	0.6112	0.1222	680	75.138	11.380	720	0.5328	0.1066
Nov. '75	400	11.825	1.637	80	0.0592	0.0118	310	6.633	1.492	320	0.1960	0.0392	410	28.506	4.222	560	0.3456	0.0691
Dec. '75	320	11.525	1.870	400	0.1704	0.0341	350	9.388	1.706	320	0.2440	0.0488	750	49.527	7.512	720	0.2828	0.0566
Jan. '76	260	15.438	2.193	80	0.0294	0.0059	150	15.176	1.532	160	0.1042	0.0208	830	79.897	7.982	480	0.1491	0.0298
Feb. '76	160	5.880	1.071	0	0	0	80	5.971	0.567	160	0.0379	0.0076	120	22.414	2.197	160	0.1137	0.0227
̄ x	298	11.604	1.741	227	0.0642	0.0128	216	7.321	1.214	617	0.2222	0.0444	396	38.582	5.173	743	0.3476	0.0695
S.D.	91	3.443	0.535	232	0.0700	0.0141	136	4.505	0.567	554	0.1652	0.0332	240	20.707	2.595	729	0.2617	0.0520
S.E.	26	0.994	0.154	67	0.0200	0.0040	39	1.300	0.164	160	0.0480	0.0100	69	5.978	0.749	211	0.0750	0.0150
May '76	190	10.757	1.424	240	0.0199	0.0040	180	47.445	4.870	720	0.0761	0.0152	220	23.131	3.699	320	0.0181	0.0036
Aug. '76	130	8.697	1.080	80	0.0162	0.0032	260	11.633	2.469	640	0.2353	0.0471	610	82.939	13.298	1360	0.2000	0.0400
Nov. '76	70	4.744	0.423	320	0.0089	0.0018	130	6.201	0.684	400	0.2710	0.0542	430	23.603	3.100	1760	0.6652	0.1330
Feb. '77	80	6.777	0.628	560	0.0842	0.0168	170	8.378	1.046	320	0.2008	0.0402	450	43.127	4.907	480	0.1373	0.0275
̄ x	127	7.632	0.944	230	0.0218	0.0044	174	18.113	2.207	500	0.1755	0.0351	386	40.611	5.912	940	0.2522	0.0505
S.D.	54	2.655	0.439	193	0.0283	0.0000	68	19.709	1.958	225	0.1039	0.0200	198	29.184	4.992	740	0.2853	0.0574
S.E.	27	1.327	0.219	96	0.0140	0.0000	34	9.854	0.979	112	0.0519	0.0100	99	14.592	2.496	370	0.1426	0.0287

Appendix 3.2 continued.

Sampling Date	Station B3					Station B4					Station B5							
	L _N	L _{TdW}	L _{FdW}	S _N	S _{TdW}	S _{FdW}	L _N	L _{TdW}	L _{FdW}	S _N	S _{TdW}	S _{FdW}	L _N	L _{TdW}	L _{FdW}	S _N	S _{TdW}	S _{FdW}
Mar. '75	180	19.060	2.866	600	0.5400	0.1080	320	36.274	3.604	1200	0.4600	0.0920	140	24.578	2.328	400	0.2400	0.0480
Apr. '75	950	108.002	12.027	800	0.4200	0.0840	420	19.643	1.833	0	0	0	310	27.782	2.973	600	0.1600	0.0320
May '75	470	36.719	7.340	200	0.0200	0.0040	680	19.583	3.459	600	0.6800	0.1360	420	49.601	7.728	0	0	0
June '75	1840	59.055	17.480	2200	0.7000	0.1400	440	22.066	2.010	0	0	0	620	42.820	6.282	200	0.0600	0.0120
July '75	1600	40.403	8.460	1600	1.3104	0.2621	470	25.959	2.675	320	0.0896	0.0179	460	43.876	6.454	240	0.0960	0.0192
Aug. '75	1180	92.294	17.347	800	0.6096	0.1219	650	24.236	4.492	320	0.1984	0.0397	360	23.685	3.803	320	0.3130	0.0626
Sep. '75	2040	67.762	12.058	560	0.4076	0.0815	350	19.657	2.720	240	0.3672	0.0734	390	35.610	4.380	0	0	0
Oct. '75	2000	51.249	8.211	1200	0.7328	0.1466	700	35.409	5.363	160	0.0228	0.0046	210	15.816	1.828	240	0.1244	0.0249
Nov. '75	1740	66.415	8.663	1360	0.7740	0.1548	440	23.923	2.868	160	0.0200	0.0040	280	19.280	2.123	80	0.0200	0.0040
Dec. '75	1140	49.180	7.244	800	0.2536	0.0507	680	35.009	3.896	80	0.0064	0.0013	560	35.367	3.983	80	0.0800	0.0016
Jan. '76	340	27.964	3.373	240	0.2610	0.0522	530	17.174	1.955	80	0.0356	0.0071	280	22.754	2.753	80	0.0459	0.0092
Feb. '76	520	22.629	2.855	160	0.0118	0.0024	280	26.144	2.266	320	0.0422	0.0084	480	43.727	3.860	80	0.0016	0.0003
\bar{x}	1167	53.394	8.994	883	0.5034	0.1007	497	25.423	3.095	290	0.1602	0.0320	376	32.075	4.066	193	0.0951	0.0178
S.D.	677	27.210	4.991	621	0.3619	0.0728	149	6.701	1.098	333	0.2241	0.0447	141	11.204	1.856	180	0.1000	0.0200
S.E.	195	7.855	1.441	179	0.1040	0.0210	43	1.934	0.317	96	0.0650	0.0130	41	3.234	0.536	52	0.0290	0.0060
May '76	310	22.881	2.730	240	0.0437	0.0087	370	38.683	3.564	160	0.0564	0.0113	320	38.809	3.852	160	0.1149	0.0230
Aug. '76	460	20.519	3.435	1680	0.4536	0.0907	350	18.926	2.121	80	0.0054	0.0011	370	24.392	2.810	160	0.2357	0.0471
Nov. '76	630	20.134	2.764	800	0.3858	0.0772	260	28.561	2.540	0	0	0	340	25.438	2.613	0	0	0
Feb. '77	470	27.510	2.973	880	0.1276	0.0255	240	9.826	0.960	320	0.0530	0.0106	170	15.429	1.546	160	0.0424	0.0085
\bar{x}	474	22.151	2.961	810	0.2382	0.0477	310	26.039	2.459	140	0.0274	0.0055	339	29.554	2.994	110	0.0932	0.0187
S.D.	132	2.692	0.328	657	0.2142	0.0424	59	10.774	0.910	137	0.0283	0.0000	92	10.479	0.883	79	0.1082	0.0200
S.E.	66	1.346	0.164	328	0.1071	0.0210	30	5.387	0.455	68	0.0140	0.0000	46	5.239	0.441	39	0.0540	0.0100

Appendix 3.2 continued.

Sampling Date	Station C1						Station C2						Station C3					
	L _N	L _{TdW}	L _{FdW}	S _N	S _{TdW}	S _{FdW}	L _N	L _{TdW}	L _{FdW}	S _N	S _{TdW}	S _{FdW}	L _N	L _{TdW}	L _{FdW}	S _N	S _{TdW}	S _{FdW}
Mar. '75	0	0	0	0	0	0	165	14.124	1.732	600	0.7400	0.1480	60	5.444	0.574	400	0.1400	0.0280
Apr. '75	20	12.643	0.797	0	0	0	20	10.216	0.832	400	0.3600	0.0720	130	12.956	1.645	1000	0.4800	0.0960
May '75	30	17.516	1.516	1000	0.5000	0.1000	130	2.483	0.638	200	0.0200	0.0040	340	4.017	0.704	600	0.1600	0.0320
June '75	20	12.136	0.657	200	0.0200	0.0040	320	7.016	2.001	800	0.3400	0.0680	260	12.641	2.091	400	0.2000	0.0400
July '75	70	21.702	3.369	240	0.0432	0.0086	190	4.032	1.176	2640	0.4960	0.0992	350	26.759	2.518	560	0.2032	0.0406
Aug. '75	50	12.227	1.521	0	0	0	290	8.316	1.645	1040	0.2936	0.0587	190	6.283	0.928	400	0.3536	0.0707
Sep. '75	60	32.365	3.982	0	0	0	270	5.771	1.549	800	0.2328	0.0466	300	15.807	3.830	160	0.0484	0.0097
Oct. '75	10	0.197	0.037	0	0	0	170	3.701	0.783	80	0.0284	0.0057	370	17.282	2.648	240	0.0656	0.0131
Nov. '75	110	63.039	5.014	80	0.0128	0.0026	120	4.528	0.714	480	0.2256	0.0451	300	13.917	1.870	320	0.1420	0.0284
Dec. '75	20	8.379	0.992	80	0.0008	0.0002	290	1.955	0.349	560	0.1856	0.0371	470	30.765	3.031	1040	0.4260	0.0852
Jan. '76	50	32.272	2.491	80	0.0118	0.0024	70	2.380	0.341	80	0.0584	0.0117	230	15.437	1.591	400	0.1502	0.0300
Feb. '76	70	17.879	1.507	0	0	0	220	4.355	0.554	80	0.0088	0.0018	250	18.428	1.588	480	0.2388	0.0478
\bar{x}	42	19.196	1.824	140	0.0491	0.0098	188	5.740	1.026	647	0.2491	0.0498	271	14.978	1.918	500	0.2173	0.0435
S.D.	32	17.229	1.583	283	0.1425	0.0283	94	3.634	0.574	703	0.2184	0.0436	111	7.997	0.971	272	0.1360	0.0265
S.E.	9	4.974	0.457	82	0.0410	0.0080	27	1.049	0.166	203	0.0630	0.0130	32	2.308	0.280	78	0.0390	0.0080
May '76	30	13.724	1.131	320	0.0115	0.0023	380	10.316	1.590	240	0.1522	0.0304	360	15.720	1.572	400	0.1372	0.0274
Aug. '76	20	5.977	0.998	0	0	0	140	4.469	0.779	880	0.1370	0.0274	160	3.875	0.527	800	0.0632	0.0126
Nov. '76	60	34.546	2.485	80	0.0014	0.0003	170	2.649	0.406	560	0.1839	0.0368	100	5.413	0.556	720	0.3211	0.0642
Feb. '77	40	0.701	0.090	80	0.1584	0.0317	50	1.023	0.144	560	0.5589	0.1118	100	1.657	0.222	160	0.0308	0.0062
\bar{x}	41	15.884	1.353	111	0.0230	0.0046	206	5.030	0.781	500	0.1893	0.0379	199	8.763	0.890	560	0.1641	0.0328
S.D.	21	13.764	0.869	146	0.0592	0.0100	127	3.750	0.584	319	0.1720	0.0346	120	7.199	0.626	253	0.1253	0.0245
S.E.	11	6.882	0.434	73	0.0296	0.0050	63	1.875	0.292	160	0.0860	0.0170	60	3.599	0.313	126	0.0630	0.0120

Appendix 3.2 continued.

Sampling Date	Station C4						Station C5					
	L _N	L _{Tdw}	L _{Fdw}	S _N	S _{Tdw}	S _{Fdw}	L _N	L _{Tdw}	L _{Fdw}	S _N	S _{Tdw}	S _{Fdw}
Mar. '75	675	95.645	10.215	1800	1.2000	0.2400	60	2.452	0.352	0	0	0
Apr. '75	110	17.798	1.904	200	0.0400	0.0080	230	7.779	1.073	0	0	0
May '75	210	23.027	2.659	200	0.0600	0.0120	210	5.775	0.819	400	0.0800	0.0160
June '75	60	7.985	0.925	0	0	0	180	4.389	0.854	400	0.1400	0.0280
July '75	70	9.879	1.214	80	0.0080	0.0016	90	1.841	0.267	240	0.0432	0.0086
Aug. '75	240	35.643	3.577	160	0.0928	0.0186	270	5.887	1.064	320	0.2784	0.0057
Sep. '75	460	15.584	1.985	160	0.0216	0.0043	180	9.176	1.316	400	0.0620	0.0012
Oct. '75	170	29.564	2.579	400	0.0756	0.0151	160	5.015	0.636	240	0.0392	0.0078
Nov. '75	290	47.393	4.137	240	0.1932	0.0386	240	11.515	1.388	80	0.0116	0.0023
Dec. '75	330	39.078	3.387	0	0	0	220	7.168	0.840	320	0.0296	0.0059
Jan. '76	290	31.084	2.587	160	0.1064	0.0213	120	3.904	0.486	240	0.2368	0.0474
Feb. '76	270	38.594	3.017	80	0.0018	0.0004	140	6.736	0.609	240	0.0704	0.0141
\bar{x}	265	32.606	3.182	290	0.1500	0.0300	175	5.970	0.809	240	0.0826	0.0114
S.D.	173	23.383	2.405	488	0.3356	0.0671	64	2.755	0.358	145	0.0911	0.0141
S.E.	50	6.750	0.694	141	0.0970	0.0190	18	0.795	0.103	42	0.0260	0.0040
May '76	210	24.180	1.536	0	0	0	150	5.126	0.508	240	0.4655	0.0931
Aug. '76	190	24.844	1.688	160	0.0061	0.0012	120	3.628	0.352	160	0.0049	0.0010
Nov. '76	250	25.952	1.605	640	0.0692	0.0138	140	3.873	0.368	480	0.1075	0.0215
Feb. '77	60	5.670	0.381	0	0	0	160	6.196	0.515	2160	0.1386	0.0277
\bar{x}	204	24.277	1.632	210	0.0191	0.0038	140	4.773	0.447	520	0.1706	0.0342
S.D.	70	9.639	0.765	295	0.0332	0.0000	15	1.315	0.107	729	0.2032	0.0412
S.E.	35	4.819	0.382	148	0.0166	0.0000	8	0.657	0.053	364	0.1020	0.0210

Appendix 3.3 Macoma balthica: The Calculations of Somatic Production for
Each Group of Stations, Cohort and Sampling Occasion.

Height = Mean and standard deviation (mm) from size-frequency data;
M.I.W. = Mean individual flesh dry weight (mg) calculated from
appropriate regression equations (see below and Appendix 3.1);

No. sampled = Total number from all stations in group;

$N \text{ m}^{-2}$ = Density of cohort;

Biomass = Flesh biomass (mg m^{-2}) as $N \text{ m}^{-2} \times \text{M.I.W.}$;

$-\Delta N$ = Negative change in density between sampling occasions;

$\Delta \bar{w}$ = Change in M.I.W. between sampling occasions;

ΔP = Production increment (mg Fdw m^{-2});

ΔM = Mortality increment (mg Fdw m^{-2});

Group 1: Stations A1, C1.

Station A1 regressions used.

Group 2: Stations B1, B2, B3.

Station B3 regressions used.

Group 3: Stations C2, C3, C4, B4, B5.

Station B4 regressions used.

Group 4: Stations A2, A3, A4.

Station A3 regressions used.

Group 5: Station C5.

Station C5 regressions used.

Appendix 3.3 continued. Example of Production Calculation: Group 1, Cohort 1975.

	\bar{x}	Height (mm)	M.I.W.	No. Sampled	$N m^{-2}$	\bar{B} ($mg m^{-2}$)	\bar{N} over Period	\bar{w} over Period	$-\Delta N$	$\Delta \bar{w}$	ΔP ($N \Delta \bar{w}$)	ΔM ($\bar{w} \Delta N$)
Mar. '75	-	-	-	-	-	-	-	-	-	-	-	-
Apr. '75	-	-	-	-	-	-	-	-	-	-	-	-
May '75	0.92	0.22	0.009	240.0	1200.0	10.800	600.00	0.0045	-1200.0	0.009	5.400	-5.400
June '75	1.13	0.24	0.036	120.0	600.0	21.600	900.00	0.0225	600.0	0.027	24.300	13.500
July '75	1.32	0.61	0.030	294.0	1470.0	44.100	1035.00	0.0330	-870.0	-0.006	-6.210	-28.710
Aug. '75	1.49	0.64	0.027	144.0	720.0	19.440	1095.00	0.0285	750.0	-0.003	-3.285	21.375
Sep. '75	1.75	0.59	0.056	195.0	975.0	54.600	847.50	0.0415	-255.0	0.029	24.577	-10.582
Oct. '75	1.76	0.65	0.061	169.0	845.0	51.545	910.00	0.0585	130.0	0.005	4.550	7.605
Nov. '75	1.73	0.62	0.052	159.0	795.0	41.340	820.00	0.0565	50.0	-0.009	-7.380	2.825
Dec. '75	1.77	0.73	0.073	160.0	800.0	58.400	797.50	0.0625	-5.0	0.021	16.747	-0.312
Jan. '76	1.64	0.83	0.075	52.5	262.5	19.687	531.25	0.0740	537.5	0.002	1.062	39.775
Feb. '76	2.03	1.23	0.132	17.0	85.0	11.220	173.75	0.1035	177.5	0.057	9.904	18.371
May '76	3.49	1.09	0.813	42.0	210.0	170.730	147.50	0.4725	-125.0	0.681	100.447	-59.062
Aug. '76	4.44	0.54	1.891	18.0	90.0	170.190	150.00	1.3520	120.0	1.078	161.700	162.240
Nov. '76	4.97	0.57	1.915	20.0	100.0	191.500	95.00	1.9030	-10.0	0.024	2.280	-19.030
Feb. '77	5.20	0.71	2.202	14.5	72.5	159.645	86.25	2.0585	27.5	0.287	24.754	56.609

Appendix 3.3 continued. Group 1₂ Production Calculation continued.

Sampling Date	Height (mm)	M.I.W.	No.	N m ⁻²	Biomass	ΔP	ΔM	Height	M.I.W.	No.	N m ⁻²	Biomass	ΔP	ΔM
COHORT 1973														
Mar. '75	5.75	0.60	3.267	10.0	50.0	163.350	-	7.97	0.29	9.285	3.0	15.0	139.275	-
Apr. '75	5.74	0.75	4.563	27.0	135.0	616.005	119.880	7.88	0.40	14.037	13.0	65.0	912.405	190.080
May '75	5.92	0.45	5.452	24.0	120.0	654.240	113.347	7.70	0.39	13.484	15.0	75.0	1011.300	-38.710
June '75	6.28	0.36	7.118	50.0	250.0	1779.500	308.210	7.49	0.32	12.239	24.0	120.0	1468.680	-121.387
July '75	6.35	0.47	6.049	39.0	195.0	1179.555	-130.952	7.90	0.52	12.632	10.0	50.0	631.600	33.405
Aug. '75	6.57	0.49	5.591	43.0	215.0	1202.065	-96.180	8.30	0.45	12.945	16.0	80.0	1035.600	20.345
Sep. '75	6.85	0.46	6.648	54.0	270.0	1794.960	256.322	8.48	0.68	14.052	11.0	55.0	772.860	74.722
Oct. '75	7.08	0.52	5.891	25.0	125.0	736.375	-149.507	8.56	0.45	10.974	10.5	52.5	576.135	-165.442
Nov. '75	7.21	0.54	7.558	58.0	290.0	2191.820	345.902	8.88	0.60	15.634	12.0	60.0	938.040	304.065
Dec. '75	7.33	0.61	8.175	32.0	160.0	1308.000	138.825	8.82	0.47	15.114	11.5	57.5	869.005	-30.550
Jan. '76	7.40	0.65	7.331	5.0	25.0	183.275	-78.070	9.30	0.71	14.693	2.5	12.5	183.662	-14.735
Feb. '76	7.30	0.71	5.696	5.0	25.0	142.400	-408.750	8.30	0	8.311	0.5	2.5	20.777	-49.372
May '76	7.34	0.26	9.178	6.5	32.5	298.285	100.107	-	-	-	-	0	0	-10.389
Aug. '76	8.15	0.45	12.819	6.5	32.5	416.617	118.332	10.30	-	26.807	2.0	10.0	268.070	134.035
Nov. '76	8.60	0.76	11.084	5.0	25.0	277.100	-48.991	11.3	-	26.569	1.0	5.0	132.845	-1.785
Feb. '77	8.55	0.29	8.467	4.0	20.0	169.340	-58.882	-	-	-	-	0	0	-66.422
COHORT 1970														
Mar. '75	9.23	0.45	14.849	7.0	35.0	519.715	-	10.55	0.35	22.772	2.0	10.0	227.720	-
Apr. '75	9.55	0.29	27.751	4.0	20.0	555.020	354.805	11.05	0.64	46.553	4.0	20.0	931.060	356.715
May '75	9.53	0.52	28.109	13.0	65.0	1827.085	15.215	11.47	0.29	53.220	3.0	15.0	798.300	116.672
June '75	9.51	0.61	25.510	19.0	95.0	2423.450	-207.920	11.09	0.39	40.930	7.0	35.0	1432.550	-307.250
July '75	9.67	0.44	24.971	8.0	40.0	1118.840	-36.382	11.57	0.36	45.715	5.5	27.5	1257.162	149.531
Aug. '75	10.53	0.32	30.434	8.5	42.5	1293.445	225.349	12.03	0.36	49.103	5.5	27.5	1350.332	93.170
Sep. '75	10.80	0.60	32.807	8.0	40.0	1312.280	97.886	11.8	-	44.752	1.0	5.0	223.760	-70.704
Oct. '75	10.66	0.61	22.522	3.5	17.5	394.135	-295.694	11.8	-	31.419	1.0	5.0	157.095	-66.665
Nov. '75	10.88	0.38	31.758	6.0	30.0	952.740	219.355	11.8	-	42.155	1.0	5.0	210.775	53.680
Dec. '75	10.92	0.48	30.720	4.0	20.0	614.400	-25.950	12.3	-	45.610	1.0	5.0	228.050	17.275
Jan. '76	10.80	0.71	23.156	2.0	10.0	231.560	-113.460	11.8	-	30.314	1.0	5.0	151.570	-78.480
Feb. '76	11.00	0.27	19.038	5.0	25.0	475.950	-72.065	12.3	-	26.449	3.0	15.0	396.735	-38.650
May '76	11.8	-	43.165	1.0	5.0	215.825	361.905	12.3	-	49.420	1.0	5.0	247.100	229.710
Aug. '76	12.3	-	46.891	3.0	15.0	703.365	37.260	-	-	-	-	0	0	-123.550
Nov. '76	-	-	-	-	0	0	-351.682	13.05	0.35	42.131	2.0	10.0	421.310	210.655
Feb. '77	-	-	-	-	0	0	0	-	-	-	-	0	0	-210.655

Appendix 3.3 continued. Group 2 Production Calculation.

Sampling Date	Height	M.I.W.	No.	N m ⁻²	Biomass	ΔP	ΔM	Height	M.I.W.	No.	N m ⁻²	Biomass	ΔP	ΔM
COHORT 1974														
Mar. '75	-	-	-	0	0	0	0	1.90	0.02	0.181	130.0	433.3	78.433	-
Apr. '75	0.8	0.023	60.0	200.0	4.600	2.300	-2.300	3.03	0.93	0.859	133.5	445.0	382.246	297.750
May '75	0.85	0.011	200.0	666.7	7.334	-5.200	-7.934	3.80	1.24	1.421	62.5	208.3	296.037	183.580
June '75	1.42	0.65	412.0	1373.3	190.889	130.560	-52.995	4.45	0.97	3.233	126.0	420.0	1357.860	569.267
July '75	1.42	0.69	587.0	1956.6	56.743	-183.150	-49.001	5.12	0.73	2.660	106.0	353.3	939.778	-221.550
Aug. '75	1.88	0.95	331.0	1103.3	144.532	156.060	68.268	5.29	0.76	3.547	100.0	333.3	1182.215	304.507
Sep. '75	2.45	1.09	265.0	883.3	193.447	87.410	38.496	5.55	0.61	3.554	139.0	463.3	1646.568	2.788
Oct. '75	2.42	0.81	354.0	1180.0	213.580	-39.205	-59.336	5.66	0.67	3.200	139.0	463.3	1482.560	-164.008
Nov. '75	2.33	1.09	300.0	1000.0	108.000	-79.570	25.920	6.05	0.71	3.313	101.0	336.7	1115.487	45.200
Dec. '75	2.21	1.21	0.064	270.5	57.706	-41.835	8.457	6.04	0.78	3.185	77.5	258.3	822.685	38.080
Jan. '76	2.45	1.04	0.119	122.0	48.392	35.979	45.045	6.09	0.74	3.374	40.0	133.3	449.754	37.006
Feb. '76	2.24	1.25	0.105	54.5	19.074	-4.118	25.200	6.08	0.73	3.077	29.0	96.7	297.546	-34.155
May '76	4.30	0.84	1.739	13.0	75.351	183.809	127.540	6.30	0.49	5.033	20.0	66.7	335.701	159.805
Aug. '76	4.57	0.74	1.940	26.0	168.140	13.065	-79.702	7.15	0.57	7.721	36.0	120.0	926.520	250.925
Nov. '76	5.30	0.61	2.216	20.0	147.741	21.161	41.560	7.49	0.49	7.433	18.0	60.0	445.980	-25.920
Feb. '77	5.77	0.68	2.842	19.0	179.984	40.885	8.447	7.47	0.45	6.139	18.0	60.0	368.340	-77.640
COHORT 1973														
Mar. '75	5.63	0.39	4.592	12.0	40.0	183.680	-	7.38	0.47	10.273	12.0	40.0	410.920	-
Apr. '75	5.76	0.33	4.960	6.5	21.7	107.632	92.177	7.86	0.56	11.586	8.0	26.7	309.346	43.788
May '75	6.35	0.38	7.474	15.5	51.7	386.406	-186.510	7.61	0.46	13.419	8.0	26.7	358.287	48.941
June '75	6.76	0.41	10.219	53.0	176.7	1805.697	-1105.750	7.97	0.32	16.077	17.5	58.3	937.289	112.965
July '75	6.94	0.45	7.777	47.0	156.7	1218.656	179.960	8.60	0.45	16.570	5.0	16.7	276.719	18.487
Aug. '75	7.33	0.50	10.040	50.0	166.7	1673.668	-89.080	8.93	0.48	18.849	15.0	50.0	942.450	76.005
Sep. '75	7.49	0.50	9.870	40.0	133.3	1315.671	332.497	9.00	0.33	18.454	7.5	25.0	461.350	-14.812
Oct. '75	7.83	0.37	9.583	33.0	110.0	1054.130	226.616	9.44	0.38	18.030	7.0	23.3	420.099	-10.240
Nov. '75	7.76	0.37	8.090	23.0	76.7	620.503	294.239	9.05	0.38	14.045	8.0	26.7	375.001	-99.625
Dec. '75	7.86	0.40	8.851	35.0	116.7	1032.912	-338.800	9.16	0.38	16.029	7.0	23.3	373.476	49.600
Jan. '76	7.97	0.35	9.059	24.0	80.0	724.720	328.648	9.17	0.38	15.159	12.0	40.0	606.360	-27.535
Feb. '76	8.04	0.38	7.914	9.5	31.7	250.874	409.874	9.04	0.26	11.940	9.0	30.0	358.200	-112.665
May '76	8.12	0.31	10.197	9.5	31.7	323.245	72.371	9.56	0.32	16.059	8.5	28.3	454.470	119.986
Aug. '76	8.73	0.41	14.297	17.5	58.3	833.515	-325.770	9.72	0.32	19.916	15.5	51.7	1029.657	154.280
Nov. '76	8.84	0.35	13.274	11.0	36.7	487.156	297.756	10.13	0.29	21.379	3.0	10.0	213.790	45.133
Feb. '77	9.12	0.45	11.131	19.0	63.3	704.592	-324.643	10.16	0.38	15.360	7.0	23.3	357.888	-100.216

Appendix 3.3 continued. Group 2 Production Calculation continued.

Sampling Date	Height	M.I.W.	No.	N m ⁻²	Biomass	ΔP	ΔM	Height	M.I.W.	No.	N m ⁻²	Biomass	ΔP	ΔM
COHORT 1971														
Mar. '75	8.30	0.00	14.571	2.0	6.7	97.626	-	10.21	0.36	26.982	17.0	56.7	1529.879	-
Apr. '75	9.13	0.25	17.436	9.0	30.0	523.080	-372.870	10.36	0.40	24.618	16.0	53.3	1312.139	-130.020
May '75	8.92	0.25	22.424	4.0	13.3	298.239	332.831	10.67	0.44	40.017	8.0	26.7	1068.454	615.960
June '75	9.70	0.58	27.604	10.5	35.0	966.140	-537.801	11.16	0.24	40.602	7.0	23.3	946.027	14.625
July '75	9.98	0.49	28.009	5.5	18.3	512.565	464.360	11.36	0.32	44.226	4.5	15.0	663.390	69.400
Aug. '75	10.34	0.33	30.088	6.5	21.7	652.910	-98.763	11.37	0.34	40.733	10.5	35.0	1425.655	-87.325
Sep. '75	10.30	0.18	29.222	9.0	30.0	876.660	-246.136	11.40	0.48	41.291	2.5	8.3	342.715	11.215
Oct. '75	10.55	0.27	26.253	6.0	20.0	525.060	277.370	11.30	0.00	33.112	6.0	20.0	662.240	-115.733
Nov. '75	10.80	0.00	26.480	5.0	16.7	442.216	87.008	11.80	0.00	36.380	2.0	6.7	243.746	43.628
Dec. '75	10.30	0.32	25.268	6.0	20.0	505.360	-85.384	11.42	0.35	37.714	8.0	26.7	1006.964	22.278
Jan. '76	10.16	0.34	22.086	5.5	18.3	404.174	40.251	11.44	0.34	34.143	5.5	18.3	624.817	-80.347
Feb. '76	10.37	0.21	18.710	3.5	11.7	218.970	-50.640	11.53	0.36	26.778	5.5	18.3	490.037	-134.779
May '76	10.47	0.26	20.681	6.0	20.0	413.620	-163.468	11.59	0.39	27.438	7.0	23.3	639.305	13.596
Aug. '76	11.03	0.39	29.421	13.0	43.3	1273.929	-583.688	11.97	0.29	37.868	3.0	10.0	378.680	173.659
Nov. '76	11.3	-	31.338	1.0	3.3	103.415	1215.160	11.8	-	36.464	1.0	3.3	120.331	-9.337
Feb. '77	11.05	0.35	19.730	2.0	6.7	132.191	-86.816	11.8	-	23.998	2.0	6.7	160.787	-62.330

COHORTS 1969+

Mar. '75	11.36	0.46	37.066	9.0	30.0	1111.980	-	-	-	-	-	0	0	0
Apr. '75	12.48	1.15	40.917	22.0	73.3	2999.216	198.904	0.92	0.33	0.024	128.0	426.7	5.120	-5.120
May '75	12.70	0.89	70.273	5.0	16.7	1173.559	-1688.310	1.56	0.68	0.070	385.0	1283.3	39.330	-40.260
June '75	12.34	0.50	53.540	12.0	40.0	2141.600	3146.677	1.91	0.96	0.062	359.0	1196.7	-9.920	5.716
July '75	13.30	0.50	77.123	3.0	10.0	771.230	-474.380	1.62	1.02	0.064	205.0	683.3	1.880	32.344
Aug. '75	13.36	1.18	68.139	8.0	26.7	1819.311	-1442.410	-	-	-	-	-	-	-
Sep. '75	12.90	0.22	62.915	5.0	16.7	1050.680	1959.930	-	-	-	-	-	-	-
Oct. '75	13.00	1.18	53.176	10.0	33.3	1770.761	-1212.938	-	-	-	-	-	-	-
Nov. '75	12.80	0.76	48.706	7.0	23.3	1134.850	655.270	-	-	-	-	-	-	-
Dec. '75	13.30	1.15	68.124	4.0	13.3	906.049	-963.547	-	-	-	-	-	-	-
Jan. '76	13.16	0.59	57.096	11.0	36.7	2095.423	509.410	-	-	-	-	-	-	-
Feb. '76	12.8	-	38.125	1.0	3.3	125.812	584.150	-	-	-	-	-	-	-
May '76	13.66	1.07	43.341	7.0	23.3	1009.845	-1465.074	0.92	0.33	0.024	128.0	426.7	5.120	-5.120
Aug. '76	12.80	0.35	46.571	5.0	16.7	777.736	1590.174	1.56	0.68	0.070	385.0	1283.3	39.330	-40.260
Nov. '76	13.30	0.71	55.425	2.0	6.7	371.347	-814.660	1.91	0.96	0.062	359.0	1196.7	-9.920	5.716
Feb. '77	13.80	0.93	38.278	5.0	16.7	639.243	296.710	1.62	1.02	0.064	205.0	683.3	1.880	32.344

COHORT 1976

Appendix 3.3 continued. Group 3 Production Calculation.

Sampling Date	Height	M.I.W.	No.	$N m^{-2}$	Biomass	ΔP	ΔM	Height	M.I.W.	No.	$N m^{-2}$	Biomass	ΔP	ΔM	
COHORT 1974															
Mar. '75	-	-	-	-	-	-	-	1.73	0.66	0.044	457.0	914.0	40.216	-	-
Apr. '75	-	-	-	-	-	-	-	1.66	0.90	0.070	249.0	498.0	18.356	23.712	
May '75	0.8	-	0.021	40.0	80.0	0.840	-0.880	2.37	0.96	0.424	175.5	351.0	150.273	36.309	
June '75	1.05	0.25	0.021	40.0	80.0	0	0	2.62	0.93	0.303	152.0	304.0	-39.627	17.061	
July '75	1.06	0.28	0.021	332.0	664.0	0	-12.264	3.14	0.97	0.550	101.5	203.0	62.614	43.026	
Aug. '75	1.46	0.41	0.059	196.0	392.0	20.064	10.880	3.59	0.86	1.122	103.0	206.0	116.974	-2.508	
Sep. '75	1.30	0.57	0.033	160.0	320.0	-9.256	3.312	3.94	0.87	1.202	75.5	151.0	14.280	63.910	
Oct. '75	1.47	0.57	0.031	117.0	234.0	-0.554	2.752	4.34	0.76	1.293	67.0	134.0	12.967	21.199	
Nov. '75	1.72	0.74	0.051	135.0	270.0	5.040	-1.476	4.72	0.72	1.679	60.0	120.0	49.022	20.804	
Dec. '75	1.98	0.92	0.077	226.5	453.0	9.399	-11.712	4.75	0.65	1.548	75.0	150.0	-17.685	-48.390	
Jan. '76	1.85	0.88	0.066	106.0	212.0	-3.657	17.111	4.96	0.52	1.713	45.5	91.0	19.882	96.170	
Feb. '76	1.55	0.87	0.028	120.0	240.0	-8.588	-1.316	5.04	0.52	1.597	51.0	102.0	-11.914	-18.205	
May '76	2.93	0.67	0.428	65.5	131.0	74.200	24.852	5.38	0.61	2.683	52.0	104.0	111.858	-4.280	
Aug. '76	3.28	0.67	0.634	28.0	56.0	19.261	39.825	5.58	0.57	3.145	43.0	86.0	43.890	46.624	
Nov. '76	4.16	0.48	1.260	24.5	49.0	32.865	6.629	6.03	0.55	3.846	34.0	68.0	53.977	62.910	
Feb. '77	4.94	0.71	1.818	11.0	22.0	19.809	41.553	6.45	0.45	3.867	16.5	33.0	1.060	134.960	
COHORT 1973															
Mar. '75	5.25	0.69	2.056	20.0	40.0	82.240	-	7.09	0.29	5.822	22.0	44.0	256.168	-	-
Apr. '75	5.17	0.69	2.188	20.0	40.0	87.520	0	7.13	0.54	5.801	12.0	24.0	139.224	-0.714	116.220
May '75	5.04	0.56	3.403	66.5	133.0	452.599	-259.935	7.16	0.45	8.968	11.0	22.0	197.296	72.841	14.768
June '75	5.20	0.49	2.241	64.0	128.0	288.128	14.135	7.15	0.34	5.720	17.0	34.0	194.480	-90.944	-88.128
July '75	5.54	0.49	3.055	57.5	115.0	351.325	34.489	7.10	0.37	6.461	11.5	23.0	148.603	21.118	66.770
Aug. '75	5.61	0.47	4.848	39.5	79.0	382.992	142.236	7.48	0.36	12.449	18.5	37.0	460.613	179.640	-132.370
Sep. '75	6.01	0.41	4.723	42.0	84.0	396.732	-23.925	7.55	0.50	9.908	17.0	34.0	336.872	-90.205	33.534
Oct. '75	6.19	0.37	4.387	42.0	84.0	368.508	0	7.77	0.40	9.595	9.5	19.0	182.305	-8.294	146.265
Nov. '75	6.17	0.37	4.233	19.0	38.0	160.854	198.260	7.82	0.37	9.593	14.5	29.0	278.197	-0.048	-95.940
Dec. '75	6.53	0.52	4.619	35.5	71.0	327.949	-146.058	7.80	0.37	8.503	23.0	46.0	391.138	-40.875	-153.816
Jan. '76	6.48	0.51	4.137	32.5	65.0	268.905	26.268	8.11	0.25	8.673	13.0	26.0	225.498	6.120	171.760
Feb. '76	6.75	0.45	4.344	22.0	44.0	191.136	89.040	7.99	0.25	7.741	14.5	29.0	224.489	-25.630	-24.621
May '76	6.83	0.43	5.519	25.5	51.0	281.469	-34.517	8.26	0.13	9.803	14.0	28.0	274.484	58.767	8.772
Aug. '76	7.18	0.44	6.725	25.0	50.0	336.250	6.122	8.48	0.25	11.105	11.0	22.0	244.310	32.550	62.724
Nov. '76	7.85	0.44	8.500	10.0	20.0	170.000	228.360	8.63	0.25	11.300	12.0	24.0	271.200	4.485	-22.404
Feb. '77	7.77	0.36	6.549	9.5	19.0	124.431	7.524	8.63	0.58	8.814	3.0	6.0	52.884	-37.290	181.026

Appendix 3.3 continued. Group 3 Production Calculation continued.

Sampling Date	Height	M.I.W.	No.	N m ⁻²	Biomass	ΔP	ΔM	Height	M.I.W.	No.	N m ⁻²	Biomass	ΔP	ΔM
COHORT 1970														
Mar. '75	8.08	0.25	9.156	25.0	50.0	457.800	-	9.59	0.43	16.575	14.0	28.0	464.100	-
Apr. '75	8.25	0.35	9.030	11.0	22.0	198.660	-4.536	9.39	0.37	13.371	11.0	22.0	294.162	-80.100
May '75	8.22	0.29	13.127	12.0	24.0	315.048	94.231	9.36	0.26	18.786	13.5	27.0	507.222	132.668
June '75	8.33	0.36	8.947	9.5	19.0	169.993	-89.870	9.40	0.39	12.745	12.5	25.0	318.625	157.066
July '75	8.33	0.32	10.465	9.5	19.0	198.835	28.842	9.63	0.29	16.214	3.0	6.0	97.284	53.769
Aug. '75	8.52	0.26	19.075	18.0	36.0	686.700	236.775	9.36	0.17	25.961	9.0	18.0	467.298	116.964
Sep. '75	8.63	0.25	15.286	7.5	15.0	229.290	-96.619	9.48	0.25	20.730	11.0	22.0	456.060	-104.620
Oct. '75	8.70	0.21	14.159	12.5	25.0	353.975	-22.540	9.61	0.25	19.941	13.0	26.0	518.466	-18.936
Nov. '75	8.63	0.25	13.480	12.0	24.0	323.520	-16.635	9.45	0.24	18.441	10.0	20.0	368.820	-34.500
Dec. '75	8.55	0.26	11.655	12.0	24.0	279.720	-43.800	9.42	0.22	16.257	17.0	34.0	552.738	-58.968
Jan. '76	8.80	0.00	11.354	8.0	16.0	181.664	-6.020	9.57	0.26	14.974	15.0	30.0	449.220	-41.056
Feb. '76	8.60	0.25	9.961	13.5	27.0	268.947	-29.949	9.57	0.26	14.365	11.0	22.0	316.030	-15.782
May '76	9.02	0.26	12.791	14.5	29.0	370.939	79.240	9.49	0.25	14.913	10.5	21.0	313.173	11.567
Aug. '76	9.30	0.00	14.667	7.0	14.0	205.338	40.334	10.08	0.28	18.697	4.5	9.0	168.273	56.760
Nov. '76	9.36	0.18	14.424	11.5	23.0	327.566	-4.495	10.21	0.20	18.731	8.5	17.0	318.427	0.442
Feb. '77	9.67	0.25	12.163	4.0	8.0	97.304	-35.045	10.30	0.00	14.541	3.0	6.0	87.246	-48.185
COHORTS 1969+														
Mar. '75	11.17	1.15	28.112	36.0	72.0	2024.064	-	-	-	-	-	0	0	0
Apr. '75	11.02	1.39	21.727	16.0	32.0	695.264	-332.020	1.20	0.27	0.029	60.0	120.0	3.480	1.740
May '75	11.03	0.85	29.555	19.5	39.0	1152.645	277.894	1.20	0.36	0.031	204.0	408.0	12.648	0.528
June '75	10.63	0.78	18.269	21.0	42.0	767.298	-457.083	1.32	0.59	0.040	197.5	395.0	15.800	3.613
July '75	11.15	1.03	25.238	23.0	46.0	1160.948	306.636	1.67	0.83	0.084	134.0	268.0	22.512	14.586
Aug. '75	10.99	0.66	43.940	13.0	26.0	1142.440	673.272	-	-	-	-	0	0	-1.680
Sep. '75	11.22	0.56	35.804	12.0	24.0	859.296	-203.400	-	-	-	-	0	0	-8.640
Oct. '75	10.97	0.75	31.449	12.0	24.0	754.776	-104.520	-	-	-	-	0	0	0
Nov. '75	10.83	0.69	29.521	17.0	34.0	1003.714	-55.912	1.20	0.27	0.029	60.0	120.0	3.480	1.740
Dec. '75	10.93	0.74	27.087	19.0	38.0	1029.306	-87.624	1.20	0.36	0.031	204.0	408.0	12.648	0.528
Jan. '76	10.99	0.65	23.635	8.0	16.0	378.160	-93.204	1.32	0.59	0.040	197.5	395.0	15.800	3.613
Feb. '76	11.12	0.66	24.024	22.0	44.0	1057.056	11.670	1.67	0.83	0.084	134.0	268.0	22.512	14.586
May '76	11.24	0.68	24.870	18.0	36.0	895.320	33.840	-	-	-	-	0	0	0
Aug. '76	11.23	1.00	25.893	7.5	15.0	388.395	26.086	1.20	0.36	0.031	204.0	408.0	12.648	0.528
Nov. '76	11.01	0.39	23.498	7.0	14.0	328.972	-34.727	1.32	0.59	0.040	197.5	395.0	15.800	3.613
Feb. '77	10.8	-	16.629	1.0	2.0	33.258	-54.952	1.67	0.83	0.084	134.0	268.0	22.512	14.586

Appendix 3.3 continued. Group 4 Production Calculation.

Sampling Date	Height	M.I.W.	No.	$N m^{-2}$	Biomass	ΔP	ΔM	Height	M.I.W.	No.	$N m^{-2}$	Biomass	ΔP	ΔM
COHORT 1974														
Mar. '75	-	-	-	-	-	-	-	3.06	0.41	0.472	29.0	96.7	45.627	-
Apr. '75	0.80	0.00	20.0	66.7	0.067	0.033	-0.033	1.97	0.91	0.039	50.5	168.3	6.565	-57.372
May '75	0.80	0.00	40.0	133.3	2.400	1.700	-0.633	2.54	0.94	0.476	35.0	116.7	55.533	62.272
June '75	1.11	0.35	160.0	533.3	37.867	17.666	-17.600	3.74	0.44	1.764	16.0	53.3	94.080	109.493
July '75	1.17	0.39	120.0	400.0	12.800	6.800	6.800	3.69	0.71	1.035	32.0	106.7	110.400	-58.327
Aug. '75	1.37	0.54	81.5	271.7	28.525	24.516	8.726	4.28	0.46	2.120	14.5	48.3	102.467	76.415
Sep. '75	1.23	0.60	120.0	400.0	11.600	-25.525	-8.598	4.49	0.36	2.084	29.0	96.7	201.520	-2.610
Oct. '75	1.97	0.82	88.0	293.3	34.027	30.159	7.680	4.62	0.61	1.925	31.0	103.3	198.916	-15.900
Nov. '75	1.94	0.89	74.5	248.3	16.887	-12.999	4.143	4.78	0.48	1.715	24.5	81.7	140.058	-19.425
Dec. '75	1.87	0.70	132.0	440.0	29.920	0	-13.036	4.44	0.56	1.324	7.0	23.3	30.893	-20.527
Jan. '76	1.94	0.82	55.0	183.3	15.583	5.298	19.509	4.80	0.39	1.548	14.0	46.7	72.240	7.840
Feb. '76	2.29	0.75	23.5	78.3	17.468	18.050	16.170	4.77	0.56	1.823	18.5	61.7	112.418	14.905
May '76	3.14	0.43	18.5	61.7	37.370	26.810	6.872	5.23	0.61	2.565	7.0	23.3	59.764	31.535
Aug. '76	3.11	0.46	8.0	26.7	15.440	-1.193	20.720	6.07	0.59	3.307	5.5	18.3	60.628	15.434
Nov. '76	3.55	0.71	8.0	26.7	23.683	8.224	0	6.55	1.06	4.171	2.0	6.7	27.807	10.800
Feb. '77	4.63	0.58	13.9	46.3	71.817	24.199	-23.873	6.80	0.71	4.495	4.0	13.3	59.933	3.240
COHORT 1972														
Mar. '75	4.80	0.44	1.950	41.7	81.250	-	-	6.41	0.31	4.852	6.5	21.7	105.127	-
Apr. '75	5.06	0.59	1.597	48.3	77.188	-15.885	-11.702	6.47	0.24	4.188	15.0	50.0	209.400	-23.804
May '75	5.35	0.50	3.886	93.3	362.693	162.061	-123.345	7.01	0.34	8.322	21.0	70.0	582.539	248.040
June '75	5.50	0.52	4.891	90.0	440.190	92.108	14.480	7.00	0.49	9.254	19.5	65.0	601.509	62.910
July '75	5.69	0.68	3.837	63.3	243.010	-80.789	116.519	7.30	0.28	8.155	14.0	46.7	380.566	-61.379
Aug. '75	5.98	0.43	5.127	83.3	427.250	94.557	-89.640	7.48	0.25	9.257	9.5	31.7	293.138	43.198
Sep. '75	6.25	0.42	6.220	93.3	580.533	96.512	-56.730	7.49	0.26	11.315	8.0	26.7	301.733	60.094
Oct. '75	6.26	0.43	5.244	83.3	437.000	-86.181	57.320	7.55	0.27	9.730	6.0	20.0	195.600	-37.010
Nov. '75	6.43	0.39	4.966	78.3	388.838	-22.462	25.525	7.77	0.13	9.789	7.5	25.0	244.725	1.327
Dec. '75	6.64	0.47	5.259	58.3	306.775	20.012	102.240	7.65	0.24	8.542	11.5	38.3	327.443	-39.467
Jan. '76	6.84	0.36	4.823	46.7	225.073	-22.890	48.476	7.63	0.25	6.849	12.0	40.0	273.960	-66.281
Feb. '76	6.59	0.47	4.604	46.7	215.007	-10.227	0	7.73	0.18	7.274	14.0	46.7	339.453	18.597
May '76	6.97	0.29	5.777	10.0	57.770	33.254	190.473	8.07	0.26	8.742	13.0	43.3	378.820	66.060
Aug. '76	7.39	0.31	5.522	48.3	266.713	-7.433	-216.357	8.42	0.23	7.757	8.0	26.7	206.853	-34.475
Nov. '76	7.67	0.25	6.216	13.3	82.880	21.375	205.415	8.47	0.27	7.988	4.5	15.0	119.820	4.816
Feb. '77	7.63	0.26	6.184	20.0	123.680	-0.533	-41.540	8.47	0.29	8.259	3.0	10.0	82.590	3.387
COHORT 1973														
Mar. '75	4.80	0.44	1.950	41.7	81.250	-	-	6.41	0.31	4.852	6.5	21.7	105.127	-
Apr. '75	5.06	0.59	1.597	48.3	77.188	-15.885	-11.702	6.47	0.24	4.188	15.0	50.0	209.400	-23.804
May '75	5.35	0.50	3.886	93.3	362.693	162.061	-123.345	7.01	0.34	8.322	21.0	70.0	582.539	248.040
June '75	5.50	0.52	4.891	90.0	440.190	92.108	14.480	7.00	0.49	9.254	19.5	65.0	601.509	62.910
July '75	5.69	0.68	3.837	63.3	243.010	-80.789	116.519	7.30	0.28	8.155	14.0	46.7	380.566	-61.379
Aug. '75	5.98	0.43	5.127	83.3	427.250	94.557	-89.640	7.48	0.25	9.257	9.5	31.7	293.138	43.198
Sep. '75	6.25	0.42	6.220	93.3	580.533	96.512	-56.730	7.49	0.26	11.315	8.0	26.7	301.733	60.094
Oct. '75	6.26	0.43	5.244	83.3	437.000	-86.181	57.320	7.55	0.27	9.730	6.0	20.0	195.600	-37.010
Nov. '75	6.43	0.39	4.966	78.3	388.838	-22.462	25.525	7.77	0.13	9.789	7.5	25.0	244.725	1.327
Dec. '75	6.64	0.47	5.259	58.3	306.775	20.012	102.240	7.65	0.24	8.542	11.5	38.3	327.443	-39.467
Jan. '76	6.84	0.36	4.823	46.7	225.073	-22.890	48.476	7.63	0.25	6.849	12.0	40.0	273.960	-66.281
Feb. '76	6.59	0.47	4.604	46.7	215.007	-10.227	0	7.73	0.18	7.274	14.0	46.7	339.453	18.597
May '76	6.97	0.29	5.777	10.0	57.770	33.254	190.473	8.07	0.26	8.742	13.0	43.3	378.820	66.060
Aug. '76	7.39	0.31	5.522	48.3	266.713	-7.433	-216.357	8.42	0.23	7.757	8.0	26.7	206.853	-34.475
Nov. '76	7.67	0.25	6.216	13.3	82.880	21.375	205.415	8.47	0.27	7.988	4.5	15.0	119.820	4.816
Feb. '77	7.63	0.26	6.184	20.0	123.680	-0.533	-41.540	8.47	0.29	8.259	3.0	10.0	82.590	3.387

Appendix 3.3 continued. Group 4 Production Calculation continued, Group 5 Production Calculation.

Sampling Date	Height	M.I.W.	No.	N m ⁻²	Biomass	ΔP	ΔM	Height	M.I.W.	No.	N m ⁻²	Biomass	ΔP	ΔM
COHORT 1976														
Mar. '75	8.02	0.83	9.830	20.0	66.7	655.333	-	-	0.00	0.013	48.0	160.0	0	0
Apr. '75	8.19	0.87	10.557	22.0	73.3	774.179	50.890	0.80	0.47	0.053	64.0	213.0	2.080	1.040
May '75	8.61	0.73	14.854	35.0	116.7	1732.965	408.215	1.24	0.19	0.024	105.0	350.0	11.307	7.466
June '75	8.87	0.66	17.306	40.5	135.0	2336.308	308.584	0.85	0.19	0.024	105.0	350.0	8.400	-8.168
July '75	8.74	0.62	14.062	26.0	86.7	1218.700	-359.597	1.25	0.59	0.041	188.0	626.7	25.693	8.302
Aug. '75	8.70	0.72	13.794	19.5	65.0	896.609	-20.328	0.80	0.00	0.013	48.0	160.0	0	0
Sep. '75	8.99	0.75	20.689	16.0	53.3	1103.412	407.839	1.24	0.47	0.053	64.0	213.0	2.080	1.040
Oct. '75	8.87	0.71	16.557	22.0	73.3	1214.179	-261.556	0.80	0.00	0.013	48.0	160.0	0	0
Nov. '75	8.83	0.67	15.484	16.0	53.3	825.812	-67.921	1.24	0.47	0.053	64.0	213.0	11.307	7.466
Dec. '75	8.76	0.42	13.588	23.0	76.7	1041.746	-123.240	0.85	0.19	0.024	105.0	350.0	8.400	-8.168
Jan. '76	8.92	0.62	11.307	25.0	83.3	942.249	-182.480	1.25	0.59	0.041	188.0	626.7	25.693	8.302
Feb. '76	8.75	0.55	10.376	10.0	33.3	345.866	-54.278	0.80	0.00	0.013	48.0	160.0	0	0
May '76	9.10	0.45	12.277	5.0	16.7	205.026	47.525	0.80	0.00	0.013	48.0	160.0	2.080	1.040
Aug. '76	9.30	0.45	10.050	6.0	20.0	201.000	-40.865	1.24	0.47	0.053	64.0	213.0	11.307	7.466
Nov. '76	9.34	0.44	10.228	5.5	18.3	187.513	3.409	0.85	0.19	0.024	105.0	350.0	8.400	-8.168
Feb. '77	9.63	0.68	11.785	6.0	20.0	235.700	29.816	1.25	0.59	0.041	188.0	626.7	25.693	8.302
COHORT 1974														
Mar. '75	-	-	-	-	-	-	-	3.37	0.53	0.553	7.0	70.0	0	0
Apr. '75	-	-	-	-	-	-	-	3.58	0.44	0.819	9.0	90.0	38.710	19.355
May '75	1.55	0.25	0.056	40.0	400.0	22.400	11.200	4.15	0.24	2.683	10.0	100.0	73.710	21.280
June '75	1.30	0.51	0.292	40.0	400.0	116.800	94.400	3.80	0.00	0.872	2.0	20.0	268.300	177.080
July '75	1.05	0.25	0.011	32.0	320.0	3.520	-101.160	3.93	0.44	0.895	15.0	150.0	17.440	-108.660
Aug. '75	2.17	0.42	0.073	32.0	320.0	23.360	19.840	4.80	0.00	1.975	2.0	20.0	134.250	1.955
Sep. '75	1.14	0.48	0.012	41.0	410.0	4.920	-22.265	4.30	0.93	1.026	5.0	50.0	39.500	91.800
Oct. '75	1.73	0.46	0.047	25.5	255.0	11.985	11.637	4.10	0.77	0.760	2.5	25.0	51.300	-33.215
Nov. '75	0.80	0.00	0.001	8.0	80.0	0.120	-7.621	4.14	0.57	0.791	9.5	95.0	19.000	-9.975
Dec. '75	1.27	0.49	0.011	33.5	335.0	3.685	1.971	4.80	0.45	1.697	6.0	60.0	75.145	1.860
Jan. '76	2.47	0.24	0.211	24.0	240.0	50.640	57.500	4.55	0.35	1.534	2.0	20.0	101.820	70.215
Feb. '76	0.93	0.48	0.018	26.0	260.0	4.680	-48.250	4.30	0.00	1.303	3.0	30.0	30.680	-6.520
May '76	1.91	0.82	0.163	28.0	280.0	45.640	39.150	5.55	0.35	2.439	2.0	20.0	39.090	-5.775
Aug. '76	3.30	0.71	0.482	5.0	50.0	24.100	52.635	6.10	0.45	3.052	5.0	50.0	48.780	28.400
Nov. '76	4.30	1.22	1.106	1.5	15.0	16.590	20.280	6.30	0.35	3.381	5.0	50.0	152.600	21.455
Feb. '77	4.30	-	1.226	1.0	10.0	12.260	1.500	6.30	0.35	3.381	5.0	50.0	169.050	16.450

Appendix 3.3 continued. Group 5 Production Calculation continued.

Sampling Date	Height	M.I.W.	No.	$N m^{-2}$	Biomass	ΔP	ΔM	Height	M.I.W.	No.	$N m^{-2}$	Biomass	ΔP	ΔM
COHORT 1972														
Mar. '75	5.30	0.00	2.0	20.0	59.040	-	-	6.30	0.00	2.0	20.0	91.540	-	-
Apr. '75	5.16	0.48	5.5	55.0	141.295	-14.362	-96.600	6.20	0.33	5.0	50.0	249.050	14.140	-143.370
May '75	4.97	0.29	3.0	30.0	70.500	-9.307	61.475	6.36	0.18	4.5	45.0	233.460	9.832	25.420
June '75	5.17	0.25	4.0	40.0	163.360	60.690	-32.170	-	-	-	0	0	-116.730	116.730
July '75	5.20	0.42	5.0	50.0	127.700	-68.850	-33.190	6.55	0.35	2.0	20.0	112.660	56.330	-56.320
Aug. '75	5.67	0.58	8.0	80.0	336.000	106.990	-101.310	7.13	0.29	3.0	30.0	331.020	135.025	-83.330
Sep. '75	6.36	0.56	4.5	45.0	240.480	71.500	167.020	7.02	0.28	4.5	45.0	341.010	-129.600	-139.590
Oct. '75	5.74	0.53	4.0	40.0	309.400	-110.882	20.195	7.20	0.26	2.5	25.0	147.525	-58.695	134.780
Nov. '75	6.06	0.49	8.5	85.0	284.665	38.375	-136.890	7.24	0.32	8.0	80.0	526.320	35.595	-343.200
Dec. '75	6.47	0.27	4.5	45.0	179.055	40.950	146.560	7.00	0.32	2.5	25.0	132.250	-67.672	326.370
Jan. '76	6.05	0.35	2.0	20.0	70.160	-15.307	93.575	7.80	0.41	4.0	40.0	311.360	81.055	-98.055
Feb. '76	6.30	0.55	6.0	60.0	228.600	12.080	-146.360	7.97	0.29	3.0	30.0	220.590	-15.085	75.680
May '76	6.63	0.29	3.0	30.0	118.530	6.345	116.400	7.80	0.45	6.0	60.0	359.920	-61.245	-200.160
Aug. '76	6.63	0.29	3.0	30.0	127.410	8.880	0	8.05	0.35	2.0	20.0	155.640	71.600	275.480
Nov. '76	7.05	0.35	2.0	20.0	92.880	9.925	44.450	8.8	-	1.0	10.0	88.350	15.795	83.080
Feb. '77	7.17	0.25	4.0	40.0	190.680	3.690	-141.150	7.80	0.00	4.0	40.0	238.440	-71.850	-221.940

COHORT 1976

COHORTS 1971+														
Mar. '75	8.30	0.00	2.0	20.0	184.240	-	-	8.30	0.00	2.0	20.0	184.240	-	-
Apr. '75	7.71	0.57	5.5	55.0	601.095	64.387	-352.450	8.3	-	1.0	10.0	209.390	104.695	-104.690
May '75	7.58	0.54	4.5	45.0	410.220	-90.650	100.220	8.13	0.41	6.0	60.0	764.160	-287.105	-841.850
June '75	8.55	0.29	4.0	40.0	427.160	66.427	49.485	8.47	0.29	3.0	30.0	307.200	-112.320	344.640
July '75	-	-	-	0	0	-213.580	213.560	8.20	0.22	5.0	50.0	527.700	12.560	-207.940
Aug. '75	8.3	-	1.0	10.0	209.390	104.695	-104.690	8.42	0.25	4.0	40.0	412.720	-10.530	104.360
Sep. '75	8.13	0.41	6.0	60.0	764.160	-287.105	-841.850	-	-	-	0	0	-206.360	206.360
Oct. '75	8.47	0.29	3.0	30.0	307.200	-112.320	344.640	9.8	-	1.0	10.0	131.060	65.530	-65.530
Nov. '75	8.20	0.22	5.0	50.0	527.700	12.560	-207.940	-	-	-	0	0	0	0
Dec. '75	8.42	0.25	4.0	40.0	412.720	-10.530	104.360	-	-	-	0	0	-65.530	65.530
Jan. '76	-	-	-	0	0	-206.360	206.360	1.05	0.26	0.013	16.0	160.0	1.040	-1.040
Feb. '76	9.8	-	1.0	10.0	131.060	65.530	-65.530	1.19	0.73	0.027	52.5	525.0	4.795	-7.300
May '76	-	-	-	0	0	0	0	0.88	0.30	0.018	218.0	2180.0	-12.172	-37.237
Aug. '76	-	-	-	0	0	0	0	-	-	-	-	-	-	-
Nov. '76	-	-	-	0	0	0	0	-	-	-	-	-	-	-
Feb. '77	-	-	-	0	0	0	0	-	-	-	-	-	-	-

Appendix 3.4 M. balthica: The Production Calculation for Station B3 Using Monthly Sampling Data, 1976-77.

Sampling Date	Height	M.I.W. No.	N m ⁻²	Biomass	ΔP	ΔM	Height	M.I.W. No.	N m ⁻²	Biomass	ΔP	ΔM
COHORT 1976												
Mar. '76	-	-	-	-	-	-	2.58	0.84	0.188	32.0	320.0	60.160
Apr. '76	-	-	-	-	-	-	3.97	0.56	0.877	9.0	90.0	78.930
May '76	1.13	0.48	0.042	24.0	240.0	10.080	3.92	0.74	1.344	8.0	80.0	107.520
June '76	0.90	0.20	0.013	120.0	1200.0	15.600	3.56	0.61	0.845	25.0	250.0	211.250
July '76	1.01	0.30	0.019	264.0	2640.0	50.160	4.88	0.79	2.301	6.5	65.0	149.565
Aug. '76	1.52	0.68	0.065	169.0	1690.0	109.850	5.01	0.97	2.445	17.0	170.0	415.650
Sep. '76	1.92	0.83	0.125	125.0	1250.0	156.250	5.22	0.95	2.735	19.0	190.0	519.650
Oct. '76	2.43	0.74	0.179	147.0	1470.0	263.130	5.16	0.67	1.977	21.0	210.0	415.170
Nov. '76	2.09	0.88	0.085	106.0	1060.0	90.100	5.42	1.00	2.397	20.0	200.0	479.400
Dec. '76	3.51	0.46	0.550	24.0	240.0	132.000	5.37	0.82	2.381	22.0	220.0	523.820
Jan. '77	3.49	0.60	0.554	15.5	155.0	85.870	5.34	0.93	2.282	12.5	125.0	285.250
Feb. '77	1.30	0.89	0.033	102.5	1025.0	33.825	5.85	0.74	2.961	14.5	145.0	429.340
COHORT 1975												
Mar. '76	-	-	-	-	-	-	2.58	0.84	0.188	32.0	320.0	60.160
Apr. '76	-	-	-	-	-	-	3.97	0.56	0.877	9.0	90.0	78.930
May '76	1.13	0.48	0.042	24.0	240.0	10.080	3.92	0.74	1.344	8.0	80.0	107.520
June '76	0.90	0.20	0.013	120.0	1200.0	15.600	3.56	0.61	0.845	25.0	250.0	211.250
July '76	1.01	0.30	0.019	264.0	2640.0	50.160	4.88	0.79	2.301	6.5	65.0	149.565
Aug. '76	1.52	0.68	0.065	169.0	1690.0	109.850	5.01	0.97	2.445	17.0	170.0	415.650
Sep. '76	1.92	0.83	0.125	125.0	1250.0	156.250	5.22	0.95	2.735	19.0	190.0	519.650
Oct. '76	2.43	0.74	0.179	147.0	1470.0	263.130	5.16	0.67	1.977	21.0	210.0	415.170
Nov. '76	2.09	0.88	0.085	106.0	1060.0	90.100	5.42	1.00	2.397	20.0	200.0	479.400
Dec. '76	3.51	0.46	0.550	24.0	240.0	132.000	5.37	0.82	2.381	22.0	220.0	523.820
Jan. '77	3.49	0.60	0.554	15.5	155.0	85.870	5.34	0.93	2.282	12.5	125.0	285.250
Feb. '77	1.30	0.89	0.033	102.5	1025.0	33.825	5.85	0.74	2.961	14.5	145.0	429.340
COHORT 1974												
Mar. '76	5.91	0.81	2.686	14.0	140.0	376.040	7.37	0.43	5.452	14.0	140.0	763.280
Apr. '76	6.33	0.77	3.395	18.5	185.0	628.075	7.89	0.36	6.435	14.5	145.0	933.075
May '76	6.30	0.64	5.033	13.0	130.0	654.290	8.30	0.00	10.838	2.0	20.0	216.760
June '76	6.70	1.19	5.847	20.0	200.0	1169.400	8.71	0.38	13.046	8.5	85.0	1108.910
July '76	7.25	0.62	7.724	34.5	345.0	2664.780	9.17	0.23	15.848	8.0	80.0	1267.840
Aug. '76	7.38	0.67	8.513	24.0	240.0	2043.120	9.20	0.48	16.808	2.5	25.0	420.200
Sep. '76	7.66	0.62	8.935	22.0	220.0	1965.700	9.23	0.38	15.888	3.5	35.0	556.080
Oct. '76	7.53	0.56	6.596	11.0	110.0	725.560	9.55	0.35	14.071	2.0	20.0	281.420
Nov. '76	7.70	0.39	8.188	10.0	100.0	818.800	8.97	0.26	13.969	6.0	60.0	838.140
Dec. '76	7.63	0.58	7.994	3.0	30.0	239.820	9.47	0.27	16.837	4.5	45.0	757.665
Jan. '77	8.01	0.26	8.794	14.0	140.0	1231.160	9.22	0.40	14.043	13.0	130.0	1825.590
Feb. '77	7.61	0.37	6.488	8.0	80.0	519.040	9.16	0.34	11.277	5.5	55.0	620.235

Column abbreviations as given in Appendix 3.3.

Appendix 3.4 continued.

Sampling Date	Height	M.I.W.	No.	N m ⁻²	Biomass	ΔP	ΔM	Height	M.I.W.	No.	N m ⁻²	Biomass	ΔP	ΔM	
COHORT 1971															
Mar. '76	8.74	0.46	9.0	90.0	847.620	-	-	9.94	0.41	14.226	3.5	35.0	497.910	-	-
Apr. '76	9.17	0.25	4.0	40.0	398.200	34.905	484.325	10.47	0.29	14.626	3.0	30.0	438.780	13.000	72.130
May '76	9.55	0.35	2.0	20.0	320.240	181.710	259.670	10.63	0.29	21.572	3.0	30.0	647.160	208.380	0
June '76	9.70	0.63	2.5	25.0	453.350	47.745	-85.365	10.63	0.29	23.995	3.0	30.0	719.850	72.690	0
July '76	10.10	0.32	2.5	25.0	532.425	79.075	0	10.86	0.50	26.589	4.5	45.0	1196.505	97.275	-379.380
Aug. '76	9.80	0.00	0.5	5.0	102.130	-13.065	417.230	11.30	0.00	31.701	1.0	10.0	317.010	140.580	1020.075
Sep. '76	10.23	0.21	3.5	35.0	763.910	28.000	-633.780	11.05	0.35	27.691	2.0	20.0	553.820	-60.150	-296.960
Oct. '76	10.05	0.35	2.0	20.0	331.120	-144.925	287.865	11.05	0.35	22.403	2.0	20.0	448.060	-105.760	0
Nov. '76	-	-	-	0	0	-165.560	165.560	-	-	-	-	0	0	-224.030	224.030
Dec. '76	10.00	0.32	2.5	25.0	507.850	253.925	-253.925	11.05	0.35	28.663	2.0	20.0	573.260	286.630	-286.630
Jan. '77	10.15	0.30	8.5	85.0	1643.305	-53.955	-1189.410	11.30	0.35	27.630	3.0	30.0	828.900	-25.825	-281.465
Feb. '77	10.30	0.35	1.0	10.0	159.990	-158.365	1324.950	11.30	0.35	21.091	1.0	10.0	210.910	-130.780	487.210

COHORTS 1970+

Mar. '76	12.47	0.96	4.5	45.0	1324.395	-	-	-	-	-	-	-	-	-	-
Apr. '76	12.40	1.24	5.0	50.0	1194.850	-262.865	-399.960	-	-	-	-	-	-	-	-
May '76	11.63	0.58	3.0	30.0	831.090	152.240	516.000	-	-	-	-	-	-	-	-
June '76	11.90	0.77	10.0	100.0	3388.800	402.025	-2155.685	-	-	-	-	-	-	-	-
July '76	11.63	0.58	3.0	30.0	983.610	-71.565	2333.625	-	-	-	-	-	-	-	-
Aug. '76	-	-	-	0	0	-491.805	491.805	-	-	-	-	-	-	-	-
Sep. '76	12.55	0.64	4.0	40.0	1640.800	820.400	-820.400	-	-	-	-	-	-	-	-
Oct. '76	-	-	-	0	0	-820.400	820.400	-	-	-	-	-	-	-	-
Nov. '76	11.8	-	1.0	10.0	364.640	182.320	-182.320	-	-	-	-	-	-	-	-
Dec. '76	12.63	0.58	3.0	30.0	1363.230	179.540	-819.050	-	-	-	-	-	-	-	-
Jan. '77	12.80	0.96	4.5	45.0	1882.305	-135.450	-654.525	-	-	-	-	-	-	-	-
Feb. '77	13.20	1.25	2.5	25.0	838.150	-290.605	753.540	-	-	-	-	-	-	-	-

Column abbreviations as given in Appendix 3.3.

Appendix 3.5 M. balthica: The Alternative Computation of Flesh Production Using the Instantaneous Weight-Specific Growth Rate, 1975-6 Data, (a) LF Stations, (b) UC Stations. (The Monthly Time Interval, $t = 0.083$).

Size Class	Sampling Date	(a)		(b)		For Period		For Period	
		x size (mm)	No. N m ⁻² Sampled	w (mg)	Biomass ΔP (mg m ⁻²)	x size (mm)	No. N m ⁻²	w (mg)	Biomass ΔP (mg m ⁻²)
0 - 5.0 mm	Mar. '75	2.627	287	410	0.070	-	-	0.070	-
	Apr. '75	2.622	405	579	0.260	81.592	494	0.165	81.592
	May '75	1.463	618	883	0.054	114.767	731	0.157	114.767
	June '75	1.925	730	1043	0.113	80.410	963	0.083	80.410
	July '75	1.667	1215	1736	0.053	115.328	1389	0.083	115.328
	Aug. '75	2.118	631	901	0.108	106.139	1318	0.080	106.139
	Sep. '75	2.403	584	834	0.157	114.943	867	0.132	114.943
	Oct. '75	2.541	553	790	0.079	95.816	812	0.118	95.816
	Nov. '75	2.356	526	751	0.061	53.935	770	0.070	53.935
	Dec. '75	2.347	526	751	0.060	48.815	751	0.065	48.815
	Jan. '76	2.556	178	254	0.064	31.155	502	0.062	31.155
	Feb. '76	2.213	92	131	0.038	9.817	192	0.051	9.817
	Mar. '75	7.373	48	69	2.607	-	-	-	-
	Apr. '75	7.080	91	130	3.797	318.599	99	3.202	318.599
	May '75	6.968	128	183	3.637	581.710	156	3.717	581.710
	June '75	7.277	281	401	4.089	1127.996	292	3.863	1127.996
	July '75	7.174	255	364	3.969	1541.092	382	4.029	1541.092
	Aug. '75	7.605	244	349	4.716	1548.101	356	4.342	1548.101
Sep. '75	7.202	351	501	4.015	1855.337	425	4.365	1855.337	
Oct. '75	7.245	317	453	2.951	1661.391	477	3.483	1661.391	
Nov. '75	7.579	272	389	3.448	1346.989	421	3.199	1346.989	
Dec. '75	7.109	223	319	2.764	1099.524	354	3.106	1099.524	
Jan. '76	7.625	100	143	2.933	657.888	231	2.848	657.888	
Feb. '76	7.283	86	123	2.497	361.095	133	2.715	361.095	
Mar. '75	12.263	41	59	15.511	-	-	-	-	
Apr. '75	13.036	70	100	19.730	1400.830	79	17.620	1400.830	
May '75	12.323	44	63	16.950	1494.710	81	18.340	1494.710	
June '75	12.345	66	94	17.032	1333.793	78	16.991	1333.793	
July '75	12.487	48	69	20.421	1526.210	81	18.726	1526.210	
Aug. '75	12.663	84	120	21.284	1970.560	94	20.852	1970.560	
Sep. '75	12.579	61	87	20.869	2181.418	103	21.076	2181.418	
Oct. '75	12.308	63	90	18.368	1736.237	88	19.618	1736.237	
Nov. '75	13.008	60	86	22.231	1786.356	88	20.299	1786.356	
Dec. '75	12.050	68	97	17.074	1798.203	91	19.652	1798.203	
Jan. '76	12.777	66	94	17.912	1670.581	95	17.493	1670.581	
Feb. '76	12.337	40	57	15.842	1274.210	75	16.877	1274.210	
>10.1 mm	Mar. '75	-	-	-	-	-	-	-	-
	Apr. '75	-	-	-	-	41.998	456	0.920	41.998
	May '75	-	-	-	-	51.205	385	0.133	51.205
	June '75	-	-	-	-	50.245	386	0.130	50.245
	July '75	-	-	-	-	31.428	388	0.081	31.428
	Aug. '75	-	-	-	-	31.941	378	0.084	31.941
	Sep. '75	-	-	-	-	26.261	314	0.083	26.261
	Oct. '75	-	-	-	-	23.463	281	0.083	23.463
	Nov. '75	-	-	-	-	30.208	256	0.118	30.208
	Dec. '75	-	-	-	-	40.878	331	0.123	40.878
	Jan. '76	-	-	-	-	34.973	331	0.105	34.973
	Feb. '76	-	-	-	-	13.050	217	0.060	13.050
	Mar. '75	-	-	-	-	506.115	103	4.890	506.115
	Apr. '75	-	-	-	-	667.222	149	4.478	667.222
	May '75	-	-	-	-	670.713	179	3.747	670.713
	June '75	-	-	-	-	604.202	173	3.492	604.202
	July '75	-	-	-	-	605.616	176	3.441	605.616
	Aug. '75	-	-	-	-	656.610	172	3.817	656.610
Sep. '75	-	-	-	-	607.112	176	3.449	607.112	
Oct. '75	-	-	-	-	503.524	183	2.744	503.524	
Nov. '75	-	-	-	-	558.646	189	2.948	558.646	
Dec. '75	-	-	-	-	545.836	174	3.128	545.836	
Jan. '76	-	-	-	-	514.692	153	3.364	514.692	
Feb. '76	-	-	-	-	1089.914	63	17.164	1089.914	
Mar. '75	-	-	-	-	1089.333	63	17.291	1089.333	
Apr. '75	-	-	-	-	1308.915	76	17.110	1308.915	
May '75	-	-	-	-	1340.718	73	18.366	1340.718	
June '75	-	-	-	-	1143.682	64	17.731	1143.682	
July '75	-	-	-	-	1003.304	58	17.151	1003.304	
Aug. '75	-	-	-	-	1093.937	62	17.503	1093.937	
Sep. '75	-	-	-	-	1236.412	75	16.485	1236.412	
Oct. '75	-	-	-	-	1460.869	88	16.507	1460.869	
Nov. '75	-	-	-	-	1343.455	89	15.095	1343.455	
Dec. '75	-	-	-	-	1171.720	80	14.464	1171.720	

Appendix 3.6 (a) *M. balthica*: Temporal Data Analysis - The Flesh and Shell Dry Weight (mg) of Standard-size (4mm and 8mm Ht.) Animals.

Date	Station A1	A2	A3	A4	B1	B2	B3	B4	B5	C1	C2	C3	C4	C5
Mar. '75	4mm. Fdw. 1.02	-	1.10	1.22	1.14	0.92	1.66	0.80	0.91	-	1.29	1.29	0.99	1.45
Apr. '75	1.27	0.74	0.64	1.27	1.32	1.03	1.83	1.00	1.22	-	-	1.47	1.82	1.03
May '75	1.41	1.61	1.71	1.99	1.89	1.86	1.68	1.80	1.51	1.62	1.90	1.58	1.96	1.17
June '75	1.78	1.43	2.11	1.29	1.49	1.60	2.41	1.04	1.62	-	1.54	1.96	1.99	2.50
July '75	1.27	1.48	1.32	1.12	1.28	1.07	1.11	1.14	1.79	1.88	1.71	1.68	1.97	1.04
Aug. '75	0.94	1.28	1.77	1.08	0.99	1.71	1.45	1.60	1.52	1.49	1.77	1.84	2.72	0.96
Sep. '75	1.01	1.47	1.42	1.32	1.46	1.26	1.16	1.26	1.03	0.82	1.84	1.55	1.74	1.04
Oct. '75	0.91	0.96	1.09	1.08	1.27	0.96	0.99	0.98	0.86	-	1.12	1.19	1.07	0.80
Nov. '75	0.97	1.23	0.91	0.63	1.41	1.23	0.75	0.95	0.70	1.24	1.16	1.33	0.97	0.69
Dec. '75	1.09	1.06	0.93	1.02	1.22	0.93	0.64	0.86	0.74	-	1.03	0.99	0.93	0.70
Jan. '76	1.13	0.96	0.86	0.82	1.34	0.52	0.72	0.84	0.96	1.30	0.98	0.98	0.87	0.96
Feb. '76	0.97	1.06	1.10	1.40	1.21	1.11	0.75	0.72	0.92	1.27	0.89	0.88	1.05	1.07
May '76	1.27	-	1.20	1.24	1.70	1.86	1.42	1.10	1.36	1.82	1.32	1.20	0.98	1.08
Aug. '76	1.36	1.20	1.12	1.10	1.37	1.12	1.29	1.15	1.09	-	1.30	1.42	1.06	0.88
Nov. '76	0.96	0.50	1.20	0.87	1.05	1.00	0.83	1.12	1.01	2.45	1.07	1.14	0.99	0.90
Feb. '77	1.08	0.73	1.03	1.57	0.99	0.86	0.95	1.00	1.03	-	0.96	1.06	0.87	1.01
Mar. '75	4mm. SW. 5.46	-	5.44	5.67	4.88	4.71	3.45	5.70	3.00	-	6.00	4.16	6.02	5.17
Apr. '75	3.14	3.85	4.36	4.93	2.98	4.13	3.92	4.88	3.76	-	-	5.23	4.88	4.72
May '75	1.45	4.31	2.01	5.32	4.26	2.14	2.14	3.25	4.41	2.22	3.15	4.61	4.40	4.13
June '75	3.18	3.24	3.08	4.50	2.71	2.42	2.45	4.68	3.96	-	2.95	3.11	3.33	4.98
July '75	3.46	5.15	4.14	5.17	2.95	2.59	2.64	4.12	4.56	3.78	3.85	4.05	7.11	5.50
Aug. '75	4.12	3.35	4.43	4.59	2.38	3.49	3.20	4.29	3.89	2.79	3.58	4.65	1.40	4.00
Sep. '75	3.78	3.50	4.45	5.93	3.36	3.79	4.08	4.29	4.06	2.00	4.05	3.93	7.62	5.54
Oct. '75	3.68	5.11	4.22	4.92	4.11	4.10	4.10	4.69	4.14	-	3.93	4.03	5.60	4.91
Nov. '75	3.88	4.76	3.84	4.79	4.35	4.74	3.70	4.77	4.23	2.46	4.63	4.56	5.79	4.77
Dec. '75	4.21	5.19	4.72	4.75	4.64	4.17	3.88	4.66	4.36	-	4.68	5.32	5.93	5.01
Jan. '76	4.18	4.54	4.47	4.54	5.10	3.33	4.30	5.08	4.49	3.97	5.24	4.66	5.47	5.49
Feb. '76	4.46	5.26	5.15	4.82	5.01	4.01	3.85	3.75	5.25	3.25	5.27	4.01	5.05	6.46
May '76	3.09	-	4.50	4.87	2.92	2.39	3.38	4.51	4.02	2.06	4.04	4.52	5.22	5.40
Aug. '76	3.41	5.58	4.66	5.85	3.61	3.35	3.02	4.25	4.98	-	4.15	4.15	6.14	6.00
Nov. '76	4.41	1.20	5.07	4.66	4.38	4.66	4.16	4.89	5.31	3.22	4.80	5.01	4.65	5.76
Feb. '77	3.98	6.15	4.79	1.79	4.04	3.12	4.23	5.41	5.35	-	4.87	5.55	7.27	6.14

Appendix 3.6 (a) continued.

Date	Station A1 8mm. Fdw	A2	A3	A4	B1	B2	B3	B4	B5	C1	C2	C3	C4	C5
Mar. '75	9.40	-	9.75	9.63	8.35	6.18	13.06	8.85	9.00	-	10.70	9.71	10.26	8.39
Apr. '75	14.81	12.69	9.63	8.63	11.06	9.25	12.16	8.23	9.51	-	-	13.07	10.99	12.48
May '75	15.38	10.31	12.08	12.01	15.49	16.17	15.77	12.18	14.75	12.07	12.56	11.89	14.69	10.84
June '75	14.99	6.54	13.17	7.98	11.18	11.68	16.24	7.95	13.06	-	16.74	14.14	12.35	9.41
July '75	13.18	7.75	10.76	7.19	11.98	11.99	12.84	9.26	14.74	15.48	20.18	11.06	12.33	11.18
Aug. '75	11.34	11.62	11.05	12.29	12.32	12.52	13.27	15.52	14.26	11.69	13.83	12.44	11.64	17.93
Sep. '75	11.46	11.46	14.07	12.09	15.99	12.32	12.35	11.95	11.13	10.88	18.78	24.69	13.35	12.03
Oct. '75	8.79	9.77	10.18	10.96	11.72	11.45	10.30	10.61	10.24	-	17.10	12.06	9.88	8.44
Nov. '75	10.86	11.49	10.87	9.47	13.98	11.83	9.02	10.38	10.28	9.65	12.02	11.34	9.21	9.61
Dec. '75	10.93	8.75	9.96	10.68	11.59	11.46	9.48	9.28	8.69	-	8.82	9.59	8.80	8.57
Jan. '76	9.29	8.14	7.89	9.81	10.49	7.17	9.18	8.29	10.20	10.07	9.10	9.14	7.99	8.43
Feb. '76	7.46	8.18	8.03	10.30	8.37	9.02	7.78	7.77	8.61	9.05	7.54	8.02	7.94	7.43
May '76	12.15	-	8.53	8.68	11.86	12.32	9.78	8.90	10.15	12.29	10.82	8.24	6.52	6.39
Aug. '76	12.09	7.65	6.79	7.43	14.64	11.70	10.92	9.32	9.68	-	11.70	7.56	6.88	7.63
Nov. '76	8.79	8.03	6.91	5.56	9.18	10.84	9.36	9.00	9.23	12.66	8.54	9.65	5.58	6.70
Feb. '77	7.07	5.58	7.05	6.85	9.82	7.84	7.53	7.11	8.80	-	7.30	7.81	6.04	6.38
Mar. '75	55.57	-	71.01	65.07	57.39	47.65	56.12	73.34	65.47	-	70.42	77.66	73.92	53.87
Apr. '75	48.04	65.68	59.37	55.58	54.66	57.22	62.80	71.33	62.06	-	-	78.49	76.80	76.60
May '75	35.13	54.07	54.60	51.92	34.98	38.18	45.47	61.00	68.84	48.68	39.88	55.19	68.84	75.14
June '75	46.36	64.42	58.88	60.02	37.26	46.05	43.43	72.08	62.18	-	47.86	59.94	75.56	52.01
July '75	49.19	70.91	58.52	65.95	50.63	48.84	46.81	76.24	71.54	58.52	55.81	72.69	76.95	72.44
Aug. '75	54.94	70.81	68.97	59.24	36.27	59.04	54.04	71.13	69.13	49.65	62.93	71.84	84.04	115.7
Sep. '75	51.22	59.46	61.76	59.59	40.53	52.11	56.62	68.19	68.94	45.99	55.08	68.08	84.76	68.78
Oct. '75	50.52	57.68	59.40	61.69	56.56	53.68	54.51	74.71	66.57	-	56.22	62.12	86.15	59.25
Nov. '75	54.86	58.70	62.03	60.11	49.01	56.18	55.01	68.69	69.19	50.38	63.91	70.16	82.98	69.89
Dec. '75	56.25	66.25	61.31	54.55	53.34	55.17	53.43	66.44	68.26	-	39.15	74.42	82.18	62.92
Jan. '76	51.68	58.77	59.49	54.14	66.76	55.15	61.59	64.61	70.02	66.70	53.91	71.58	77.95	62.27
Feb. '76	57.22	61.82	59.14	48.55	66.02	62.20	51.84	71.74	70.82	59.24	54.15	71.57	77.61	71.11
May '76	44.26	-	61.75	56.65	51.90	47.85	53.91	73.21	69.20	50.80	55.99	66.42	79.80	68.62
Aug. '76	51.33	58.87	54.19	51.58	50.49	50.02	53.06	68.42	65.00	-	60.39	60.73	79.86	71.83
Nov. '76	47.02	63.45	56.68	52.63	57.41	62.28	55.07	76.37	70.16	59.76	48.55	66.86	70.47	63.90
Feb. '77	48.75	74.26	52.94	52.12	55.39	47.47	51.80	64.82	73.92	-	50.62	58.91	79.08	60.10

8mm. sw.

Appendix 3.6 (b) M. balthica : Temporal Data Analysis - Linear Regression Equations of Flesh Condition, 4_{fdw} , 4_{sw} , 8_{fdw} , 8_{sw} (mg)

With Mean Monthly Temperature ($^{\circ}$ C).

Stn. n.	Dependent Variable	Dependent Variable				Dependent Variable											
		b	S.E.	a	r	p	b	S.E.	a	r	p						
A1 16	CF_H	0.600	0.255	14.867	0.600	*	0.019	0.012	0.957	0.404	n.s.	4_{sw}	-0.080	0.043	4.548	-0.447	n.s.
	8_{fdw}	0.337	0.112	7.741	0.626	**	-0.236	0.301	52.511	-0.205	n.s.	8_{sw}					
A2 14	CF_H	0.279	0.207	15.641	0.363	n.s.	0.044	0.014	0.664	0.673	**	4_{sw}	-0.035	0.073	4.735	-0.137	n.s.
	8_{fdw}	0.099	0.120	8.121	0.230	n.s.	0.031	0.342	62.900	0.026	n.s.	8_{sw}					
A3 16	CF_H	0.494	0.181	14.471	0.590	*	0.049	0.016	0.724	0.626	**	4_{sw}	-0.075	0.041	5.085	-0.435	n.s.
	8_{fdw}	0.231	0.105	7.472	0.507	*	0.093	0.265	59.069	0.093	n.s.	8_{sw}					
A4 16	CF_H	0.162	0.211	16.578	0.201	n.s.	0.001	0.017	1.179	0.015	n.s.	4_{sw}	0.073	0.048	4.089	0.376	n.s.
	8_{fdw}	0.078	0.110	8.564	0.186	n.s.	0.408	0.259	52.739	0.388	n.s.	8_{sw}					
B1 16	CF_H	0.414	0.174	17.587	0.536	*	0.014	0.013	1.183	0.272	n.s.	4_{sw}	-0.148	0.029	5.340	-0.807	***
	8_{fdw}	0.306	0.101	8.685	0.630	**	-1.489	0.362	66.106	-0.739	**	8_{sw}					
B2 16	CF_H	0.601	0.175	15.200	0.676	**	0.046	0.017	0.728	0.581	*	4_{sw}	-0.087	0.042	4.446	-0.486	n.s.
	8_{fdw}	0.325	0.105	7.595	0.637	**	-0.345	0.035	55.911	-0.258	n.s.	8_{sw}					
B3 16	CF_H	0.755	0.249	13.713	0.629	**	0.048	0.024	0.743	0.473	n.s.	4_{sw}	-0.087	0.029	4.410	-0.624	**
	8_{fdw}	0.343	0.113	7.745	0.632	**	-0.391	0.264	57.395	-0.368	*	8_{sw}					
B4 16	CF_H	0.529	0.173	13.132	0.632	**	0.036	0.012	0.720	0.623	**	4_{sw}	-0.055	0.030	5.132	-0.444	n.s.
	8_{fdw}	0.263	0.094	7.020	0.601	*	0.140	0.242	68.738	0.153	n.s.	8_{sw}					

Appendix 3.6 (b) Continued.

Stn. n.	Dependent Variable				Dependent Variable													
	b	S.E.	a	r	p	b	S.E.	a	r	p								
B5 16	CF _H	0.654	0.170	14.069	0.716	**	4 _{fdw}	0.046	0.013	0.682	0.674	**	4 _{sw}	-0.034	0.034	4.697	-0.255	n.s.
	8 _{fdw}	0.340	0.081	7.361	0.747	***	8 _{sw}	-0.200	0.171	70.209	-0.297	n.s.						
C1 9	CF _H	0.704	0.249	15.420	0.730	*	4 _{fdw}	-0.008	0.035	1.621	-0.081	n.s.	4 _{sw}	-0.042	0.053	3.297	-0.284	n.s.
	8 _{fdw}	0.213	0.123	9.321	-0.547	n.s.	8 _{sw}	-0.794	0.423	62.723	-0.579	n.s.						
C2 15	CF _H	1.066	0.207	11.551	0.818	***	4 _{fdw}	0.053	0.012	0.786	0.768	***	4 _{sw}	-0.135	0.028	5.713	-0.805	***
	8 _{fdw}	0.627	0.152	6.031	0.753	**	8 _{sw}	0.243	0.468	51.843	0.144	n.s.						
C3 16	CF _H	0.716	0.264	14.663	0.586	*	4 _{fdw}	0.055	0.010	0.795	0.837	***	4 _{sw}	-0.062	0.030	5.100	-0.483	n.s.
	8 _{fdw}	0.332	0.210	7.945	0.389	n.s.	8 _{sw}	-0.339	0.373	71.319	-0.236	n.s.						
C4 16	CF _H	0.465	0.217	13.661	0.497	n.s.	4 _{fdw}	0.087	0.021	0.498	0.737	**	4 _{sw}	-0.106	0.080	6.428	-0.332	n.s.
	8 _{fdw}	0.297	0.131	6.675	0.518	*	8 _{sw}	-1.473	0.843	88.964	-0.423	n.s.						
C5 16	CF _H	0.445	0.173	13.182	0.568	*	4 _{fdw}	0.020	0.023	0.883	0.224	n.s.	4 _{sw}	-0.060	0.034	5.854	-0.426	n.s.
	8 _{fdw}	0.377	0.129	5.705	0.614	*	8 _{sw}	1.524	0.689	53.735	0.509	*						
ALL 214	CF _H	0.561	0.059	14.502	0.544	***	4 _{fdw}	0.038	0.005	0.844	0.471	***	4 _{sw}	-0.069	0.015	4.984	-0.302	***
	8 _{fdw}	0.301	0.036	7.505	0.503	***	8 _{sw}	-0.189	0.166	62.500	-0.078	n.s.						

Appendix 4.1 The Mean Flesh Condition of C. edule and M. arenaria.

Date	<u>Cerastoderma edule</u>				<u>Mya arenaria</u>			
	CF _H	S.D.	S.E.	n	CF _H	S.D.	S.E.	n
1975								
March	9.893	0.745	0.166	20	4.874	0.803	0.328	6
April	14.612	6.995	1.256	31	6.237	0.065	0.015	19
May	18.112	6.131	1.051	34	7.534	0.951	0.198	23
June	13.580	4.163	0.512	66	8.233	1.685	0.281	36
July	14.873	3.828	0.766	25	7.067	1.089	0.257	18
Aug.	12.843	2.172	0.384	32	6.559	1.852	0.586	10
Sept.	12.519	3.723	0.507	54	5.054	0.861	0.209	17
Oct.	10.755	3.324	0.436	58	4.407	1.049	0.397	7
Nov.	11.194	3.464	0.455	58	5.073	0.852	0.348	6
Dec.	11.016	3.448	0.575	36	5.396	0.600	0.212	8
1976								
Jan.	10.458	2.254	0.329	47	5.333	1.687	0.689	6
Feb.	9.424	1.830	0.279	43	4.502	0.743	0.248	9
May	10.729	2.764	0.426	42	6.221	0.687	0.178	15
Aug.	13.712	4.309	0.690	39	5.922	1.918	0.858	5
Nov.	14.217	3.519	0.401	77	5.273	0.836	0.264	10
1977								
Feb.	10.584	2.359	0.373	40	5.511	-	-	1

Appendix 4.2(a) C. edule: Regression Analyses of the Field Population, Reference Regression Equations.

$$Tdw(mg) = Ht(mm) \frac{b + S.E.}{a}$$

$$Fdw(mg) = Ht(mm) \frac{b + S.E.}{a}$$

$$Tdw(mg) = Fdw(mg) \cdot a \quad CF_H = b \pm S.E.Ht(mm) + a$$

Date	n	b	S.E.	a	p	r	b	S.E.	a	p	r	b	S.E.	a	p	r					
Mar.'75	20	3.294	0.085	9.397	***	0.994	2.861	0.001	75.911	***	0.990	1.151	0.030	15.524	***	0.994	-0.133	0.009	11.130	***	-0.958
Apr.'75	31	3.366	0.080	12.417	***	0.992	2.976	0.097	69.984	***	0.985	1.116	0.023	10.069	***	0.994	-0.137	0.206	15.846	ns	-0.123
May '75	34	3.276	0.077	11.940	***	0.991	2.925	0.092	49.945	***	0.985	1.097	0.033	6.982	***	0.986	-0.184	0.224	19.572	ns	-0.144
June'75	66	3.513	0.059	22.522	***	0.991	3.021	0.079	80.929	***	0.978	1.118	0.032	8.126	***	0.974	0.005	0.098	13.528	ns	0.006
July'75	25	3.289	0.083	11.749	***	0.993	2.785	0.099	41.191	***	0.986	1.148	0.050	7.598	***	0.979	-0.265	0.130	18.240	ns	-0.392
Aug.'75	32	3.468	0.064	18.302	***	0.995	3.026	0.084	84.430	***	0.988	1.126	0.031	9.421	***	0.989	0.056	0.086	12.067	ns	0.118
Sep.'75	54	3.297	0.043	11.108	***	0.996	2.728	0.039	44.969	***	0.995	1.198	0.020	9.171	***	0.992	-0.338	0.066	16.351	***	-0.577
Oct.'75	58	3.243	0.038	9.337	***	0.996	2.803	0.072	61.760	***	0.982	1.126	0.024	13.659	***	0.987	-0.155	0.062	12.708	*	-0.318
Nov.'75	58	3.190	0.029	8.270	***	0.998	2.754	0.047	54.980	***	0.992	1.144	0.018	12.927	***	0.993	-0.244	0.057	13.807	***	-0.492
Dec.'75	36	3.244	0.050	9.072	***	0.996	2.738	0.073	50.839	***	0.988	1.165	0.027	12.193	***	0.991	-0.218	0.086	13.820	*	-0.398
Jan.'76	46	3.280	0.048	10.155	***	0.995	2.830	0.075	63.228	***	0.984	1.132	0.027	13.083	***	0.987	-0.126	0.079	12.195	ns	-0.232
Feb.'76	43	3.176	0.048	7.645	***	0.995	2.933	0.063	91.771	***	0.991	1.069	0.021	18.093	***	0.992	-0.012	0.054	9.575	ns	-0.034
May '76	42	3.398	0.051	14.825	***	0.996	2.706	0.079	45.814	***	0.983	1.220	0.035	9.141	***	0.983	-0.240	0.075	13.993	**	-0.454
Aug.'76	39	3.273	0.036	10.139	***	0.998	2.826	0.054	56.754	***	0.993	1.145	0.023	10.715	***	0.993	-0.269	0.090	15.876	**	-0.442
Nov.'76	77	3.112	0.029	6.653	***	0.997	2.780	0.026	47.863	***	0.997	1.116	0.011	11.508	***	0.997	-0.301	0.047	16.859	***	-0.591
Feb.'77	40	3.187	0.041	8.035	***	0.997	2.798	0.037	63.826	***	0.997	1.136	0.013	14.223	***	0.997	-0.188	0.050	12.439	***	-0.523

Appendix 4.2(b) M. arenaria: Regression Analyses of the Field Population, Reference Regression Equations.

$$Tdw(mg) = L(mm) \frac{b + S.E.}{a}$$

$$Fdw(mg) = L(mm) \frac{b + S.E.}{a}$$

$$Tdw(mg) = Fdw(mg) \cdot a \quad CF_L = b \pm S.E.L(mm) + a$$

Date	n	b	S.E.	a	p	r	b	S.E.	a	p	r	b	S.E.	a	p	r					
Mar. '75	6	2.773	0.095	12.701	***	0.998	2.792	0.141	139.61	***	0.991	0.993	0.034	10.632	***	0.998	-0.098	0.009	5.776	***	-0.984
Apr. '75	19	2.732	0.128	11.112	***	0.982	2.982	0.047	155.20	***	0.998	0.916	0.043	9.156	***	0.982	-0.012	0.001	6.323	***	-0.981
May '75	23	2.901	0.122	24.908	***	0.982	3.090	0.096	161.62	***	0.990	0.931	0.037	4.807	***	0.984	0.056	0.087	7.057	ns	0.138
June '75	36	2.967	0.065	25.894	***	0.992	2.913	0.088	101.62	***	0.985	0.999	0.027	4.454	***	0.988	-0.056	0.049	8.847	ns	-0.192
July '75	18	2.879	0.109	19.784	***	0.989	2.935	0.113	119.86	***	0.988	0.963	0.046	5.848	***	0.982	-0.025	0.060	7.463	ns	-0.103
Aug. '75	10	2.659	0.104	11.182	***	0.994	2.859	0.201	106.03	***	0.981	0.909	0.043	7.333	***	0.991	-0.111	0.103	8.539	ns	-0.353
Sep. '75	17	3.218	0.103	63.037	***	0.992	3.447	0.113	748.17	***	0.992	0.927	0.029	7.841	***	0.993	0.099	0.034	3.111	*	0.604
Oct. '75	7	2.922	0.086	26.080	***	0.998	3.154	0.158	348.34	***	0.994	0.919	0.035	8.827	***	0.996	0.027	0.047	3.976	ns	0.245
Nov. '75	6	2.848	0.168	18.117	***	0.993	3.000	0.380	199.48	**	0.969	0.904	0.103	10.069	**	0.975	Not calculated	-Signif.	too low		
Dec. '75	8	2.871	0.088	18.625	***	0.997	2.844	0.059	128.23	***	0.999	1.009	0.024	7.209	***	0.998	-0.063	0.024	6.187	*	-0.733
Jan. '76	6	2.798	0.196	15.059	***	0.990	3.143	0.207	275.61	***	0.991	0.890	0.025	9.915	***	0.998	0.064	0.085	4.444	ns	0.354
Feb. '76	9	2.973	0.159	23.324	***	0.990	2.790	0.141	139.19	***	0.991	1.056	0.057	8.358	***	0.990	-0.091	0.057	5.464	ns	-0.516
May '76	15	2.907	0.077	22.085	***	0.995	2.982	0.047	155.28	***	0.998	0.973	0.026	6.212	***	0.995	0.006	0.017	6.145	ns	0.091
Aug. '76	5	3.410	0.220	67.732	***	0.994	3.324	0.331	405.60	***	0.985	1.013	0.052	7.226	***	0.996	0.251	0.182	2.351	ns	0.623
Nov. '76	10	2.798	0.072	14.211	***	0.997	2.980	0.074	182.14	***	0.998	0.937	0.022	9.374	***	0.998	-0.006	0.027	5.372	ns	-0.078
Feb. '77																					

Insufficient Data

Appendices 4.3 and 4.4 C. edule : The Mean Height, Flesh Weight, Density and
Biomass of Each Cohort at Each Sampling Occasion.

Sampling Date	Cohort	Mean Ht. (mm)	S.D.	Mean fdw (mg)	Nos. m ⁻²	Biomass ₂ mg fdw m ⁻²
Mar. '75	1974	2.695	1.555	0.420	44.99	18.89
	1973	8.475	1.197	6.248	5.71	35.70
	1972	13.700	0.726	23.130	5.71	132.17
	>1972	21.433	0.635	84.973	2.14	182.08
Apr. '75	1974	2.242	1.330	0.492	45.71	22.49
	1973	9.114	1.248	11.029	5.00	55.14
	1972	15.200	1.885	48.925	2.86	139.79
	>1972	21.425	1.328	131.350	2.86	375.29
May '75	1974	3.497	1.706	1.276	25.69	32.79
	1973	9.062	1.000	14.362	5.71	82.07
	1972	15.100	1.530	65.050	2.86	185.86
	>1972	20.150	1.343	124.400	1.43	177.71
June '75	1974	5.592	1.214	2.550	17.14	43.71
	1973	9.961	1.559	15.681	18.57	291.21
	1972	15.480	2.131	47.520	7.14	339.43
	>1972	22.467	1.722	159.283	4.29	682.64
July '75	1975	0.850	0.155	0.013	11.43	0.15
	1974	5.643	0.810	3.233	5.00	16.16
	1973	11.912	1.643	25.162	5.71	143.79
	1972	16.117	1.698	61.033	4.29	261.57
	>1972	21.450	0.733	129.225	2.86	369.21
Aug. '75	1975	1.171	0.457	0.067	40.00	2.66
	1974	8.792	1.716	9.008	8.57	77.21
	1973	15.767	1.701	50.093	10.71	536.71
	1972	20.200	0.538	119.660	3.57	427.36
Sept. '75	1975	1.285	1.079	0.188	197.85	37.14
	1974	10.918	1.211	15.052	7.86	118.26
	1973	15.369	1.295	37.706	11.43	430.92
	1972	18.950	1.202	86.080	1.43	122.97
	>1972	23.480	2.044	137.490	3.57	491.04
Oct. '75	1975	1.727	1.555	0.334	123.56	41.24
	1974	11.767	1.413	14.754	8.57	126.46
	1973	15.729	1.309	37.889	10.00	378.89
	1972	19.400	0.520	84.523	2.14	181.12
	>1972	23.678	2.332	138.047	6.43	887.44
Nov. '75	1975	2.373	1.725	0.513	66.42	34.11
	1974	11.056	1.593	12.360	6.43	79.45
	1973	15.850	1.618	35.737	4.29	153.16
	1972	19.111	0.891	63.086	6.43	405.55
	>1972	23.900	1.221	147.576	3.57	527.06
Dec. '75	1975	1.667	1.502	0.328	35.00	11.47
	1974	11.609	1.252	15.389	7.86	120.92
	1973	15.562	0.529	32.324	5.71	184.71
	1972	19.040	0.770	69.680	3.57	248.86
	>1972	24.967	1.270	203.193	2.14	435.41

Appendices 4.3 and 4.4 (Continued).

Sampling Date	Cohort	Mean Ht. (mm)	S.D.	Mean fdw (mg)	Nos. m ⁻²	Biomass mg fdw m ⁻²
Jan. '76	1975	2.470	1.050	0.467	33.57	15.68
	1974	12.682	1.791	19.874	15.71	312.30
	1973	16.583	0.740	45.522	12.14	552.77
	1972	18.1		63.570	0.71	45.41
	>1972	21.467	0.551	114.667	2.14	245.71
Feb. '76	1975	2.884	2.129	0.807	17.86	14.41
	1974	12.445	1.507	17.309	15.71	272.00
	1973	17.133	1.109	49.882	6.43	320.67
	1972	19.567	0.416	73.987	2.14	158.54
	>1972	30.2		326.200	0.70	233.00
May '76	1975	2.288	2.258			
	1974	12.405	1.788			
	1973	17.875	1.310			See Appendix 4.5
	1972	20.925	0.885			
	>1972	29.1				
Aug. '76	1976	1.256	0.593			
	1975	8.875	2.563			
	1974	16.925	0.562			See Appendix 4.5
	1973	18.800	0.374			
	1972	21.650	0.071			
Nov. '76	1976	2.122	1.571			
	1975	10.014	1.832			
	1974	15.460	1.831			See Appendix 4.5
	1973	20.467	0.458			
	1972	24.067	1.701			
Feb. '77	1976	2.298	1.760			
	1975	11.917	1.947			
	1974	17.143	1.189			See Appendix 4.5
	1973	21.400	1.131			
	1972	23.200	0.000			

Appendix 4.5 C. edule : The Computation of Production, e.g. 1976-77 Data.

Age Class	Sampling Date	Nos. m^{-2}	Mean Indiv. fdw (mg)	$\Delta \bar{w}$. (mg)	$\bar{N} m^{-2}$	ΔP ng fdw m^{-2}	B_{fdw} $mg m^{-2}$
1976	Feb. '76	-	-	-	-	-	-
	May '76	-	-	-	-	-	-
	Aug. '76	640.00	0.036	0.036	320.00	11.520	23.040
	Nov. '76	122.14	0.169	0.133	381.07	50.682	20.641
	Feb. '77	95.71	0.161	-0.008	108.92	-0.871	14.409
					Total P	61.331	\bar{B} 20.554
1975	Feb. '76	17.86	0.243	-	-	-	4.340
	May '76	35.00	0.205	-0.038	26.43	-1.004	7.175
	Aug. '76	2.86	8.424	8.219	18.93	155.586	24.093
	Nov. '76	5.00	12.639	4.215	3.93	16.565	63.195
	Feb. '77	4.29	16.073	3.434	4.64	15.951	68.953
						187.098	32.777
1974	Feb. '76	15.71	17.740	-	-	-	278.695
	May '76	15.00	19.873	2.133	15.35	32.752	298.095
	Aug. '76	2.86	52.219	32.346	8.93	288.850	149.346
	Nov. '76	7.14	42.267	-9.952	5.00	-49.760	301.786
	Feb. '77	5.00	44.460	2.193	6.07	13.311	222.300
						285.153	249.931
1973	Feb. '76	6.43	45.305	-	-	-	291.311
	May '76	5.71	53.407	8.102	6.07	49.179	304.954
	Aug. '76	3.57	70.271	16.864	4.64	78.249	250.867
	Nov. '76	6.43	92.196	21.925	5.00	109.625	592.820
	Feb. '77	1.43	82.699	-9.497	3.93	-37.323	118.260
						199.730	338.357
1972	Feb. '76	2.14	66.883	-	-	-	143.130
	May '76	2.86	81.794	14.911	2.50	37.277	233.931
	Aug. '76	1.43	104.715	22.921	2.14	49.165	149.742
	Nov. '76	2.14	143.656	38.914	1.78	69.510	307.424
	Feb. '77	1.43	103.666	-39.990	1.78	-71.382	148.242
						84.570	209.196
1972	Feb. '76	0.71	238.866	-	-	-	169.594
	May '76	0.71	199.662	-39.204	0.71	-27.835	141.760
	Aug. '76	-	-	-199.662	0.30	-70.880	-
	Nov. '76	-	-	-	-	-	-
	Feb. '77	-	-	-	-	-	-
						-98.715	151.038

Appendix 4.6 Mya arenaria: Data Incorporated in the Production Estimates.

Sampling Date	Age Class	Mean Length (mm)	S.E.	Total No. Sampled	Mean Fdw. (mg)	S.E.	Nos. m ⁻²	Total Fdw. (mg m ⁻²)
Mar. '75	1974	2.285	0.111	46	0.183	0.016	32.84	6.010
	1973	20.033	1.367	3	41.017	8.213	2.14	87.858
Apr. '75	1974	2.870	0.174	96	0.703	0.265	68.54	48.176
	1973	18.770	0.841	3	40.612	5.016	2.14	87.026
May '75	1974	8.587	0.492	23	4.803	0.855	16.43	78.908
June '75	1974	9.961	0.195	46	9.086	0.961	32.86	298.528
	1973	26.0	-	1	126.8	-	0.71	9.057
	>1973	36.2	-	1	307.0	-	0.71	219.826
July '75	1975	1.533	0.095	113	0.138	0.013	80.68	11.126
	1974	15.660	0.811	17	31.291	5.011	12.14	379.967
	1973	25.6	-	1	115.4	-	0.71	82.429
Aug. '75	1975	2.019	0.044	241	0.137	0.004	172.07	23.579
	1974	18.420	1.165	8	43.387	5.382	5.71	247.929
	1973	26.4	-	1	82.70	-	0.71	59.071
	>1973	60.4	-	1	1474.1	-	0.71	1052.929
Sep. '75	1975	2.416	0.115	181	0.284	0.038	129.23	36.689
	1974	20.414	0.895	14	48.883	6.762	10.00	488.833
	1973	28.850	0.050	2	134.805	8.785	1.43	192.579
Oct. '75	1975	2.464	0.153	144	0.348	0.073	102.82	35.814
	1974	22.400	5.200	2	69.550	43.230	1.43	99.357
	1973	30.267	0.393	3	97.197	6.886	2.14	208.280
Nov. '75	1975	2.465	0.097	169	0.330	0.022	120.67	39.298
	1974	20.000	1.109	5	42.310	8.459	3.57	151.106
	1973	32.200	0.800	2	165.415	8.983	1.43	236.308
Dec. '75	1975	2.486	0.138	123	0.322	0.043	87.82	28.276
	1974	20.767	0.809	3	43.740	3.048	2.14	93.729
Jan. '76	1975	3.106	0.154	125	0.433	0.059	89.25	38.683
	1974	23.167	2.841	3	66.130	27.801	2.14	141.708
Feb. '76	1975	3.046	0.157	127	0.499	0.093	90.68	45.282
	1974	17.175	0.728	4	22.892	2.970	2.86	65.405
May '76	1975	4.905	0.450	37	1.550	0.551	26.42	40.956
	1974	27.100	3.371	3	127.963	41.384	2.14	274.206
	1973	37.6	-	1	382.9	-	0.71	273.500
Aug. '76	1976	1.429	0.077	121	0.062	0.011	86.39	5.366
	1975	16.175	1.149	4	30.486	13.265	2.86	87.102
Nov. '76	1976	1.560	0.077	149	0.121	0.024	106.39	12.918
	1975	18.700	1.955	4	39.397	12.994	2.86	112.564
	1974	32.950	0.250	2	179.050	32.850	1.43	255.786
Feb. '77	1976	2.619	0.125	75	0.361	0.073	53.55	19.360

Appendix 4.7 M. arenaria : The Computation of Production

Sampling Date	Age Class	N. m ⁻²	\bar{w} . (mg)	$\Delta\bar{w}$.	\bar{N}	$\frac{P}{N\Delta\bar{w}}$	Age Class	N. m ⁻²	\bar{w} . (mg)	$\Delta\bar{w}$.	\bar{N}	$\frac{P}{N\Delta\bar{w}}$
Mar. '75	1973	2.14	41.017	-	-	-	1974	32.84	0.183	-	-	-
Apr. '75		2.14	40.612	-0.404	2.14	-0.865		68.54	0.703	0.520	50.69	26.349
May '75		-	-	-40.612	1.07	-43.455		16.43	4.803	4.100	42.48	174.201
June '75		0.71	126.80	126.80	0.36	45.014		32.86	9.086	4.283	24.64	105.545
July '75		0.71	115.40	-11.40	0.71	-8.094		12.14	31.291	22.206	22.50	499.628
Aug. '75		0.71	82.70	-32.70	0.71	-23.217		5.71	43.388	12.096	8.92	107.958
Sept. '75		1.43	134.855	52.105	1.069	55.700		10.00	48.883	5.496	7.85	43.169
Oct. '75		2.14	97.197	-37.601	1.785	-67.099		1.43	69.550	20.667	5.71	118.110
Nov. '75		1.43	165.416	68.218	1.785	121.769		3.57	42.310	-27.240	2.50	-68.101
Dec. '75		-	-	-68.218	0.71	-48.435		2.14	43.740	1.430	2.85	4.084
Jan. '76		-	-	-	-	-		2.14	66.130	22.390	2.14	47.915
Feb. '76		-	-	-	-	-		2.86	22.892	-43.239	2.50	-108.096
						<u>31.318</u>						<u>950.762</u>
May '76		0.71	382.9	-	-	-		2.14	127.963	105.071	2.50	262.678
Aug. '76		-	-	-	-	-		-	-	-127.963	1.07	-136.920
Nov. '76		-	-	-	-	-		1.43	197.05	197.05	0.71	140.891
Feb. '77		-	-	-	-	-		-	-	-197.05	0.71	-140.891
												<u>125.758</u>

(Legend as Appendix 3.3)

Appendix 6.1 M. & R. Expt. Final and Initial Size, Weight and Condition Data.

	Final		Initial		Final		Initial		CF _H		Modified H _{t+1} (mm)
	L. (mm)	H. (mm)	L. (mm)	H. (mm)	Fdw. (mg)	sw. (mg)	Fdw. (mg)	sw. (mg)	Final	Initial	
(B31)	15.1	12.1	14.5	11.9	45.9	318.0	52.1	243.6	25.91	30.92	12.23
	7.9	6.6	6.1	5.1	6.6	26.5	2.6	7.2	22.96	19.78	7.61
	8.2	6.4	6.0	4.7	7.2	21.1	2.0	5.1	27.47	18.95	7.54
	9.9	8.0	8.5	6.8	10.3	52.3	7.2	24.1	20.12	23.02	8.80
	8.7	7.0	7.1	5.7	7.4	27.0	3.8	11.5	21.57	20.98	7.87
	10.0	8.3	8.2	6.9	13.8	49.7	7.6	25.6	24.13	23.20	9.24
	7.0	6.0	5.6	4.5	5.0	11.1	1.7	4.3	23.15	18.52	7.01
	9.1	7.5	7.6	6.2	7.4	34.2	5.2	16.4	17.54	21.93	8.37
	8.6	7.2	7.5	6.0	7.2	27.5	4.6	14.3	19.29	21.55	8.00
	8.4	7.0	7.2	6.0	6.5	29.5	4.6	14.3	18.95	21.55	7.67
	12.6	10.4	11.7	9.6	20.0	132.5	24.4	100.5	17.78	27.61	10.94
	10.4	8.4	8.6	6.9	13.9	50.0	7.6	25.6	23.45	23.20	9.40
	9.2	7.5	8.1	6.6	8.5	51.6	6.5	21.2	20.15	22.66	8.10
	7.7	6.5	6.2	5.1	5.6	21.5	2.6	7.2	20.39	19.78	7.44
	6.9	5.5	5.0	3.9	4.1	11.7	1.0	2.3	24.64	17.17	6.57
	7.6	6.1	6.0	4.7	5.7	23.8	2.0	5.1	25.11	18.95	7.04
	8.3	7.0	7.0	6.0	6.6	29.7	4.6	14.3	19.24	21.55	7.67
	Animals lost over period 8.7, 5.5, 5.1, 4.8, 4.9, 4.3, 4.8 mm Ht. initially.										
(B32)	16.4	12.7	15.9	12.5	58.9	365.7	62.0	298.2	28.75	31.73	12.83
	13.9	11.3	13.6	11.1	25.3	255.1	40.8	182.9	17.53	29.80	11.43
	11.9	9.6	11.0	8.9	15.4	121.8	18.7	73.5	17.41	26.53	10.07
	6.9	5.9	5.5	4.7	5.0	15.6	2.0	5.1	24.35	18.95	6.70
	8.1	6.8	6.4	5.4	7.5	25.0	3.2	9.2	23.85	20.39	7.74
	7.6	6.4	5.6	4.8	3.9	18.6	2.1	5.6	14.88	19.16	7.47
	10.0	8.2	9.1	7.5	8.9	61.6	10.2	36.1	16.14	24.24	8.67
	8.4	7.1	7.3	6.2	6.9	31.3	5.2	16.4	19.28	21.93	7.70
	8.5	6.9	6.5	5.3	7.0	23.5	3.0	8.5	21.31	20.19	7.97
	10.4	8.5	9.7	8.0	12.9	72.3	12.8	47.2	21.01	25.08	8.83
	7.8	6.1	5.6	4.4	5.8	18.7	1.6	3.9	25.55	18.30	7.24
	8.2	6.3	6.2	4.9	6.4	20.7	2.3	6.1	25.60	19.37	7.24
	8.9	7.2	8.3	6.8	8.0	34.0	7.2	24.1	21.43	23.02	7.47
	8.2	6.7	7.7	6.3	6.4	21.7	5.5	17.5	21.28	22.11	6.97
	8.9	7.5	7.6	6.5	8.8	47.5	6.2	19.9	20.86	22.48	8.17
	9.3	7.6	7.7	6.3	9.3	36.3	5.5	17.5	21.19	22.11	8.47
	9.0	7.4	8.1	6.7	7.9	35.5	6.9	22.6	19.50	22.84	7.87
	7.9	6.6	6.7	5.8	6.6	23.7	4.1	12.4	22.96	21.17	7.14
	8.4	6.7	7.5	5.9	6.1	21.3	4.4	13.3	20.28	21.36	7.24
	10.3	8.5	9.5	7.8	11.2	62.6	11.7	42.5	18.24	24.75	8.97
	Animals lost over period 7.5, 4.7, 4.2, 4.1 mm Ht. initially.										
(B33)	16.3	13.0	16.0	12.8	46.5	469.0	67.4	328.8	21.17	32.13	13.13
	7.3	6.0	5.7	4.7	5.6	19.2	1.9	5.1	25.93	18.95	6.87
	9.8	8.3	8.8	7.5	9.5	50.7	10.2	36.1	16.61	24.24	8.84
	8.4	6.7	5.7	4.5	9.0	29.7	1.7	4.3	29.92	18.52	8.17
	9.2	7.5	6.7	5.4	8.0	36.7	3.2	9.2	18.96	20.39	8.91
	10.4	8.5	10.0	8.1	11.8	72.8	13.4	49.7	19.21	25.24	8.77
	10.2	8.4	8.4	6.8	9.6	45.2	7.2	24.1	16.20	23.02	9.47
	7.9	6.4	5.7	4.6	5.4	18.7	1.8	4.7	20.60	18.73	7.61
	8.4	7.0	7.0	5.8	6.4	30.6	4.1	12.4	18.66	21.17	7.80-
	8.6	6.5	6.2	4.9	6.9	19.6	2.3	6.1	25.13	19.37	7.57
	9.0	7.6	8.0	6.7	7.7	38.2	6.9	22.6	17.54	22.84	8.20
	9.6	8.0	8.6	7.0	9.6	56.2	8.0	27.1	18.75	23.37	8.67
	11.0	8.6	10.1	7.8	13.0	84.4	11.7	42.5	20.44	24.75	9.14

Appendix 6.1 continued.

	9.0	7.7	8.0	7.0	7.7	41.9	8.0	27.1	16.87	23.37	8.17
	7.4	6.0	5.8	4.5	6.1	19.0	1.7	4.3	28.24	18.52	7.01
	6.4	5.4	3.7	3.1	4.4	9.7	0.4	0.9	27.94	15.22	6.94
	7.0	5.1	5.0	4.1	4.7	15.1	1.2	2.9	35.43	17.63	5.77
	7.7	6.1	5.3	4.0	5.0	16.5	1.1	2.6	22.03	17.40	7.51
	Animals lost over period 3.9, 3.9 mm Ht. initially.										
(B34)	13.2	11.4	12.4	10.2	21.6	215.9	30.2	129.0	14.58	28.50	12.20
	9.9	8.1	8.1	6.7	12.2	53.1	6.9	22.6	22.96	22.84	9.04
	11.0	9.0	9.6	7.9	13.6	88.6	12.3	44.8	18.66	24.91	9.74
	10.3	8.4	9.3	7.6	10.7	69.3	10.7	38.2	18.05	24.41	8.94
	10.3	8.3	9.0	7.3	14.5	67.0	9.3	32.3	25.36	23.90	8.97
	9.0	7.4	8.2	6.9	7.0	37.9	7.6	25.6	17.27	23.20	7.74
	7.0	5.7	5.5	4.2	5.2	12.7	1.3	3.2	28.08	17.86	6.90
	6.7	5.3	5.0	4.0	4.7	13.1	1.1	2.6	31.57	17.40	6.17
	9.0	7.3	7.1	5.6	8.9	29.2	3.6	10.7	22.88	20.78	8.44
	10.3	8.2	8.7	7.0	11.1	48.3	8.0	27.1	20.13	23.37	9.00
	8.0	6.4	6.6	5.5	5.9	20.5	3.4	9.9	22.51	20.58	7.00
	8.0	6.3	5.9	4.8	6.7	20.9	2.1	5.6	26.79	19.16	7.31
	8.1	6.4	6.4	5.2	6.7	20.3	2.8	7.9	25.56	19.98	7.20
	7.9	6.4	6.5	5.4	5.6	23.2	3.2	9.2	21.36	20.39	7.07
	6.4	5.2	5.0	4.3	4.5	10.8	1.4	3.5	32.00	18.08	5.80
	Animals lost over period 5.0, 4.7, 5.0, 4.1, 4.6, 3.9, 4.2 mm Ht. initially.										
(B35)	14.1	11.8	13.8	11.5	27.0	277.6	46.2	211.5	16.43	30.36	12.00
	14.1	11.5	13.5	11.1	29.4	202.2	40.8	182.9	19.33	29.80	11.77
	13.2	11.0	12.2	10.1	34.0	222.2	29.2	123.9	25.54	28.36	11.60
	11.9	9.6	11.5	9.2	23.5	128.2	21.0	84.3	26.56	26.99	9.87
	10.6	8.4	9.9	7.9	9.8	71.2	12.3	44.8	16.53	24.91	8.73
	9.3	7.5	7.2	5.8	8.6	33.3	4.1	12.4	20.39	21.17	8.64
	10.2	8.3	8.3	7.2	11.5	42.2	8.8	30.5	20.11	23.72	9.04
	Animals lost over period 4.6, 3.8, 4.5, 4.7, 5.2, 4.4, 3.4 mm Ht. initially.										

Appendix 6.2 10°C C.T. Expt. Mean Condition and Change With Time in Replicate

Treatments; Significance of Replicates From t-tests.

Removal	Pot No.	N.	FCF _H	SE	CCF _H	SE	Pot No.	N.	FCF _H	SE	CCF _H	SE	p
1st. Rem.	5C1	4	12.99	1.54	-4.55	1.57	5C5	5	12.41	0.96	-5.12	0.95	n.s.
	5C9	4	14.58	1.45	-2.96	1.43	5C13	5	14.58	1.10	-2.96	1.09	n.s.
	10C1	9	12.58	0.73	-4.95	0.71	10C5	10	12.89	0.99	-4.64	0.98	n.s.
	15C1	12	13.90	0.85	-3.66	0.85	15C5	15	14.84	0.44	-2.70	0.44	n.s.
	10F1	10	12.96	0.74	-4.57	0.74	10F5	9	14.49	0.95	-3.05	0.95	n.s.
	20F1	20	13.87	0.41	-3.67	0.42	20F5	19	13.82	0.49	-3.73	0.49	n.s.
	30F1	27	14.75	0.46	-2.80	0.46	30F5	30	13.01	0.47	-3.73	0.47	*
2nd. Rem.	5C2	5	9.35	1.19	-8.21	1.21	5C10	5	10.16	0.67	-7.38	0.67	n.s.
	5C6	5	8.96	1.19	-8.60	1.19	5C14	5	12.39	0.87	-5.17	0.87	*
	10C2	10	9.72	0.85	-7.82	0.85	10C6	9	10.75	0.85	-6.80	0.84	n.s.
	15C2	13	9.99	0.67	-7.57	0.67	15C6	15	12.69	0.63	-4.85	0.63	***
	10F2	9	11.21	0.88	-6.33	0.88	10F6	9	11.37	0.39	-6.17	0.39	n.s.
	20F2	18	9.24	0.38	-8.31	0.38	20F6	19	11.33	0.33	-6.21	0.33	***
	30F2	28	11.80	0.57	-5.74	0.57	30F6	28	10.38	0.41	-7.14	0.40	*
3rd. Rem.	5C3	5	14.29	1.21	-3.26	1.20	5C7	5	18.29	0.85	0.74	0.87	*
	5C11	4	17.00	2.86	-0.53	2.88	5C15	5	19.04	1.94	1.51	1.96	n.s.
	10C3	9	15.91	0.70	-1.63	0.71	10C7	9	17.53	1.22	-0.02	1.23	n.s.
	15C3	13	13.45	1.05	-4.10	1.04	15C7	15	15.02	0.94	-2.53	0.95	n.s.
	10F3	10	14.68	1.54	-2.86	1.55	10F7	9	13.64	1.28	-3.90	1.30	n.s.
	20F3	18	10.35	0.67	-7.20	0.67	20F7	20	11.85	0.79	-5.69	0.79	n.s.
	30F3	25	11.47	0.58	-6.08	0.59	30F7	26	11.36	0.67	-6.17	0.69	n.s.
4th. Rem.	5C4	5	22.31	2.42	4.76	2.45	5C8	5	26.69	2.24	9.15	2.23	n.s.
	5C12	5	24.17	2.25	6.63	2.24	5C16	5	24.00	3.02	6.44	3.03	n.s.
	10C4	10	19.64	1.50	2.10	1.51	10C8	9	19.27	1.08	1.73	1.09	n.s.
	15C4	14	17.78	1.29	0.24	1.30	15C8	15	17.54	1.45	-0.01	1.46	n.s.
	10F4	10	17.38	1.79	-0.17	1.80	10F8	9	22.38	1.41	4.85	1.41	*
	20F4	13	16.27	1.63	-1.27	1.64	20F8	19	16.65	0.87	-0.90	0.87	n.s.
	30F4	24	15.72	0.71	-1.82	0.71	30F8	26	11.66	0.69	-5.88	0.69	***

Where FCF_H = final flesh condition;

CCF_H = change in flesh condition from start of expt.;

SE = standard error of mean values;

p = significance level of difference between replicates, all other permutations of 5C replicates also not-significantly different from each other.

Appendix 6.3 T.T. Expt. Mean Condition and Change With Time in Replicate Treatments and Pooled Treatments. (Legend as Appendix 6.2).

Removal	Pot No.	N.	FCF _H	SE	CCF _H	SE	N.	FCF _H	SE	CCF _H	SE	
1st. Rem.	LC1'	14	10.42	0.82	-1.91	0.81	29	12.06	0.58	-0.38	0.60	
	LC1''	15	13.58	0.61	1.05	0.72						
	LF4'	18	13.68	0.61	1.48	0.53	38	13.23	0.35	-0.97	0.35	
	LF4''	20	12.83	0.37	0.52	0.44						
	MC1'	11	12.52	0.50	-0.05	0.55	30	12.26	0.45	-0.25	0.53	
	MC1''	19	12.10	0.67	-0.36	0.79						
	MF4'	15	13.10	0.97	1.08	1.00	32	13.02	0.63	0.94	0.69	
	MF4''	17	12.76	0.83	0.82	0.97						
	HC1'	16	13.41	1.15	1.05	1.10	27	12.52	0.78	0.07	0.79	
	HC1''	11	11.23	0.86	-1.36	0.99						
	HF4'	8	10.75	0.86	-1.81	1.12	16	9.84	0.53	-2.82	0.67	
	HF4''	8	8.93	0.50	-3.84	0.60						
	2nd. Rem.	LC2'	7	9.02	0.68	-3.57	0.71	16	9.00	0.36	-3.78	0.38
		LC2''	9	8.98	0.40	-3.94	0.44					
		LF5'	17	10.04	0.75	-2.44	0.86	34	9.51	0.48	-2.99	0.52
LF5''		17	8.98	0.59	-3.54	0.59						
MC2'		3	10.20	1.68	-1.66	2.19	8	9.22	0.74	-3.19	1.01	
MC2''		5	8.62	0.67	-4.11	0.94						
MF5'		6	11.53	0.97	-0.43	0.87	15	10.11	0.82	-2.14	0.93	
MF5''		9	9.16	1.14	-3.29	1.34						
HC2'		2	9.38	1.97	-2.99	3.50	2	9.38	1.97	-2.99	3.50	
HC2''		Insufficient Data										
HF5'		"	"	"	"	"	Insufficient Data					
HF5''		"	"	"	"	"	Insufficient Data					
3rd. Rem.		LC3'	9	7.08	0.91	-5.29	0.92	19	8.12	0.58	-4.36	0.62
		LC3''	10	9.05	0.64	-3.53	0.78					
		LF6'	8	9.28	1.59	-3.39	1.73	21	12.04	0.95	-0.40	1.03
	LF6''	13	13.75	0.94	1.44	1.02						
	MC3'	1	10.14	0	-3.21	0	1	10.14	0	-3.21	0	
	MC3''	Insufficient Data										
	MF6'	7	16.25	2.27	3.83	2.36	13	16.93	1.63	4.40	1.71	
	MF6''	6	17.73	2.54	5.05	2.68						
	HC3'	Insufficient Data					Insufficient Data					
	HC3''	"	"	"	"	"	Insufficient Data					
	HF6'	"	"	"	"	"	Insufficient Data					
	HF6''	"	"	"	"	"	Insufficient Data					

Appendix 6.4 10°C C.T. Expt. (a): The Reference Regression Equations for Each Replicate of Each Treatment.

Final s.w. = $b + S.E.$ Initial s.w. + a F. Hd = $b + S.E.$ I. Hd + a

T'ment.	n	b	S.E.	a	r	p	b	S.E.	a	r	p	b	S.E.	a	r	p
1st. Removal																
5C1	4	1.362	0.026	0.214	1.000	***	0.674	0.023	0.357	0.999	**	1.005	0.030	0.063	0.999	***
5C5	5	1.775	0.061	-14.349	0.998	***	0.636	0.075	1.185	0.980	**	1.013	0.035	0.005	0.998	***
5C9	4	1.293	0.067	-4.597	0.997	**	1.005	0.120	-0.820	0.986	*	1.006	0.016	-0.022	1.000	***
5C13	5	1.648	0.116	-14.131	0.993	***	0.873	0.035	0.028	0.997	***	1.012	0.005	-0.065	1.000	***
10C1	9	1.260	0.023	-4.271	0.999	***	0.793	0.042	0.010	0.990	***	1.011	0.020	-0.044	0.999	***
10C5	10	1.297	0.045	-2.256	0.995	***	0.739	0.071	0.574	0.964	***	0.852	0.038	1.204	0.992	***
15C1	12	1.285	0.045	-1.569	0.994	***	0.713	0.078	1.142	0.945	***	1.007	0.011	0.021	0.999	***
15C5	15	1.832	0.089	-24.870	0.985	***	0.847	0.017	0.086	0.997	***	0.989	0.015	0.150	0.998	***
10F1	10	1.614	0.059	-12.013	0.995	***	0.624	0.071	1.246	0.952	***	1.031	0.015	-0.080	0.999	***
10F5	9	1.847	0.069	-20.780	0.995	***	0.704	0.059	1.817	0.977	***	1.013	0.017	0.120	0.999	***
20F1	20	1.468	0.067	-8.513	0.982	***	0.657	0.044	1.609	0.963	***	1.000	0.018	0.213	0.997	***
20F5	19	1.235	0.037	1.905	0.992	***	0.658	0.049	1.722	0.956	***	0.994	0.015	0.228	0.998	***
30F1	27	1.462	0.037	-9.674	0.992	***	0.857	0.029	0.600	0.986	***	1.002	0.016	0.187	0.997	***
30F5	30	1.219	0.053	-3.335	0.974	***	0.717	0.066	0.879	0.899	***	1.008	0.018	0.139	0.995	***
2nd. Removal																
5C2	5	1.554	0.022	-11.138	1.000	***	0.328	0.071	2.097	0.936	*	1.024	0.018	-0.185	0.999	***
5C6	5	1.362	0.040	-5.185	0.999	***	0.595	0.065	-0.777	0.982	**	1.029	0.005	-0.160	1.000	***
5C10	5	1.442	0.041	-3.470	0.999	***	0.526	0.034	0.453	0.994	***	1.003	0.015	0.018	1.000	***
5C14	5	1.702	0.083	-16.450	0.996	***	0.586	0.060	1.210	0.984	**	1.015	0.015	-0.044	1.000	***
10C2	10	1.385	0.093	-5.328	0.982	***	0.707	0.046	-0.894	0.984	***	1.011	0.012	0.038	0.999	***
10C6	9	1.398	0.058	-1.042	0.994	***	0.665	0.088	0.388	0.944	***	1.000	0.032	0.176	0.996	***
15C2	13	1.293	0.050	-2.985	0.992	***	0.393	0.086	1.977	0.810	***	0.969	0.032	0.435	0.994	***
15C6	15	1.662	0.067	-12.455	0.989	***	0.649	0.043	0.740	0.972	***	0.987	0.018	0.213	0.998	***
10F2	9	1.329	0.073	-3.801	0.989	***	0.900	0.081	-1.052	0.973	***	1.019	0.033	0.092	0.996	***
10F6	9	1.077	0.057	0.707	0.990	***	0.717	0.049	0.041	0.984	***	0.926	0.031	-0.789	0.996	***
20F2	18	1.430	0.066	-7.884	0.983	***	0.559	0.042	0.140	0.958	***	1.030	0.018	-0.031	0.997	***
20F6	19	1.260	0.053	-3.124	0.985	***	0.746	0.027	-0.252	0.989	***	1.019	0.019	0.026	0.997	***
30F2	28	1.300	0.055	1.988	0.977	***	0.656	0.049	0.805	0.934	***	0.964	0.018	0.490	0.995	***
30F6	28	1.577	0.048	-9.581	0.988	***	0.625	0.023	0.237	0.983	***	0.991	0.014	0.245	0.997	***

Appendix 6.4 10°C C.T. Expt. (a) continued.

T'ment. n	F. s.w. = b + S.E.				F. fdw = b + S.E.				F. Ht = b + S.E.				Bertalanffy Parameters				
	b	S.E.	a	p	b	S.E.	a	p	b	S.E.	a	p	r	Ht	K	H _∞	
3rd. Removal																	
5C3	5	1.580	0.074	-16.767	0.997	0.778	0.068	0.575	0.989	**	1.000	0.000	0.000	1.000	***	0.126	12.22
5C7	5	1.721	0.051	-12.166	0.999	0.817	0.036	2.112	0.996	***	0.912	0.048	0.883	0.996	***	0.350	12.95
5C11	4	1.540	0.070	-2.122	0.998	0.591	0.265	2.922	0.844	n.s.	0.839	0.168	1.565	0.962	*	0.276	11.21
5C15	5	1.432	0.033	0.993	0.999	0.560	0.065	4.909	0.980	**	0.801	0.079	2.308	0.986	**	0.445	11.39
10C3	9	1.751	0.073	-11.334	0.994	0.855	0.066	1.007	0.980	***	0.973	0.025	0.508	0.998	***	0.145	11.90
10C7	9	1.782	0.046	-8.088	0.998	0.735	0.036	2.560	0.992	***	0.907	0.031	1.101	0.996	***	0.292	10.18
15C3	13	1.461	0.043	-6.917	0.995	0.673	0.060	1.298	0.958	***	1.022	0.016	-0.035	0.999	***	0.187	10.26
15C7	15	1.662	0.081	-7.509	0.985	0.657	0.086	1.659	0.903	***	0.933	0.021	0.808	0.997	***	0.147	10.61
10F3	10	1.731	0.062	-16.309	0.995	0.610	0.073	1.253	0.947	***	0.963	0.012	0.391	0.999	***	0.223	11.25
10F7	9	1.254	0.038	-2.570	0.997	0.438	0.091	2.541	0.876	**	0.944	0.022	0.692	0.998	***	0.232	10.29
20F3	18	1.658	0.092	-14.618	0.976	0.544	0.072	1.103	0.884	***	0.969	0.020	0.597	0.997	***	0.042	15.85
20F7	20	1.643	0.071	-16.909	0.984	0.623	0.046	0.658	0.954	***	0.991	0.012	0.163	0.999	***	0.091	10.55
30F3	25	1.441	0.045	-6.321	0.989	0.516	0.047	1.456	0.916	***	0.989	0.016	0.308	0.997	***	0.091	11.86
30F7	26	1.403	0.045	-5.668	0.988	0.774	0.039	-0.392	0.971	***	0.978	0.014	0.330	0.997	***	0.077	11.69
4th. Removal																	
5C4	5	1.413	0.036	0.681	0.999	0.686	0.068	5.784	0.985	**	0.882	0.062	1.442	0.993	***	0.126	12.22
5C8	5	1.708	0.043	20.931	0.999	1.512	0.136	7.344	0.988	**	0.705	0.109	3.821	0.966	**	0.350	12.95
5C12	5	1.455	0.120	8.210	0.990	1.411	0.426	3.878	0.886	*	0.759	0.091	2.702	0.979	**	0.276	11.21
5C16	5	1.445	0.098	27.322	0.993	0.401	0.244	14.882	0.687	n.s.	0.641	0.090	4.089	0.972	**	0.445	11.39
10C4	10	1.391	0.067	12.675	0.991	0.511	0.145	5.645	0.780	**	0.865	0.064	1.606	0.979	***	0.145	11.90
10C8	9	1.283	0.056	14.185	0.993	0.692	0.109	4.511	0.923	***	0.747	0.049	2.575	0.985	***	0.292	10.18
15C4	14	1.702	0.092	-3.365	0.983	0.626	0.083	3.496	0.909	***	0.829	0.033	1.755	0.990	***	0.187	10.26
15C8	15	1.591	0.047	-1.066	0.994	0.665	0.069	3.099	0.937	***	0.863	0.026	1.453	0.994	***	0.147	10.61
10F4	10	1.375	0.074	1.879	0.989	0.532	0.063	4.322	0.948	***	0.800	0.062	2.251	0.977	***	0.223	11.25
10F8	9	1.453	0.077	-0.450	0.990	1.352	0.200	1.723	0.931	***	0.793	0.054	2.130	0.984	***	0.232	10.29
20F4	13	1.516	0.071	-10.269	0.988	0.887	0.112	0.460	0.922	***	0.959	0.025	0.650	0.996	***	0.042	15.85
20F8	19	1.398	0.080	-0.272	0.973	0.828	0.082	1.824	0.926	***	0.848	0.027	1.603	0.991	***	0.165	10.55
30F4	24	1.389	0.038	-3.021	0.992	0.702	0.060	2.289	0.929	***	0.913	0.024	1.032	0.992	***	0.091	11.86
30F8	26	1.169	0.039	3.350	0.982	0.734	0.062	0.071	0.923	***	0.926	0.026	0.865	0.991	***	0.077	11.69

Appendix 6.4 10°C C.T. Expt. (b): The Reference Linear Regression Equations (Pooled Data) of Each Treatment, from which the Change in Size and Weight of Initial 4 and 8 mm Animals were Calculated; the Results of the t-Test Analysis to Detect Growth are also Given (see text). All Equations Significant at p *** Level.

Treatment	n	F. Ht = b + S.E. I. Ht + a					F. fdw = b + S.E. I. fdw + a					F. s.w. = b + S.E. I. s.w. + a					
		b	S.E.	a	r	t-test Results	b	S.E.	a	r	t-test Results	b	S.E.	a	r	t-test Results	
1st. Removal																	
5C	18	1.009	0.011	-0.011	0.999	n.s.	0.695	0.035	1.020	0.981	***	1.503	0.055	-6.555	0.989	***	+
10C	19	0.921	0.029	0.646	0.991	*	0.763	0.041	0.304	0.976	***	1.283	0.026	-3.306	0.996	***	+
15C	27	0.996	0.010	0.108	0.999	n.s.	0.803	0.032	0.309	0.980	***	1.673	0.078	-21.869	0.974	***	+
10F	19	1.022	0.011	0.016	0.999	n.s.	0.684	0.045	1.316	0.965	***	1.790	0.050	-19.460	0.993	***	+
20F	39	0.996	0.011	0.226	0.998	n.s.	0.658	0.032	1.656	0.959	***	1.309	0.039	-1.302	0.984	***	+
30F	57	1.005	0.012	0.162	0.996	n.s.	0.808	0.036	0.583	0.950	***	1.376	0.035	-7.791	0.982	***	+
2nd. Removal																	
5C	20	1.017	0.007	-0.081	1.000	*	0.446	0.041	1.352	0.931	***	1.520	0.030	-9.344	0.996	***	+
10C	19	1.007	0.015	0.091	0.998	n.s.	0.689	0.045	-0.306	0.965	***	1.390	0.055	-3.236	0.987	***	+
15C	28	0.983	0.016	0.279	0.996	n.s.	0.529	0.053	1.262	0.889	***	1.487	0.060	-8.426	0.980	***	+
10F	18	0.970	0.024	0.460	0.995	n.s.	0.804	0.050	-0.463	0.971	**	1.196	0.058	-1.194	0.982	**	+
20F	37	1.026	0.013	-0.010	0.997	n.s.	0.616	0.033	0.176	0.953	***	1.373	0.044	-6.291	0.983	***	+
30F	56	0.979	0.012	0.348	0.996	n.s.	0.651	0.029	0.452	0.954	***	1.421	0.040	-4.099	0.979	***	+
3rd. Removal																	
5C	19	0.888	0.042	1.226	0.982	*	0.716	0.044	2.525	0.969	***	1.577	0.039	-7.446	0.995	***	+
10C	18	0.938	0.021	0.817	0.996	**	0.772	0.034	1.962	0.985	***	1.778	0.037	-10.297	0.997	***	+
15C	28	0.971	0.017	0.447	0.996	n.s.	0.666	0.050	1.485	0.935	***	1.532	0.050	-5.457	0.989	***	+
10F	19	0.956	0.014	0.522	0.998	**	0.542	0.058	1.704	0.916	***	1.561	0.072	-13.518	0.982	***	+
20F	38	0.983	0.015	0.347	0.996	n.s.	0.579	0.042	0.925	0.916	***	1.653	0.056	-15.994	0.979	***	+
30F	51	0.985	0.011	0.309	0.997	n.s.	0.639	0.035	0.471	0.934	***	1.424	0.031	-5.996	0.988	***	+
4th. Removal																	
5C	20	0.754	0.053	2.952	0.959	***	0.879	0.150	8.456	0.810	n.s.	1.510	0.058	13.642	0.989	**	+
10C	19	0.815	0.042	2.020	0.978	***	0.586	0.091	5.197	0.842	***	1.348	0.045	13.009	0.991	***	+
15C	29	0.848	0.020	1.590	0.992	***	0.654	0.050	3.233	0.929	***	1.615	0.042	-0.795	0.991	***	+
10F	19	0.802	0.040	2.154	0.979	***	0.657	0.119	4.894	0.801	*	1.386	0.050	1.723	0.989	***	+
20F	32	0.898	0.021	1.180	0.992	***	0.857	0.066	1.229	0.921	*	1.459	0.053	-5.001	0.981	***	+
30F	50	0.920	0.018	0.941	0.991	***	0.724	0.047	1.083	0.911	***	1.328	0.030	-1.814	0.988	***	+

Appendix 6.5 10°C C.T. Expt.: The Exponential Regression Equations of Flesh and Shell Dry Weight (mg) with Shell Height (mm). All equations Significant at p *** Level.

$$fdw = Ht \frac{b}{a} \pm S.E.$$

$$s.w. = Ht \frac{b}{a} \pm S.E.$$

Removal	Treatment	n	b	S.E.	a	r	b	S.E.	a	r
1st. Removal	5C	18	3.063	0.103	84.37	0.991	3.744	0.111	41.98	0.993
	10C	19	3.418	0.107	177.40	0.992	3.882	0.113	59.81	0.993
	15C	27	2.947	0.087	63.03	0.989	3.736	0.103	41.34	0.991
	10F	19	3.034	0.121	79.16	0.987	3.799	0.118	48.74	0.992
	20F	39	2.941	0.069	64.77	0.990	3.672	0.087	38.08	0.990
	30F	57	3.025	0.070	74.79	0.986	3.652	0.066	39.57	0.991
2nd. Removal	5C	20	2.830	0.164	71.66	0.972	3.868	0.116	54.17	0.992
	10C	19	3.153	0.159	136.61	0.979	3.702	0.108	39.51	0.993
	15C	28	2.796	0.159	59.71	0.960	3.729	0.129	41.04	0.985
	10F	18	3.217	0.153	137.12	0.982	3.561	0.110	33.90	0.992
	20F	37	3.080	0.104	115.61	0.981	3.618	0.095	35.56	0.988
	30F	56	3.218	0.077	141.02	0.985	3.587	0.080	31.52	0.987
3rd. Removal	5C	19	2.814	0.165	41.05	0.972	3.954	0.160	65.75	0.986
	10C	18	2.773	0.131	38.33	0.982	3.977	0.163	63.93	0.987
	15C	28	2.795	0.179	47.85	0.951	3.649	0.117	32.61	0.987
	10F	19	2.320	0.153	19.04	0.965	3.640	0.146	35.45	0.986
	20F	38	2.987	0.157	91.40	0.953	3.714	0.114	40.65	0.984
	30F	51	3.027	0.134	96.49	0.955	3.664	0.075	37.95	0.990
4th. Removal	5C	20	2.674	0.224	20.95	0.942	4.121	0.124	93.93	0.992
	10C	19	2.521	0.187	19.80	0.956	3.943	0.132	58.28	0.991
	15C	29	2.637	0.233	28.59	0.909	3.937	0.101	56.14	0.991
	10F	19	2.472	0.254	17.87	0.921	3.861	0.148	55.97	0.988
	20F	32	2.591	0.189	27.38	0.929	3.800	0.105	49.32	0.989
	30F	50	3.028	0.185	81.66	0.921	3.636	0.075	36.47	0.990

Appendix 6.6 T.T. Expt.: Linear Regression Equations of Final Height with Initial Height (mm) for Both Single and Pooled Replicate Treatments, with Results of the t-Test Analysis (see Text).

F. Ht = b + S.E. I. Ht + a

Treatment	Single Replicate				Pooled Replicates				t-test Results				
	b	S.E.	a	n	b	S.E.	a	n		r	p		
1st. Removal													
LC1'	0.974	0.013	0.346	14	0.967	0.009	0.409	29	0.999	***	-110.14	***	
LC1''	0.961	0.013	0.474	15	0.970	0.012	0.417	38	0.997	***	-82.36	***	
LF4'	0.990	0.010	0.236	18	0.986	0.003	0.191	30	1.000	***	-332.35	***	
LF4''	0.956	0.020	0.562	20	0.980	0.007	0.301	32	0.999	***	-141.88	***	
MC1'	0.994	0.006	0.122	11	0.988	0.003	0.175	27	1.000	***	-332.35	***	
MC1''	0.984	0.004	0.205	19	0.982	0.007	0.238	16	1.000	***	-141.88	***	
MF4'	0.978	0.010	0.330	15	0.997	0.007	0.136	16	1.000	***	-141.86	***	
MF4''	0.977	0.013	0.299	17	0.967	0.012	0.469	34	0.997	***	-82.37	***	
HC1'	0.989	0.004	0.161	16	0.990	0.007	0.209	8	1.000	***	-141.87	***	
HC1''	0.986	0.005	0.200	11	0.968	0.021	0.445	15	0.997	***	-46.65	***	
HF4'	0.975	0.012	0.293	8	Insufficient Data								
HF4''	0.994	0.007	0.140	8	Insufficient Data								
LC2'	0.998	0.008	0.133	7	Insufficient Data								
LC2''	0.997	0.012	0.125	9	Insufficient Data								
LF5'	0.943	0.022	0.716	17	Insufficient Data								
LF5''	0.987	0.008	0.238	17	Insufficient Data								
MC2'	0.987	0.029	0.195	3	Insufficient Data								
MC2''	0.985	0.004	0.278	5	Insufficient Data								
MF5'	0.972	0.005	0.343	6	Insufficient Data								
MF5''	0.953	0.033	0.612	9	Insufficient Data								
HC2'	Insufficient Data				Insufficient Data								
HC2''	No Data				Insufficient Data								
HF5'	No Data				Insufficient Data								
HF5''	No Data				Insufficient Data								
LC3'	0.973	0.010	0.333	9	0.977	0.008	0.345	19	0.999	***	-124.02	***	
LC3''	0.978	0.011	0.373	10	0.964	0.010	0.568	21	0.999	***	-99.04	***	
LF6'	0.984	0.007	0.314	8	Insufficient Data								
LF6''	0.954	0.015	0.690	13	Insufficient Data								
MC3'	No Data				Insufficient Data								
MC3''	Insufficient Data				Insufficient Data								
MF6'	0.704	0.094	2.838	7	0.818	0.060	1.881	13	0.971	***	-15.85	***	
MF6''	0.957	0.022	0.600	6	Insufficient Data								
HC3', HC3''	No Data				Insufficient Data								
HF6', HF6''	No Data				Insufficient Data								

Appendix 6.7 T.T. Expt. : Linear Regression Equations of Final Flesh Weight with Initial Flesh Weight (mg) for Both Single and Pooled Replicate Treatments, with Results of the t-Test Analysis (see Text).
 $F. \text{ fdw} = b - S.E. \cdot I. \text{ fdw} + a$

Treatment	Single Replicate					Pooled Replicates					t-test Results				
	b	S.E.	a	n	r	b	S.E.	a	n	r		p			
1st. Removal	LC1'	0.969	0.092	-0.429	14	0.950	0.835	0.052	0.995	29	0.951	***	-18.40	***	
	LC1''	0.757	0.057	2.149	15	0.966	0.966	0.030	0.893	38	0.983	***	-32.37	***	
	LF4'	1.111	0.063	0.510	18	0.975	0.975	0.042	1.040	30	0.962	***	-23.02	***	
	LF4''	0.933	0.026	0.690	20	0.993	0.993	0.063	0.585	32	0.939	***	-14.94	***	
	MC1'	0.757	0.069	1.660	11	0.965	0.965	0.130	-1.147	27	0.877	***	-6.50	***	
	MC1''	0.794	0.053	0.727	19	0.964	0.964	0.029	1.270	16	0.982	***	-33.91	***	
	MF4'	0.915	0.101	1.073	15	0.928	0.928	0.042	0.392	16	0.973	***	-23.14	***	
	MF4''	0.931	0.061	0.298	17	0.969	0.969	0.039	0.891	34	0.946	***	-25.00	***	
	HC1'	1.506	0.185	-2.030	16	0.908	0.908	0.025	0.476	8	0.995	***	-39.40	***	
	HC1''	0.874	0.051	-0.116	11	0.985	0.985	0.058	0.173	15	0.963	***	-16.49	***	
	HF4'	0.634	0.027	1.048	8	0.995	0.995	Insufficient Data							
	HF4''	0.540	0.042	1.325	8	0.982	0.982	Insufficient Data							
	LC2'	0.718	0.061	0.124	7	0.982	0.982	Insufficient Data							
	LC2''	0.646	0.067	0.642	9	0.964	0.964	Insufficient Data							
2nd. Removal	LF5'	0.732	0.057	0.376	17	0.958	0.958	0.048	0.992	19	0.934	***	-20.32	***	
	LF5''	0.603	0.053	1.087	17	0.946	0.946	0.063	2.905	21	0.884	***	-15.36	***	
	MC2'	0.458	0.125	0.932	3	0.965	0.965	Insufficient Data							
	MC2''	0.601	0.031	0.467	5	0.996	0.996	Insufficient Data							
	MF5'	0.938	0.054	0.329	6	0.993	0.993	Insufficient Data							
	MF5''	0.758	0.067	-0.531	9	0.974	0.974	Insufficient Data							
	HC2'	Insufficient Data			2			Insufficient Data							
	HC2''	No Data			-			No Data							
	HF5'	No Data			-			No Data							
	HF5''	No Data			-			No Data							
	LC3'	0.504	0.054	0.538	9	0.962	0.962	0.516	0.048	0.992	19	0.934	***	-20.32	***
	LC3''	0.526	0.082	1.409	10	0.916	0.916	0.517	0.063	2.905	21	0.884	***	-15.36	***
	LF6'	0.546	0.080	1.256	8	0.942	0.942	Insufficient Data							
	LF6''	0.583	0.104	3.275	13	0.862	0.862	Insufficient Data							
MC3'	No Data			-			Insufficient Data								
MC3''	Insufficient Data			1			Insufficient Data								
MF6'	1.372	0.346	0.454	7	0.871	0.871	0.941	0.238	3.446	13	0.766	***	-3.26	**	
MF6''	0.707	0.365	5.621	6	0.695	0.695	No Data								
HC3', HC3''	No Data			-			No Data								
HF6', HF6''	No Data			-			No Data								

Appendix 6.8 T.T. Expt. : Linear Regression Equations of Final Shell Weight with Initial Shell Weight (mg) for Both Single and Pooled Replicate Treatments, with Results of the t-Test Analysis (see Text.)

$$F. \text{ sw.} = b + S.E. \cdot I. \text{ sw.} + a$$

Treatment	Single Replicate					Pooled Replicates					t-test Results			
	b	S.E.	a	n	r	b	S.E.	a	n	r		p		
1st. Removal	LC1'	1.128	0.043	-4.446	14	0.991	1.120	0.021	-2.434	29	0.995	***	-46.50	***
	LC1''	1.114	0.025	-0.549	15	0.997	1.127	0.034	-3.694	38	0.984	***	-28.28	***
	LF4'	1.022	0.040	3.667	18	0.988	1.111	0.047	-1.583	30	0.976	***	-20.17	***
	LF4''	1.152	0.048	-6.853	20	0.985	1.080	0.030	-1.949	32	0.989	***	-32.25	***
	MC1'	1.262	0.063	-6.758	11	0.989	1.232	0.041	-8.929	27	0.986	***	-23.16	***
	MC1''	1.087	0.059	-2.729	19	0.976	1.021	0.032	1.544	16	0.993	***	-30.23	***
	MF4'	1.083	0.032	-0.917	15	0.994	1.000	0.055	2.340	16	0.980	***	-17.18	***
	MF4''	0.942	0.136	1.129	17	0.873	0.989	0.017	-0.431	34	0.995	***	-57.83	***
	HC1'	1.209	0.066	-7.404	16	0.980	1.105	0.026	-1.432	8	0.998	***	-37.36	***
	HC1''	1.260	0.048	-11.638	11	0.993	1.163	0.031	-2.896	15	0.995	***	-31.10	***
	HF4'	1.075	0.028	1.397	8	0.998	Insufficient Data							
	HF4''	1.000	0.047	-0.945	8	0.993	Insufficient Data							
	LC2'	1.110	0.014	1.076	7	1.000	Insufficient Data							
	LC2''	0.954	0.089	2.102	9	0.971	Insufficient Data							
	LF5'	0.955	0.029	-1.441	17	0.993	Insufficient Data							
	LF5''	0.997	0.019	2.445	17	0.997	Insufficient Data							
MC2'	0.824	0.041	7.072	3	0.999	Insufficient Data								
MC2''	1.112	0.029	-1.985	5	0.999	Insufficient Data								
MF5'	1.241	0.016	1.327	6	1.000	Insufficient Data								
MF5''	1.175	0.037	-8.783	9	0.996	Insufficient Data								
HC2'	Insufficient Data						Insufficient Data							
HC2''	No Data						No Data							
HF5'	No Data						No Data							
HF5''	No Data						No Data							
3rd. Removal	LC3'	0.843	0.015	8.632	9	0.999	0.882	0.027	13.508	19	0.992	***	-36.16	***
	LC3''	0.933	0.041	16.031	10	0.992	1.095	0.048	3.715	21	0.982	***	-19.74	***
	LF6'	1.129	0.100	2.332	8	0.977	Insufficient Data							
	LF6''	0.991	0.026	8.201	13	0.996	Insufficient Data							
	MC3'	No Data						Insufficient Data						
	MC3''	Insufficient Data						Insufficient Data						
	MF6'	0.753	0.058	16.408	7	0.986	1.015	0.094	3.731	13	0.972	***	-9.62	***
	MF6''	1.103	0.097	0.762	6	0.985	Insufficient Data							
HC3', HC3''	No Data						No Data							
HF6', HF6''	No Data						No Data							

Appendix 6.9 T.T. Expt. : Exponential Regression Equations of Flesh and Shell Weight (mg) with Shell Height (mm) for the

Pooled Replicate Treatment.

$$F_{dw} = \frac{H^b}{a} \pm \text{S.E.}$$

$$sw = \frac{H^b}{a} \pm \text{S.E.}$$

Treatment	n	b	S.E.	a	r	p	b	S.E.	a	r	p
1st. Removal											
LC1	29	3.009	0.194	87.52	0.948	***	3.951	0.610	73.78	0.780	***
LF4	38	3.136	0.076	100.18	0.989	***	3.612	0.092	32.41	0.939	***
MC1	30	2.564	0.126	33.91	0.968	***	3.715	0.206	39.44	0.959	***
MF4	32	2.827	0.144	57.46	0.963	***	3.265	0.425	20.31	0.814	***
HC1	27	2.978	0.179	79.66	0.957	***	3.852	0.110	51.08	0.990	***
HF4	16	2.393	0.127	28.52	0.981	***	3.932	0.160	62.49	0.989	***
2nd. Removal											
LC2	16	3.012	0.190	115.45	0.973	***	4.155	0.191	105.54	0.985	***
LF5	34	2.876	0.173	84.83	0.947	***	3.572	0.103	31.33	0.987	***
MC2	8	2.589	0.161	48.30	0.989	***	3.569	0.245	26.79	0.986	***
MF5	15	2.635	0.287	50.76	0.931	***	3.777	0.154	44.80	0.989	***
HC2	2	Insufficient Data					Insufficient Data				
HF5	-	No Data					No Data				
3rd. Removal											
LC3	19	2.988	0.250	126.33	0.945	***	3.597	0.093	29.08	0.994	***
LF6	21	2.519	0.278	33.03	0.901	***	3.811	0.142	46.83	0.987	***
MC3	1	Insufficient Data					Insufficient Data				
MF6	13	2.501	0.699	22.46	0.699	**	3.866	0.196	56.84	0.986	***
HC3	-	No Data					No Data				
HF6	-	No Data					No Data				

Appendix 6.10 Data Used in the Calculation of Elimination ($\Delta M = \Sigma f_{dw}$ of Animals Lost over Experimental Period) From Each Treatment at the Final Removal: 10°C C.T. Expt.(a), and T.T. Expt.(b). (The Projected Weight = Theoretical Weight at Removal Following Death as Calculated from Weight and Growth Equations for Appropriate Removal.)

(All weights as flesh dry weight.)

T'ment.	Initial Size			Initial Projected Mean			Initial			Projected Mean			Initial			Projected Mean						
	L. (mm)	Ht. (mm)	Weight (mg)	Weight (mg)	Weight (mg)	Weight (mg)	T'ment.	Ht. (mm)	Weight (mg)	Weight (mg)	Weight (mg)	T'ment.	Ht. (mm)	Weight (mg)	Weight (mg)	Weight (mg)	T'ment.	Ht. (mm)	Weight (mg)	Weight (mg)	Weight (mg)	
(a) 10C8	4.2	3.3	0.627	4.945	2.786	2.786	(b) LC3'	6.6	3.48	2.29	2.89	(b) LF6''	4.9	1.34	4.06	2.70						
15C4	10.5	8.4	10.412	10.014	10.213	10.213	continued	4.9	1.34	1.21	1.27	continued	2.9	0.25	3.42	1.83						
10F8	14.3	12.3	32.791	46.056	39.423	39.423		4.8	1.26	1.17	1.22	MF6'	12.6	27.41	82.83	55.12						
20F4	14.2	11.1	24.080	21.819	22.949	22.949	LC3''	13.0	30.29	17.34	23.81		12.0	23.46	32.64	28.05						
	9.8	7.6	7.706	7.295	7.500	7.500		7.9	6.18	4.66	5.42		11.4	19.92	27.78	23.85						
	6.6	5.4	2.756	2.905	2.830	2.830		7.7	5.69	4.40	5.05		7.5	5.23	7.63	6.43						
	6.6	5.4	2.756	2.905	2.830	2.830		7.3	4.80	3.93	4.36		6.9	4.01	5.96	4.98						
	6.2	5.0	2.187	2.400	2.293	2.293		6.7	3.65	3.33	3.49		7.0	4.20	6.22	5.21						
	7.8	6.0	3.784	3.816	3.800	3.800		6.7	3.65	3.33	3.49		7.1	4.39	6.48	5.44						
	5.2	4.2	1.294	1.608	1.451	1.451		6.4	3.15	3.07	3.11		6.8	3.83	5.71	4.77						
20F8	7.2	5.6	3.075	4.370	3.722	3.722		4.7	1.18	2.03	1.61		6.7	3.65	5.46	4.56						
30F4	14.2	12.0	30.444	23.661	27.052	27.052		3.8	0.60	1.72	1.16		6.4	3.15	4.78	3.96						
	9.6	7.5	7.405	7.487	7.446	7.446		2.8	0.22	1.52	0.87		4.8	1.26	2.18	1.72						
	9.0	7.4	7.112	7.282	7.197	7.197	LF6'	11.2	18.82	11.53	15.17		3.2	0.34	0.92	0.63						
	6.6	5.2	2.461	4.017	3.239	3.239		8.4	7.51	5.36	6.44		11.5	20.48	20.10	20.29						
	4.3	3.5	0.748	2.814	1.781	1.781		7.8	5.93	4.49	5.21		11.4	19.92	19.70	19.81						
	4.0	3.2	0.571	2.690	1.630	1.630		7.3	4.80	3.88	4.34		8.6	8.10	11.35	9.72						
30F8	13.3	10.9	22.798	16.805	19.801	19.801		7.1	4.39	3.65	4.02		7.9	6.18	9.99	8.08						
	9.1	7.4	7.112	5.291	6.201	6.201		7.0	4.20	3.55	3.88		7.4	5.01	9.16	7.09						
	6.9	5.7	3.243	2.451	2.847	2.847		6.7	3.65	3.25	3.45		7.5	5.23	9.32	7.27						
	6.8	5.6	3.075	2.186	2.630	2.630		6.7	3.65	3.25	3.45		7.0	4.20	8.59	6.39						
(b) LC3'				14.35	20.95	20.95		6.2	2.85	2.81	2.83		6.8	3.83	8.33	6.08						
				10.58	15.25	15.25		4.8	1.26	1.94	1.60		6.7	3.65	8.20	5.93						
				8.26	11.79	11.79		3.9	0.65	1.61	1.13		6.6	3.48	8.08	5.78						
				2.65	3.42	3.42		3.0	0.28	1.41	0.84		5.0	1.43	6.63	4.03						
				2.56	3.28	3.28		11.8	22.23	16.23	19.23		4.8	1.26	6.51	3.88						
				2.47	3.15	3.15		11.1	18.29	13.94	16.11		4.8	1.26	6.08	3.88						
				2.05	2.52	2.52		10.7	16.27	12.76	14.51		3.9	0.65	6.08	3.36						
				1.70	2.00	2.00		6.7	3.65	5.40	4.52		3.4	0.42	5.92	3.17						
								5.8	2.30	4.62	3.46		4.6	1.10	1.96	1.53						

Appendix 6.11 Size, Weight and Heavy Metal Content and Concentration of M. balthica.

L. (mm)	H. (mm)	Shell Wt. (mg)	Flesh Wt. (mg)	CF ^H	FES (ppm)	FEF (ppm)	FEFC (µg)	ZNS (ppm)	ZNF (ppm)	ZNFC (µg)	CUS (ppm)	CUF (ppm)	CUFC (µg)	PBS (ppm)	PBF (ppm)	PBFC (µg)	CDS (ppm)	CDF (ppm)	CDFC (µg)	
C4	10.2	8.3	79.49	5.336	9.33	285	2811	15.0	54	1382	7.4	33	676	3.6	70	155	0.8	12	47	0.2
	10.3	8.2	81.92	5.202	9.43	280	3570	18.6	76	1614	8.4	20	454	2.4	62	389	2.0	12	81	0.4
	8.5	6.6	37.16	3.120	10.85	404	3606	11.2	108	1066	3.3	40	401	1.2	89	248	0.8	14	80	0.2
	8.7	7.1	50.02	3.185	8.90	284	3755	12.0	170	1413	4.5	22	524	1.7	66	345	1.1	15	107	0.3
	7.9	6.5	29.99	3.277	11.93	315	4742	15.5	133	3242	10.6	28	525	1.7	83	496	1.6	20	143	0.5
	6.5	5.4	15.49	2.546	16.17	611	2498	6.3	186	1443	3.7	44	271	0.7	111	412	1.0	33	169	0.4
	7.4	6.0	19.22	3.159	14.63	557	2624	8.3	257	1369	4.3	29	456	1.4	105	617	1.9	24	136	0.4
B3	14.1	11.2	262.4	23.40	16.66	192	2411	56.4	22	607	14.2	18	368	8.6	63	99	2.3	9	22	0.5
	12.2	9.9	186.88	9.465	9.75	151	2980	28.2	31	610	5.8	12	367	3.5	48	193	1.8	7	39	0.4
	8.6	6.9	22.12	4.931	15.01	638	3295	16.2	123	1577	7.8	19	168	0.8	119	213	1.0	29	51	0.2
	9.2	7.2	24.50	5.962	15.97	415	3175	18.9	123	776	4.6	22	131	0.8	95	88	0.5	21	33	0.2
	7.8	6.1	15.39	4.353	19.18	638	3117	13.6	292	609	2.6	27	255	1.1	104	241	1.0	28	62	0.3
	6.9	5.5	10.86	2.837	17.05	756	5478	15.5	207	1339	3.8	39	293	0.8	97	458	1.3	31	130	0.4
	5.1	4.0	4.479	0.999	15.60	3150	15562	15.5	681	3455	3.4	62	280	0.3	463	1302	1.3	103	421	0.4

Where FES, FEF, FEFC = Iron: shell concⁿ, flesh concⁿ, flesh content, respectively;
 ZNS, ZNF, ZNFC = Zinc: " " " "
 CUS, CUF, CUFC = Copper: " " " "
 PBS, PBF, PBFC = Lead: " " " "
 CDS, CDF, CDFC = Cadmium: " " " "

Appendix 6.12 M. balthica Heavy-metal Analysis: (a) Linear Regression Equations of Shell and Flesh Concentration (ppm) with Height (mm), Condition Factor and Flesh and Shell Dry Weight (mg), (Abbreviations as Appendix 6.11).

Dep. Var. = b + S.E. Ind. Var. + a

Dep. Var.	Station C4 Animals					Station B3 Animals					Total Animals				
	a	b	S.E.	r	p	a	b	S.E.	r	p	a	b	S.E.	r	p
	Independent Variable: Height														
FES	1144.4	-109.7	30.6	-0.848	*	3047.5	-303.0	127.0	-0.730	n.s.	2427.7	-255.9	89.93	-0.635	*
ZNS	493.6	-51.4	17.6	-0.794	*	750.7	-74.33	23.35	-0.818	*	655.0	-67.81	16.63	-0.762	**
CUS	62.81	-4.65	3.01	-0.568	n.s.	68.29	-5.493	1.802	-0.806	*	67.59	-5.372	1.312	-0.763	**
PBS	194.1	-16.06	3.36	-0.906	**	424.6	-39.03	18.84	-0.680	n.s.	347.8	-33.31	11.79	-0.603	*
CDS	62.17	-6.328	1.451	-0.890	**	105.12	-9.989	3.644	-0.775	*	88.47	-8.891	2.620	-0.700	*
	Independent Variable: Height														
FEF	2473.7	130.8	322.4	0.178	n.s.	14366.0	-1270.6	615.2	-0.678	n.s.	11225.6	-986.2	435.7	-0.547	*
ZNF	2008.7	-52.6	298.1	-0.079	n.s.	3382.7	-289.5	131.7	-0.701	n.s.	3304.1	-260.4	113.2	-0.553	*
CUF	-105.9	84.17	35.31	0.729	n.s.	144.4	16.75	14.37	0.462	n.s.	222.1	20.82	22.40	0.259	n.s.
PBF	948.5	-82.69	51.34	-0.584	n.s.	1237.9	-119.5	54.68	-0.699	n.s.	1171.8	-112.7	35.08	-0.680	*
CDF	348.3	-34.84	8.500	-0.878	**	397.1	-39.79	18.08	-0.701	n.s.	381.2	-38.58	10.94	-0.713	*
	Independent Variable: Condition Factor														
FEF	4868.8	-128.9	111.3	-0.460	n.s.	4103.3	66.79	721.7	0.041	n.s.	2318.3	142.6	278.6	0.146	n.s.
ZNF	1526.5	10.38	114.2	0.041	n.s.	1117.3	10.54	159.2	0.030	n.s.	1823.7	-26.41	73.14	-0.104	n.s.
CUF	826.8	-30.53	14.25	-0.692	n.s.	412.4	-9.381	13.33	-0.300	n.s.	794.2	-31.24	8.726	-0.719	*
PBF	-4.569	33.16	19.12	0.613	n.s.	245.9	7.991	65.85	0.054	n.s.	212.0	12.01	25.66	0.134	n.s.
CDF	-35.996	12.49	3.857	0.823	*	50.76	3.691	21.81	0.075	n.s.	40.30	5.024	8.324	0.172	n.s.
	Independent Variable: Flesh Dry Weight														
FEF	3432.4	-16.30	319.9	-0.023	n.s.	7393.2	-302.9	244.0	-0.485	n.s.	5379.5	-201.7	166.0	-0.331	n.s.
ZNF	1805.1	-42.86	291.3	-0.066	n.s.	1813.2	-71.60	52.55	-0.520	n.s.	1877.2	-74.30	40.63	-0.467	n.s.
CUF	201.2	73.51	38.19	0.652	n.s.	220.2	6.178	4.368	0.512	n.s.	370.0	-0.150	7.840	-0.005	n.s.
PBF	618.7	-64.63	54.60	-0.468	n.s.	586.6	-29.11	21.90	-0.511	n.s.	522.6	-26.50	14.25	-0.473	n.s.
CDF	221.9	-30.62	10.62	-0.790	*	178.9	-9.513	7.304	-0.503	n.s.	157.3	-8.752	4.635	-0.479	n.s.
	Independent Variable: Shell Dry Weight														
FES	574.2	-4.097	1.399	-0.795	*	1206.1	-4.752	3.910	-0.477	n.s.	849.8	-3.836	2.671	-0.383	n.s.
ZNS	234.1	-2.090	0.676	-0.810	*	307.8	-1.283	0.787	-0.589	n.s.	246.2	-1.171	0.541	-0.530	n.s.
CUS	38.39	-0.168	0.125	-0.515	n.s.	35.23	-0.090	0.061	-0.553	n.s.	35.32	-0.095	0.042	-0.541	n.s.
PBS	111.67	-0.625	0.148	-0.889	**	186.2	-0.598	0.554	-0.434	n.s.	141.8	-0.489	0.370	-0.356	n.s.
CDS	29.26	-0.286	0.070	-0.833	*	45.18	-0.167	0.116	-0.540	n.s.	34.25	-0.143	0.081	-0.454	n.s.

Appendix 6.12 continued: (b) Logarithmic Regression Equations of Flesh and Shell Concentration (ppm) with Flesh and Shell Weight (mg), and Flesh Content (μg) with Flesh Weight (mg); (c) Exponential Regression Equations for Same Variables of Total Specimens Analysed, (Abbreviations as Appendix 6.11).

(b) Dep. Var. = $b + \text{S.E. Ind. Var.} + a$

Dep. Var.	Station C4 Animals				Station B3 Animals				Total Animals				
	b	S.E.	a	r	b	S.E.	a	r	b	S.E.	a	r	p
Log.FEF	0.063	0.366	3.483	0.076	n.s.	-0.580	0.131	4.021	-0.892	**	3.853	-0.921	**
Log.ZNF	Not Calculated,	p too high			n.s.	-0.561	0.168	3.409	-0.831	*	3.453	-0.727	**
Log.CUF	0.683	0.333	2.283	0.676	n.s.	0.080	0.174	2.343	0.200	n.s.	2.524	0.014	n.s.
Log.PBF	-0.836	0.430	3.006	-0.511	n.s.	-0.829	0.202	2.968	-0.878	**	2.994	-0.830	**
Log.CDF	-1.293	0.406	2.717	-0.819	*	-0.954	0.150	2.483	-0.943	**	2.534	-0.925	**
Log.FES	-0.462	0.100	3.299	-0.900	**	-0.631	0.106	3.652	-0.936	**	3.584	-0.921	**
Log.ZNS	-0.700	0.199	3.201	-0.843	*	-0.799	0.070	3.266	-0.981	**	3.271	-0.952	**
Log.CUS	-0.251	0.165	1.870	-0.563	n.s.	-0.315	0.083	1.859	-0.862	*	1.878	-0.754	**
Log.PBS	-0.330	0.050	2.433	-0.942	**	-0.399	0.122	2.615	-0.824	*	2.576	-0.829	**
Log.CDS	-0.559	0.073	2.124	-0.960	**	-0.554	0.083	2.182	-0.948	**	2.163	-0.945	**
Log.FEFC	1.063	0.366	0.483	0.792	*	0.420	0.131	1.021	0.819	*	0.853	0.748	**
Log.ZNFC	1.013	0.556	0.183	0.632	n.s.	0.438	0.168	0.409	0.760	*	0.453	0.641	*
Log.CUFC	1.683	0.333	-0.717	0.914	**	1.080	0.174	-0.657	0.941	**	-0.476	0.847	**
Log.PBFC	0.164	0.630	0.006	0.115	n.s.	0.171	0.202	-0.032	0.354	n.s.	-0.006	0.266	n.s.
Log.CDFC	-0.293	0.406	-0.283	-0.307	n.s.	0.046	0.150	-0.517	0.135	n.s.	-0.466	0.005	n.s.

(c)

$$\text{FEF} = \frac{7128.5}{\text{fdw}} 0.458 \pm 0.139 \quad \text{ZNF} = \frac{2837.9}{\text{fdw}} 0.559 \pm 0.152 \quad \text{CUF} = 334.2 \text{ fdw} 0.009 \pm 0.183 \quad \text{PBF} = \frac{986.3}{\text{fdw}} 0.844 \pm 0.164$$

$$\text{CDF} = \frac{342.0}{\text{fdw}} 0.998 \pm 0.118 \quad \text{FES} = \frac{3837.1}{\text{sw}} 0.615 \pm 0.075 \quad \text{ZNS} = \frac{1866.4}{\text{sw}} 0.773 \pm 0.072 \quad \text{CUS} = \frac{75.51}{\text{sw}} 0.291 \pm 0.073$$

$$\text{PBS} = \frac{494.3}{\text{sw}} 0.521 \pm 0.170 \quad \text{CDS} = \frac{145.5}{\text{sw}} 0.563 \pm 0.056 \quad \text{FEFC} = 7.128 \text{ fdw} 0.541 \pm 0.139 \quad \text{ZNFC} = 2.838 \text{ fdw} 0.441 \pm 0.152$$

$$\text{CUFC} = \frac{\text{fdw} 1.009 \pm 0.183}{2.992} \quad \text{PBFC} = \frac{\text{fdw} 0.156 \pm 0.163}{1.014} \quad \text{CDFC} = \frac{\text{fdw} 0.002 \pm 0.118}{2.924}$$

Appendix 7.1 Macrofaunal Species List for Torry Bay.

Coelenterata :

Peachia hastata.

Nemertea, Nematoda - unidentified.

Annelida :

Oligochaeta - unidentified.

Polychaeta :

Nereis virens
N. diversicolor
Nephtys hombergi
Arenicola marina
Phyllodoce maculata

Pectinaria (koreni)
Lanice conchilega
Scoloplos armiger
Polydora ciliata
+ other Spionid spp.

Mollusca :

Macoma balthica
Cerastoderma edule
Cardium lamarcki
Scrobicularia plana
Mya arenaria
M. truncata
Abra alba
A. nitida
A. prismatica
Retusa obtusa

Littorina littorea
L. littoralis
L. saxatilis
Nucella lapillus
Tellina tenuis
T. fabula
Limapontia depressa
M. edulis
Hydrobia ulvae

Arthropoda :

Corophium volutator
Ligia oceanica
Bathyporeia sp.
Crangon vulgaris
Carcinas maenas
Mysidacea

Gammarus sp.
Haustorius sp.
Eurydice sp.
Balanus balanoides
Pagurus bernhardus