METAZOAN DETRITIVORES AND UNDERWATER DECOMPOSITION PROCESSES OF DETACHED SUBLITTORAL MACROPHYTES

(One volume)

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A thesis submitted for the degree of Doctor of Philosophy in the University of Glasgow, following research conducted at the University Marine Biological Station, Millport.

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DECLARATION

I hereby declare that the work embodied in this thesis, for the degree of Doctor of Philosophy, is a result of my own work, which has not previously been submitted for a degree.

Signed............. ....

A.P. Bedford.

I cerify that this study has been performed under my supervision.

Signed......   ....

Dr. P.G. Moore.

SUMMARY

A great deal of attention has been paid to the importance of marine angiosperm litter to coastal marine ecosystems, its decomposition and the role played by associated metazoans in this process. In the Clyde Sea area, autumn storms result in large quantities of kelp being detached. This kelp forms large accumulations on the sea bed in certain areas. This project sought to examine the involvement of metazoans in the decomposition of this algal material.

The fauna associated with sea-bed accumulations of decomposing *Laminaria saccharina* has been studied by year-round SCUBA diving at two sites in the Clyde Sea Area. Seasonal changes in the densities of 64 species were recorded. The *Laminaria* carries with it to the sea-bed a large part of its normal fauna. Additional species settle onto the weed from the plankton whilst others migrate onto it from the surrounding sea-bed. Peak densities of associated species were recorded in autumn.

Three species were selected for detailed investigation in the laboratory concerning their importance in the decomposition process. These were the polychaete *Platynereis dumerilii*, the echinoid *Psammechinus miliaris* and the amphipod *Gammarus locusta*. The roles of both *Platynereis* and *Psammechinus* were examined by comparing their responses (behavioural choice, growth rates, absorption efficiencies of both carbon and protein, gut retention times and faecal output) to fresh and rotting kelp. *Platynereis* builds its parchment tubes preferentially on the fresh weed and feeds at the mouth of this tube. It grows faster on this diet. *Platynereis* is a detritivore which exploits the substratum directly. *Psammechinus*, although showing a behavioural preference for the rotting weed, grows equally well on either diet once it has reached a particular size. Substratum digestion is of paramount importance for *Psammechinus* when feeding on either diet.

Gammarus locusta's responses to the two diets (examined by comparing survival and growth rates in juveniles, fecundity, fertility and breeding behaviour in adults) illustrated the importance of the rotting weed (with its associated micro-organisms) to this organism. The relative importance of interactive cropping by these three detritivores was studied by *in situ* containment of different species combinations. The presence of *Gammarus* with *Psammechinus* resulted in less weed being lost than when *Psammechinus* was isolated. This is because *Gammarus* selectively crops rotting weed, retarding frond disintegration by microbes. *Platynereis* retards microbial colonization of frond tissues ruptured during its feeding by repeated cropping of the same region. These results reflect the situation found in the field with the complete detached weed fauna present. Litter bag experiments *in situ* showed that , except during the summer, weed is lost from sea-bed accumulations at a faster rate when macrofaunal animals are excluded. Macrofaunal cropping prevents the weed from decomposing very rapidly. Macroalgal decay thus differs profoundly from that of vascular plants. The ecological consequences of this difference are discussed.

INTRODUCTION

The importance of macrophyte productivity in coastal waters has been known since the work of Petersen and Boysen-Jensen (1911), though for various reasons (see Fenchel, 1972; Fenchel and Jørgensen, 1977) it has only been fully appreciated in recent years. Blinks (1955) commented on the high productivity of macroalgae and Ryther (1963) considered that there could be little doubt that productivity of the benthic macrophyte community plays an important, if not dominant, role in the organic production of coastal regions. More recently, Mann (1972) and Teal (1980) have stated that coastal macrophyte productivity may be up to 40X that of the open sea (see also Jupp and Drew, 1974; Johnston et al., 1977; Hatcher et al., 1977). Characteristically, herbivores graze only a small proportion of this production (Teal, 1962; Odum and de la Cruz, 1967; Heald, 1969; Kikuchi and Pérès, 1977; Velimirov et al., 1977), perhaps no more than 10% (Odum, Zieman and Heald, 1971; Mann, 1972). The remainder enters detrital food chains, which act as the main link between primary and secondary producers. In the following work, detritus is defined as all types of biogenic material in various stages of microbial decomposition which represent potential energy sources for consumer species (Darnell,1967).

Macrophyte detrital food chains have received a great deal of attention in recent years. Much of this work has concentrated on the highly productive, shallow water sea-grasses Zostera marina (L) (Adams and Angelovic , 1970; Rasmussen, 1973; Harrison and Mann, 1975; Tenore, 1975, 1977; Harrison, 1977; Thayer, 1977; Godshalk and Wetzel, 1978), Spartina spp. (Odum and de la Cruz, 1967; Gosselink and Kirby, 1974; de la Cruz, 1975; Haines, 1977; Lopez et al., 1977; Christian and Wetzel, 1978; Haines and Hanson, 1979) and Thalassia testudinum (König) (Zieman, 1968; Fenchel, 1970). Being vascular plants, the sea-grasses contain a combination of resistant tissues dominated by cellulose and lignin. Cell walls contain inhibitory chemicals (Valiela et al., 1979; Harrison and Chan, 1980;

Harrison, 1982) and unpalatable waxes cover the epidermis (Odum, Zieman and Heald, 1971). They are low in nitrogen (Tenore, 1977) and decomposition rates of dead material are generally slow, being in the order of 6-12 months (Odum and de la Cruz, 1967; Wood et al., 1969; Odum, Zieman and Heald, 1971; Tenore, 1977). This organic debris represents a non-circulating nutrient supply and a potential energy source for consumers which stabilizes pulsed inputs. It can also represent a 'bottle-neck' to energy flow (Macfadyen, 1961). So processes which mobilize this material are crucial for ecosystem functioning (Hargrave, 1975). In recent years, it has become clear that much of the organic detritus suspended in marine systems originates from the bottom (Ansell, 1974) and hence benthic detrital ecosystems are important also in the supply of nutrients to the water column. The living, highly structural, low nitogen sea-grasses with a C/N ratio above 22, are generally unpalatable to animals (Tenore, 1975). Such a C/N ratio is considered to be too high for adequate nutrition of herbivores and detritivores. Microbial activity not only degrades this material (but note Christian and Wetzel,1978), but also increases its nitrogen content (Hanson, 1982). Many authors have shown that detritivores, ingesting organic detritus, have very low assimilation efficiencies for the substratum but very high efficiencies for the associated epibionts found on aged material (Newell, 1965; Hargrave, 1970; Fenchel, 1970, 1972; Lopez et al., 1977; Harrison, 1977; Levinton, 1972 Kofoed, 1975). Kristensen (1972) noted that a number of marine invertebrate detritivores lacked the enzymes necessary to digest plant structural components. This work has led to the general view that they digest solely the detritus epibionts (Hargrave, 1977) though not all microbes are digested (Lopez and Levinton, 1978). This pattern is certainly exhibited by a large number of detritivores, but there are exceptions . Adams and Angelovic, (1970) showed that two estuarine invertebrates assimilated the substratum more efficiently than the associated bacteria. Kofoed (1975) found 34% assimilation efficiency for Hydrobia feeding on sterile barley hay. Yokoe and Yasumosa (1964) demonstrated cellulase activity in a number of marine invertebrates and work has shown that many invertebrates contain enzymes suitable for digesting other macrophyte structural components, such as alginic acid (Favron and Vaskovsky, 1971). Lewis and Whitney (1968) demonstrated cellulase activity in Nereis virens and further showed that the production of this enzyme was stimulated by passage of algae through the gut.

In temperate waters and on rocky coasts, large brown algae (Phaeophyta) are the dominat macrophytes. The fronds of these algae resemble moving belts of tissue (Mann, 1972) with erosion from the senescent, distal region of the frond being compensated for by meristematic activity at the frond base. In a single year, these fronds may replace their length up to five times (Mann, 1972), contributing large quantities of dissolved organic matter (D.O.M.) (Khailov and Burlakova, 1969; Brylinsky, 1977; Newell, et al., 1980; Linley et al., 1981; Lucas et al., 1981) and particualate detritus to the sediments and water column (Sutcliffe, 1972; Ansell, 1974; Webster et al., 1975; Johnston et al., 1977; Raine and Patching, 1980). In addition to this process, winter storms can detach large numbers of intact kelp plants (Kitching, 1937; Johnston, 1971; Field et al., 1977). These plants can either be washed ashore, fuelling littoral detrital food chains (Backlund, 1945; Velimirov et al., 1977; Griffiths and Stenton-Dozey, 1981; Koop, Newell and Lucas, 1982), or sink to the sea-bed below the photic zone, there to decay by routes as yet little known. On the sea-bed, large accumulations of this material can be produced by tidal currents acting over irregular topography. Algae lack the large quantities of strengthening materials found in angiosperms and tend to be high in nitrogen (Tenore, 1977; Godshalk and Wetzel, 1978). As a result, decomposition rates are relatively fast (Hunter, 1974; Tenore and Hanson, 1980; Griffiths and Stenton-Dozey, 1981), releasing large quantities of fine organic material into the sediments. This investigation examines the role of metazoan detritivores in the decomposition of these accumulations of coarse detritus and complements Benwell's (1980) study on meiofaunal nematodes.

Locally, such macrophyte accumulations are dominated by the alga *Laminaria saccharina* (L.) Lamour (Table 1). The decomposition of this alga has been studied. The regions of the frond which are actively growing exude large quantities of phenolic substances (Gelbstoff) which are toxic to saprophytic and pathogenic organisms and which also prevent larval settlement by sessile invertebrates (Sieburth, 1964, 1968; Sieburth and Conover, 1965; Sieburth and Jensen, 1969; Hornesly and Hide, 1974; Withers *et al*., 1975). The numbers of bacteria increase progressively along the algal frond (Laycock, 1974; Mazure and Field, 1980) corresponding to reduced exudation of these phenolic substances. When the weed is carried below the photic zone however, these protective mechanisms no longer function (Tenore and Rice, 1980) and bacteria and associated consumers flourish. The leaching rate of inhibitor plant-chemicals may be a rate-limiting factor in decomposition processes (Valiela *et al*., 1979). A sea-bed accumulation of detached weed can therefore be considered to consist of; (i) fresh or undamaged material from newly-detached weed and (ii) rotting weed displaying extensive signs of decay. *Psammechinus miliaris* (Gmelin), *Platynereis dumerilii* (Audouin and Milne-Edwards) and *Gammarus locusta* (L.) are the three most important macroscopic detritivores exploiting these accumulations locally. Their responses to these two diets have been investigated in detail both in the laboratory and in the field. Fresh material was presented as epibiont-free tissue derived from freshly detached *L. saccharina*. Rotting weed was identical material which had decomposed aphotically in running sea water until it lost its rigidity and turned green/brown in colour. The length of time this took varied with water temperature and therefore could not be standardized. The production of rotting weed in this way ensured that only micro-organisms involved in decomposition were present.

Table 1

Percentage composition of detached macrophyte beds found at four sites.

LOCH RANZA (13-20 metres)

	4.11.76	17.11.76	3.12.76	17.12.76	27.1.77	4.5.77	31.5.77	14.7.77
Laminaria saccharina	100	100	100	94	100	76	85	100
Others	-	-	-	6	-	24	15	-
	2.9.77	5.10.77	21.10.77	30.11.77	20.1.78	10.3.78		
Laminaria saccharina	100	100	100	95	100	100		
Others	-	-	-	5	-	-		

TOMONT END (16-24 metres)

	11.11.76	2.12.76	26.1.77	3.2.77	24.3.77	18.5.77	13.7.77	31.8.77	12.10.77
Laminaria saccharina	100	100	100	94	100	100	100	87	100
Others	-	-	-	6	-	-	-	13	-

KAMES BAY (24-33 metres)

	21.7.77	7.9.77	27.10.77	1.12.77	19.1.78	20.2.78	11.4.78
Laminaria saccharina	62	100	53	46	38	31	49
L. digitata	-	-	-	19	11	14	15
Desmarestia sp.	22	-	16	3	13	25	11
Chlorophyceae + Rhodophyceae	15	-	16	12	9	6	-
Fucaceae	-	-	15	19	29	22	-
Others	1	-	-	1	-	2	25

FAIRLIE CHANNEL (50-57 metres)

	21.7.77	7.9.77	27.10.77	1.12.77	19.1.78	20.2.78	11.4.78
Laminaria saccharina	100	100	100	74	29	32	100
Fucaceae	-	-	-	17	18	25	-
Desmarestia sp.	-	-	-	9	35	8	-
Ascophyllum nodosum	-	-	-	-	18	35	-

CHAPTER 1

THE ROLE OF PSAMMECHINUS MILIARIS (GMELIN)

INTRODUCTION.

Although sea urchins have varied diets,they are predominantly herbivorous (Lawrence, 1975). Some sea-urchins eat sea-grasses (Ogden, Brown and Salesky, 1973; Kikuchi and Pérez, 1973; Rasmussen, 1973; Greenway, 1976) but the majority appear to eat algal material, particularly large brown algae (Miller and Mann, 1973). This material is often loose-lying when ingested (Lees, 1970; Lowry and Pearce, 1973; Rosenthal *et al.*, 1974; Field *et al.*, 1977; Mattison *et al.*, 1977; Velimirov *et al.*, 1977). *Echinus esculentus* (L.) is the dominant grazer of attached sublittoral weeds (especially settled sporelings) locally, but in a few areas it also consumes significant amounts of detached *Laminaria saccharina* (L.) Lamour on the sea bed. *Psammechinus miliaris* (Gmelin) is found under stones in the littoral and immediate sublittoral zones and very young individuals have been recorded in the holdfasts of attached *Laminaria* spp. (Scarratt, 1961; Moore, 1971). These animals may eat part of the holdfast; promoting the detachment of plants in rough weather. This notwithstanding, in general, *Psammechinus* seems to consume little attached weed; indeed it is reported to have predilection for boring sponges and worms (Hancock, 1957) and bryozoans (Jensen, 1969; Rasmussen, 1973). In the Clyde Sea area, however, large numbers of *Psammechinus* are found consistently on sublittoral beds of detached kelp (see also Larsson, 1968); prompting the present investigation.

MATERIALS AND METHODS.

Psammechinus miliaris occurred locally in large numbers (<18 animals per 100 g^{-1} weed dry weight) on sublittoral beds of detached *L. saccharina*. The animals used in the laboratory experiments were collected from the littoral population at White Bay, Isle of Cumbrae (O.S. Grid ref. NS 178592, see Fig. 1). There, animals from a large size range are available (Fig. 15). They can be collected easily and transported to the laboratory with minimun disturbance. Prior to experimental use, animals were allowed to acclimatize to laboratory conditions for 14 days.

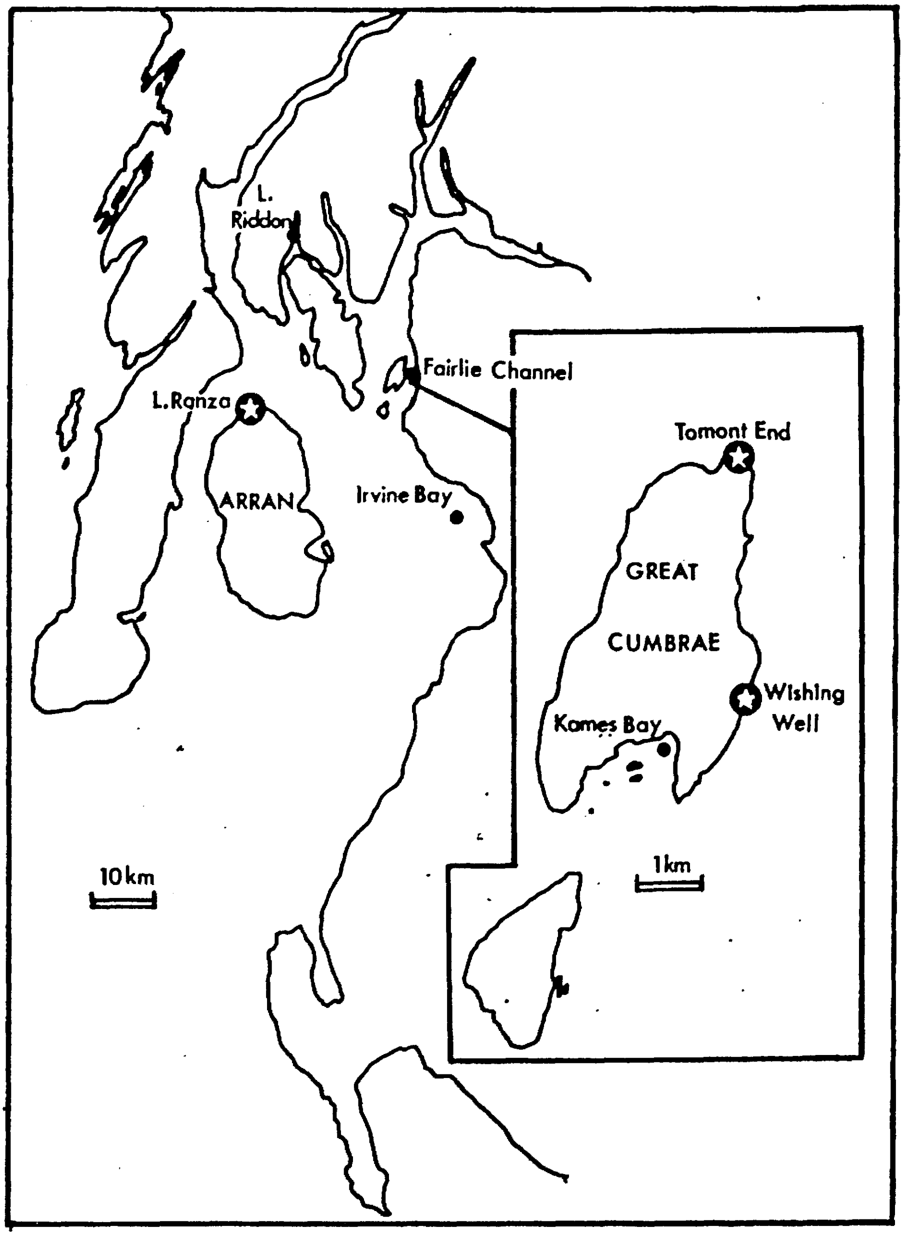
The gut retention time in echinoids appears to depend on food availability, being shorter when food is plentiful (Lewis, 1964; Lawrence, 1975). Animals starved after feeding have very long gut retention times (Lasker and Giese, 1954). Animals starved prior to experimental use show reduced absorption efficiencies for algal material (Lawrence, 1975). Since the purpose of this work was to establish the role which *Psammechinus* feeding played in the decomposition of detached weed, it was important that animals responded to weed presented in experiments in the same way as in the field. Animals in the field normally live amongst an abundant food supply: laboratory *Psammechinus* were thus always fed *ad libidum* both before and during experiments.

1) Comparison of growth rates

Psammechinus were divided into various size classes, each class having a range of test diameter of not more than 4 mm. Within each class, groups were fed on either fresh or rotting weed (as defined in the Introduction), and a third (control) group was starved. Each group contained not less than five individuals. Groups were kept separately in mesh cages (8 meshes/cm) under running seawater

Figure 1.

The Firth of Clyde, showing major collecting and experimental sites (✪) and other sites of detached weed accumulation (●).


L. Riddon
Fairlie Channel
L. Ranza
ARRAN
Irvine Bay
Tomont End
GREAT
CUMBRAE
Wishing Well
Kames Bay
1km
10km

(supplied from an open system). The animals were given an excess of their particular food. Fresh weed was changed every day to prevent any build-up of micro-organisms. Test diameter was measured to the nearest 0.05 mm using modified dial calipers. Pins mounted at right-angles to the jaws penetrated between the spines of the urchin, allowing accurate measurement of test diameter. These measurements were made every 35 days, the mean of three measurements being recorded for each animal. Intermittent handling did no damage to Psammechinus. From these data, the mean size and mean increase over the experimental period were determined for each size group.

2) Comparison of Gut Retention Times

Continuously-fed Psammechinus generally produces faeces in the sequence that materials were ingested; individual meals remaining as discrete units within the gut. Individual Psammechinus were initially fed Ulva lactuca (L.). Subsequent production of green faeces indicated that the gut contained no other material (confirmed by dissection of a number of individuals). The diet was then changed to either fresh or rotting kelp; the time at which feeding re-commenced being noted. Animals were observed every 30 minutes and the time at which the faecal colour changed was recorded. For a number of individuals the change in faeces colour was indistinct presumably due to some mixing of meals within the gut.

3) Comparison of Absorption Efficiencies (Protein and Organic Carbon)

Animals from the growth experiments were also used for this work. For the four size groups investigated, rotting or fresh weed was changed every day and the faeces produced in the previous 24 hours were collected. Before presentation to the urchins, the frond material was cut into 3 portions, the middle portion being kept as a reference sample. Both the collected faeces and the reference weed samples were rinsed in filtered seawater and dried. The weed was always cut across the width of the frond to include any lateral variations. The dried weed and faeces were thus always contaminated by small quantities of salt. Obviously this could have been prevented by use of a fresh water rinse, but it was observed with rotting weed, that most of the motile micro-organisms were lost when this was done. The loss of these organsisms would obviously affect any biological assays. No loss occurred, however, when filtered seawater was used. The effect of salt contamination would be the same for both weed and faecal samples. Thus, although the absolute values for the biochemical components of both weed and faeces are lower as a result of salt contamination, relative computations, e.g. the determination and comparison of absorption efficiencies for the two diets, remain unaffected. The rotting weed, although showing extensive signs of decay (e.g. general softening, large micro-organism populations etc.), did not disintegrate so readily that detrital contamination of the faeces resulted. The faeces and reference weed samples were oven dried (35°C, 7 days) before being transferred to an evacuated desiccator for a further week. The dry weights of faeces produced each day by the groups of Psammechinus were determined (see section 4) before these and the reference weed samples were ground in a mortar. Since this material absorbs moisture readily, it was redried in an evacuated desiccator for 7 days before analysis. The protein content of both weed and faeces were determined using Lowry's method (Lowry et al, 1951), standardized against Bovine Serum Albumen Fraction V (Kaushik and Hynes, 1968). Organic carbon was determined using Walkley and Black's wet oxidation method (Holme and McIntyre, 1971). The absorption efficiency (for protein or organic carbon) is defined as:-

$$\text{ABS. EFF. } (\%) = \frac{\text{Content of Weed} - \text{Content of Faeces}}{\text{Content of Weed}} \times 100$$

The absorption effeciency is thus determined by comparing the appropriate content of the weed with that of the faeces produced in the following 24 hours, after the gut retention time has been taken into account. The organic fraction of the weed and faeces corresponds to the cell wall component and there is a direct relationship between this fraction and the energy content of the weed (Fig. 2) as determined using a Phillipson oxygen microbomb calorimeter. Energy values have been left in original units (4.2 J≃1 cal; 4.2kJ≃1kcal).

4) Comparison of Dry Weight of Faeces Produced

The faeces consist principally of cell wall components, which also make up the bulk of the dry weight of intact weed. Thus the dry weight of faeces produced can be considered as an index of the weight of food eaten. The mean dry weight of faeces produced per animal per day was determined, for animals fed on fresh and rotting weed (see section 2), allowing comparative feeding rates to be assessed.

5) Choice Experiments

The food preference of Psammechinus was tested in two experimental arrangements: (a) in a closed system and (b) in an open system (Fig.3). In the former, a shallow plastic tray filled with aerated seawater was used. The fresh and rotting weeds were anchored at opposite ends of the tray. At the beginning of the experiment, Psammechinus (n=18 or 12) were placed at the centre of the tray and the experiment was enclosed in a light-proof cover. The position of the animals with respect to the two diets was recorded on successive days for 7-10 days. The water and faecal pellets were siphoned out every day and fresh seawater added. This prevented the build-up of metabolites and the development of anaerobic conditions, without disturbing the animals unduly. Lawrence (1975) considered that this form of experiment is most efficient for studying urchin food preferences.

Figure 2.

Energy content (kcal. g^{-1}) of kelp (<u>L. saccharina</u>) frond tissue related to organic carbon content (mg. mg^{-1} dry wt.) of fresh weed (○), faeces from <u>Psammechinus</u> fed fresh weed (□) and faeces of <u>Platynereis</u> fed fresh weed (●). Equation of line of best fit $y = 11.13x - 0.44$ ($r=0.95$, df. 25, $P<0.001$).

Note; units of energy retained as originally measured,

(1 Joule=2.38846×10^{-4} kcal.).

Equivalent equation for rotting weed; $y = 16.73x - 1.60$

($r=0.85$, df. 23, $P<0.001$).

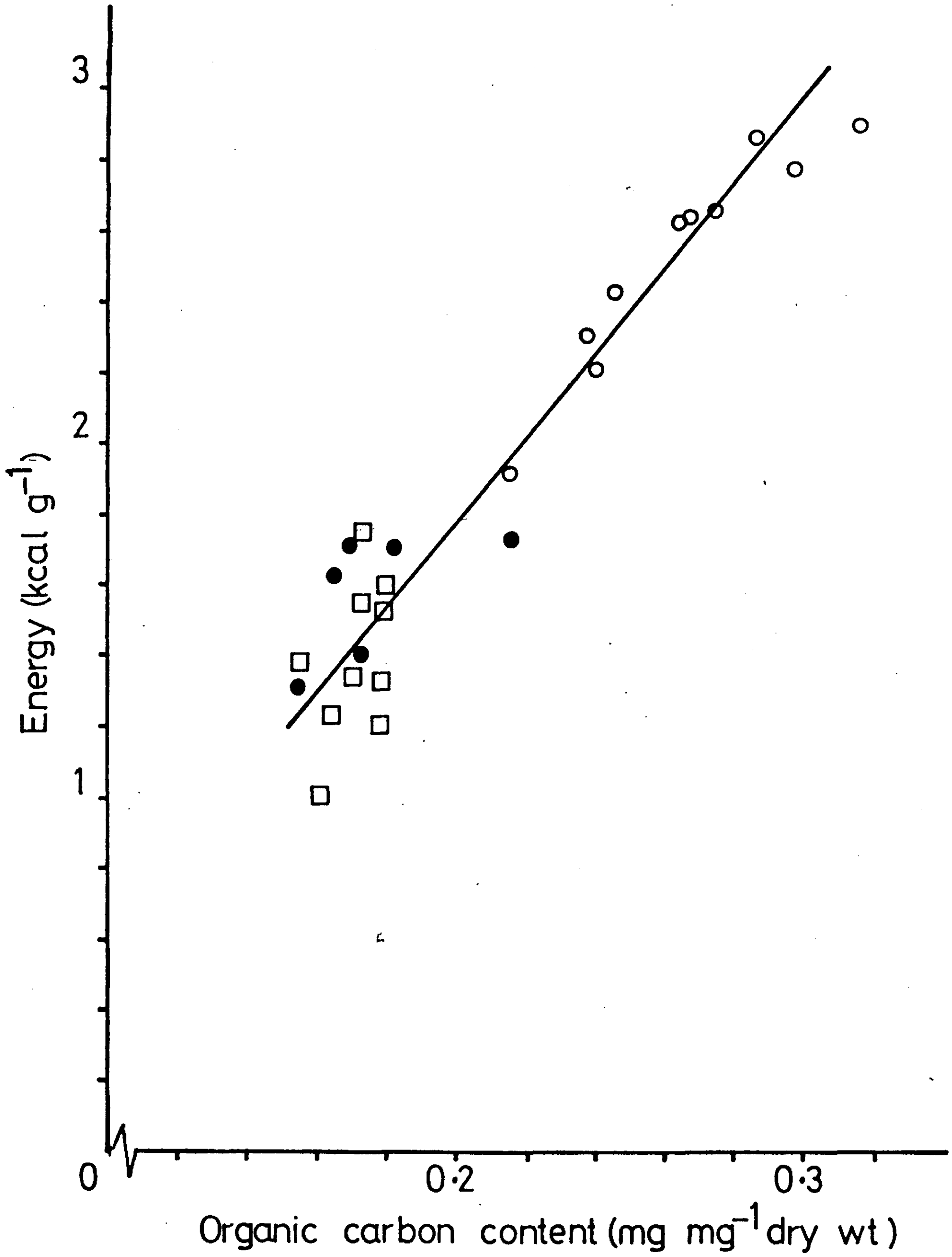

3
2
1
0
Energy (kcal g^{-1})
0·2
0·3
Organic carbon content (mg mg^{-1} dry wt)

Figure 3.

Choice chambers used in Psammechinus experiments, (a) closed system, (b) open system.

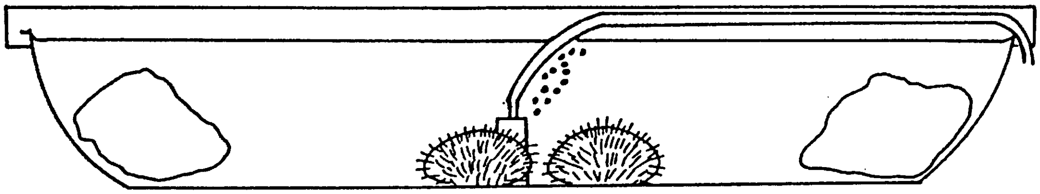
A = 'Y' tube,

B = container with mesh bag of one kelp type (contrasting kelp in identical apparatus leading to other Y-arm not shown),

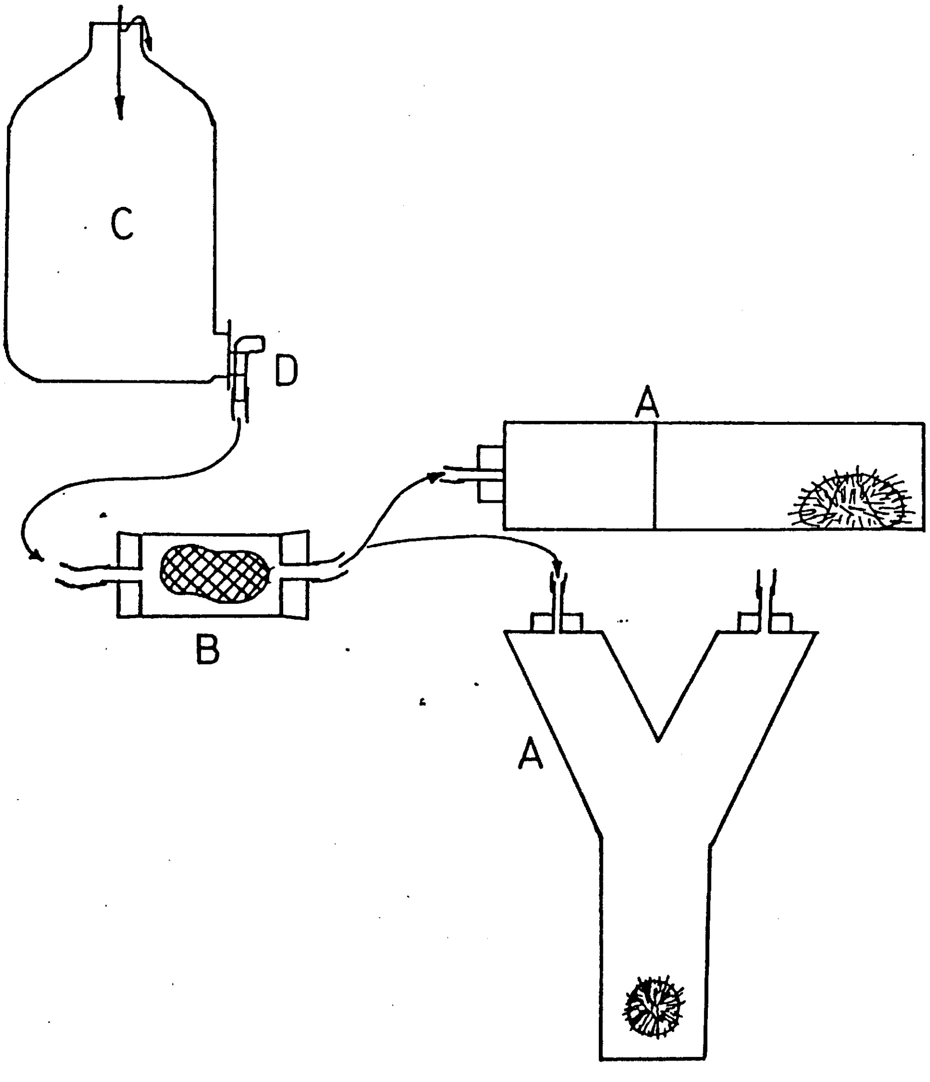
C = overflowing 5l aspirator giving constant head,

D = flow balancing tap.

(a)



(b)



In the open system, a 'Y' tube apparatus was used (Fig. 3b-A). The water flowing to the two arms passed through tubular containers (Fig. 3b-B) containing mesh bags of either fresh or rotting weed. The rate of flow was kept constant using two overflowing 5 l aspirators (Fig. 3b-C). The rates of flow were first balanced, with the aid of water-soluble dye, using two taps (Fig, 3b-D). The animals were placed in the mouth of the 'Y' and then the apparatus was enclosed in a light-proof cover. Movement of the animals with respect to each arm was inspected every 30 min.

6) The Decomposition of Psammechinus Faeces

Decomposing plant material is characterized by an initial rise in bacterial numbers, followed by a rise in the numbers of ciliates (Fenchel, 1970; Linley *et al.*, 1981). By examining changes in the ciliate populations of *Psammechinus* faeces with time, decomposition can be monitored. Fresh *Psammechinus* faeces were placed in plastic, fine mesh cylindrical containers "Toby-Teaboys" (5.5 cm, 4.5 cm. diam) (Aldridge Plastics Ltd., Staffs) and left in running seawater. At 2-3 day intervals, a faecal sample was removed and the ciliates extracted by mixing with 5% formalin. This resulted in the extraction of both the surface and the internal ciliates from the faeces. The faecal pellets were filtered-off using plankton netting (mesh size 0.1 mm) and oven dried at 35°C. The ciliates were counted over 50 micro-transects using the method described by Vollenweider (1971). The estimate of total ciliate density was expressed as numbers per mg. dry weight of faeces. Ciliates extracted by this technique retained their general body form; the cilia being readily visible. To give some indication of the impact of *Psammechinus* on decomposition rate, faecal decompostion was compared with, (i) intact *Laminaria saccharina* and (ii) *L. saccharina* which had been homogenized to a size equivalent to that of faecal pellets.

7) Comparison of the Size Structure of Populations of *P. miliaris* on Detached Weed Beds in the Field

The test diameters of *P. miliaris* randomly sampled from beds of detached weed at Loch Ranza -O.S. Grid ref. NR930510 (15m depth), Tomont End - NS181593 (20m), Kames Bay - NS171549 (20m) and Irvine Bay -lat, 55° 36'N: long. 4° 46'W (35m) (see introduction, Fig. 1) were measured to determine the structure of these populations. These animals were collected either by beam trawling (2m beam with 25 mm mesh) or by S.C.U.B.A. diving. These populations were compared (i) with the stable littoral population found at White Bay and (ii) with the population which developed on bags of kelp suspended 3m above the sea-bed at a depth of 20m, at the Wishing Well, Gt. Cumbrae, in July 1976 (Fig. 1). *P. miliaris* is not usually found at the Wishing Well, hence colonization of this weed must have occurred by the settlement of larvae. Thus, comparisons between these populations, aided by laboratory data on size-specific growth rates, would shed light on the age structure of *Psammechinus* populations and on the mode of colonization of detached weed beds by urchins.

RESULTS

1) Comparison of Growth Rates

The relationships between mean test diameter and growth increment for animals fed fresh or rotting weed are shown in Fig. 4 (a, b). The animals fed rotting weed showed a significant negative relationship with size ($r= 0.59$, df. 29, $P<0.001$)., with younger individuals increasing their test diameters at a faster rate than older urchins. The animals fed fresh weed showed no size relationship ($r=0.22$, df.29, $P<0.05$). Considerable variation was shown, however, in both trials. These data are a summary of information collected at all times of year and this variation can be attributed largely to seasonal effects. Seasonal variation is illustrated in Fig. 5 showing the mean 35 day increases in test diameter for 16 mm urchins over 12 months. The data for each particular 35 day period are plotted on the last day of that period. Clearly, faster growth occurred in June-August with little or no growth being made during December-February, irrespective of diet. These animals spawned in June-July. No growth was observed in the control animals, which died in October. For each size class, growth rate data are available for animals fed either diet over identical periods of time. It can be seen from Fig. 5 that animals on both diets are subject to identical seasonal effects. Thus, by dividing the mean increases in weight achieved on rotting weed by the corresponding increases achieved on fresh weed, we obtain a true dietary response comparison which is independent of seasonal effects. These growth ratios are shown plotted against the mean test diameter for the corresponding size class in Fig. 6. A ratio of unity indicates that the two diets promoted identical growth rates. The results show clearly that rotting weed promoted much faster growth rates in younger individuals than did fresh weed. For older individuals (>14 mm diam.)

Figure 4.

The relationships between mean test diameter of *Psammechinus* and mean growth increment (mm) over 35 day intervals irrespective of time of year, for animals fed rotting and fresh *L.saccharina*.

Equation for line of best fit (rotting); $y = 1.76 - 0.04x$

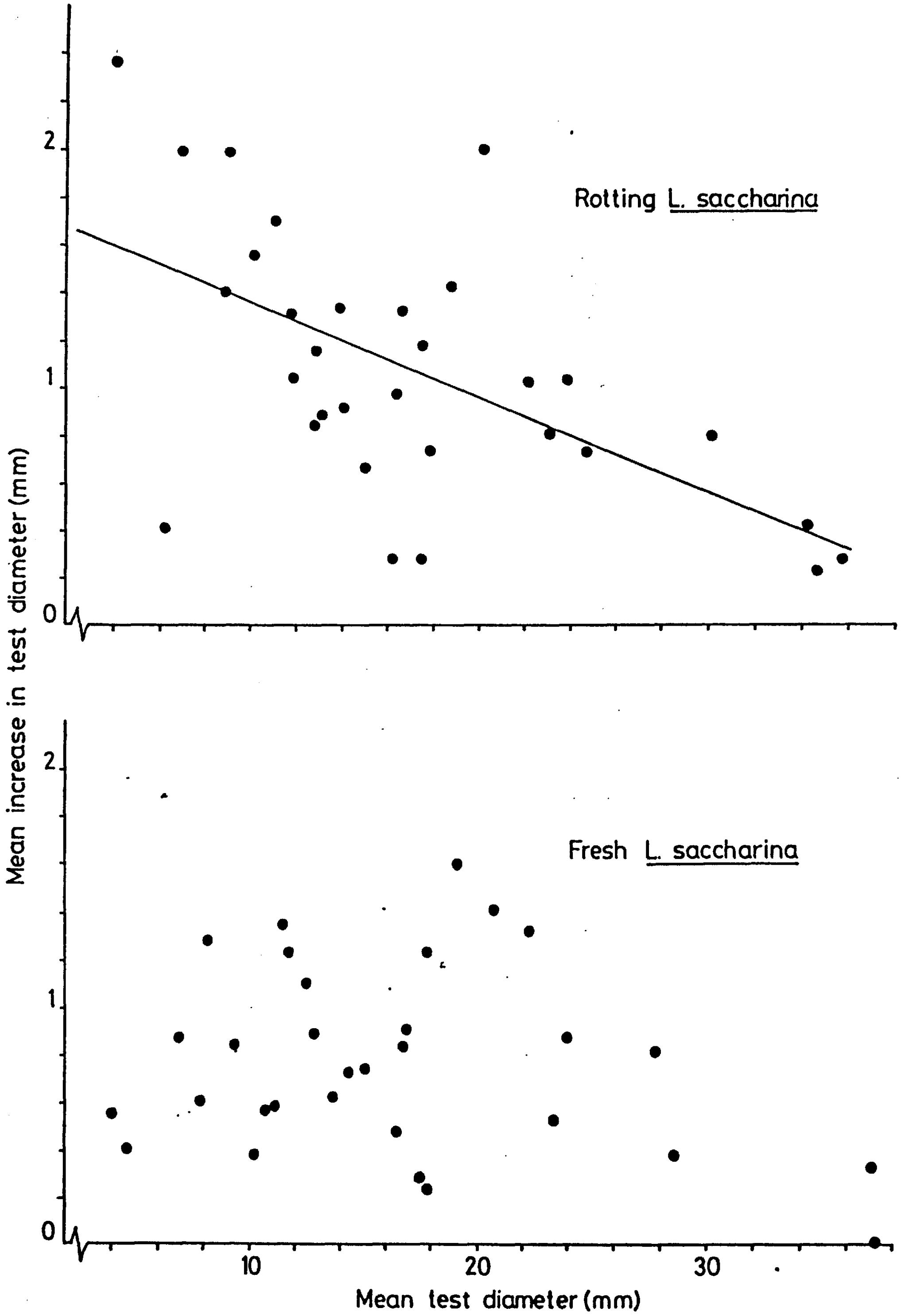

Rotting L. saccharina
Fresh L. saccharina
0
1
2
0
1
2
10
20
30
Mean increase in test diameter (mm)
Mean test diameter (mm)

Figure 5.

Seasonal variation in mean growth increment (mm) over 35 day intervals for _Psammechinus_ of 16 mm test diameter, fed either rotting (○) or fresh (●) _L. saccharina_ or starved (☐).

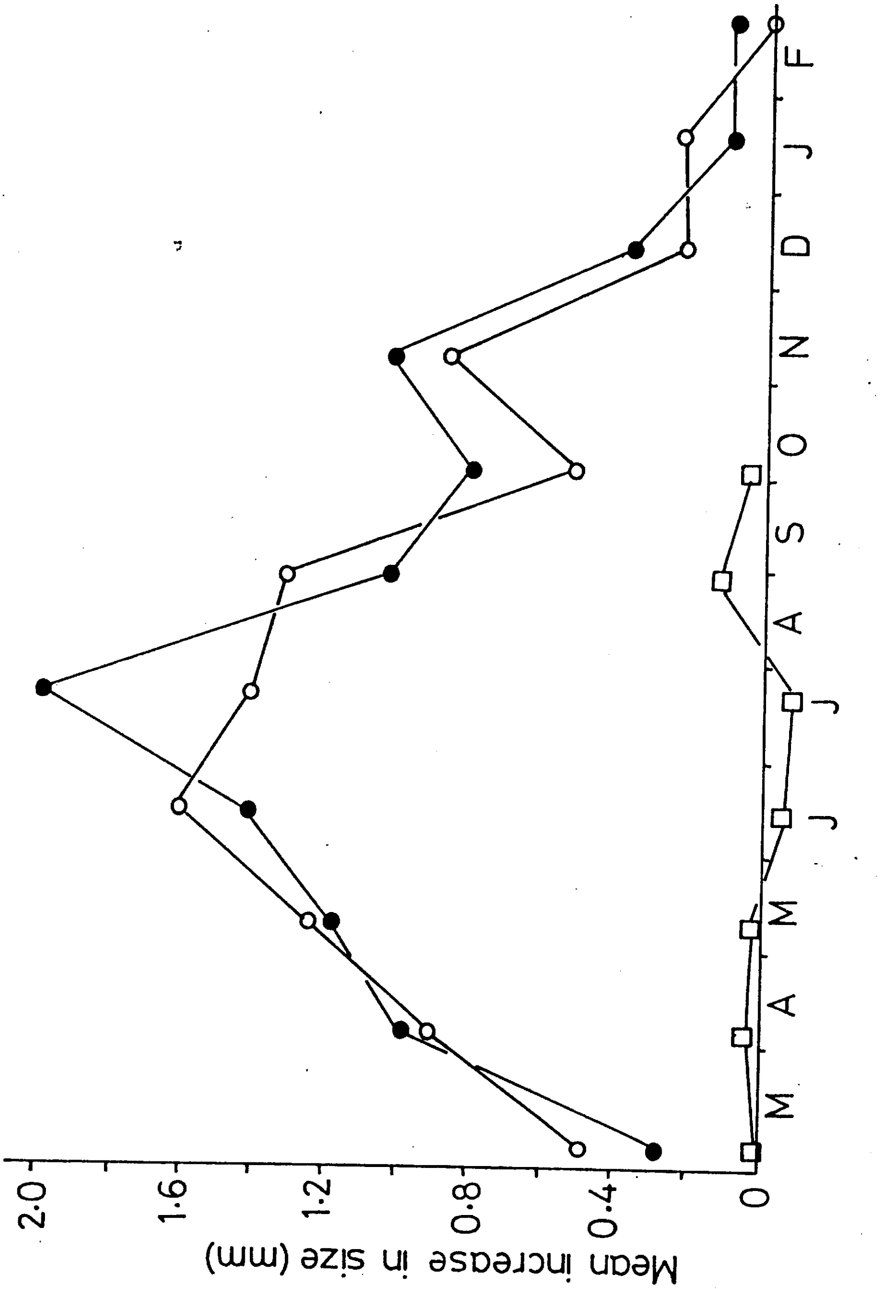
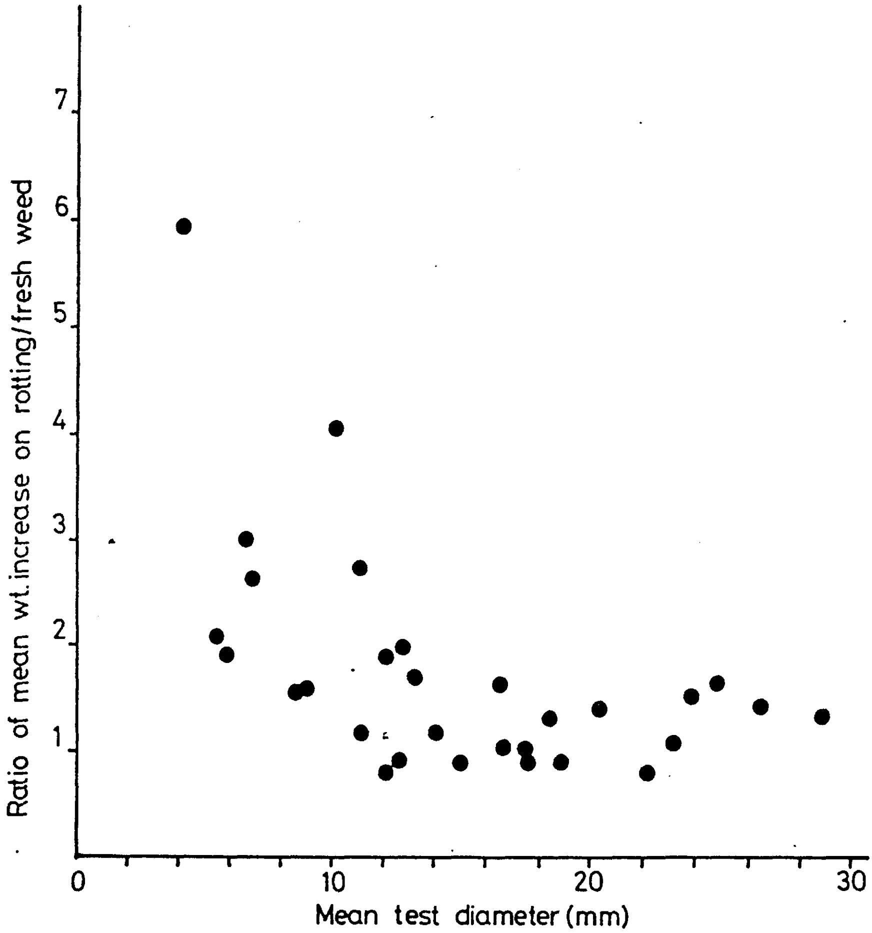

Mean increase in size (mm)
0
0·4
0·8
1·2
1·6
2·0
M
A
M
J
J
A
S
O
N
D
J
F

Figure 6.

Ratio of growth on rotting kelp: fresh kelp as a function of body size within corresponding size classes in _Psammechinus_.


Ratio of mean wt. increase on rotting/fresh weed
7
6
5
4
3
2
1
0
10
20
30
Mean test diameter (mm)

however, there was little or no difference.

2) Comparison of Gut Retention Times (G. R.T.)

Psammechinus fed on fresh weed had significantly longer gut retention times (16.26h ± 0.18 (S.E.), n=40) than animals fed on rotting weed (11.94h ± 0.12, n=16). (note: in some individuals, faecal colour change was gradual, not abrupt. The minimum value for these animals has been included in the calculation of means. G.R.T. values quoted are thus minimum values).

3) Comparison of Absorption Efficiencies

(a) Protein. The mean protein values for fresh (40. 3 ± 1.28 $mg.g^{-1}$ dry wt. (S.E.), n=74) and rotting weed (39.8 ± 1.42, n=74) used in these experiments were compared and found to be not significantly different ($P > 0.05$). The protein absorption efficiencies for animals (size classes combined) on the two diets were found to be significantly different (two tailed Mann-Whitney U test, z=10.06, $P < 0.00006$), mean values being 90.3% and 61.7% for animals feeding on the fresh and rotting weed respectively. The relationships between the absorption efficiency and the protein content of the ingested weed were examined for animals fed either fresh or rotting kelp; the results are shown in Figs. 7(A-D) and 8(A-D) respectively. The data for each size class (mean test diameter indicated) are presented separately. There was a significant positive relationship between these parameters for animals from all size classes feeding on fresh weed ((A) r=0.74, df.21, $P < 0.001$; (B) r=0.57, df.20, $P < 0.01$; (C) r=0.88, df.30, $P < 0.001$; (D) r=0.41, df.16, $P < 0.05$). Clearly though, the relationship exhibited by the smaller animals (A) differed markedly from groups B-D. Covariance analysis (Snedecor and Cochran, 1967) was used to compare the regression lines fitted to these data (Table 2). The regression line for Group A differed significantly in slope and elevation

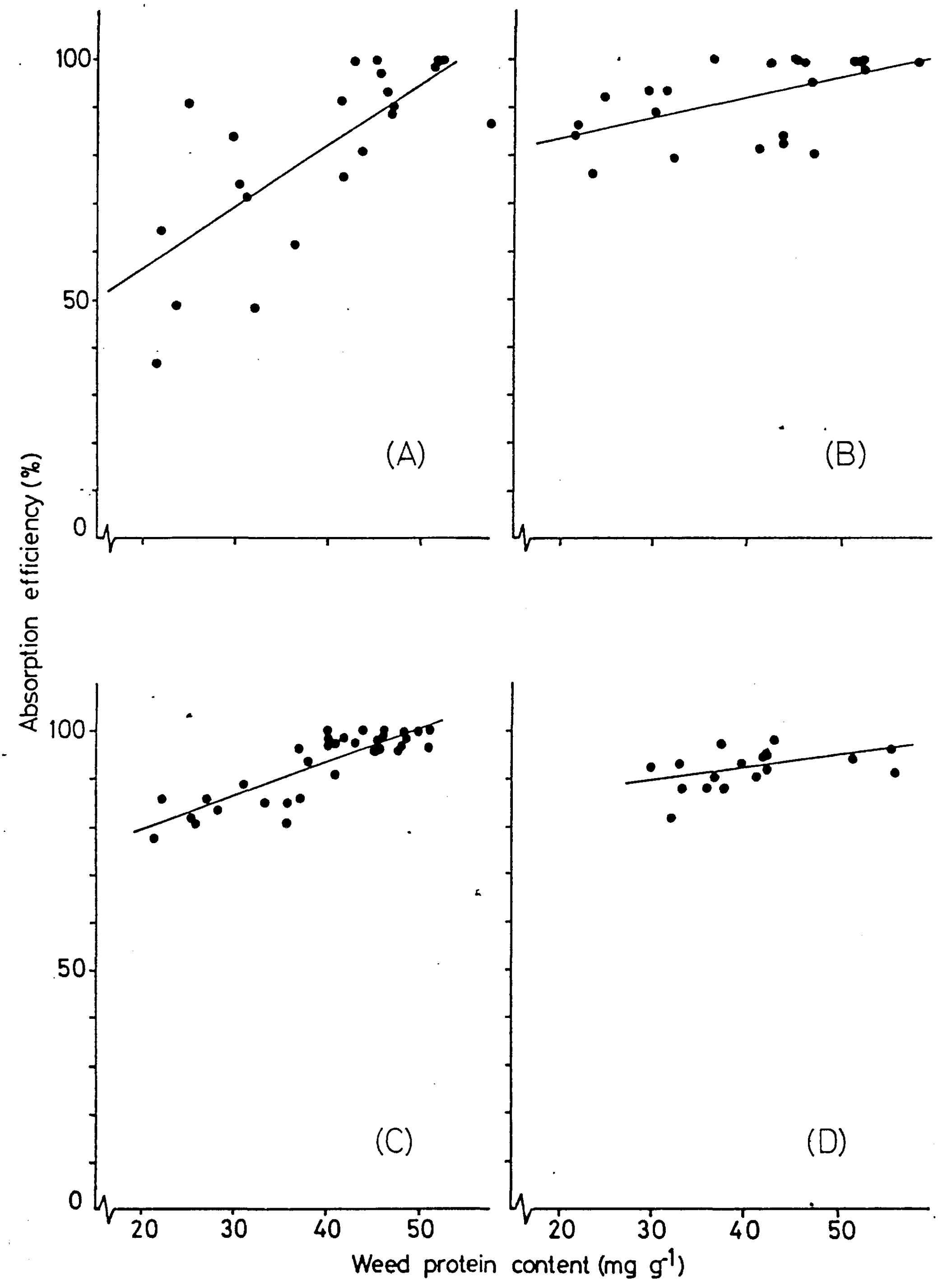
Figure 7.

Absorption efficiency (%) as a function of weed protein content ($mg.g^{-1}$ dry wt.) in fresh L. saccharina for Psammechinus from four size classes (A-D). Mean test diameters are: (A) 8.0 mm; (B) 12.9 mm; (C) 20.0 mm; (D) 27.9 mm.

Equations for lines of best fit:

(A) $y = 31.22 + 1.27x$, (B) $y = 75.6 + 0.42x$,

(C) $y = 64.95 + 0.71x$, (D) $y = 82.17 + 0.26x$.



Absorption efficiency (%)
100
50
0
(A)
(B)
(C)
(D)
20
30
40
50
Weed protein content (mg g^{-1})

Table 2

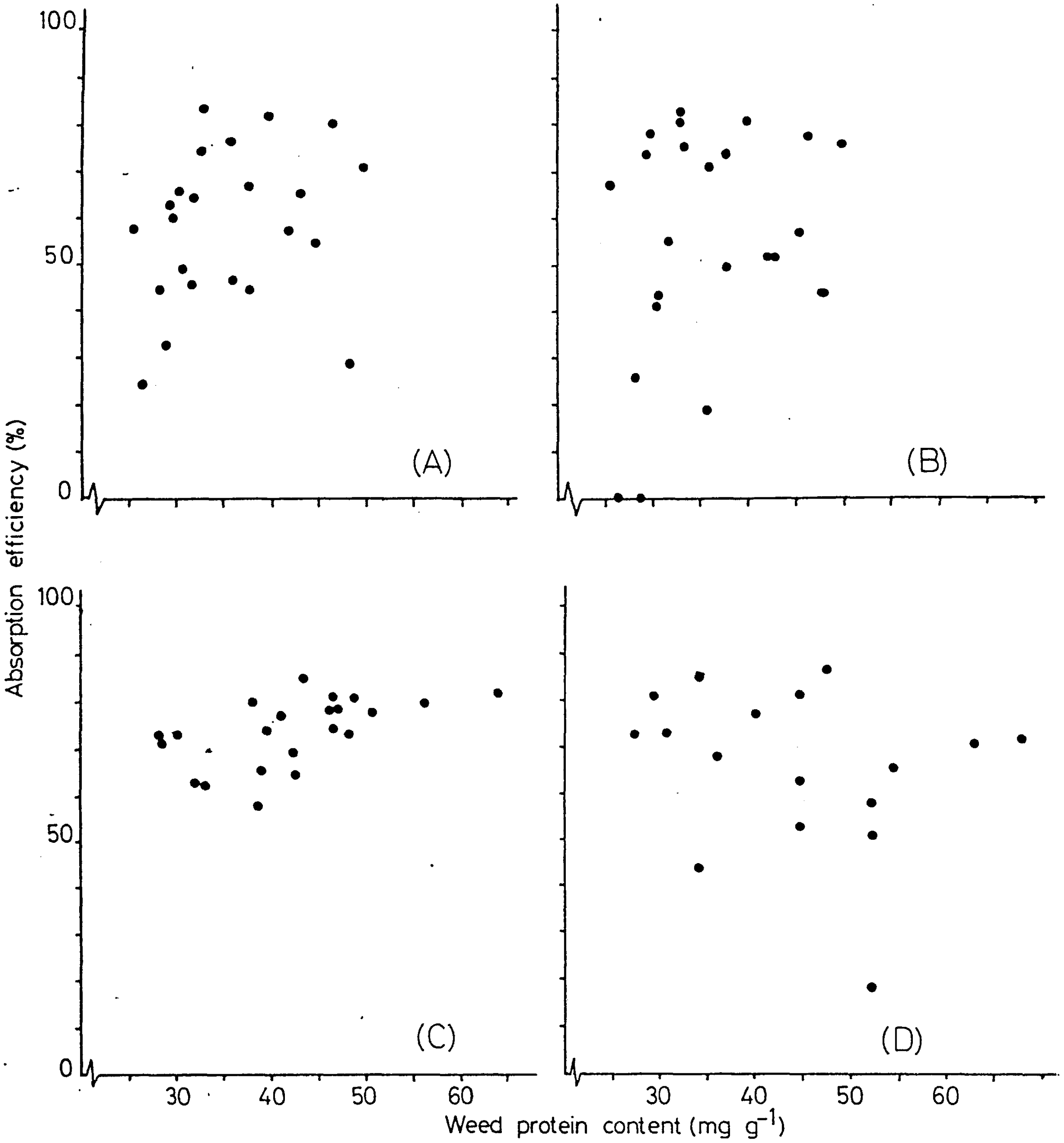
Covariance analysis of regression lines A-D in Fig. 7.

ns. = $P > 0.05$, $^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

	Slope		Elevation	
Comparisons	F_1	df.	F_2	df
A v B	8.80 **	1,41	9.33 **	1,42
A v C	5.33 **	1,51	20.41 ***	1,52
A v D	7.16 *	1,37	7.86 **	1,38
B v C	3.92 ns	1,50	0.30 ns	1,51
B v D	0.57 ns	1,36	0.01 ns	1,37
C c D	11.40 **	1,46	1.11 ns	1,47

Figure 8.

Absorption efficiency (%) as a function of weed protein content (mg g^{-1} dry wt.) in rotting L. saccharina for Psammechinus from four size classes (A-D). Mean test diameters are: (A) 9.0 mm; (B) 12.9 mm; (C) 19.4 mm; (D) 30.1 mm.


100
50
0
(A)
(B)
(C)
(D)
Absorption efficiency (%)
30
40
50
60
Weed protein content (mg g^{-1})

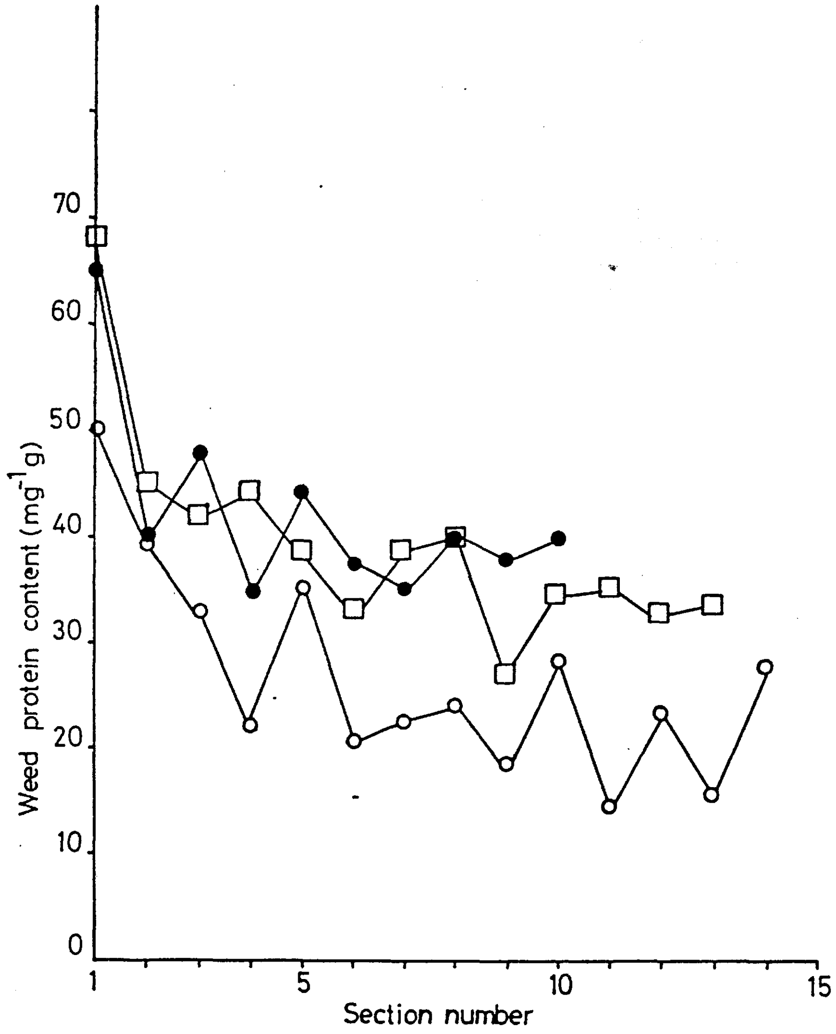
from those of the other three groups. Although the slope of line C differed significantly from line D, there was no significant difference between the elevation of lines B,C or D. Thus, within the natural range of protein values, there was little difference between the three larger size groups, which are all generally efficient protein digesters. The very young individuals (Group A), however, can only digest the high protein weeds efficiently. Only one group (C) of animals feeding on rotting weed showed a significant relationship ($r=0.61$, df.20, $P<0.01$) between protein absorption efficiency and protein content of ingested weed.

The protein content of a fresh Laminaria saccharina frond varies along its length. Fig. 9 shows data for 3 fronds, cut into 8 cm. sections, with position 1 corresponding with the meristem region at the base of the frond. The low protein material, which young Psammechinus cannot digest effeciently comes from the older, tougher material away from the meristem.

(b) Organic Carbon. The mean organic carbon value for rotting weed (239.1 ± 3.12 (S.E.) $mg.g^{-1}$ dry wt. n=67) was found to be significantly ($P<0.001$) lower than that for fresh weed (266.9 ± 2.82, n=67). The organic carbon absorption efficiencies were also found to be significantly different (two tailed Mann-Whitney U test, z=7.59, $P<0.00006$), for animals feeding on the fresh (mean 39.3%) and rotting weed (mean 21.2%) respectively. These differences, however, may be due simply to the changed chemical composition of rotting weed. The relationship between organic carbon absorption efficiency and organic carbon content of ingested weed is illustrated in Fig. 10 for animals fed both diets. These composite data relate to animals of all four size classes. There was a significant ($P<0.001$) positive relationship between these two parameters in animals fed either diet (r (fresh)=0.62, df. 43; r (rotting)=0.78, df.49). Covariance analysis showed that

Figure 9.

Variation in protein content of 3 fresh L. saccharina fronds ($mg. g^{-1}$ dry wt.) with position along the frond. Section 1 corresponds with basal meristem: subsequent sections are at 8 cm. intervals.



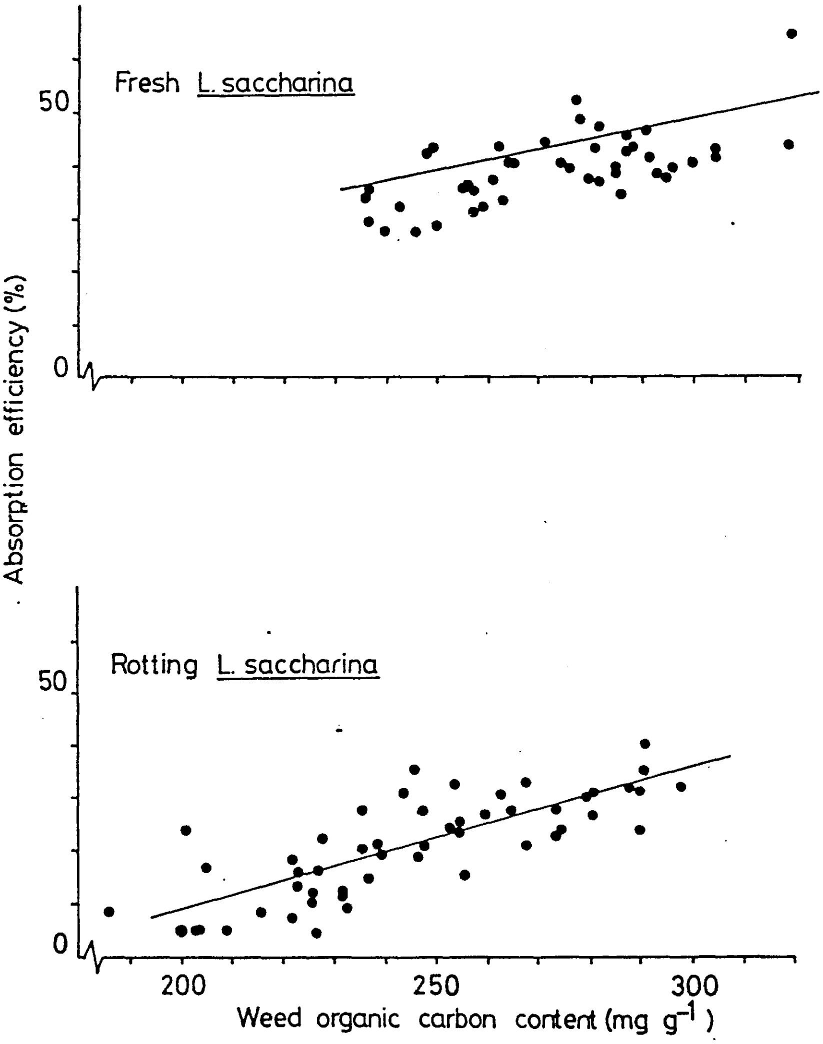
Weed protein content (mg^{-1}g)
0
10
20
30
40
50
60
70
1
5
10
15
Section number

Figure 10.

Absorption efficiency (%) in Psammechinus as a function of weed organic carbon content (mg.g^{-1} dry wt.) in fresh and rotting L. saccharina.

Equations of lines of best fit:

fresh, $y = -13.90 + 0.20x$;   rotting, $y = -43.40 + 0.26x$.


Fresh L. saccharina
Rotting L. saccharina
Absorption efficiency (%)
50
0
50
0
200
250
300
Weed organic carbon content (mg g⁻¹)

although these regression lines did not differ signifcantly in slope (F_1=2.00, df.1,92, $P>0.05$), they did differ significantly in elevation (F_2=71.66, df.1,93, $P<0.001$). Thus, animals feeding on fresh weed digested organic carbon more efficiently.

4) Comparison of Faecal Output Rate

Fig. 11 illustrates the relationship between the rate of faecal output of individual *Psammechinus* and body size. Faecal output rate was positively correlated with test diameter in animals fed either rotting (r=0.93, df.10) or fresh (r=0.93, df.10) weed ($P<0.001$). Covariance analysis showed that these regression lines differed significantly in both slope (F_1=6.829, df.1,20, $P<0.025$), and elevation (F_2=5.133, df.1,21, $P<0.05$), with standard-sized animals fed rotting weed producing larger quantities of faeces. Thus, *Psammechinus* feeding on rotting weed ingested more food than did counterparts fed fresh weed.

5) Choice Experiments

(a) The results obtained using the closed system are shown in Fig. 12 (a-f). Here, the percentages of animals found on rotting weed on successive days have been illustrated for six trials (χ^2 values calculated from raw data). The percentage of urchins found on rotting weed rose quickly and stabilized at a high level (approx. 80%) on all occasions. In this experiment, *Psammechinus* consistently displayed a significant ($P<0.05$) preference for rotting weed.

(b) The results obtained using the 'Y' tube arrangement are presented in Table 3. Here, however, *Psammechinus* showed no preference for weed type (χ^2=0.02, df.1, $P>0.05$); the significant movement (χ^2=4.03, df.1, $P<0.05$) being downcurrent, away from the stimuli. Current speed was not recorded but was cerainly not such as would impede urchin movement upstream. Food choice thus seems to be the result of a kinesis rather than a taxis.

Figure 11.

Rate of faecal output by individual Psammechinus as a function of body size for animals fed either rotting (○) or fresh (●) L. saccharina.

Equations for lines of best fit;

fresh, $y = -3.76 + 0.68x$; rotting, $y = -6.99 + 1.09x$.

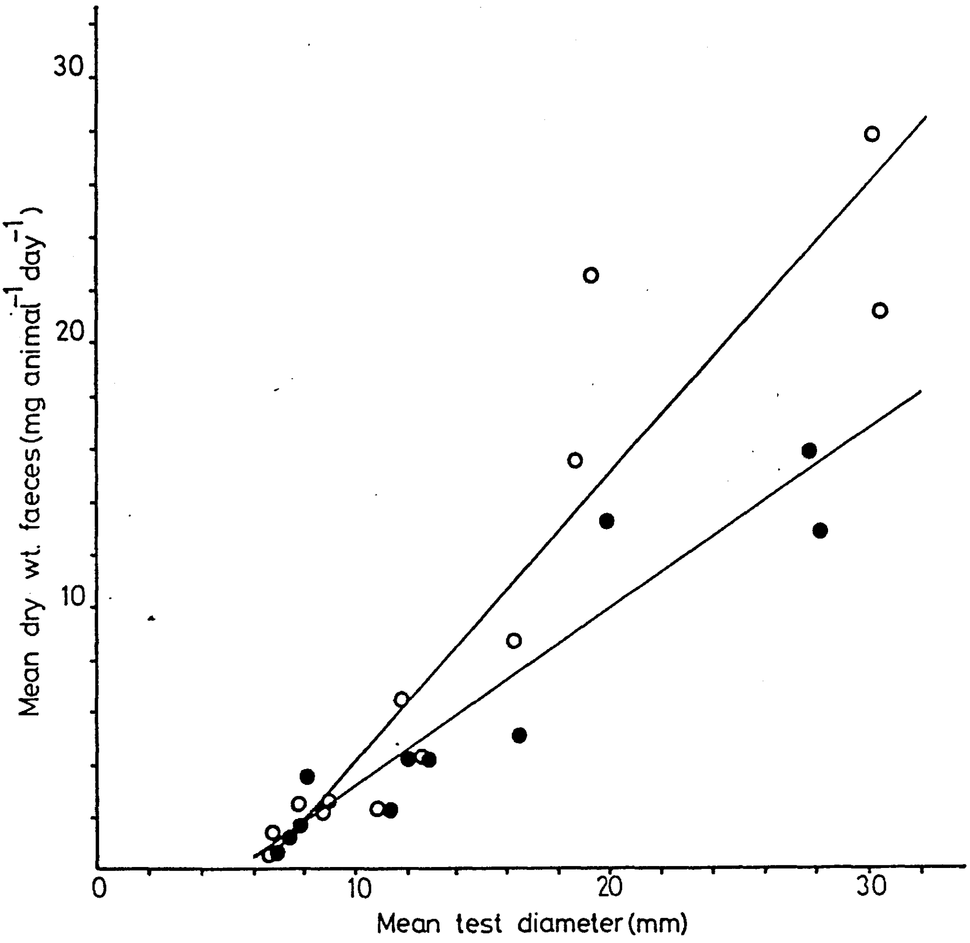

Mean dry wt. faeces (mg animal^{-1} day^{-1})
30
20
10
0
10
20
30
Mean test diameter (mm)

Figure 12.

Closed-system (max. duration, 10 days) choice experiment data for Psammechinus given a choice of fresh vs. rotting weed. Six trials (a-f), no. of animals = 18 (a,b,c) or 12 (d,e,f).

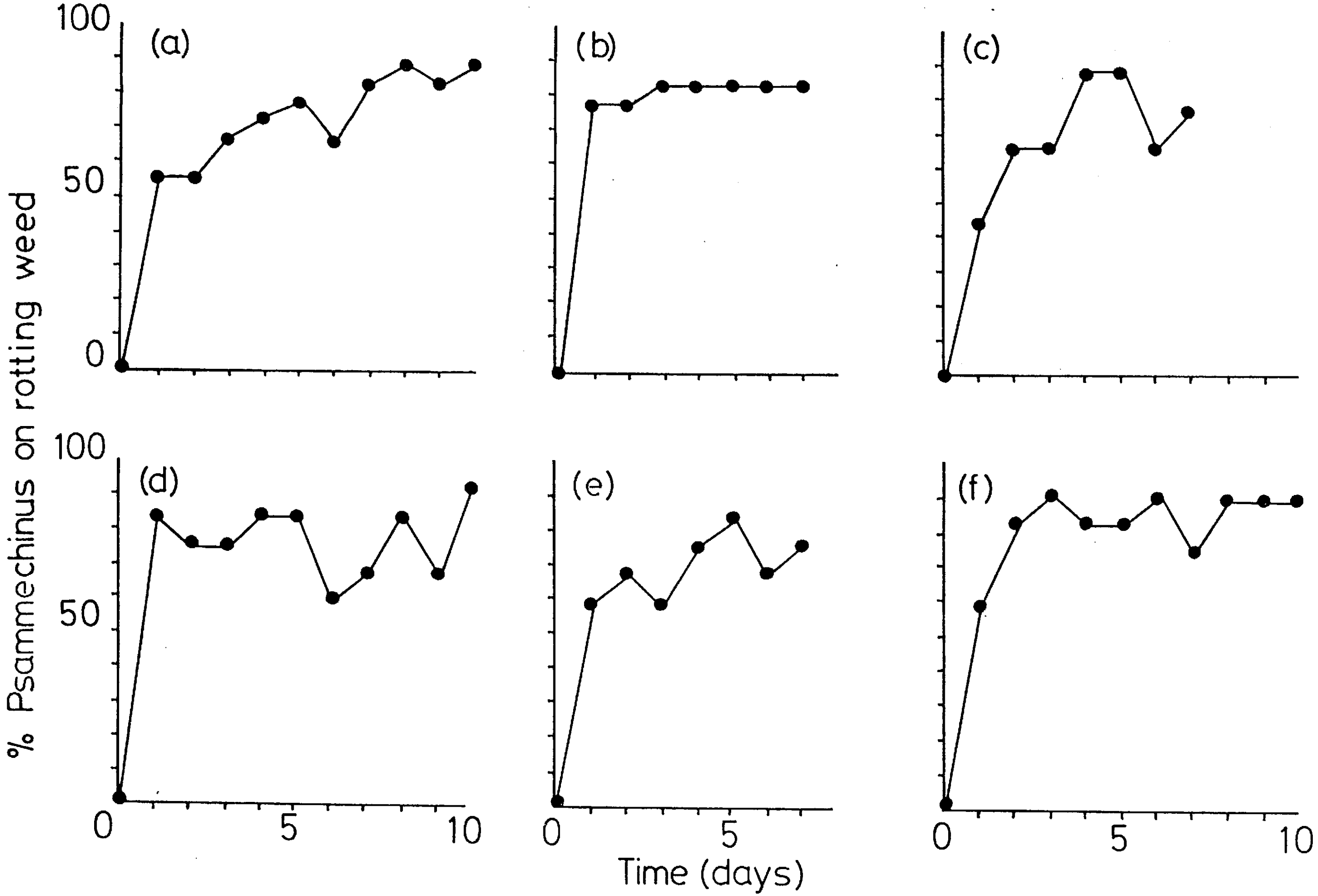

% Psammechinus on rotting weed
100
50
0
100
50
(a)
(b)
(c)
(d)
(e)
(f)
0
5
10
0
5
0
5
10
Time (days)

Table 3.

Open-system (Y-tube) choice experiment data for *Psammechinus* given a choice between fresh and rotting weed.

Trial	Number of animals tested	Number moving towards rotting weed	Number moving towards fresh weed	Number moving downstream
1	30	6	7	17
2	30	7	5	18
3	30	4	4	22
4	30	7	9	14

6) The Decomposition of Psammechinus Faeces

The changes in ciliate numbers with time found for the three experimental substrata are illustrated in Figs. 13 and 14. The population peak for Psammechinus faeces occurred after approximately the same length of time (c. 10 days) as that for homogenized L. saccharina. Both these substrata reached peak ciliate densities before the intact weed, indicating the importance of surface area and D.O.M. to microbial decomposition. The peak ciliate number found on Psammechinus faeces, however, was much smaller than that on homogenized weed and, presumably, also on intact weed. There were, however, large differences between the actual population sizes found on the same substratum from one trial to another, The two trials reported were carried out at different times of the year: November 1976 (Fig. 13) and March 1977 (Fig, 14), when the mean perentage dry weights of living L. saccharina were very different (16.9% (Nov.) and 4.9% (March)). This difference in tissue density may, at least in part, account for the difference in ciliate carrying capacity observed between trials.

7). Comparison of the Size Structure of Field Populations of P. miliaris on Detached Weed Beds

Size-frequency histograms for the various field populations of Psammechinus are shown in Fig. 15. The population which developed on suspended bags of weed at the Wishing Well had a size range of 2-13 mm. These individuals can only have settled from the plankton within the period of exposure and so they must have been less than one year old. The populations at Tomont End and Loch Ranza had similar size ranges (1-9 mm.), but much wider size ranges were found at Kames Bay (3-28 mm.) and Irvine Bay (4-20 mm.). The structure of these populations resembled more closely that of the stable, littoral population found at White Bay (size range, 8-35 mm.).

Figure 13.

Population density changes with time of ciliated Protozoa on (a) Psammechinus faeces (□-□), (b) intact L. saccharina (●—●) and (c) homogenized L. saccharina (○—○) (Nov.-Dec. 1976).

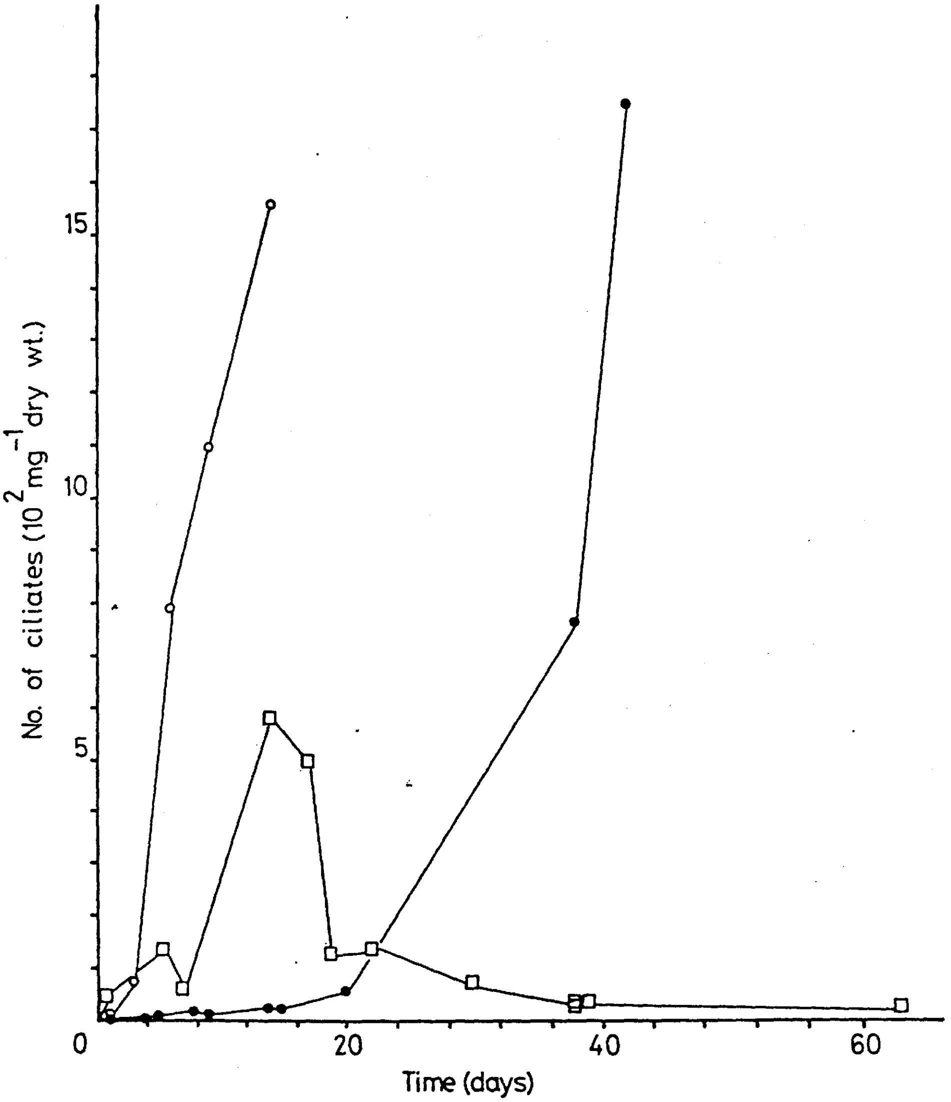
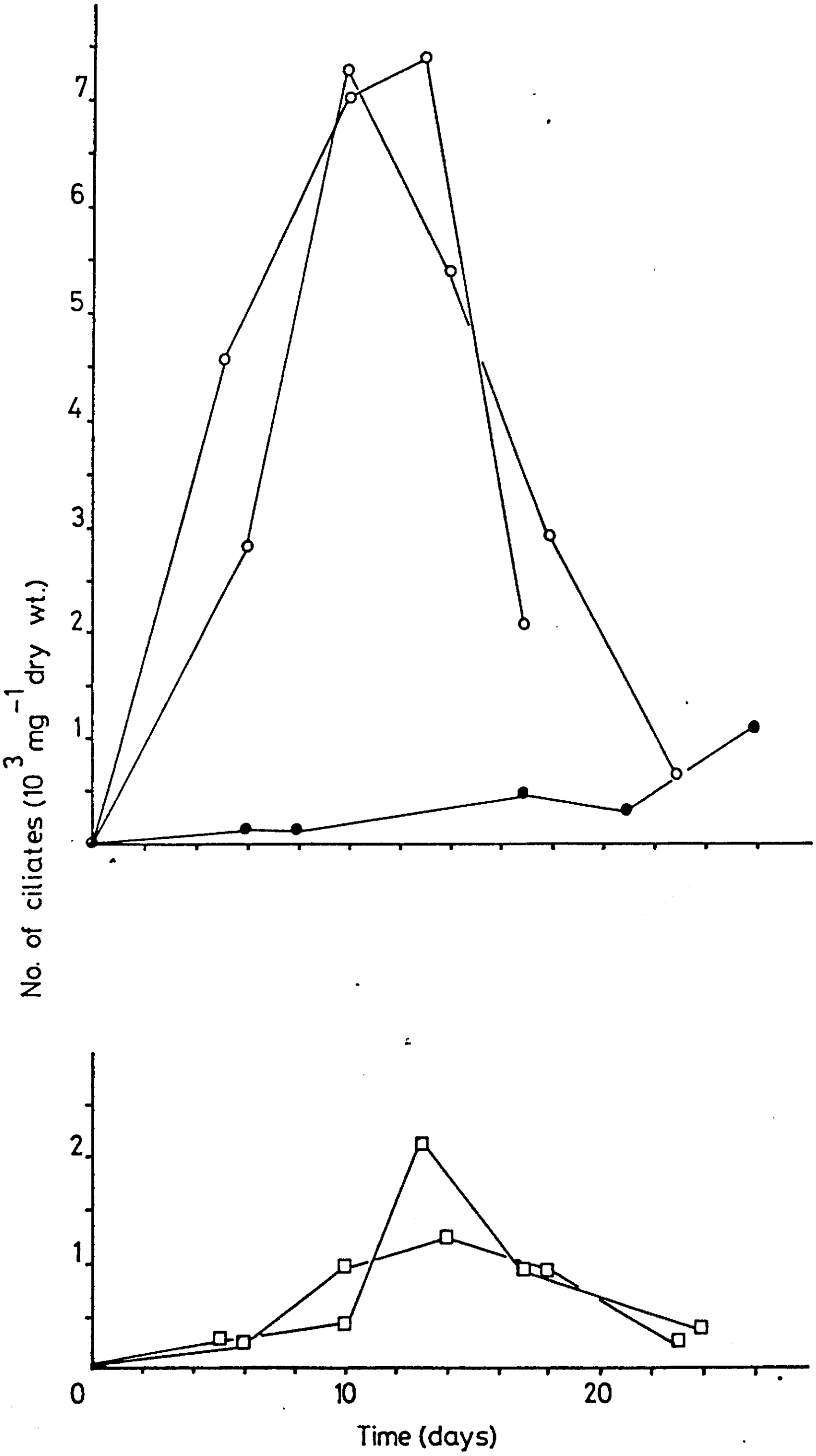

No. of ciliates (10^2 mg^{-1} dry wt.)
15
10
5
0
20
40
60
Time (days)

Figure 14.

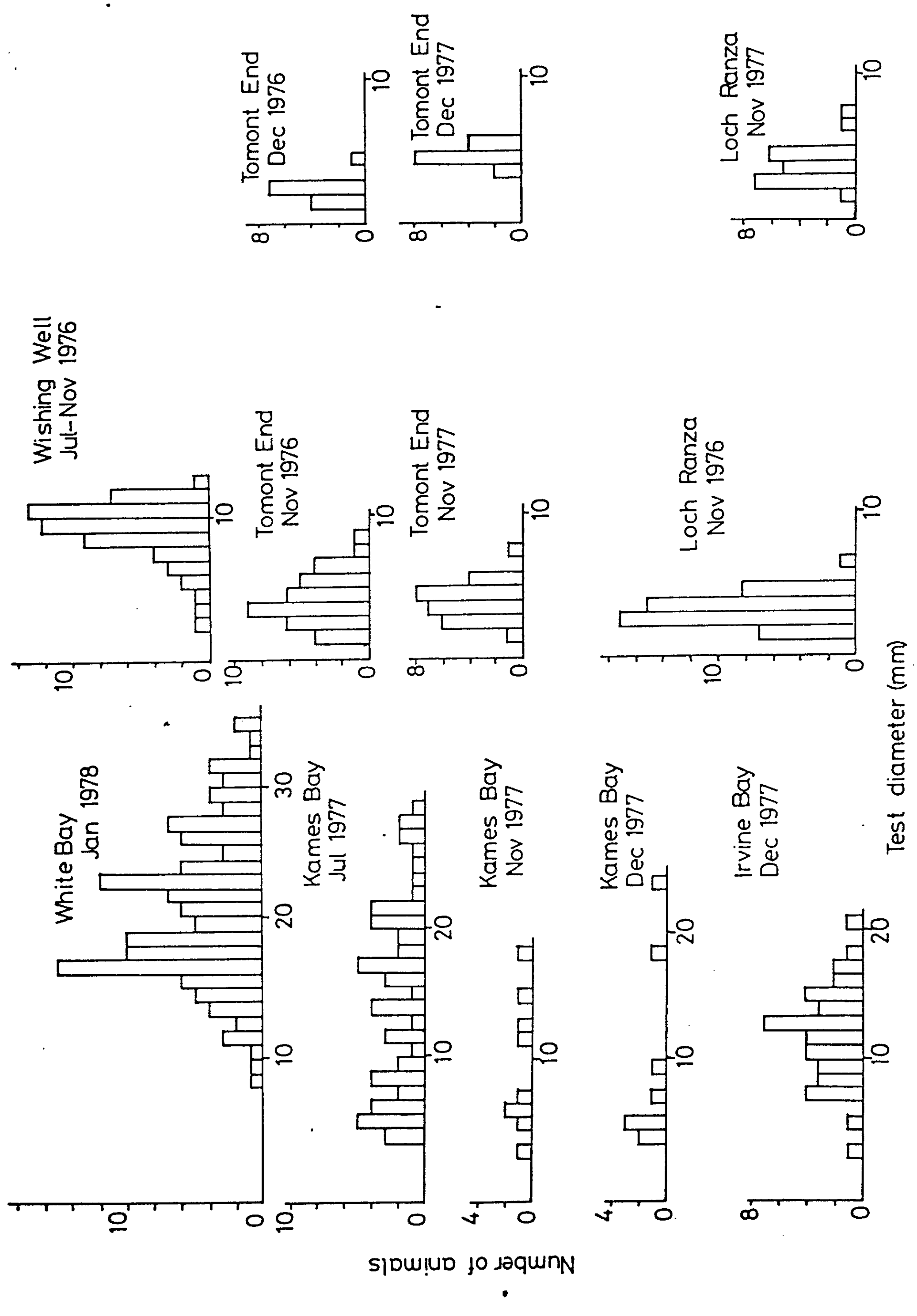
Population density changes with time of ciliated Protozoa on (a) Psammechinus faeces (□—□; two replicates), (b) intact L.saccharina (●—●) and (c) homogenized L. saccharina (o—o ; two replicates). (Feb.-Mar. 1977).



7
6
5
4
3
2
1
No. of ciliates (10^3 mg^{-1} dry wt.)
2
1
0
10
20
Time (days)

Figure 15.

Size-frequency histograms for various field populations of Psammechinus miliaris in the Clyde Sea area.


Number of animals
Test diameter (mm)
White Bay
Jan 1978
Kames Bay
Jul 1977
Kames Bay
Nov 1977
Kames Bay
Dec 1977
Irvine Bay
Dec 1977
Wishing Well
Jul-Nov 1976
Tomont End
Nov 1976
Tomont End
Nov 1977
Loch Ranza
Nov 1976
Tomont End
Dec 1976
Tomont End
Dec 1977
Loch Ranza
Nov 1977
0
10
20
30
4
8

DISCUSSION

Psammechinus aggregates by kinetic responses (cf. Mattison et al., 1977; Ott and Maurer, 1977; Russo, 1979) on the decaying areas of kelp fronds in seabed drift accumulations and actively ingests this material. By re-cropping the damaged edges of rotting weed it will exert some control over the rate at which decompostion occurs, although not to the same extent as Gammarus locusta (L.) (see chapter 3).

Jensen (1969) noted that great variation in growth rate of young Psammechinus is a normal feature of animals in the sea as well as in the aquarium. Such vaiations depend on diet and thus make it impossible to separate a population into age groups solely on the basis if size-frequency distributions. Larval settlement appears to be the main method by which Psammechinus colonizes detached weed beds. That adults were found in such situations as Kames Bay and Irvine Bay, reflects previous years settlement onto drift accumulations which have a predictable year-round availability of drift kelp, as they face prevailing SW winds (Fig. 15).

The similar growth rates of larger (presumed older) Psammechinus fed either fresh or rotting kelp in the laboratory, suggests that these diets are nutritionally equivalent. From this, it follows that the relatively poor growth rates exhibited by young Psammechinus feeding on fresh weed, derived from an inability to digest this material efficiently rather than from any inherent nutritional deficiency of fresh weed.

The period of maximum urchin growth (Fig. 5) occurred in the months of June, July and August. This corresponds with the breeding season of Psammechinus in the Firth of Clyde (Elmhirst, 1922; personal observations). Jensen (1969) suggested that seasonal variation in growth rate also occurred in Danish Psammechinus and that mature individuals did not grow during the breeding season (a period of six months). She saw gonad maturation as being responsible for growth cessation (see also Lewis, 1958). Other authors (Fuji, 1962, 1967; Ebert, 1968; Miller and Mann, 1973) have found reduced feeding rates in various Strongylocentrotus spp. during the breeding season. Leighton (1968) suggested that the swelling gonads compress the gut, preventing it from functioning normally.

Psammechinus from the Firth of Clyde, however, feed voraciously throughout the breeding season. It is proposed that at this time Psammechinus expands its test to accommodate the swelling gonads, thereby leaving the gut free to function normally. McPherson (1969) found the highest feeding rate in Eucidaris when the gonads were largest and the results obtained by Bull (1939) for Psammechinus are in agreement with those presently obtained. Jensen (1969) drew her conclusions from comparisons of size-frequency histograms for four samples taken in the period January-October. She assessed the age of her Psammechinus by counting the rings on interabulacral plates, then she separated year classes on this basis in her histograms (some containing less than 8 individuals). Considering the wide variation in individual size that can occur with age (as recognised by Jensen), much larger numbers would be required before unambiguous conclusions could be drawn using her method. Her data on growth rates, and mine, are thus not properly comparable. Jensen(1969) and Bull (1939) both found reduced (or zero) growth in laboratory-maintained Psammechinus during the winter. Jensen again attributed this to the onset of gonad maturation. It would seem most likely, however, that this was simply a response to low water temperatures.

Various authors (see Clark, 1969) have considered that dissolved organic material (D.O.M.) may play an important part in echinoid nutrition. The lack of growth and eventual death of the control group in the present study (Fig. 5) however, illustrate that this material plays no important part in the nutrition of Psammechinus. Animals can survive for lengthy periods only at the expense of tissue resorption. Indeed, Field (1972) noted that Strongylocentrotus fed Laminaria released dissolved organic carbon carbon into the water in large quantity. D.O.M. may , however, play a minor role in the regional nutrition of echinoid spines (West, de Burgh and Jeal, 1976; de Burgh, West and Jeal, 1977).

External digestion has been demonstrated in Psammechinus (Pequignat, 1966, 1972). In the present work, food was generally changed every 24 hours and no signs of surface digestion of algae were observed. Considering too, the large output of faeces, there can be little doubt that "skin digestion" was of very minor (if any) importance to Psammechinus in the present study.

That there was no significant difference between the protein values for fresh and rotting kelp is perhaps contrary to expectation. Previous workers (Odum and de la Cruz. 1967; Heald, 1969) have shown that the protein content of decaying angiosperm material increased as decomposition progressed; caused by a build-up in numbers of saprophagous microbes. A large range of protein values was found for fresh weed (10-65 mg.g^{-1} dry wt.) and this would tend to conceal any overall differences between rotting and fresh weed. The protein values for fresh weed here reported are lower than those found by Black (1950). The maximum value presently found was 6.5% (dry weight) compared with 10-11% found by Black at the same time of year. Black obtained his data from estimates of the total (Kjeldahl) nitrogen content of the weed x 6.25. Mann (1972) noted that this procedure overestimates protein values and this no doubt accounts for much of the resultant difference. In addition, contamination by salt (see Methods), will result in lower protein values. This effect was found, however, to be very small.

The absorption efficiencies recorded for organic carbon illustrate the ability of Psammechinus to digest kelp structural polysacharides. Alginic acid is the principal structural component found in the Phaeophyceae (Percival, 1968), comprising 13-21% of the dry solids in L. saccharina (Black, 1950). Cellulose accounts for no more than 5% (Percival, 1968). Alginase activity has been demonstrated in Psammechinus by Franssen and Jeunioux (1965). Cellulose digestion, however, has not been specifically demonstrated in Psammechinus, but Yokoe and Yasumosa (1964) and Elykova (1972) have demonstrated the digestion of sodium carboxymethylcellulose, a soluble cellulose derivative, in other echinoids. Most recently, Fong and Mann (1980) have demonstrated the digestion of cellulose in Strongylocentrotus droebachiensis. Their work strongly implied that this facility was a property of a gut microflora. In fresh weed, much of the protein fraction is confined to the cell contents. Although some cells will rupture during ingestion, digestion of the cell walls must take place in order to account for the high protein absorption efficiencies recorded. By contrast, for animals feeding on rotting weed, protein will be readily available in the form of epibionts and the action of microbes in weakening the cell walls will make the remaining algal cell protein even more readily accessible. Thus, organic carbon digestion is of lesser importance to animals feeding on rotting weed. The older, tougher material will have relatively larger quantities of structural polysaccharides and hence, in order to release the protein fraction, more efficient organic carbon digestion would be required. Thus, not surprisingly, a direct relationship was found to exist between organic carbon content of ingested weed and the resulting absorption effeciency for all animals. This will, in part at least, account for the lower organic carbon absorption efficiencies found in animals fed rotting weed.

Much interest has been shown in recent years in the possible importance of echinoid gut bacteria in algal decomposition (reviewed by Lawrence, 1975). It is considered by some that, under normal feeding conditions, bacteria are of little importance, and that with an adequate food supply, material passes quickly through the gut (taking from 8 to 12 hours (Lewis, 1964)): too quickly for bacteria to make any significant contribution. Guerinot, Fong and Patriquin (1977), however, reported that <u>Strongylocentrotus droebachiensis</u> in kelp beds might receive about 8-15% of their daily N requirements from N_2 fixed by bacteria in the gut. They gave no data on gut retention times. Odintsov (1981), on the other hand, reported that bacterial N-fixation in the gut of <u>Stichopus japonicus</u> made no significant contribution to the N balance at least in the cold season. Bacteria may also have a cellulolytic ability and a capacity to synthesize essential amino acids (Fong and Mann, 1980). With a limited food supply, however, material is retained for longer periods. Starved animals may retain material for up to two weeks (Lasker and Giese, 1954). Farmanfarmaian and Phillips (1962) and Prim and Lawrence (1975) considered that, with these longer gut retention times, bacterial digestion may become especially important. It is generally considered that bacteria in the gut of echinoids are derived directly from ingested weed (Lawrence, 1975). Fresh weed has only a very limited bacterial population (Laycock, 1974). Thus, if bacteria were of importance, it would be expected that high organic carbon absorption effeciencies would be recorded for animals feeding on rotting weed - with its very large bacterial populations - and this is not the case. The results presented here suggest that bacteria play no important part in carbohydrate digestion in <u>Psammechinus</u>, but this does not preclude the possibility of a microbial role in amino-N availability. Bacteriological data on <u>Psammechinus</u>

guts would be of great interest.

The young (immature) Psammechinus feeding on fresh weed returned poor protein absorption efficiencies when confronted with the older, tougher, low-protein kelp tissue. These animals are only capable of digesting the high-protein, soft-walled meristem tissue effeciently. Presumably, the reduced protein absorption efficiencies returned on low-protein, older kelp thalli reflect the inability of young individuals to macerate or digest the thicker cell walls. In turn, it would seem likely that it is this inability which accounts for the relatively poor growth rates found in young Psammechinus fed fresh weed. Older individuals fed this material can digest low protein substrates efficiently and they maintained similar, if not identical, growth rates to their counterparts fed rotting weed.

Seasonal differences have been recorded in echinoid absorption efficiencies (Fuji, 1967; Miller and Mann, 1973). Such variations are of no present significance, since comparative data were collected simultaneously and over a relatively short period of time. Psammechinus absorption efficiencies showed direct correlations with both the protein and organic carbon values of ingested fresh weed. Since these two fractions vary seasonally (Black, 1950), seasonal variation would be anticipated were the absorption efficiencies to be followed throughout the year.

For Psammechinus feeding on rotting weed, protein is readily available (see above). But, these animals returned much lower absorption efficiencies than their counterparts fed on fresh weed. The residual algal protein is easily digestible and, presumably, will be efficiently extracted. Therefore, some of the micro-organism protein present in rotting weed must be in a form which cannot be digested by Psammechinus; possibly bacterial protein enclosed within refractory bacterial cell walls (cf. Birkbeck and McHenery, 1982). This would explain why no correlation emerged between the overall protein content of rotting weed and the resulting absorption efficiency of Psammechinus. Presumably, a direct relationship would have existed between that fraction of total protein attributable to the alga (if this could have been determined) and absorption efficiency.

The fact that mature P. miliaris feeding on rotting weed can maintain similar growth rates to those feeding on fresh weed, whilst digesting their food less efficiently, appears at first sight to be contradictory. These animals, however, produced larger quantities of faeces than those feeding on fresh weed, indicating faster rate of feeding, with shorter gut retention time. It is interesting though that Traer (1980) found little difference between the weight of green (live) Posidonia tissue bitten off by P. microtuberculatus Blainville compared with brown (decayed) tissue. Mature P. miliaris seemingly adopt different 'strategies' when feeding on fresh and rotting weed. Fresh weed is relatively difficult to digest; the protein fraction being confined to the contents of intact cells. The relatively long gut retention time employed by animals feeding on fresh weed allows for the digestion of algal cell walls; the necessary prelude to the digestion of algal protein. By this means, high protein absorption efficiencies are obtained. Rotting weed is easily digestible, with abundant protein present in the form of micro-organisms, and with the organic carbon fraction being reduced by microbial catabolism, allowing for easier extraction of the remaining algal protein. Of the total protein, however, some is apparently in a form unavailable to digestion by Psammechinus, resulting in the relatively low protein absorption efficiencies recorded. On such a diet, Psammechinus reduces its gut retention time, passing more food through the gut, allowing residual proteins to be extracted. In this way, Psammechinus maintains its protein intake and conserves its growth rate irrespective of diet. Psammechinus then does not fulfil the 'classic' role of a microbe-stripping detritivore. Substratum digestion is of paramount importance for animals feeding either on fresh or rotting weed (cf. Fenchel, 1972).

CHAPTER 2

THE ROLE OF PLATYNEREIS DUMERILII (AUDOUIN AND MILNE-EDWARDS)

INTRODUCTION.

Although the feeding habits of the Nereidae are varied (Fauchald and Jumars, 1979), most species ingest algal material to some degree. A number of these polychaetes live in close association with algae, using the plant substratum both for tube attachment and as a food source.

In the Clyde Sea area, two species in particular are found in association with Laminaria saccharina (L.) Lamour, viz. Nereis pelagica (L.) and Platynereis dumerilii (Audouin and Milne-Edwards). N. pelagica is commonly found in holdfasts of attached kelp (Scarratt, 1961; Moore, 1971, 1973) and is omnivorous (Goerke, 1971). If holdfasts are deliberately detached, N. pelagica vacates them rapidly (personal observations) and this species is rarely found sublittorally in beds of detached L. saccharina. P. dumerilii on the other hand, is rarely found in association with attached L. saccharina (Clark, 1960; Moore, 1971). Rather it is abundant locally in sublittoral drift weed accumulations. It constructs its tubes on all regions of the plant (personal observation). Clark and Milne (1955) stated that this worm was found in a well-marked narrow zone in Kames Bay, at a water depth of 20m, in association with decaying Laminaria. Personal records showed quite a wide depth range (15-80m) for Platynereis in the Clyde Sea area at large. This species is considered to be mainly herbivorous (Korringa, 1951; Rasmussen, 1973) and all individuals taken from detached weed had exclusively algal material in their guts. The tough, chitinous jaws of this worm produce a characteristic "scalloping" of frond edges which is readily observable in situ.

Platynereis also produces easily-recognizable, tough, parchment-like tubes (Pettibone, 1963; Daly, 1973) which often extend over more than one algal frond.

MATERIALS AND METHODS.

P. dumerilii (referred to interchangeably as *Platynereis* herein) was found locally in large numbers on beds of detached weed (densities <45 animals/100g weed dry weight). Experimental animals were collected either by beam-trawling (2m beam with 25mm mesh) or by S.C.U.B.A. diving. Detached kelp was collected from water depths of 15-20m. The membrane tubes of *Platynereis* are readily visible and worms were easily extracted by gentle pressure on the posterior. Too much pressure resulted in autotomy of the tail segments. Prior to experimental use, animals were allowed to acclimatize for 14 days in the laboratory. Mortality only occurred in experimental animals when the breeding season approached.

At this time,heteronereids generally left their tubes to take part in courtship behaviour. This was followed by the release of gametes (by body rupture) and ultimately by death. Release of chemicals by these adults generally stimulated all other worms in close proximity, irrespective of age (Hauenschild, 1955), to mature quickly, as found by Boilly-Marer (1974). In the laboratory, spawning of first *Platynereis* individuals usually started in April each year. In the field, the timing of maturation varies with the severity of the winter (Rasmussen, 1973). Thus, all laboratory experiments were carried out before February.

All experimental animals were fed continuously, since Lewis and Whitney (1968) found that digestive efficiency was reduced in previously starved animals.

1) Comparison of growth rates.

Monitoring changes in the size of living polychaetes is difficult, with changes in coelomic pressure altering their relative dimensions. Equally, changes in wet weight are unsatisfactory owing to difficulty in removing all surface-held water, particularly from larvae (Bass and Brafield, 1972). Sarvala (1971) considered that counting the numbers of segments was the best indicator of age in small worms and this method has been used in the past, e.g. by Hemplemann (1911) for Platynereis dumerilii (since referred to P. massiliensis (Moquin-Tandon) by Hauenschild (1955)). Certainly, in P. dumerilii, there is a highly significant ($r = 0.94$, df. 58, $P < 0.001$) relationship between body dry weight (whole animals dried at 60°C and weighed on a Beckman Microbalance LM 500) and number of body segments (Fig. 16), determined using preserved specimens. The difficulty of distinguishing the posteriormost segments, however, makes this method inappropriate for live animals.

Many polychaetes, including P. dumerilii, possess tough chitinous jaws. These jaws increase in size with age (Kirkegaard, 1970) but their measurement can only be carried out directly on dead specimens. Platynereis though makes distinctive semi-circular bites in fresh L. saccharina (Fig. 25). The width of these bites is related to mouth size and hence to worm body size. Bite width was measured under a stereo-microscope with an eyepiece graticule (to the nearest 0.04mm). Bites from individual worms varied greatly in diameter. By examining a large number (ca. 50) of bites from individuals, a maximum bite size was obtained. The relationship between the maximum bite size and worm dry weight was then established (Fig. 17), and used to estimate the dry weight of living P. dumerilii. Animals were isolated in running seawater in individual mesh-walled, cylindrical containers (5.5cm x 4.5cm diam.)("Toby-Teaboys":Aldridge Plastics, Staffs.) with either fresh or rotting weed. Bites were most distinctive on fresh weed. With rotting weed, fragmentation at bite edges can occur and the weed itself may stretch during handling. Thus, prior to bite measurements, all animals were fed on fresh weed for 1-2 days. Since feeding is an essential part of this technique, no starved control group could be kept. Ten animals were kept on each of the two diets and bite measurements

Fig. 16

The relationship between log. body dry weight (µg) and log. number of body segments in Platynereis dumerilii.

Equation of line of best fit: log. $y = -6.325 + 5.597 \log.x$

(Note: all worms whole, no autotomized individuals included)

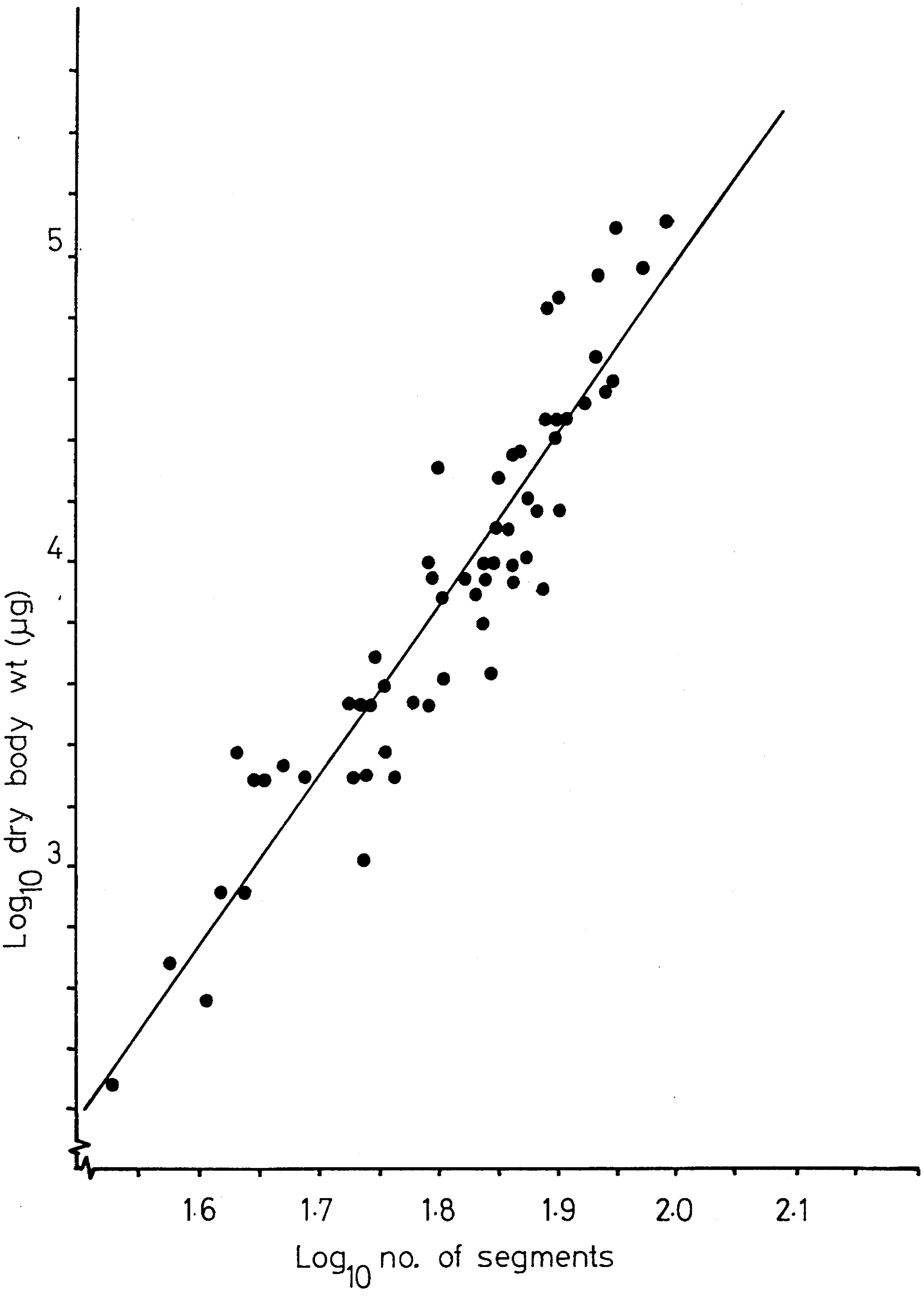
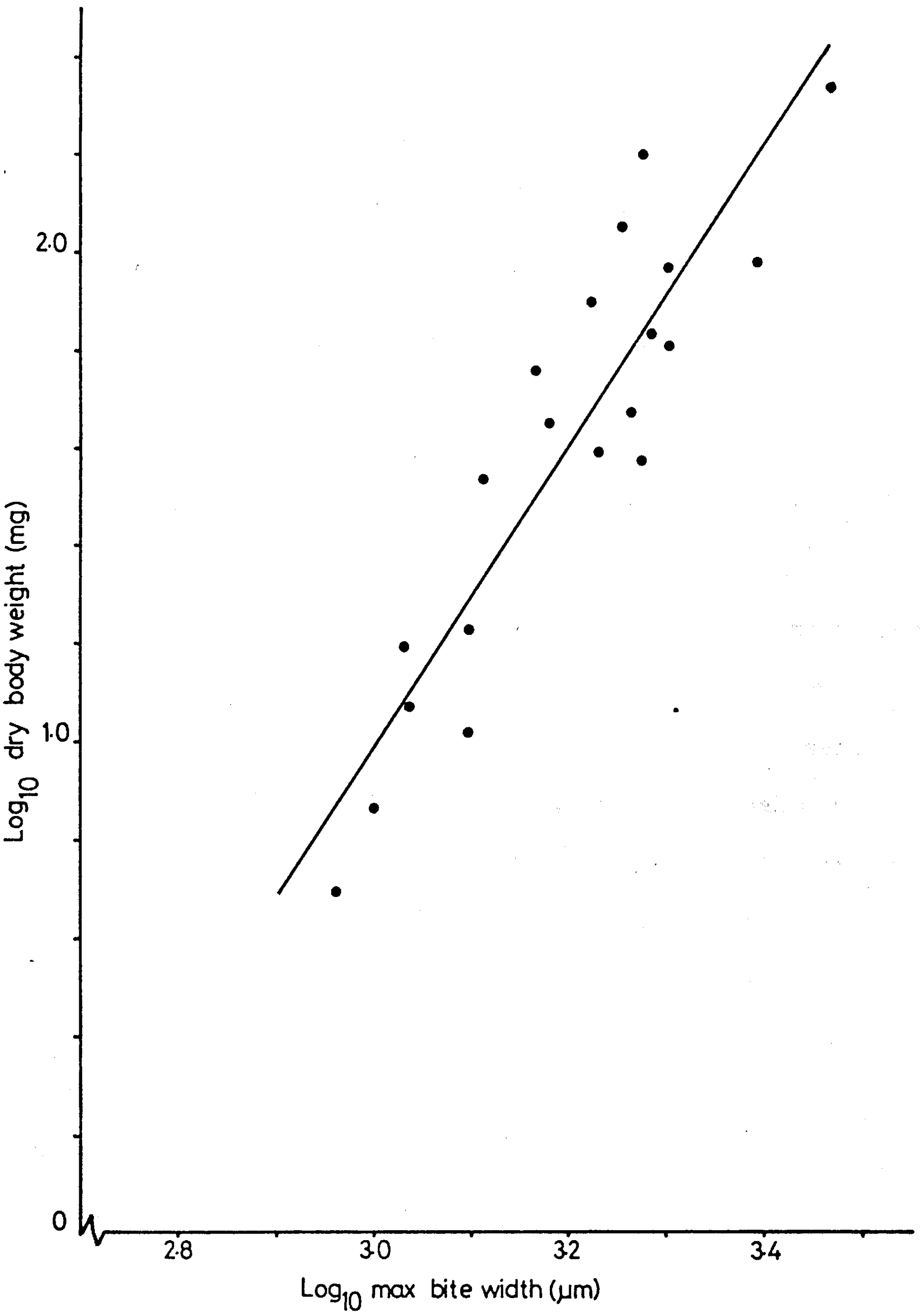

5
4
3
Log10 dry body wt (μg)
1·6
1·7
1·8
1·9
2·0
2·1
Log10 no. of segments

Fig. 17

The relationship between log. body dry weight (mg) and log. maximum bite width (µm) in Platynereis dumerilii.

Equation of line of best fit: log. $y = -8.35 + 3.11$ log. x


2·0
1·0
0
Log$_{10}$ dry body weight (mg)
2·8
3·0
3·2
3·4
Log$_{10}$ max bite width (µm)

taken every 28 days. This work was carried out during October-December so that seasonal effects were minimized.

2) Comparison of Absorption Efficiencies.

P. dumerilii were kept in individual, short lengths of 5mm bore glass tubing (see also Clark, 1959) in shallow, plastic trays with aerated seawater. Keeping the animals in glass tubes allowed (i) for easy handling without damage and (ii) for the immediate recognition of any heteronereids. Within these tubes *Platynereis* constructed their own chitinous tubes which they ventilated at intervals by dorso-ventral undulations (see Wells and Dales, 1951; Clark, 1959). Defaecation always occurred outside the glass tube and at the opposite end to that at which food was presented. Thus, especially in the case of animals feeding on rotting weed, detrital contamination of the faeces was avoided. The animals feeding on fresh and rotting weed were kept in separate trays. The food and water were changed, and the faecal material collected every day. A reference sample of weed was retained. The selection of this sample; its treatment together with the treatment of the faecal material and the determination of absorption efficiencies (both for protein and organic carbon) were carried out as indicated for *Psammechinus* in similar experiments (see Chapter 1, section 3). Absorption efficiency was calculated after allowance had been made for gut retention time.

3) Comparison of Gut Retention Time.

The sections of algal material ingested by *Platynereis* filled the whole width of the gut and their passage through the body was readily observable. Faeces were egested in synchrony with the ingestion of food, with individual meals remaining as discrete units within the gut. Individual *P. dumerilii* were kept in glass tubing (as above) and fed initially on *Ulva lactuca* (L.) (Korringa, 1951). Once green faeces were produced, the diet was changed to either fresh or rotting

L. saccharina. The animals were then observed every 30 minutes. The time at which feeding recommenced and the colour of the faeces changed were recorded.

4) Comparison of Dry Weight of Faeces Produced.

Individual *Platynereis* were isolated in "Toby-Teaboys" on either fresh or rotting weed in running seawater. The faecal pellets were collected each day from individual animals over a 14 day period. These were washed with fresh water and oven dried at 60°C. The dry weight of individual *Platynereis* were assessed by measuring the maximum bite diameter on fresh *L.saccharina* (see above).

5) Choice Experiments.

Twelve *Platynereis* were placed in the centre of a tray of aerated seawater with fresh and rotting weed at opposite ends. Experiments (n=10) were enclosed in a light-proof cover and left for 4 hours. At the end of this period, the number of animals found on both weed types was recorded. Provided that an adequate food supply is present, *Platynereis* will remain in the same tube (Clark, 1959; pers. obs.) and feed in that area. Thus, "settling" preference will also indicate likely diet.

6) The Decomposition of *Platynereis* Faeces.

The rate of decomposition of *Platynereis* faeces was examined by monitoring changes in the ciliate populations associated with this material. Their rate of decomposition was compared with that of intact fresh *L.saccharina* and of weed which had been homogenized to an equivalent particle size. The method used was identical to that employed for examining the decomposition of *Psammechinus* faeces (see Chapter 1, section 6).

7) Examination of Feeding Behaviour.

It appeared from casual observations that whilst feeding, *Platynereis* recropped the same area of algal frond successively. To test this, individual Platynereis (in glass tubes, see above) were isolated in trays of aerated seawater with a section of Laminaria frond. The amounts of frond removed by individuals were mapped on successive days.

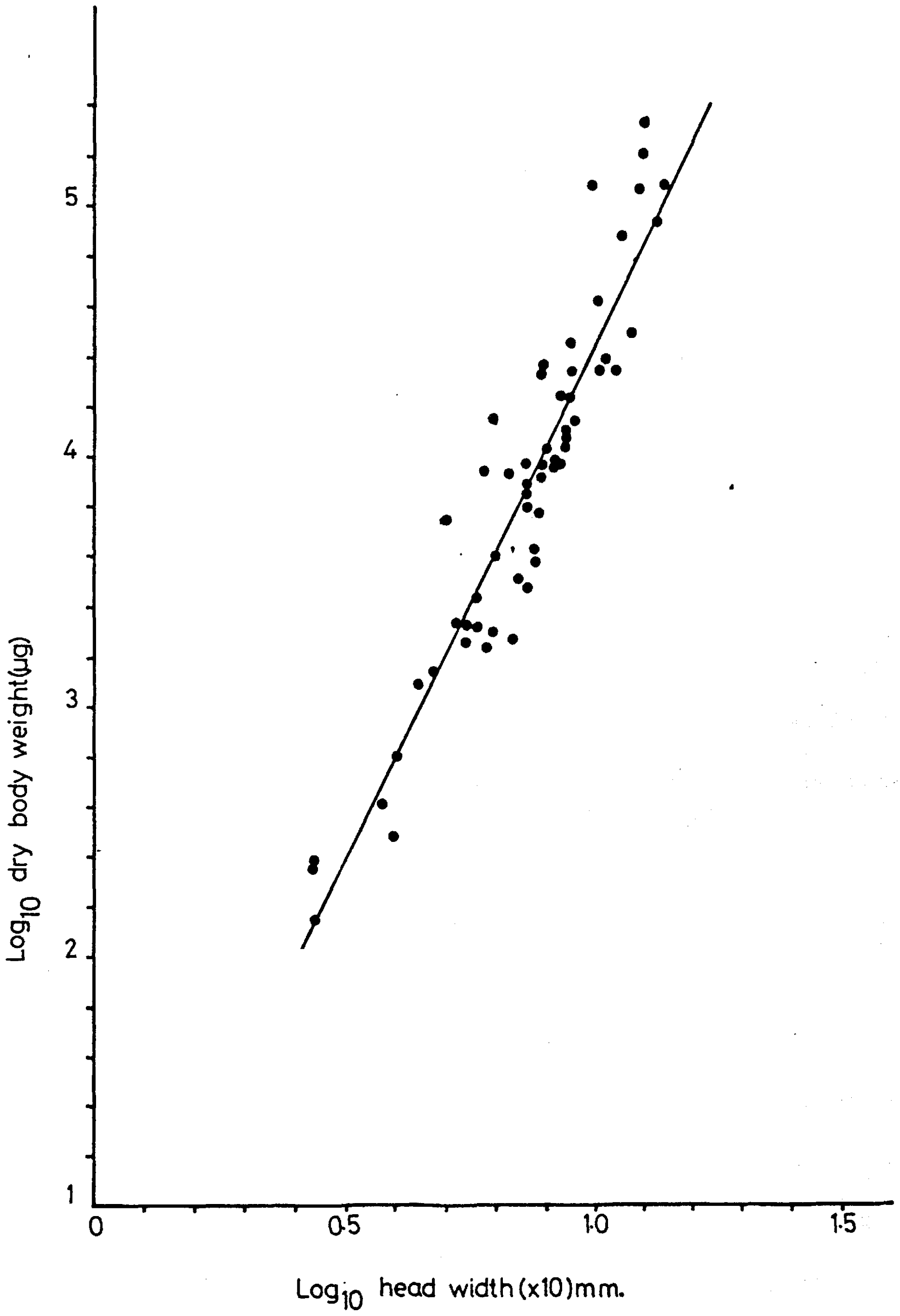
8) Comparisons of size structure of field populations of Platynereis dumerilii on detached weed beds.

Platynereis were collected by S.C.U.B.A. diving on beds of detached weeds at two localities, Loch Ranza (Isle of Arran; O.S. Grid ref. NR 930510) and Tomont End (Isle of Cumbrae; Grid ref. NS 181593) (see Fig. 1). Worms were extracted from the weed using 5% formalin. The width of the head (measured to the nearest 0.025mm, under a dissecting microscope, using an eye-piece graticule), was found to be the most easily measured size function in preserved material. The relationship between head width and Platynereis dry weight is shown in Fig. 18. Width measurements were converted into dry weight using the regression equation fitted to these data (Fig. 18).

Fig. 18

The relationship between log. body dry weight (µg) and log. head width ($X10^{1}$mm) in Platynereis dumerilii.

Equation of line of best fit : log. y = 0.294 + 4.17 log. x


Log$_{10}$ dry body weight(µg)
5
4
3
2
1
0
0·5
1·0
1·5
Log$_{10}$ head width (x10) mm.

RESULTS.

1) Comparison of growth rates.

The relationships between the dry weight of individual Platynereis and their increases over a 28 day period for animals feeding on both fresh and rotting L. saccharina are shown in Fig. 19 (a,b). Animals grew significantly on both diets (r(fresh) = 0.75, df. 23, $P < 0.001$; r(rotting) = 0.47, df.20, $P < 0.05$); the larger (older) individuals increasing their dry weight (in absolute terms) at a faster rate than the smaller individuals. Covariance analysis (Snedecor and Cochran, 1967) was used to compare the regression equations fitted to these data. The regression line for animals feeding on fresh weed had a significantly greater slope ($F = 4.81$, df. 1.43, $P < 0.05$) than that for animals feeding on rotting weed. Thus, animals of a standard size, feeding on fresh weed, grow faster than animals feeding on rotting weed. From the positions of the two lines, however, there is some indication that this situation may be reversed in very young individuals.

2) Comparison of Absorption Efficiencies.

a. Protein

The mean protein values for experimental fresh (28.06 ± 1.81 (SE) $mg.g^{-1}$ dry wt, n=51) and rotting (30.79 ± 1.54, n=46) weed were compared and found to be not significantly different ($d = 1.15$, $P > 0.05$). The protein absorption efficiencies for animals feeding on these two diets (mean = 80.86% (fresh), 47.38% (rotting)) were significantly different (two tailed Mann-Whitney U test, $z = 5.66$, $P < 0.00006$). (Note: a non-parametric test was used owing to variance in homogneity in angular transformed data, see Siegel (1956)). The absorption efficiency of protein was linearly related ($r = 0.35$, df. 47, $P < 0.05$) to the protein content of ingested weed for animals

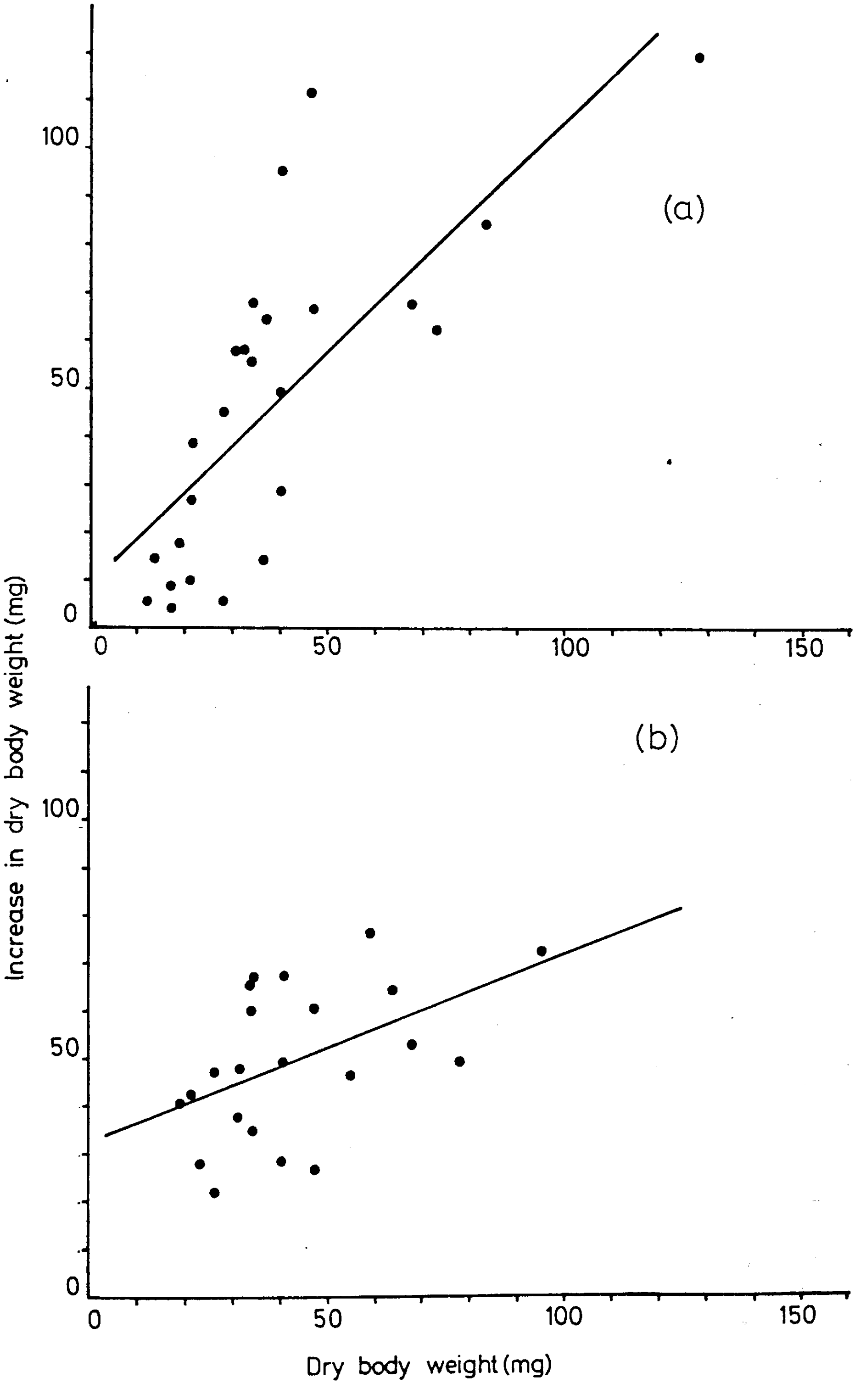
Fig. 19

Increase in body dry weight (mg) of worms of different body weight (mg), fed (a) fresh L. saccharina and (b) rotting L. saccharina, over a 28 day period.

Equations of lines of best fit:

Fresh, $y = 8.99 + 0.97x$

Rotting $y = 32.50 + 0.39x$


(a)
(b)
100
50
0
0
50
100
150
Increase in dry body weight (mg)
Dry body weight (mg)

feeding on fresh but not on rotting weed ($r = 0.23$, df. 42, $P > 0.05$) (Fig.20 a,b). The former group showed lower absorption efficiencies on lower protein substrates.

b. Organic Carbon

The mean organic carbon values for experimental fresh (253.15 ± 10.36 (S.E.) mg. g^{-1} dry wt, n=20) and rotting weed (246.69 ± 6.75, n=26) were compared and found not to be significantly different ($P > 0.05$). The organic carbon absorption efficiencies (mean = 28.79% (fresh), 24.00% (rotting)) were also found not to differ significantly (variances homogeneous, percentages transformed to angles: $t = 1.63$, df. 36, $P > 0.05$) for animals feeding on fresh and rotting weed. The relationships between organic carbon absorption efficiency and organic carbon content of ingested weed for animals on both diets are shown in Fig.21 (a,b). The regression line for animals feeding on rotting weed was significantly different from horizontal ($r = 0.53$, df. 14, $P < 0.05$), that for fresh weed was not ($r=0.38$, df. 20, $P > 0.05$). Lower absorption efficiencies on lower organic carbon weeds was thus a general trend.

3) Comparison of Gut Retention Times.

The gut retention times of Platynereis feeding on fresh (9.33h ± 0.15 (S.E.)) and rotting weed (9.6h ± 0.19) were not significantly ($P > 0.05$) different (n=20 in each case).

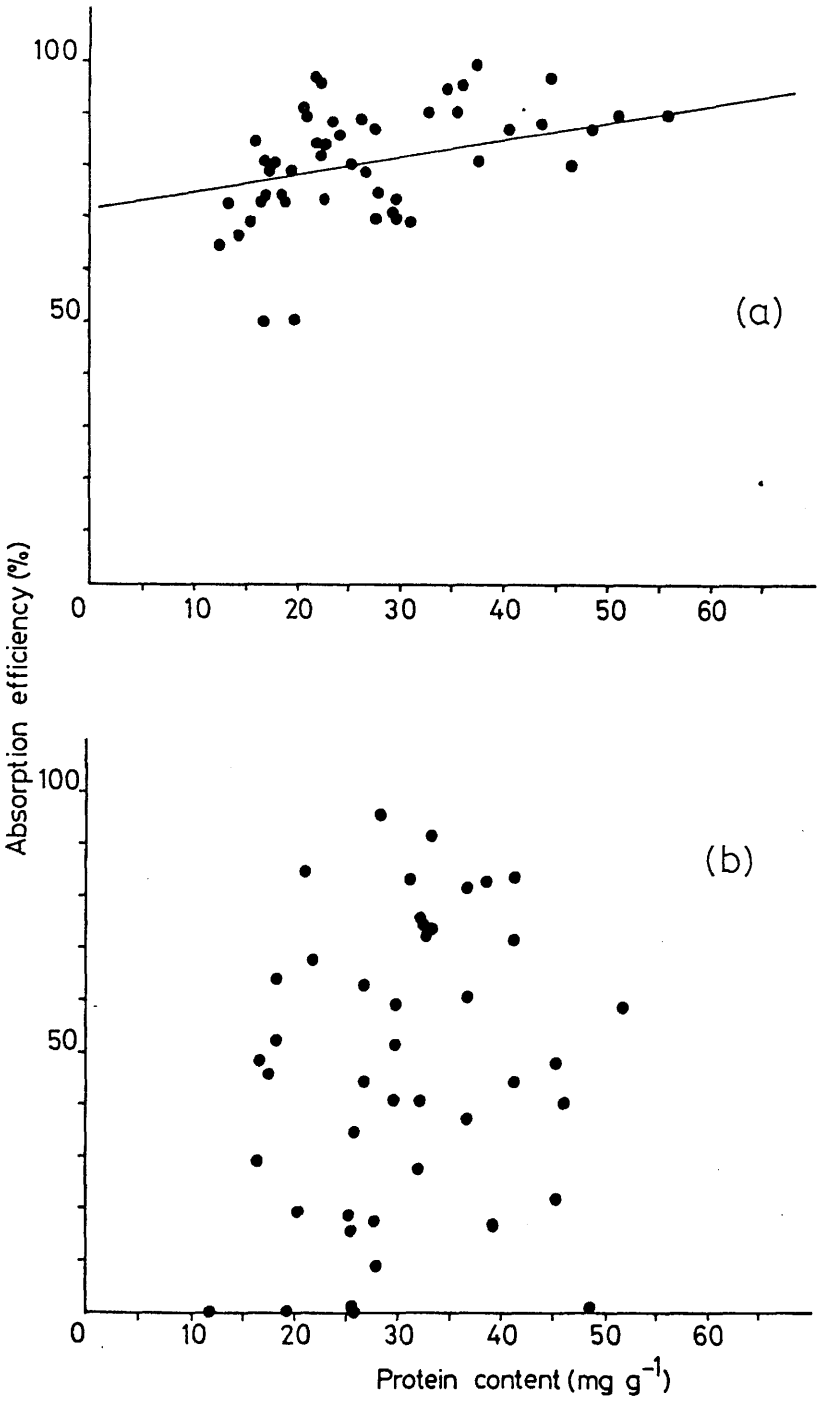
4) Comparisons of Dry Weight of Faeces Produced.

Significant relationships existed between the mean dry weight of faeces produced per day by Platynereis and worm dry weight for animals fed on both fresh ($r = 0.82$, df. 8, $P < 0.01$) and rotting ($r = 0.82$, df. 8, $P < 0.01$) weed (Fig. 22). The regression equations fitted to these data were compared using covariance analysis and were found not to differ significantly either in slope or elevation ($F_1 = 0.05$, df. 1, 16, $P > 0.05$; $F_2 = 1.27$, df. 1,17, $P > 0.05$). Thus,

Fig. 20

Absorption efficiency (%) in Platynereis dumerilii as a function of protein content (mg. protein g^{-1} dry wt.) of (a) fresh, or (b) rotting Laminaria

Equation of line of best fit for (a): $y = 71.85 + 0.32\ x$



100
50
0
10
20
30
40
50
60
(a)
Absorption efficiency (%)
100
50
0
10
20
30
40
50
60
(b)
Protein content (mg g^{-1})

Fig. 21

Absorption efficiency (%) in Platynereis dumerilii as a function of organic carbon content (mg. C g^{-1} dry wt.) of (a) fresh, or (b) rotting Laminaria.

Equations of lines of best fit:

(a) Fresh, $y = 2.50 + 107.21\ x$

(b) Rotting $y = -9.45 + 136.60\ x$

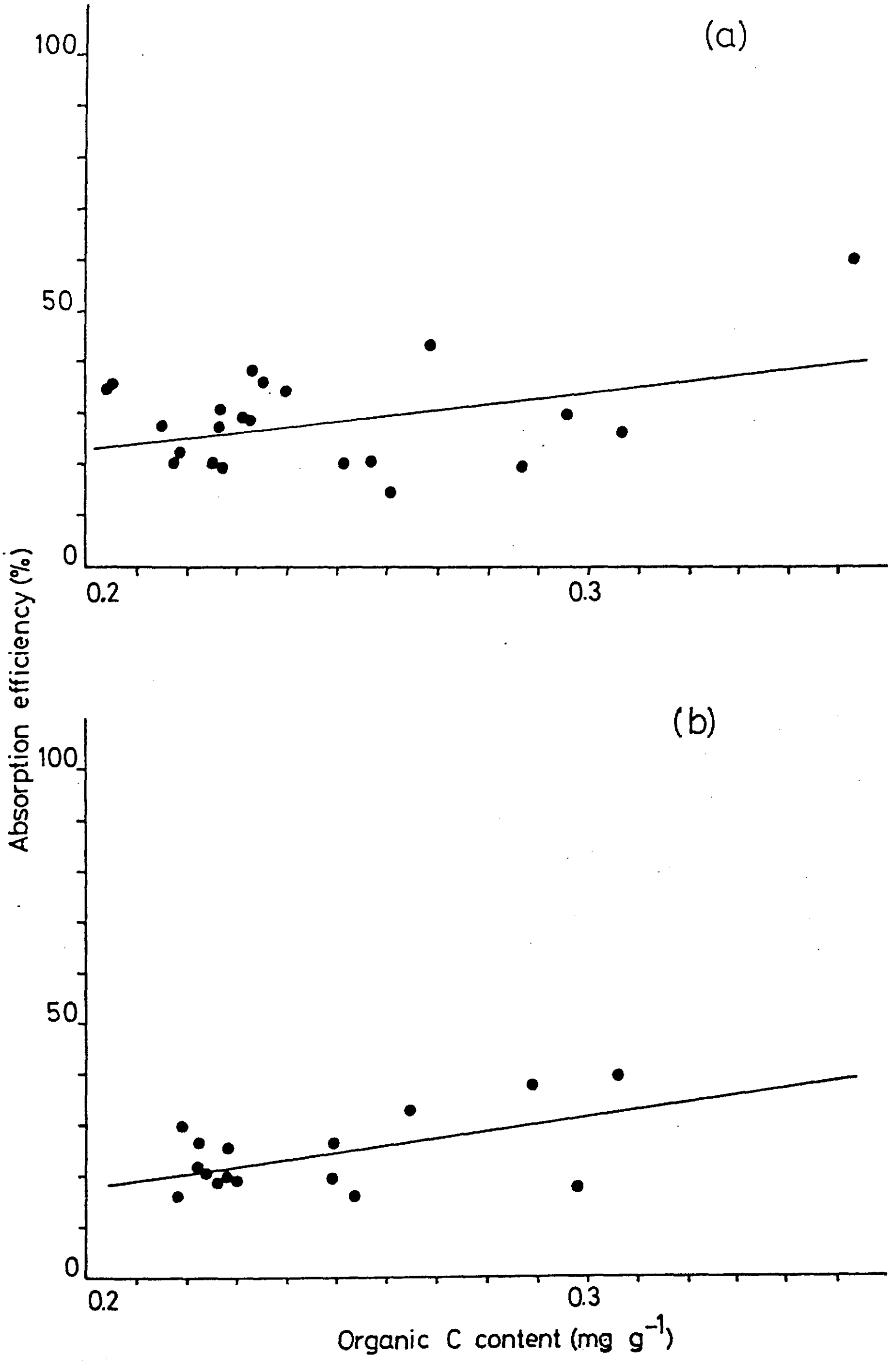

(a)
100
50
0
0.2
0.3
Absorption efficiency (%)
(b)
100
50
0
0.2
0.3
Organic C content (mg g^{-1})

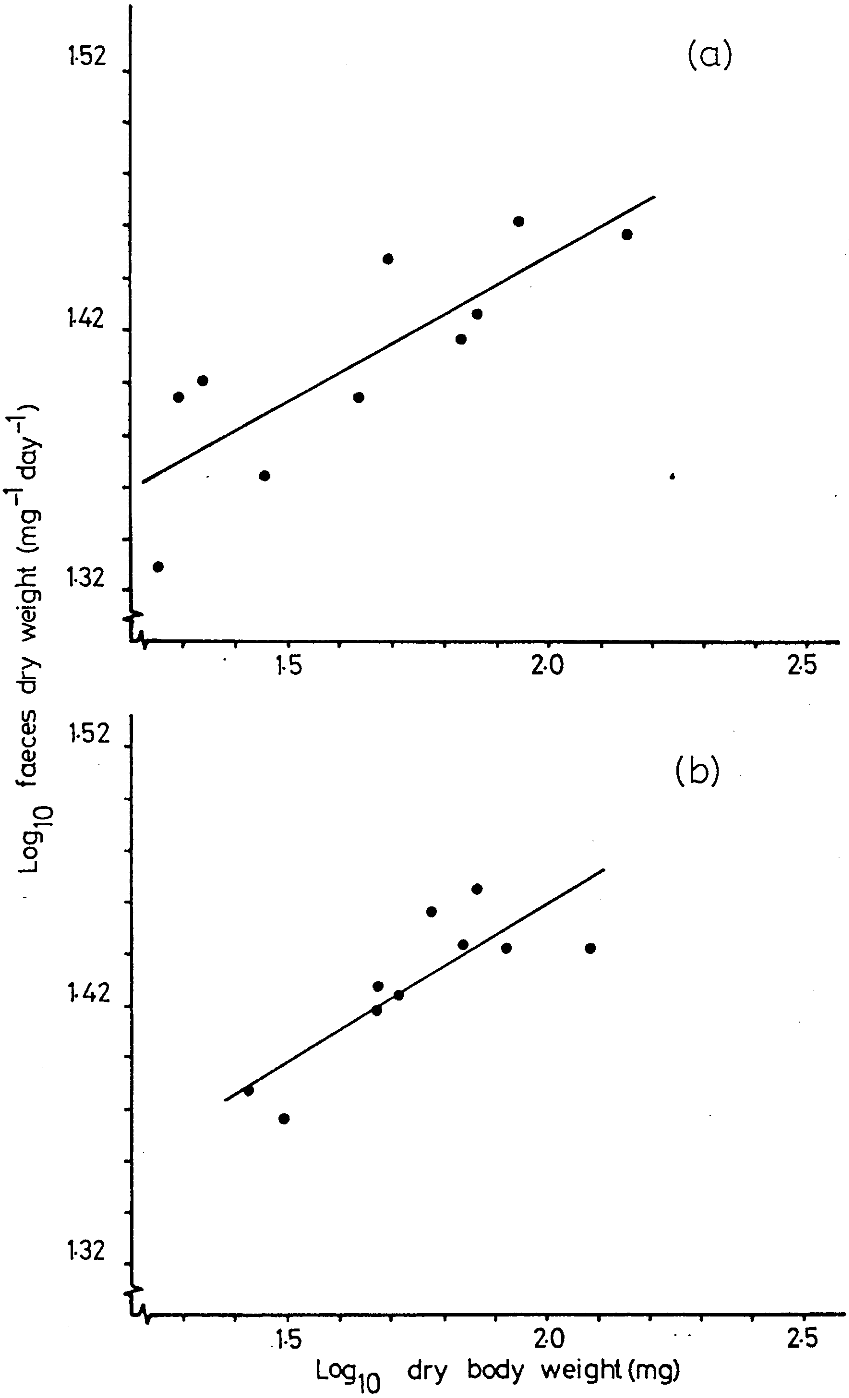
Fig. 22

Rate of faecal production (mean dry wt. faeces mg. day^{-1}) in *Platynereis dumerilii* as a function of body dry weight (mg) in worms fed, (a) fresh or (b) rotting *Laminaria*.

Equations of lines of best fit:

(a) Fresh, $y = 1.23 + 0.11\ x$,

(b) Rotting $y = 1.22 + 0.12\ x$


(a)
(b)
1·52
1·42
1·32
1·5
2·0
2·5
Log$_{10}$ faeces dry weight (mg^{-1} day^{-1})
Log$_{10}$ dry body weight (mg)

standard-size animals feeding on both diets produce similar quantities of faeces and hence ingest similar quantities of weed.

5) Choice Experiments.

Platynereis showed a clear preference (χ^2 (on raw numbers) = 38.53, df. 1, $P < 0.001$) for constructing tubes on fresh weed.

6) The Decomposition of Platynereis faeces.

The changes in ciliate numbers with time were followed for three experimental substrata: (a) faeces, (b) intact weed and (c) homogenized weed. The results are illustrated in Figs.23 and 24 (in Fig. 24, two experimental trials are illustrated for Platynereis faeces and homogenized weed). The timing of peak ciliate populations on the Platynereis faeces coincided approximately with that for the homogenized weed. Both these substrata promoted peaks earlier than did intact weed. The sizes of peak populations (in Figs. 23a and 23b), however, varied considerably. These trials were carried out at different times of year (Nov. 1976 and March 1977).

7) Feeding Behaviour.

The diagrams in Fig. 25 represent sections of frond which have been eaten by Platynereis. The portions removed on successive days are marked individually. Platynereis will recrop the same portion of algal frond for 2-3 days but will then ignore sections of previously exposed algal tissue. These then become open to attack by saprophagous micro-organisms.

8) Comparison of Size Structure of field populations of Platynereis dumerilii found on detached weed beds.

The weight-frequency histograms derived from field populations of P. dumerilii at Loch Ranza and Tomont End are illustrated in Fig. 26. The results consistently indicated two size classes. The adult size-class was lost in the late spring (April-June). Later in the year, this size-class reappeared and the proportion of very

Fig. 23

Population density changes with time of ciliated Protozoa on (a) Platynereis dumerilii faeces (□—□), (b) intact L. saccharina (●—●) and (c) homogenized L. saccharina (o—o) (Nov. - Dec. 1976).

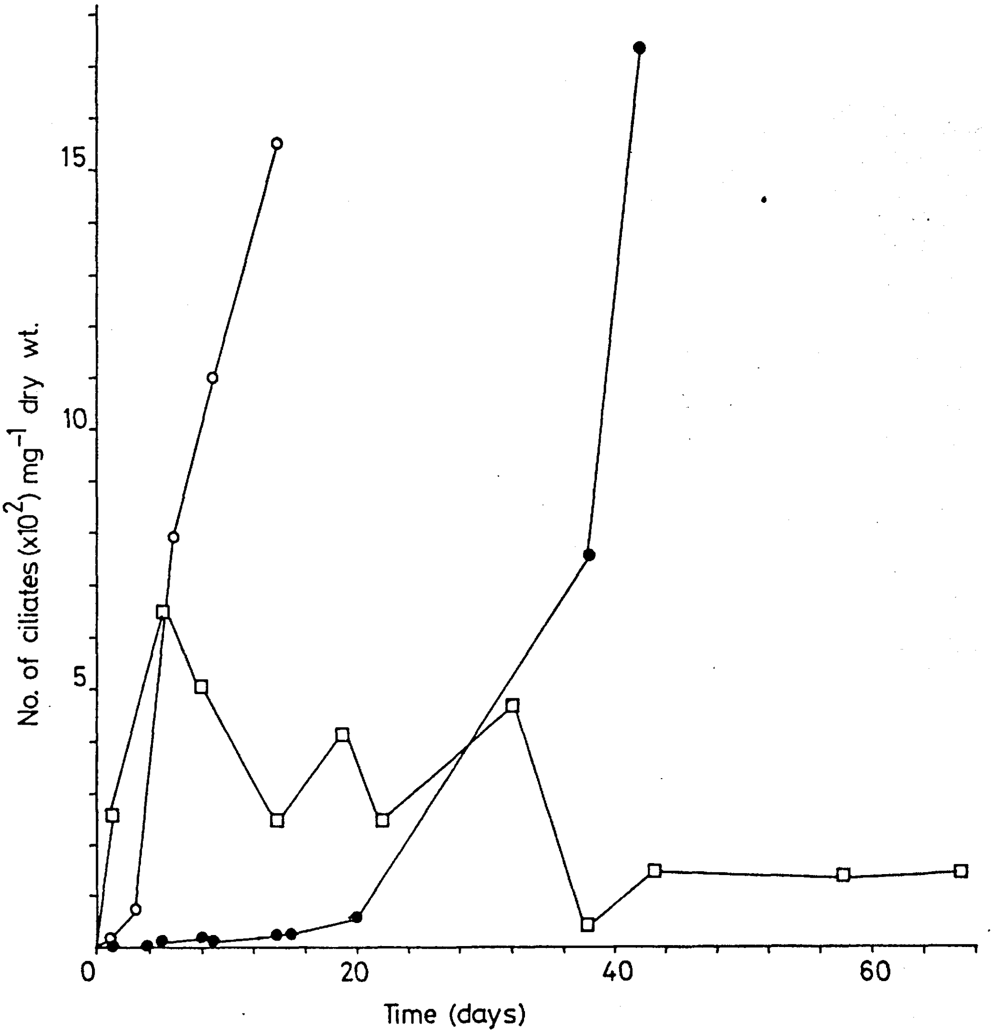

No. of ciliates ($\times10^2$) mg^{-1} dry wt.
15
10
5
0
20
40
60
Time (days)

Fig. 24

Population density changes with time of ciliated Protozoa on (a) intact L. saccharina (●——●) and homogenized L. saccharina (○——○ , two replicates) and (b) Platynereis dumerilii faeces (□——□, two replicates) (Feb. - Mar. 1977)

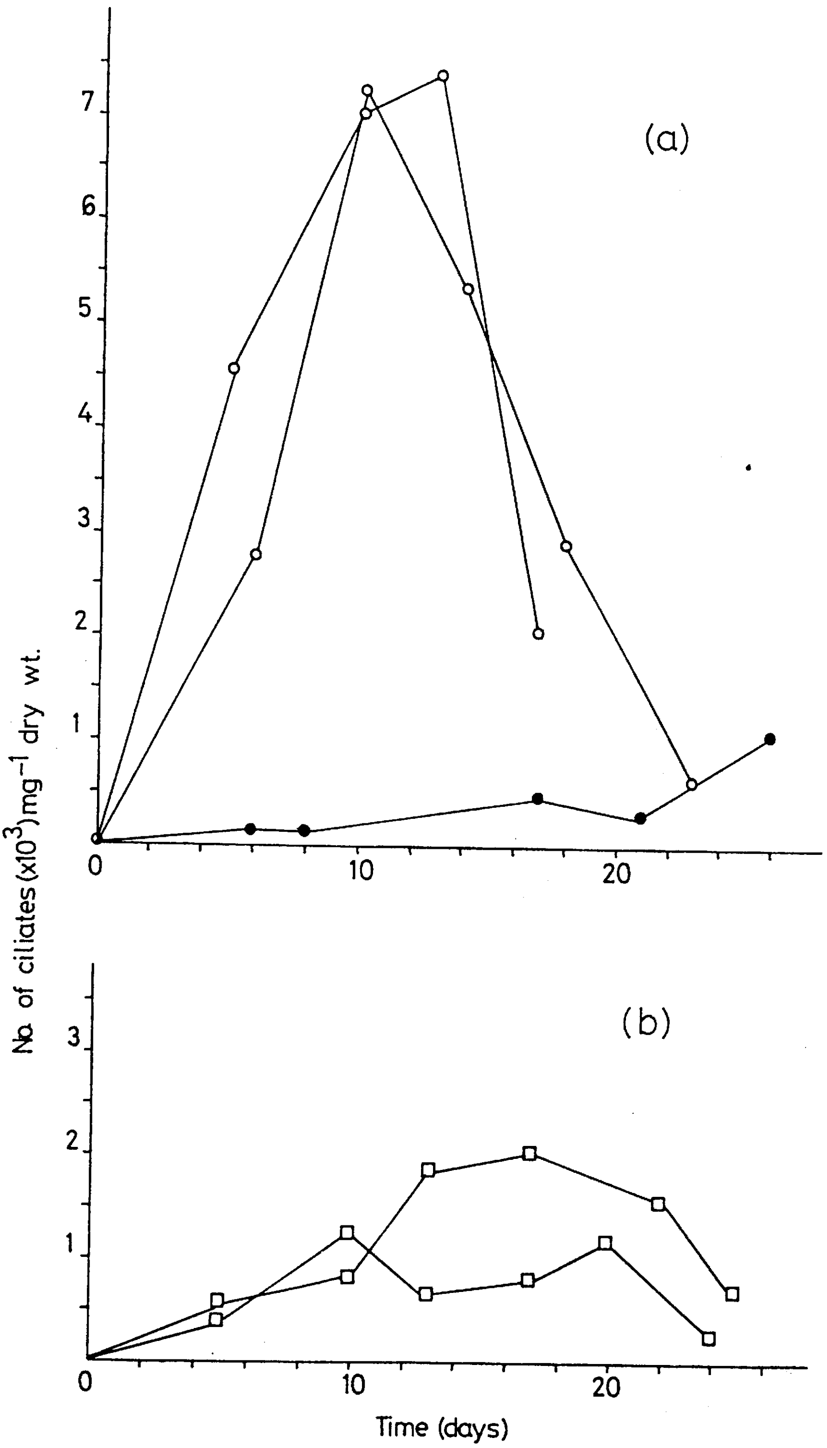

(a)
7
6
5
4
3
2
1
0
10
20
No. of ciliates (x10^3) mg^{-1} dry wt.
(b)
3
2
1
0
10
20
Time (days)

Fig. 25

Sequence of kelp consumption of three different pieces of *L. saccharina* by individual *Platynereis dumerilii*. Dates of sequences, A = Dec. 1977; B and C = Nov. 1977.

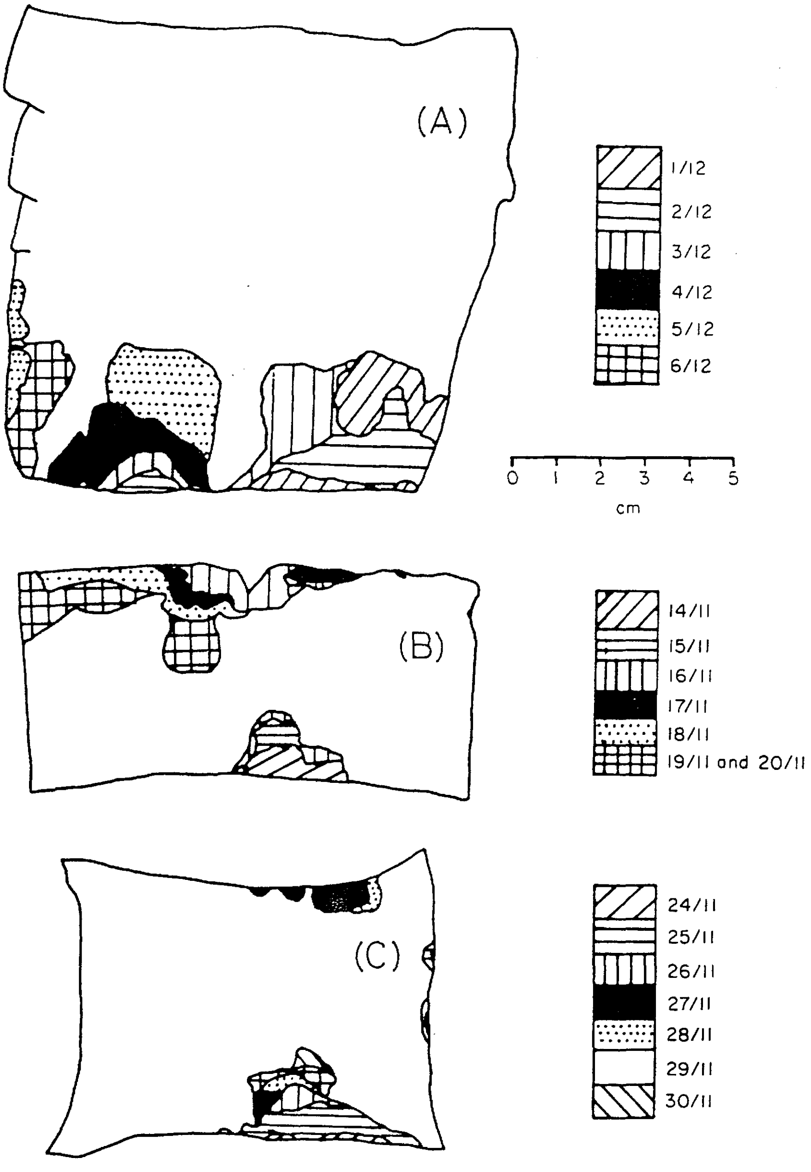
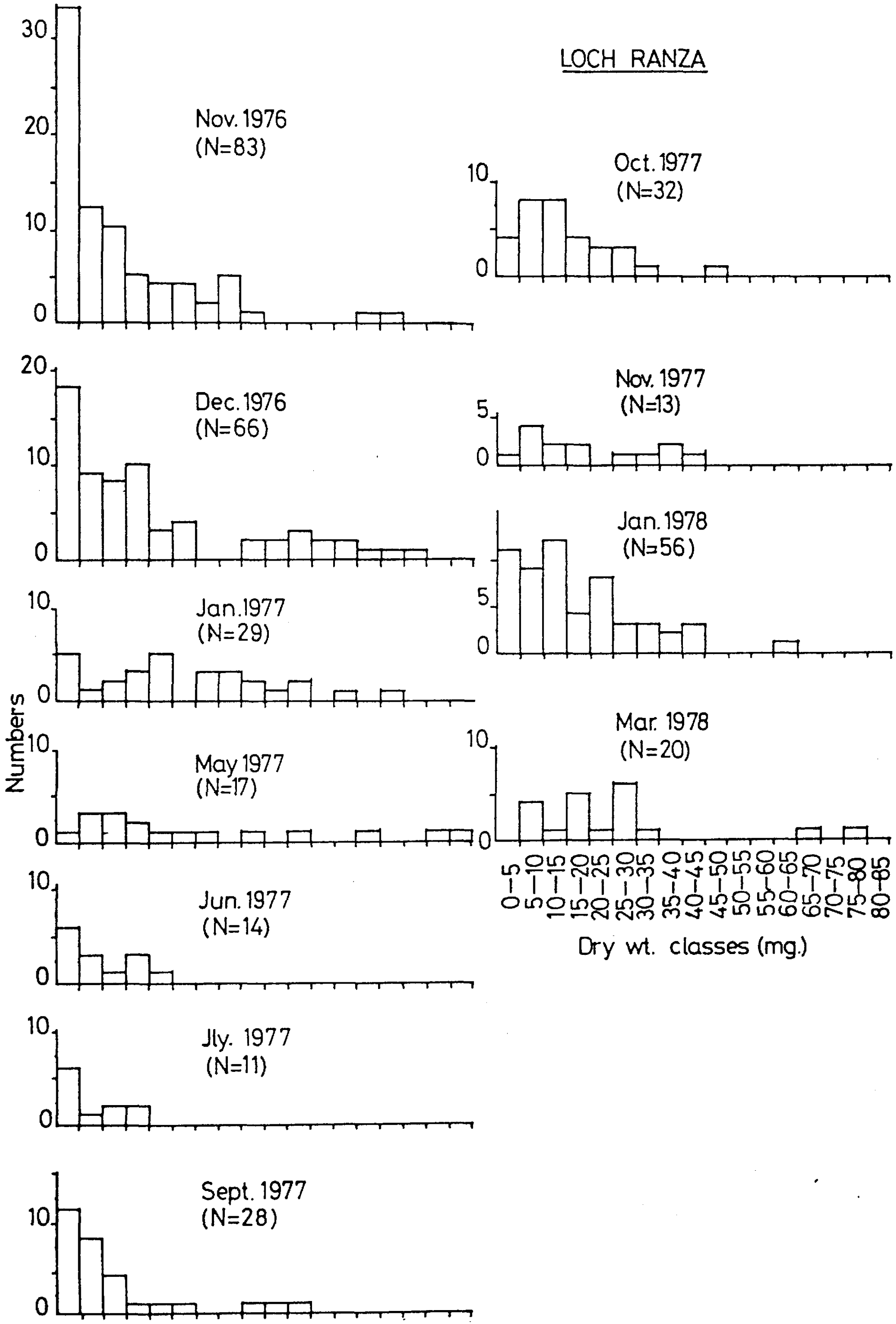
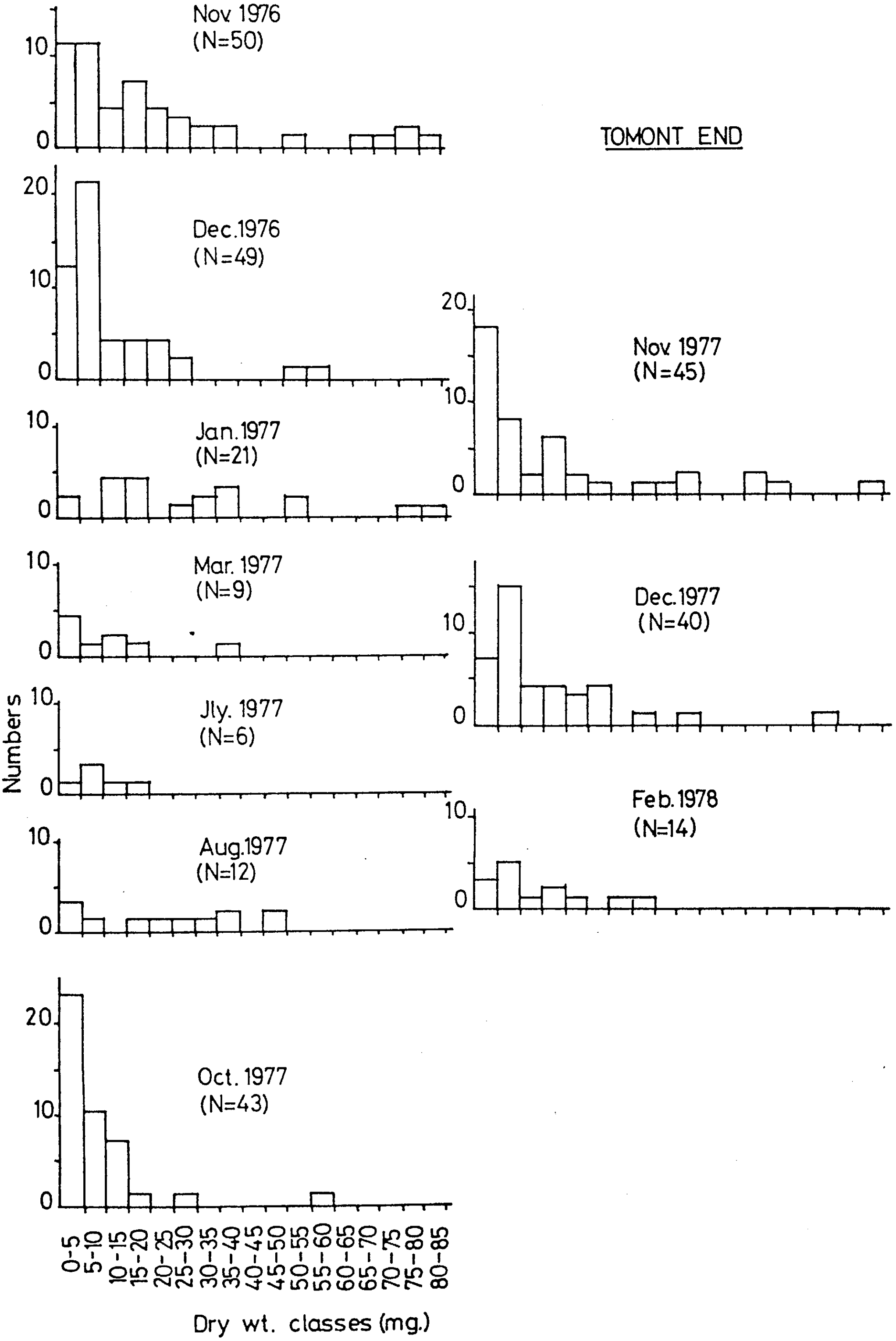

(A)
1/12
2/12
3/12
4/12
5/12
6/12
0 1 2 3 4 5
cm
(B)
14/11
15/11
16/11
17/11
18/11
19/11 and 20/11
(C)
24/11
25/11
26/11
27/11
28/11
29/11
30/11

Fig. 26

Population histograms for Platynereis dumerilii from sublittoral beds of detached kelp at two sites: (a) Loch Ranza and (b) Tomont End in the Clyde Sea Area.

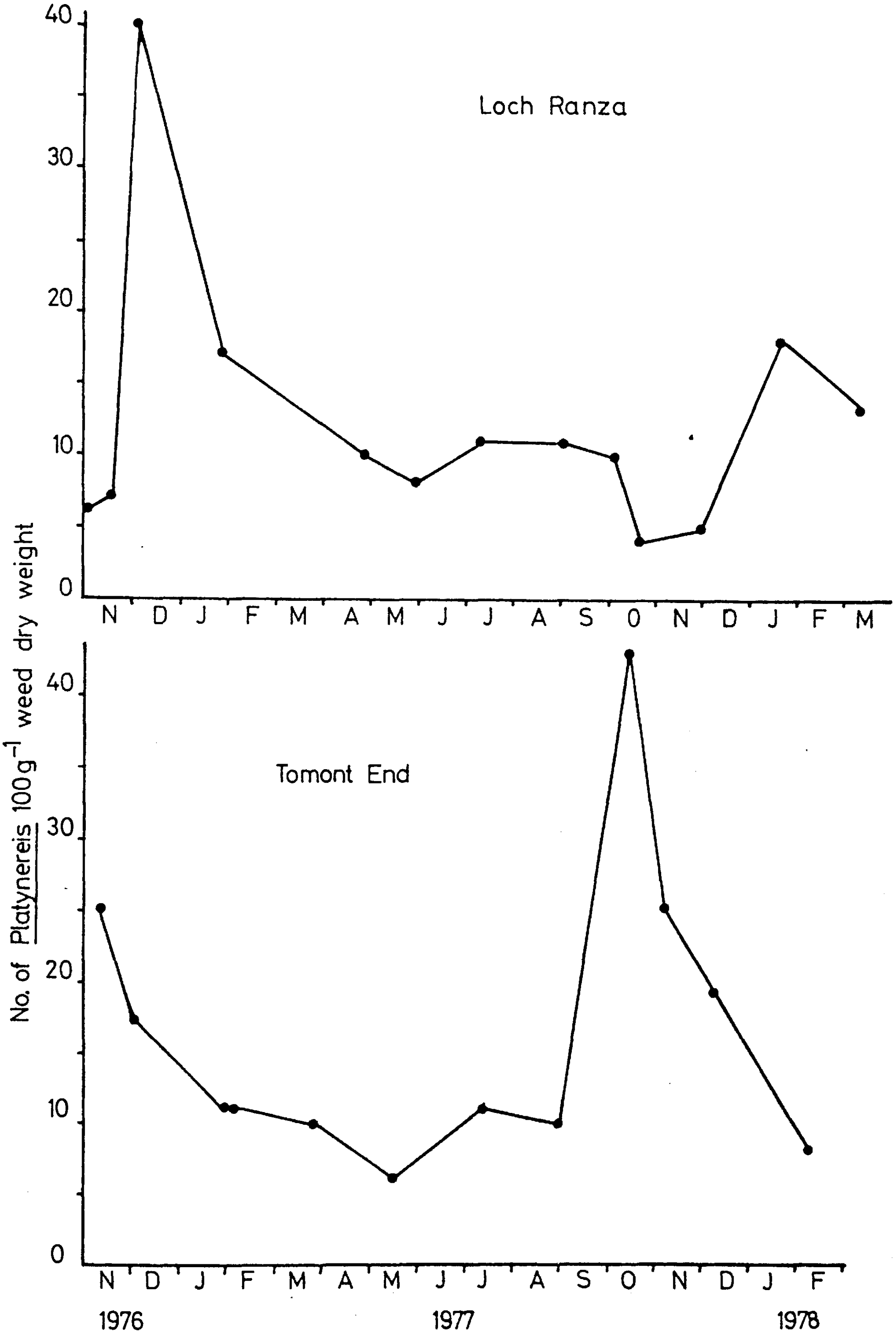

LOCH RANZA
Numbers
Nov. 1976
(N=83)
Dec. 1976
(N=66)
Jan. 1977
(N=29)
May 1977
(N=17)
Jun. 1977
(N=14)
Jly. 1977
(N=11)
Sept. 1977
(N=28)
Oct. 1977
(N=32)
Nov. 1977
(N=13)
Jan. 1978
(N=56)
Mar. 1978
(N=20)
30
20
10
5
0
0–5
5–10
10–15
15–20
20–25
25–30
30–35
35–40
40–45
45–50
50–55
55–60
60–65
65–70
70–75
75–80
80–85
Dry wt. classes (mg.)


TOMONT END
Nov. 1976
(N=50)
Dec.1976
(N=49)
Jan.1977
(N=21)
Mar. 1977
(N=9)
Jly. 1977
(N=6)
Aug.1977
(N=12)
Oct. 1977
(N=43)
Nov. 1977
(N=45)
Dec.1977
(N=40)
Feb.1978
(N=14)
Numbers
0
10
20
0-5
5-10
10-15
15-20
20-25
25-30
30-35
35-40
40-45
45-50
50-55
55-60
60-65
65-70
70-75
75-80
80-85
Dry wt. classes (mg.)

young individuals also increased. Figure 27 shows changes in population densities of P. dumerilii throughout the year at both sites. Large numbers of Platynereis were present during the late autumn/winter period, with relatively small populations being present during the early spring and summer.

Fig. 27

Changes in population density of Platynereis dumerilii on detached kelp at two sites in the Clyde Sea area.


Loch Ranza
Tomont End
No. of Platynereis 100g^{-1} weed dry weight
0
10
20
30
40
N D J F M A M J J A S O N D J F M
1976
1977
1978

DISCUSSION

A number of workers have shown that polychaetes (larvae especially) actively absorb amino-acids and other small organic molecules (D.O.M.) from the surrounding medium (Chapman and Taylor, 1968; Bass *et al.*, 1969; Taylor, 1969; Stephens, 1975; Jørgensen, 1979; Jørgensen and Kristensen, 1980). D.O.M. may thus also be of some importance to *Platynereis*, i.e. growth may not be related solely to that material which is ingested. Since animals on both diets were kept in identical media, however, comparisons between growth rates should remain valid. D.O.M., of course, will be released from the food ration, more so (presumably) from rotting material, but differences are likely to be small and are overshadowed by the worms' performance on fresh weed. Exudates from fresh weed include polysaccharides and polyphenolics (Johnston, 1971; Tenore and Rice, 1980) although the exact chemical nature of individual substances is largely unknown.

Worms (particularly older individuals) feeding on fresh weed grew faster than their counterparts fed rotting material. This situation may be reversed in very young individuals, but insufficient data exist for rotting weed for any clear conclusions to be drawn as yet. The results, however, point to substratum digestion as being of primary importance to *Platynereis*.

No significant difference was found between the mean protein contents of fresh and rotting weed. This was contrary to expectation: an increase in protein is generally associated with the build-up of micro-organisms on rotting material. The reasons for this similarity and an assessment of the accuracy of protein estimation procedure have been fully discussed in Chapter 1 in relation to similar experiments carried out with *Psammechinus miliaris*. Also in the *Psammechinus* study, a significant reduction in the mean organic carbon content of rotting weed was found which, it was conjectured, corresponded with bacterial digestion of the structural and reserve polysaccharides of the weed. Here, although the mean organic carbon value for rotting weed was lower than for fresh, the difference was not statistically significant. A smaller number of determinations was made during the Platynereis study though (20 and 26, for fresh and rotting weed respectively) as compared with 51 and 46 during the Psammechinus work (see Chapter 1). Given the variability of fresh weed organic carbon values, the failure of the Platynereis data to reach statistical significance could simply be due to the smaller number of observations.

The organic carbon absorption efficiencies recorded illustrate the ability of Platynereis to digest kelp structural polysaccharides. Alginic acid is the principal structural polysaccharide in the Phaeophyceae (Percival, 1968), comprising 13-21% of dry solids in L. saccharina (Black, 1950). Cellulose accounts for no more than 5% (Percival, 1968). Some digestion of reserve polysaccharide may be accounted for in the absorption efficiencies recorded. The bulk of Laminaria protein is confined within the cell. Platynereis is a very "tidy" feeder, its jaws making clean cuts in the weed, resulting in little cell disfigurement. Thus, cell wall digestion must occur to account for the high protein absorption efficiencies recorded.

It is pertinent to recall that Cammen (1980) found that Nereis succinea (Frey and Leuckart) was able to assimilate carbon from sterile plant detritus (Spartina) and that only 25% of its carbon requirement was derived from microbial sources. Tenore and Hanson (1980) and Tenore (1981) also considered that the sedentary polychaete Capitella capitata derives some nourishment directly from the alga Gracilaria. Neither alginase nor cellulase enzymes have yet been demonstrated in Platynereis, although cellulase activity has been reported in the related Nereis virens (Lewis and Whitney, 1968).

Interestingly, in *Nereis,* cellulase activity proved to be latent; release being stimulated by the passage of algae through the gut. Thus dietry history could greatly influence experimental conclusions and induction mechanisms may account for the dearth of reports concerning cellulase activity in other polychaetes. Lewis and Whitney (1968) also showed, in *Nereis*, that cellulase was derived exclusively from the gut wall and not from bacteria living in the gut. The older, tougher weeds have larger quantities of structural polysaccharides and hence, more efficient organic carbon digestion is required for the efficient release of cell-content protein. *Platynereis* on both diets showed similar capabilities of organic carbon digestion, presumably related to their similar gut retention times.

Animals feeding on fresh weed, however, showed markedly higher protein absorption efficiencies than animals on rotting weed and showed a direct relationship between weed protein content and protein absorption efficiency. The high-protein samples were the thinner, softer, basal frond tissues where the levels of structural and reserve polysaccharides are lowest (see Johnston *et al.*, 1977) and from which protein may be extracted more efficiently. Animals feeding on rotting weed showed no relationship betweed absorption efficiency and the protein content of ingested weed. In rotting weed, protein is readily available in the form of microbes. Bacterial digestion of the algal cell walls will also faciliatate extraction of the remaining algal protein. Given the high protein absorption efficiencies of *Platynereis* on fresh weed, one can assume that algal proteins remaining in rotting weed will also be extracted efficiently. The explanation for the independence of absorption efficiency and protein content of rotting weed must then be that some micro-organism protein is not available to *Platynereis*, i.e. bacterial protein enclosed within tough bacterial cell walls (cf. Birkbeck and McHenery's (1982) data on bacterial lysis by *Mytilus*). Thus, in *Platynereis* , substratum rather than micro-organism digestion is of paramount importance (see also Cammen, 1980; Tenore et al., 1982). Presumably, the absorption efficiency is related to the level of algal protein remaining. Since animals feeding on both diets, i) produce the same quantities of faeces, and ii) have the same gut retention times, animals feeding on fresh weed will be obtaining larger quantities of protein per unit time. This explains their increased rate of growth (cf. Briggs et al., 1979).

Polychaetes envelop their faeces in a peritrophic membrane (Fretter and Graham, 1976). This membrane consists of a gelatinous protein stabilized by chitin fibres. Thus, absolute values for faecal protein and organic carbon will be elevated, resulting in absorption efficiencies lower than reality. This error, however, does not affect relative comparisons between diets.

Platynereis constructed tubes preferentially amongst fresh weed. Although Platynereis may occasionally leave its tube to feed (Casanova and Coulon-Ross, 1967), it generally feeds in the vicinity of the tube entrance. In the field, vacating its tube would make Platynereis vulnerable to attack by predators. Having constructed its tube on fresh weed, it is clearly adaptive to eat this material also. Tube longevity would be severely prejudiced by selecting disintegrating material as a foundation. Once such a foundation had lost its rigidity, the weed bed would gradually consolidate, blanketing Platynereis, restricting water movement and reducing the oxygen tension in the water around the worms due to microbial B.O.D. Additionally, the construction of tubes on fresh weed plays an important part in maintaining the cohesion of detached weed beds. Often, tubes are built across more than one frond: they may also incorporate other material such as stones and shells etc. In this way, present and future resources for Platynereis and other detritivores are preserved from the dispersive action of tidal currents.

Platynereis feeds in the same area for 2-3 days, recropping previously exposed algal tissue. After a few days, however, a worm may alter its feeding area altogether or it may concentrate on only a part of the total area previously exposed. In this way, Platynereis ultimately generates new areas for colonization by saprophagous micro-organisms. Its effectiveness in this respect though, is substantially less than that of other animals which graze randomly. Kohlmeyer (1971) noted that Platynereis tube fibres were often found in association with diseased bladders of Sargassum spp. He considered that the attachment of these fibres to the alga possibly resulted in physical damage and promoted colonization by saprophagous micro-organisms. This may be an additional method whereby Platynereis effects decomposition of detached kelp fronds.

Substratum comminution by Platynereis, however, remains its most important contribution to kelp decay processes. The results presented indicate that Platynereis faeces decompose much faster than intact weed, but that this rate is comparable with that for weed homogenized to an equivalent size. Clearly, surface area available for colonization by saprophagous micro-organisms is the prime regulator of faecal decomposition rate. Ciliate population densities on Platynereis faeces are much lower than on either homogenized or intact weed, due to the reduced nutritional value of faeces following digestion. Although bacteria appear to be of no importance in nereid digestive processes (Lewis and Whitney, 1968), viable bacteria associated with the egested faeces will multiply rapidly after defaecation. Actively-feeding Platynereis will be enriching underlying sediments with a steady output of faecal material which, following maturation, will be rich in micro-organisms. Infaunal deposit feeders underlying the weed piles will thus benefit from a continuous supply of nutrient-rich detritus. In this way, Platynereis helps to stabilize the input of fine detritus to the sediments (see also Chapter 3 and the role of Gammarus locusta (L.)).

Platynereis generally spawns in its second year (Hauenschild, 1955), although in the laboratory, it can spawn at 3 months old (Hauenschild, 1955). Spawning occurs around June (Rasmussen, 1973; Boilly-Marer, 1974) but its onset can be brought forward in response to a previous mild winter (Rasmussen, 1973). *Platynereis* is noted for its extreme reproductive plasticity (Pettibone, 1963; Crothers, 1966; Mercer and Dunne, 1973). *Platynereis* populations found on detached weed will thus consist of individuals which have (i) settled as larvae from the plankton, (ii) migrated over the seabed as larvae onto the weed, (iii) migrated as adults onto the weed and (iv) matured into adults from (i) and (ii).

CHAPTER 3

THE ROLE OF GAMMARUS LOCUSTA (L.)

INTRODUCTION.

Amphipods have featured prominently in much of the recent work concerning detritivore involvement in aquatic plant litter decomposition (Fenchel, 1970; Hargrave, 1970; Mann, 1972; Bärlocher and Kendrick, 1973a, b, 1975; Kostalos and Seymour, 1976; Harrison, 1977; Lopez et al, 1977; Levinton et al., 1976; Zimmerman et al., 1979; Robertson and Mann, 1980; Morrison and White, 1980). They are considered to be important links in plant-detritus based food chains (Odum and Heald, 1972). The family Gammaridae has been studied extensively, both in freshwater (Bärlocher and Kendrick, 1973a,b, 1975; Moore, 1975; Monk, 1977; Sutcliffe et al., 1981) and marine (Dahl, 1948; Martin, 1966; Jazdzewski, 1973; Harrison, 1977; Zimmerman et al., 1979; Morrison and White, 1980) ecosystems. The marine amphipods such as Gammarus oceanicus Segerstråle, Lagunogammarus salinus Spooner and L. zaddachi Sexton are commonly found in accumulations of decaying macrophyte material, both littorally and sublittorally (Jazdzewski, 1973; Rasmussen, 1973; Harrison, 1977).

In the Clyde Sea area, Gammarus locusta (L.) is an important sublittoral gammaridean amphipod. In the immediate sublittoral, it is found in association with various filamentous algae (pers. obs.). Withers et al. (1975) found this amphipod in association with Sargassum muticum (Yendo) Fensholt. As found by Steen (1951), this animal is absent from the Laminaria zone and it does not contribute significantly to the kelp holdfast fauna (Moore, 1973, 1978). G. locusta is found in abundance, however, in sublittoral accumulations of detached L. saccharina (approximate water depth 17-25m). Sars (1890-1895) and Stephensen (1940) also noted the occurrence of this amphipod among similar beds of decaying algae in Norwegian waters. The following work examines the role of G. locusta in sublittoral algal decomposition.

Identification of Gammarus spp. has caused difficulties in the past, as illustrated by the problems that Rasmussen (1973) experienced. Help is provided by Rygg's (1974) useful key to juvenile gammarids from the Baltic. A number of other authors have provided guidelines for identifying the various northern Gammarus spp. (Sexton, 1942; Segerstrale, 1947; Spooner, 1947, 1951) and Lincoln (1979) has summarized the British species. Lagunogammarus zaddachi is the species most commonly confused with G. locusta although these two species can be readily separated following Sexton (1942) or Lincoln (1979). They occupy different habitats, G. locusta being mainly marine whilst L. zaddachi prefers brackish waters (Serventy, 1935; Sexton, 1942; Jazdzewski, 1973). G. locusta can tolerate salinities as low as 15°/oo but L. zaddachi inhabits much lower salinity water (4-10°/oo) (Fenchel and Kolding, 1979).

MATERIALS AND METHODS

Gammarus locusta occurred locally in large numbers (< 40 adults/100g dry wt. of weed) on beds of detached Laminaria saccharina, particularly in Kames Bay (Isle of Cumbrae, see Fig. 1). Observations on G. locusta feeding in the laboratory and gut content analysis from freshly-collected animals demonstrated that L. saccharina constitutes the major component of this animal's diet. The role of Gammarus in weed decomposition was examined by comparing its responses to both fresh and rotting weed (as defined in the Introduction). Choice experiments and comparisons of juvenile growth and survival, copulatory behaviour and fecundity of adults were made in animals feeding continuously on each diet. In addition, the direct effect of Gammarus on decomposition and its possible coprophagous habits were examined. All experimental animals were collected by beam trawling (2 metre beam, mesh 25mm) over the beds of detached weed in Kames Bay (depth range 17-25m). G. locusta is very hardy and suffered no damage during collection. It survived in the laboratory for several months. Sexton (1924, 1928) and Greze (1971) found that G. chevreuxi Sexton and G. subtypicus Stock respectively also survived well in captivity. Prior to experimental use, wild-caught G. locusta were allowed to acclimatize to laboratory conditions for 14 days on their experimental diet.

1) Comparison of growth and survival in juvenile G. locusta

Comparisons of juvenile growth rates have been used to indicate the relative importance of different diets to G. locusta. Following copulation, gravid females were isolated in aerated seawater on a diet of rotting kelp. These females were examined daily and the liberated juveniles collected. Juveniles to be isolated on different diets, were picked at random from a mixture of different broods. No less than fifteen juveniles were present in each dietary group.

In addition, ten juveniles were collected and killed to determine mean size at the beginning of the experiment. Each group of amphipods was kept in 1-litre beakers with 800ml of Millipore-filtered (0.3µm pore size) seawater together with their respective food. The beakers were aerated and placed in constant temperature water baths. The temperature was varied between experiments. Diets used were: (i) rotting *L. saccharina*, (ii) fresh, intact *L. saccharina*, (iii) homogenized fresh weed, (iv) fresh faeces of the polychaete *Platynereis dumerilii*, (v) aged faeces of *P. dumerilii*, (vi) fresh faeces of the sea urchin *Psammechinus miliaris* and (vii) aged faeces of *P. miliaris*. (In (iv) to (vii), both urchins and worms had been feeding on fresh *L. saccharina*). A starved group served as a control. Martin (1966) found that food texture was important in food selection by *Marinogammarus* spp. (sens. lat.). These animals avoided the tough laminarian and fucoid algae. It was considered that the intact, fresh *L. saccharina* might be too tough for newly hatched juveniles and, for this reason, homogenized fresh weed was used in these experiments. Thus, the ability of *G. locusta* to digest this diet was examined, not their ability to ingest the substratum in nature. A number of comparisons between the intact and homogenized weed were made, however, to establish the validity of this assumption. The aged faecal pellets of *P. dumerilii* and *P. miliaris* were pellets which had been left in running seawater for 10-15 days. This corresponded with the period required for the largest micro-organism populations to develop on such material (see Chapters 1 and 2). The number of diets to be compared in any one experiment depended on the numbers of juveniles available at any time. The water and food material were changed every day. In addition to preventing the build-up of waste metabolites, this allowed for the removal of any carcasses (which would otherwise be cannibalized) and the counting of remaining animals. The removal of carcasses was particularly important with the starved group. The experiments were concluded when obvious size differences could be seen between amphipods on different diets or when copulating couples were found. The dry weights of amphipods on the different diets was then determined. Some of the adult amphipods produced by feeding juveniles on fresh and rotting weed were needed alive for other experiments (see the following section) and so some indirect method for determining dry body weight was needed. Kinne (1961), Vlasblom (1969) and Greze (1972) used body length as a size index. Stretching of the body during handling or contraction during killing, however, can cause great inaccuracy. Moore (1978, 1981) used the sizes of particular body tagmata as indices of total length in the amphipods Corophium bonnellii Milne Edwards and Lembos websteri (Bate) to counter the effects of body curling. Figure 28 shows the relationship between head length and dry weight of freshly collected G. locusta (including gut contents) (oven dried at 60°C). Head length was measured under a binocular microscope with an eye-piece graticule. Live animals were placed in a watch glass with all but a drop of water removed so that they were immobilised. Amphipods not required alive were killed in 5% formalin. As indirect measurements were used for the living amphipods, it was considered inappropriate to use direct methods to determine the dry weight. As a result, head length measurements were also used for the dead amphipods. It was found that with careful handling, measurements of head length taken before and after killing were identical.

2) Comparison of fecundity of G. locusta.

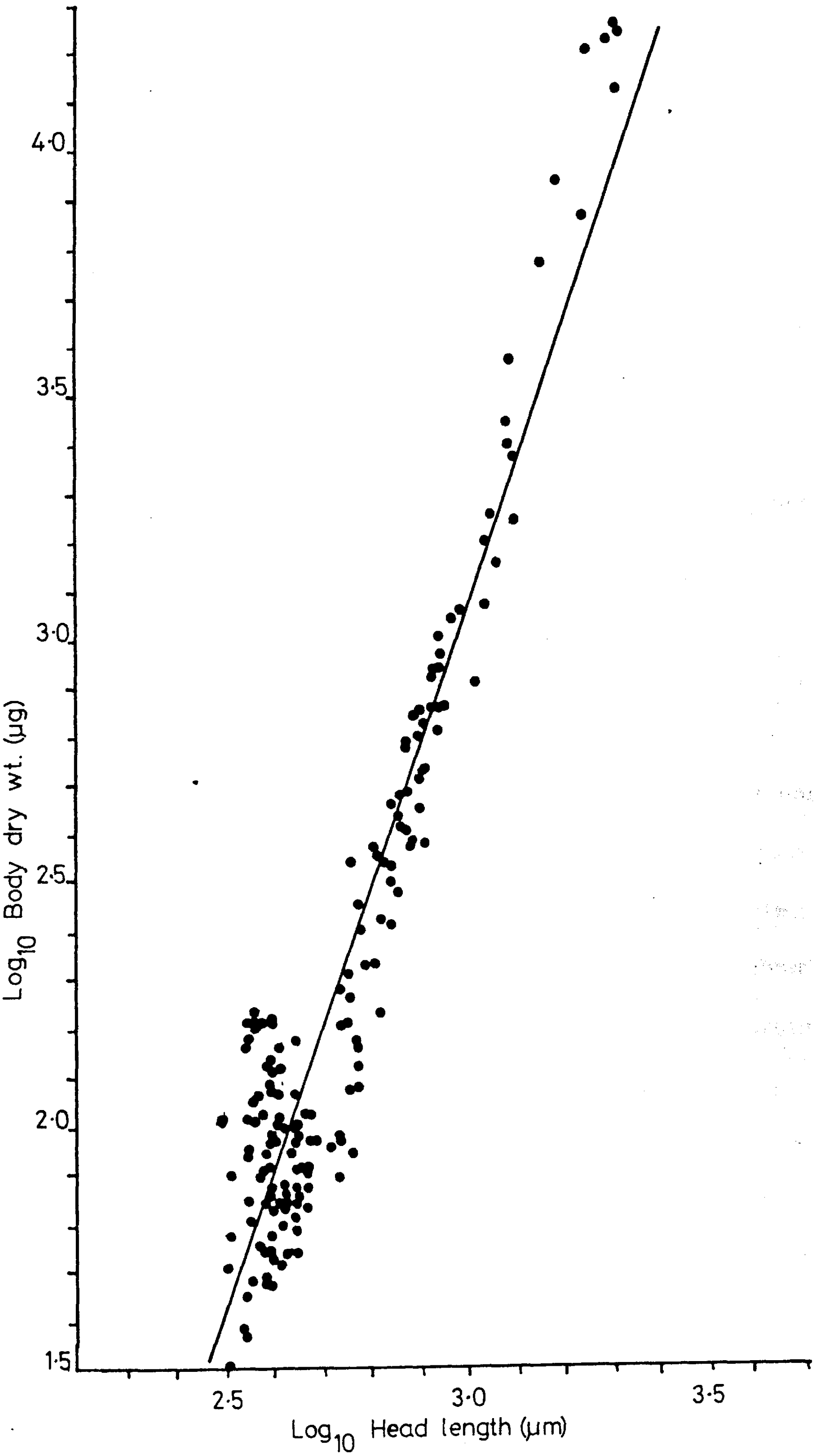
Fecundity was used as an index of nutritional quality of fresh and rotting weed. A relationship between female dry weight and the numbers of eggs produced was derived for amphipods feeding on each diet. Two groups of amphipods were used, (i) animals that had been fed both as adults and juveniles (see above) on either fresh or rotting weed and (ii) adults that had been taken from the field

Fig. 28

The relationship between head length (μm) and body dry weight (μg) in freshly collected Gammarus locusta

Equation of line of best fit: $\log y = 2.94 \log x - 5.77$

($r = 0.943$, d.f. = 198, $P < 0.001$)



4·0
3·5
3·0
2·5
2·0
1·5
Log$_{10}$ Body dry wt. (µg)
2·5
3·0
3·5
Log$_{10}$ Head length (µm)

and subsequently isolated on either of these two diets. It can be assumed that the wild amphipods had all been reared on similar diets. Thus four different categories offemales were confined in groups with an excess of their particular diet and an arbitrary number of males. In all cases, wild males collected from Kames Bay were used. Whenever coupling occurred, that pair of amphipods was isolated in a container of aerated seawater with food. When the couple separated following copualtion and egg laying, the female was killed in 5% formalin. All eggs were removed from the brood pouch (using a blunt seeker) and counted. Head length was measured under a dissecting microscope and dry weight was derived as above. Various errors are inherent in this procedure, viz. (i) variations in gut fullness were ingored in dry weight determinations, (ii) head length will usually increase after a moult, whereas number of eggs laid by that individual after the moult should correctly be referred to pre-moult head size, but moults are often broken and even measurement of intact moults may be unrealistic due to flattening, and (iii) the same calibration curve has been used irrespective of diet. Dry weight of the mother will vary during the intermoult period depending inter alia on degree of cuticular calcification after the previous moult. Any post-moult assessment of pre-moult dry weight is thus difficult and would at least need to include the weight of the cast cuticle. This was often damaged, e.g. by male feeding, since it was impossible to supervise all moult activity. In the interests of uniformity, these constraints have been by-passed presently by optimizing dry weight estimations to post-moult head size field equivalents. Results should therefore be regarded as preliminary, but errors should be comparable between groups. The initial acclimation period ensured the liberation of pre-existing broods. Experiments were conducted at a constant temperature of 15°C.

3) Comparison of the number of young produced

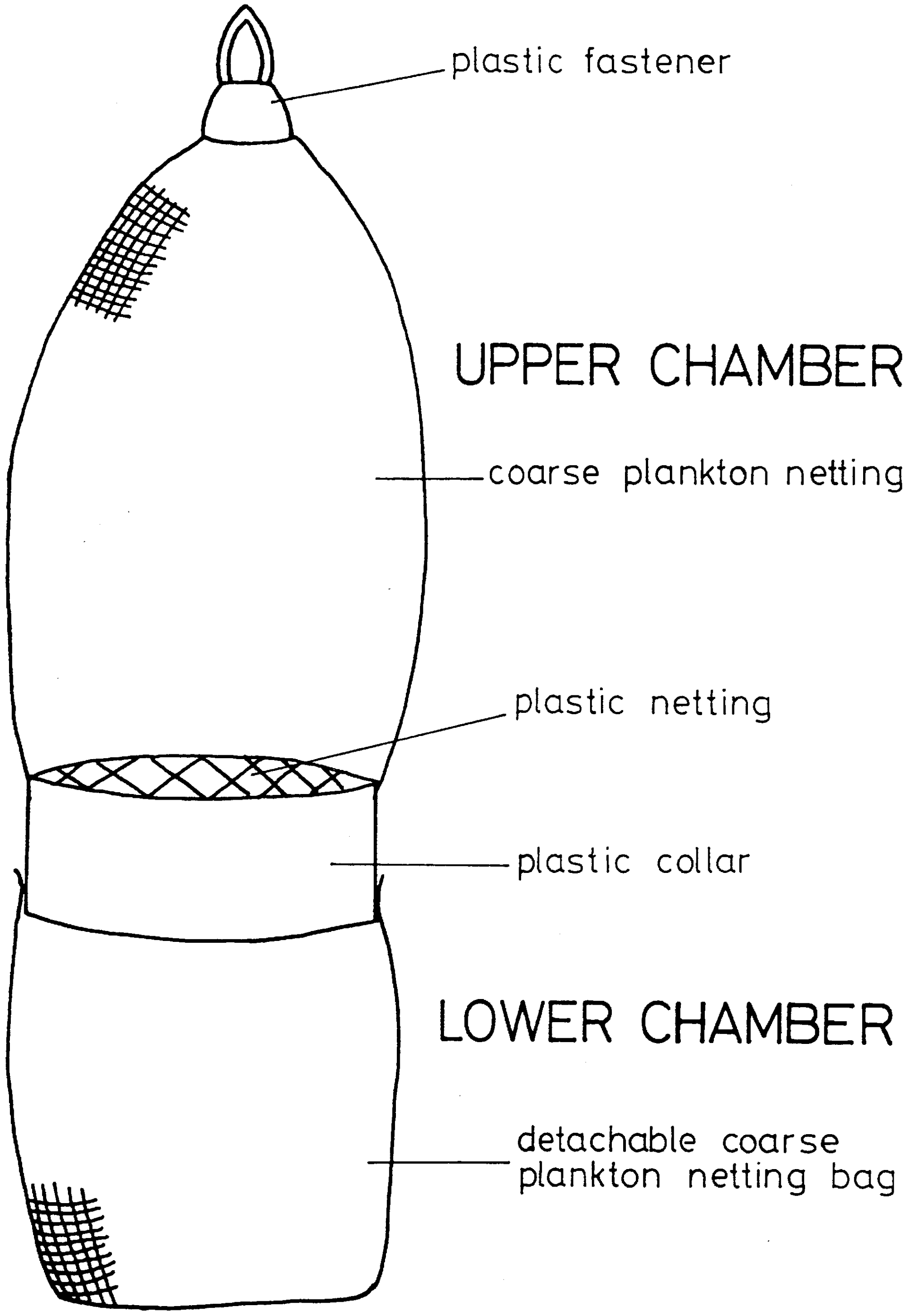
The fertility of females feeding on fresh or rotting weed was also compared. Equal numbers of males and females, collected from Kames Bay, were isolated on one of the two diets. Following 14 days acclimatization, couples were isolated in separate vessels of aerated seawater with their respective diet. The male was removed once it had released the female following copulation. Each day, the water and food were replaced and the female examined for brood hatching. The colour of the brood changed from greyish green (the colour of the eggs) to reddish brown (corresponding to the newly hatched individuals) when this occurred. Hatching was confirmed by examination of the female under a dissecting microscope. The juveniles were collected and counted on successive days, as they were released from the brood pouch. Female's head length was measured live (see previous section) and she was returned to the original container to mate again. The measurement of the head did not appear to cause any physical damage and no deaths resulted. A number of females, however, did die when copulating. When this occurred, these females were replaced.

4) The effect of G. locusta on decomposition

G. locusta was observed in the laboratory to feed at the edges of Laminaria fronds, particularly where decompoaition was occurring. The following work was designed to assess the importance of this behaviour in decomposition. Three (A,B and C), two-chamber, coarse plankton net cages (8 meshes/cm) were used (Fig. 29), The two chambers were separated by coarse plastic netting (1 cm mesh). Fresh L. saccharina was placed in the upper chamber of all three cages. The previous chapters have established that Platynereis dumerilii and Psammechinus miliaris (in particular) aid decomposition by exposing algal tissue to saprophagous micro-organisms. These

Fig. 29

Design of two-chamber net cages used to study the effect of Gammarus locusta on decomposition (see text for details).


plastic fastener
UPPER CHAMBER
coarse plankton netting
plastic netting
plastic collar
LOWER CHAMBER
detachable coarse plankton netting bag

animals (two of each) were added to the upper chamber of cages A and B. The Psammechinus used had test diameters greater than 15.0mm and thus were physically restricted to the upper chamber. Upon admission to the upper chamber, Platynereis readily constructed a tube within the weed and was thus also restricted (behaviourally) to this chamber. The faecal pellets of these animals dropped through into the lower chamber. Into cage B also, five Gammarus were added. These could migrate freely between the two chambers. The three cages were kept in total darkness in a tank of running seawater for about a month. At convenient intervals (see Fig. 36), weed samples were removed from the upper chambers of cages A, B and C and faeces from the lower chamber of A and B. The number of amphipods found in association with the faeces was also noted on each occasion. The samples were mixed with 5% formalin and the numbers of associated ciliates determined (by Vollenweider's (1969) method) and used as an index of decomposition rate. Cage C, with no animals present, indicated the rate of weed decomposition due to microbes alone. By comparing the different graphs, both the effects on decomposition of Platynereis and Psammechinus combined with G. locusta can be demonstrated, as well as an indication be gained of whether G. locusta indulges in coprophagy by choice.

5) Choice experiment

Choice tests were carried out to examine whether or not Gammarus showed a preference for decaying L. saccharina. Two large mesh bags (8 meshes/cm) each containing either fresh or rotting L. saccharina were connected horizontally by a short length of plastic tubing. The bags were secured to the plastic tube using rubber bands. The experiment was conducted in total darkness in a large tank of running seawater. The apparatus was placed across the current of water so that there was no flow between the two chambers. Thirty adult amphipods were placed into the apparatus (as follows) and left for one day. The animals were tipped into the central plastic tube with the rotting weedbag attached and prevented from moving into the bag by throttling its neck. The fresh weed bag was replaced on the other end of the tube and its neck also throttled. The whole apparatus was submerged and the two bags released gently and simultaneously. The animal's mobility necessitated care in handling this apparatus. The following day, both mesh bags were carefully removed from the plastic tubing, their contents emptied separately and the numbers of amphipods in each bag counted.

All regressions were calculated by the method of least squares and regression lines compared by covariance analysis (Snedecor and Cochran, 1967). Chi-squared values were calculated without Yate's correction.

RESULTS.

1a) Comparison of survival

Table 4 shows the percentage survival of juvenile Gammarus on different diets at 21 days, to allow comparison of runs of differing duration. Each section of the Table compares two diets and each row relates to a separate experimental run. Considerable variation in survivorship is apparent for any one diet, due mainly to intrinsic differences between the various groups of juveniles used. Comparisons should therefore only be made between different diets within the same experiment. Table 4 has been constructed (from a number of multi-diet experiments) to demonstrate the different effects of these diets on survivorship using these within-experiments comparisons. Homogenized fresh weed promoted greater survival than intact material, but lower survival than rotting weed. The remaining diets, excluding fresh Psammechinus faeces, all induced lower survival than homogenized fresh weed. The fresh Psammechinus faeces produced similar survival to this latter material. Overall, rotting kelp promoted the greatest survival in juvenile Gammarus. Temperature seemed to have little effect on survival.

1b) Comparison of growth

Table 5 compares the projected dry weights of amphipods at the end of the experimental period for groups of animals reared on different diets. The mean dry weights of amphipods were compared using Student's "t" tests and illustrate significant differences between the various diets. Homogenized fresh weed promoted faster growth than intact material but slower growth than rotting kelp. The fresh faeces of Platynereis and Psammechinus produced faster growth than did similar, aged material but produced slower growth than homogenized fresh material. Rotting weed promoted the fastest growth of all diets tested. Comparing the faeces of the urchin and the worm, the fresh

Table 4

Percentage survival of juvenile *Gammarus locusta* on different diets at 21 days in growth experiments of variable duration.

Trial	Diets		Control group	Temperature (°C)
	Homogenized fresh weed	Intact fresh weed		
1	40	13	7	15
2	40	13	0	15
3	47	40	0	15
4	57	39	39	19
	Rotting weed	Homogenized fresh weed		
5	67	67	7	9
6	93	100	7	12
7	93	40	0	15
8	100	73	0	15
9	87	40	27	15
10	100	73	0	17
11	53	40	-	18
	Homogenized fresh weed	*Psammechinus* faeces (fresh)		
12	100	93	7	12
13	93	80	0	14
14	40	87	27	15
15	94	38	31	18
	Psammechinus faeces (fresh)	*Psammechinus* faeces (aged)		
16	93	80	7	12
17	87	40	27	15
	Homogenized fresh weed	*Platynereis* faeces (fresh)		
18	93	80	0	14
19	40	27	7	15
20	33	7	0	15
21	40	87	27	15
22	73	0	0	17
23	93	63	31	18
	Platynereis faeces (fresh)	*Platynereis* faeces (aged)		
24	87	87	27	14
25	7	7	0	15
26	20	0	7	18

Table 5

Comparison of derived dry weights (mg) of G.locusta fed different diets in experiments of differing temperature and duration.

Diets: Rotting weed v. Fresh weed (homogenized)

Temp. (°C)	Mean dry weight of amphipod on Rotting weed (mg)	SD	Mean dry weight of amphipods on fresh weed (mg)	SD	t	df	Days
9	0.082	0.003	0.066	0.002	4.085***	65	17
12	1.701	0.273	0.985	0.125	2.443*	25	30
14	2.264	0.344	0.854	0.078	2.844*	19	40
15	2.400	0.182	0.850	0.119	5.121***	30	34
15	2.557	0.369	1.166	0.23	2.409*	14	27

Diets: Fresh (homogenized) v. Fresh (intact)

Temp. (°C)	Mean dry weight on homogenized weed (mg)	SD	Mean dry weight on intact weed (mg)	SD	t	df	Days
15	1.166	0.230	0.237	0.035	4.406**	9	27
19	0.387	0.079	0.292	0.079	0.315^{ns}	18	26

Diets: Fresh (homogenized) v. Psammechinus faeces (fresh)

Temp. (°C)	Mean dry weight on fresh(h) weed (mg)	SD	Mean dry weight on fresh Psamm. faeces (mg.)	SD	t	df	Days
12	0.985	0.125	0.626	0.089	2.261*	24	30
15	1.166	0.230	0.609	0.056	3.404**	16	27
18	1.392	0.169	0.622	0.108	2.761*	19	19

Diets: Psammechinus faeces (fresh) v. Psammechinus faeces (aged)

Temp. (°C)	Mean dry weight on Psammechinus faeces (fresh) (mg)	SD	Mean dry weight on Psammechinus faeces (aged) (mg)	SD	t	df	Days
12	0.626	0.089	0.126	0.047	4.967***	22	30
15	0.609	0.056	0.321	0.068	3.060**	17	27

Diets: Fresh weed (homogenized) v. Platynereis faeces (fresh)

Temp. (°C)	Mean dry weight on fresh weed (mg)	SD	Mean dry weight on Platynereis faeces (mg)	SD	t	df	Days
15	1.166	0.230	0.399	0.046	4.826***	15	27
18	1.392	0.169	0.376	0.054	4.770***	18	19

cont.

Diets: Platynereis faeces (fresh) v. Platynereis faeces (aged)

Temp. (°C)	Mean dry weight on Platynereis faeces (fresh) (mg)	SD	Mean dry weight on Platynereis faeces (aged) (mg)	SD	t	df	Days
15	0.399	0.046	0.166	0.059	3.780***	22	27

Diets: Psammechinus faeces (fresh) v. Platynereis faeces (fresh)

Temp. (°C)	Mean dry weight on Psammechinus faeces (fresh) (mg)	SD	Mean dry weight on Platynereis faeces (fresh) (mg)	SD	t	df	Days
15	0.609	0.056	0.399	0.046	2.870**	23	27
18	0.622	0.108	0.376	0.054	2.284*	14	18

Diets: Psammechinus faeces (aged) v. Platynereis faeces (aged)

Temp. (°C)	Mean dry weight on Psammechinus faeces (aged) (mg)	SD	Mean dry weight of Platynereis faeces (aged) (mg)	SD	t	df	Days
15	0.321	0.068	0.116	0.059	2.198*	17	27

Diets: Control group (no food) v. Beginning size.

Temp. (°C)	Mean dry weight of control group (mg)	SD	Mean dry weight of beginning group (mg)	SD	t	df	Days
19	0.092	0.007	0.506	0.008	3.26**	13	26

Note: Mean dry weight of newly hatched G. locusta kept from all experiments was 0.0577 ± 0.0057 mg.

n.s. = $P > 0.05$

* = $P < 0.05$

** = $P < 0.01$

*** = $P < 0.001$

and aged faeces of Psammechinus promoted faster growth than similar forms of Platynereis faeces. The control group also grew during the experiment (cf. animals killed at the beginning). Temperature affects growth of juvenile Gammarus. Figure 30 illustrates the relationships between mean increase in body weight per day and temperature for amphipods feeding on either the fresh (homogenized) or rotting kelp. Animals feeding on both diets showed significantly faster growth at higher temperatures (fresh, $r = 0.88$, df. 5, $P < 0.01$; rotting, $r = 0.95$, df. 4, $P < 0.01$). The regression equation for animals feeding on the rotting weed had a significantly higher elevation than for the fresh weed ($F_1 = 21.48$, df. 1,9, $P < 0.01$), illustrating that growth was significantly faster on rotting weed at higher temperature.

2) Comparison of fecundity in G. locusta

The relationships between numbers of eggs produced and female body weight (feeding on either the fresh (F) or rotting (R) weed) for animals (i) reared as juveniles and adults on the same diet (A) and (ii) isolated only as adults on one particular diet (B) are shown in Figs 31 and 32 respectively. The two parameters were significantly correlated in females of both categories and on both diets (fresh (A_F), $r = 0.82$, df. 9. $P < 0.01$; rotting (A_R), $r = 0.85$, df. 20, $P < 0.001$; fresh (B_F), $r = 0.55$, df. 11, $P < 0.05$; rotting (B_R), $r = 0.52$, df. 24, $P < 0.01$). In the first category, the regression equations for females feeding on the fresh (A_F) and rotting (A_R) kelp were compared using covariance analysis. The latter (A_R) was found to have a significantly higher elevation ($F_2 = 14.34$, df. 1,30, $P < 0.001$). Similarly, in the second category, the regression line for females feeding on the rotting weed (B_R) had a significantly higher elevation ($F_2 = 12.12$, df. 1,36, $P < 0.01$) than that for females feeding on fresh material (B_F). Thus, in both categories, for any given size of female, individuals

Fig. 30

Mean increase in body dry weight day^{-1} (µg) in <u>Gammarus locusta</u> fed either rotting kelp (R) or fresh kelp (F) at different water temperatures.

Equations of lines of best fit:

R: $y = 0.014x - 0.121$

F: $y = 0.008x - 0.073$

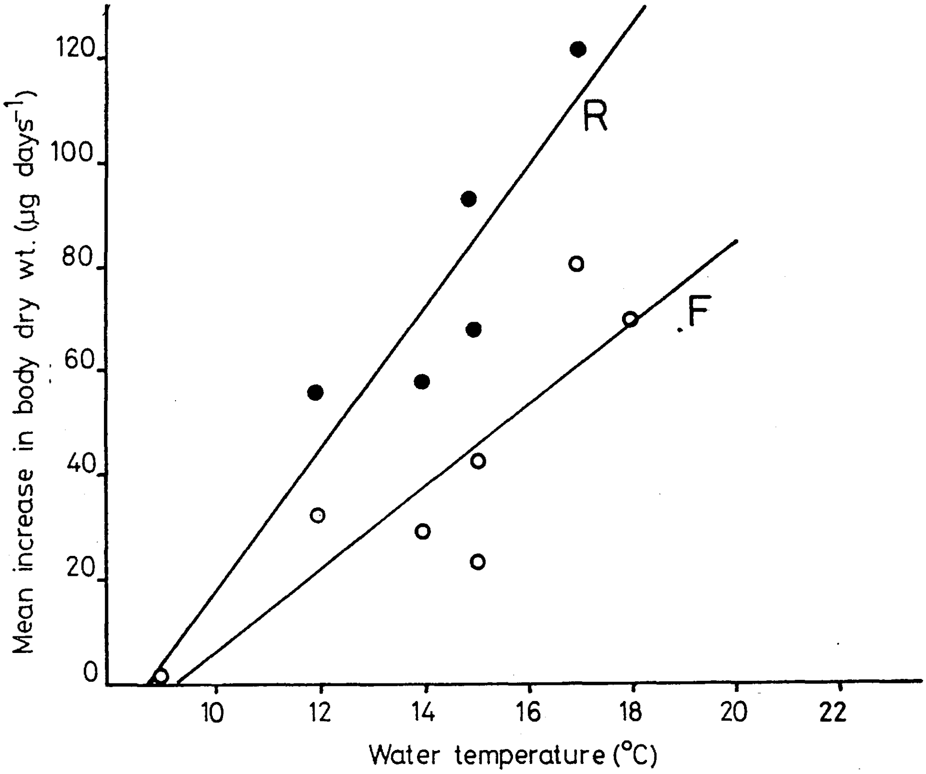

Mean increase in body dry wt. (μg days^{-1})
120
100
80
60
40
20
0
R
F
10
12
14
16
18
20
22
Water temperature (°C)

Fig. 31

Fecundity of female Gammarus locusta in relation to body dry weight (mg) for animals reared as juveniles and adults (cf. Fig. 32) on the same diet of either fresh kelp (A_F) or rotting kelp (A_R).

Equations of lines of best fit:

A_F: $y = 18.32x - 32.70$

A_R: $y = 35.18x - 60.13$

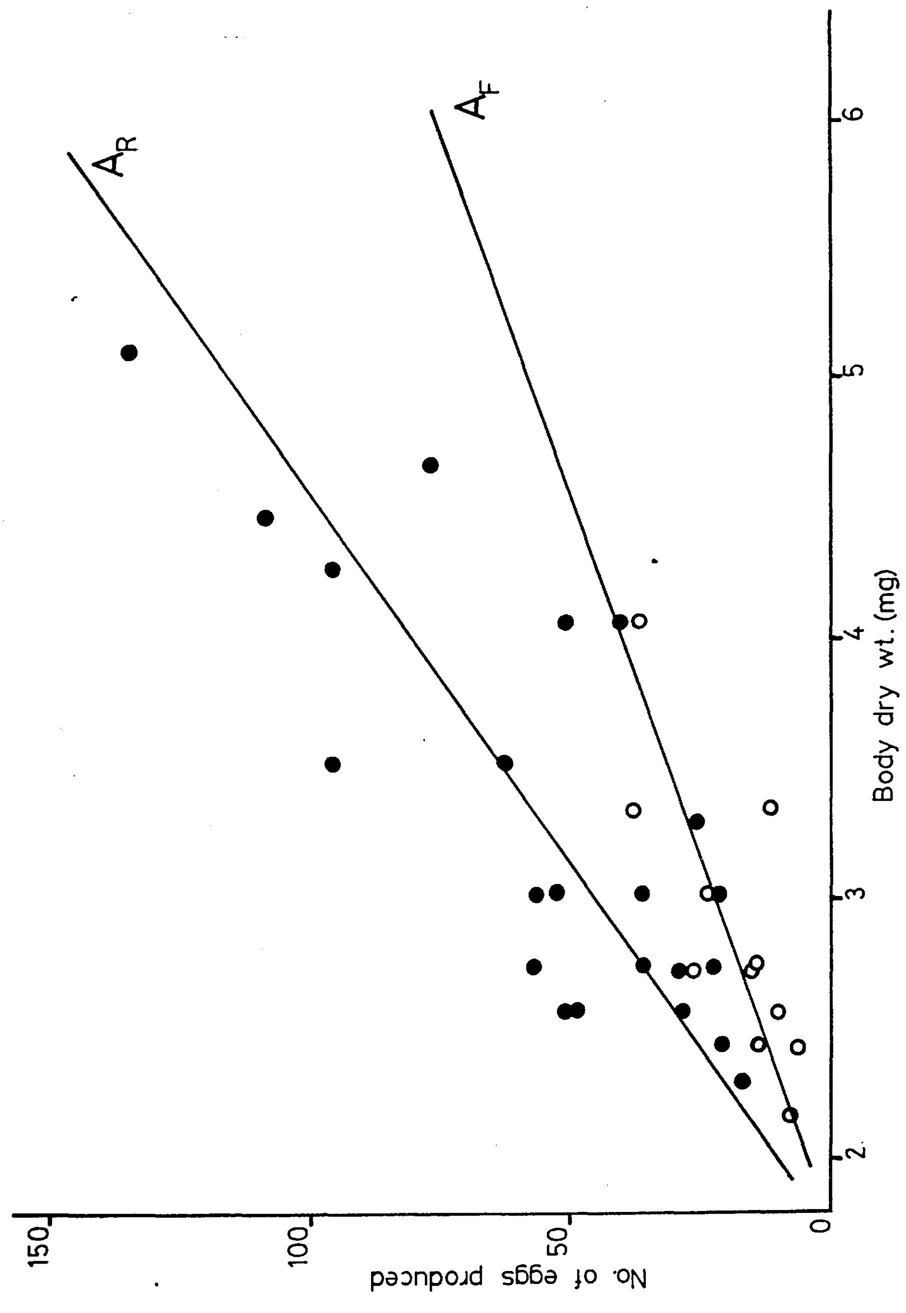

No. of eggs produced
0
50
100
150
Body dry wt. (mg)
2
3
4
5
6
A_R
A_F

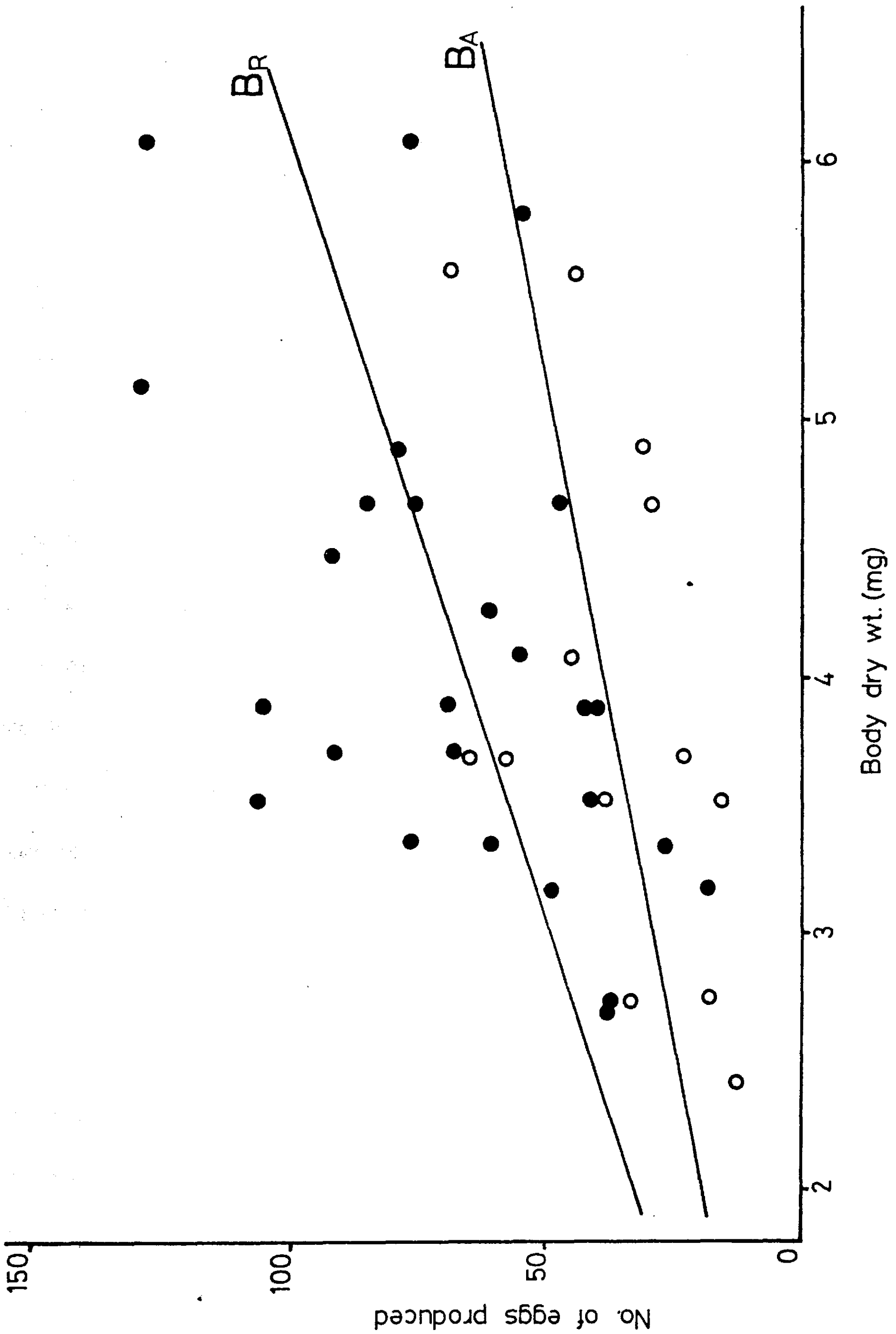
Fig. 32

Fecundity of female Gammarus locusta in relation to body dry weight (mg) for animals isolated only as adults (cf. Fig. 31) on a diet of either fresh kelp (B_F) or rotting kelp (B_R).

Equations of lines of best fit:

B_F: $y = 9.34x + 0.67$

B_R: $y = 16.30x + 0.29$


B_R
B_A
No. of eggs produced
0
50
100
150
Body dry wt. (mg)
2
3
4
5
6

fed on rotting weed produced more eggs. Comparing all four categories (Table 6), no significant difference existed between the regression lines A_F and B_F, suggesting that both groups of females were reared on similar diets. The slope of the regression line A_R however, was significantly higher than line B_R, suggesting that these animals were reared on diets of differing nutritional value. Figure 33 shows the significant correlation ($r = 0.86$, df. 27, $P < 0.001$) between numbers of eggs produced and body dry weight of wild females collected from the beds of detached weed in Kames Bay. All of these females had large quantities of algal material in their guts. This regression line (C) was compared with the previous relationships (A_F, A_R, B_F and B_R) using covariance analysis (Fig. 34 and Table 7). No significant difference was found between lines C and B_R. The elevation of line C however, was significantly ($P < 0.001$) higher than for A_F and B_F and the slope of C was significantly ($P < 0.01$) less than A_R. These results suggest that the females in B_R and C had consumed diets of similar nutritional value.

3) Comparison of numbers of young produced

Table 8 compares data on the various stages of the breeding cycle for amphipods feeding on either fresh or rotting weed. Generally, the time periods for the various stages were independent of diet. Differences between the two dietary groups, however, did occur in (i) the total number of copulations, (ii) the percentage of broods which were unsuccessful (with eggs being shed prematurely) and (iii) the number of the females which died during copulation. In all these instances, females feeding on fresh weed were the least successful. Figure 35 shows the relationship between the numbers of young produced and body dry weight of females feeding on either fresh or rotting weed. These parameters were significantly linked, only for females feeding on rotting kelp (fresh, $r = 0.32$, df. 6, $P > 0.05$; rotting, $r = 0.84$,

Table 6

F-ratios from covariance analysis comparing regressions of fecundity on projected female dry weight in two experimental categories (A and B - see text for details) and on two diets - fresh (F) and rotting (R) weed.

n.s. = $P > 0.05$,
* = $P \leqslant 0.05$
*** = $P \leqslant 0.001$

Regressions compared	Slope		Elevation	
	F_1	df	F_2	df
A_F v B_F	1.35 ns	1,20	0.47 ns	1,21
A_F v B_R	0.03 ns	1,33	8.39 *	1,34
A_R v B_R	6.00 *	1,44	0.67 ns	1,45
A_R v B_F	13.73 ***	1,31	15.14 ***	1,32

Fig. 33

Fecundity of wild female Gammarus locusta from detached weed in Kames Bay.

Equation of line of best fit: $y = 18.95x - 11.76$

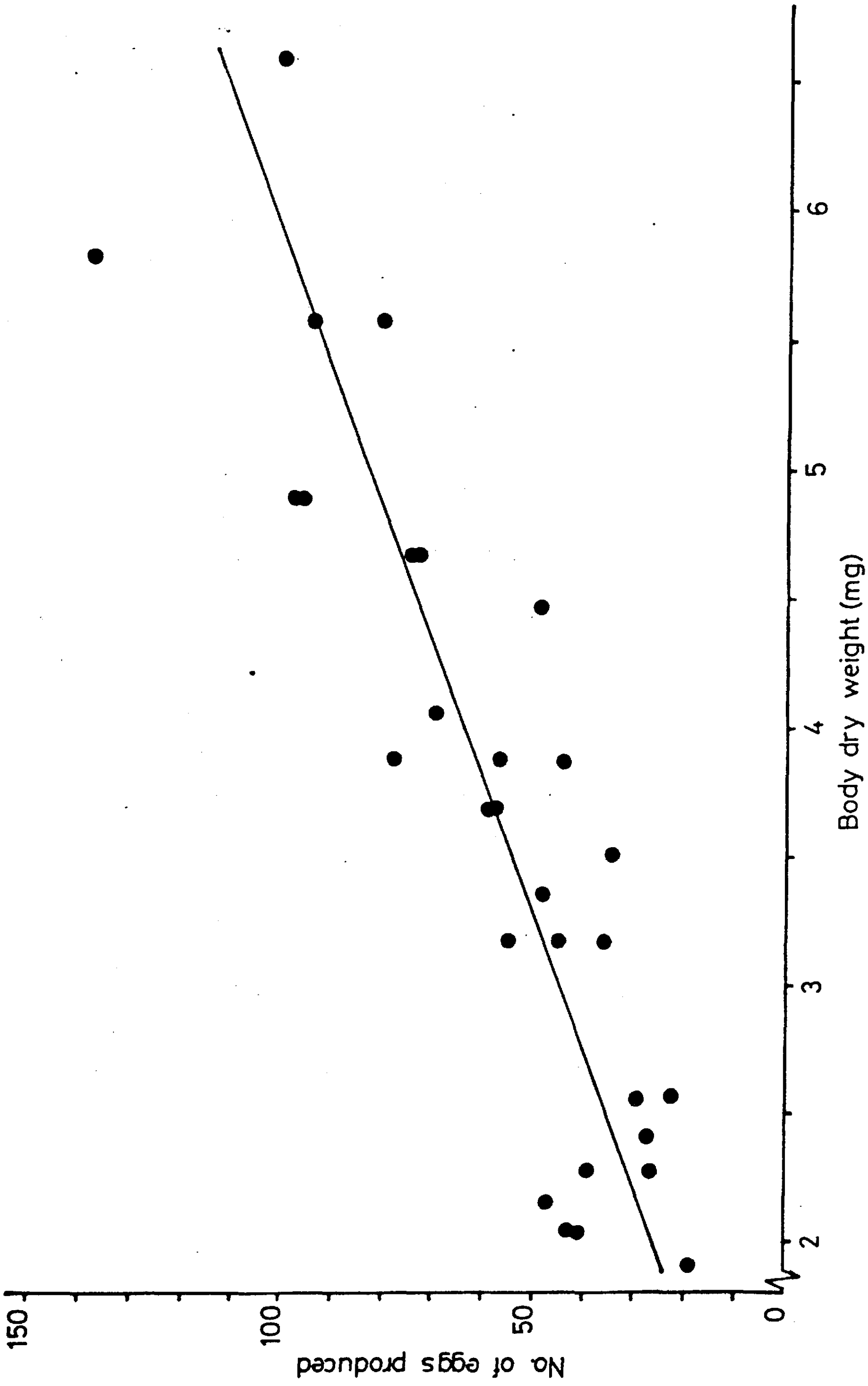

No. of eggs produced
0
50
100
150
Body dry weight (mg)
2
3
4
5
6

Fig. 34

Fecundity/dry weight relationships compared for experimental (A_F, A_R, B_F and B_R) and control (C) female Gammarus locusta, see Figs. 31, 32 and 33 and Tables 6 and 7.

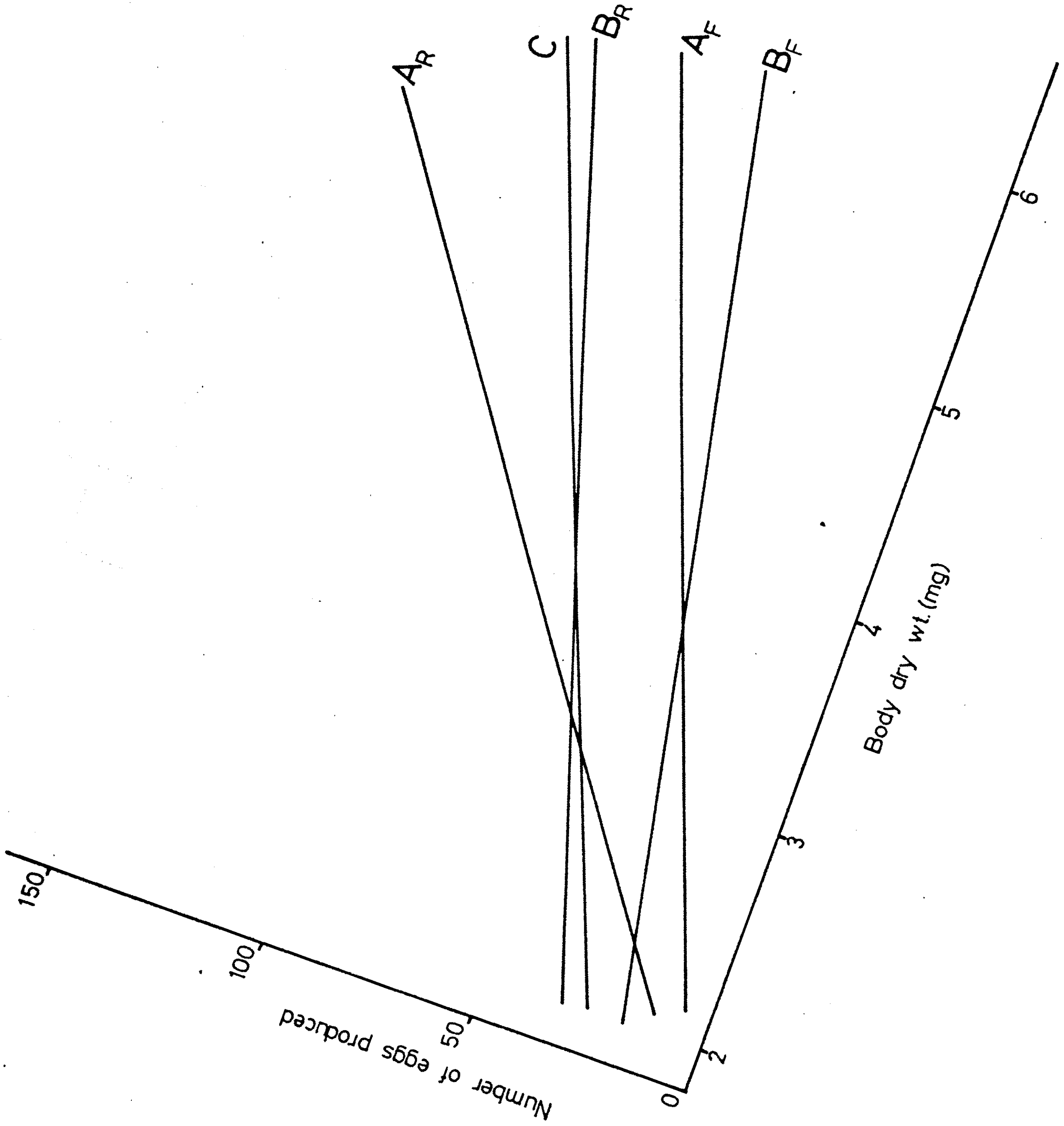

A$_R$
C
B$_R$
A$_F$
B$_F$
Number of eggs produced
0
50
100
150
Body dry wt.(mg)
2
3
4
5
6

Table 7

F-ratios from covariance analysis comparing regressions of fecundity on projected female dry weight in two experimental categories (A and B - see text for details) and on two diets, fresh (F) and rotting (R) weed with field-collected females (C).

n.s. = $P > 0.05$
* = $P \leqslant 0.05$
** = $P \leqslant 0.01$
*** = $P \leqslant 0.001$

Regressions compared	Slope		Elevation	
	F_1	df	F_2	df
C v A_F	0.01 ns	1,36	23.13***	1,37
C v A_R	10.74**	1,47	0.96ns	1,48
C v B_F	4.03*	1,38	22.45***	1,39
C v B_R	0.02 ns	1,51	0.08 ns	1,52

Table 8

Reproductive history of a group of 20 female *Gammarus locusta* fed either fresh or rotting *L. saccharina*.

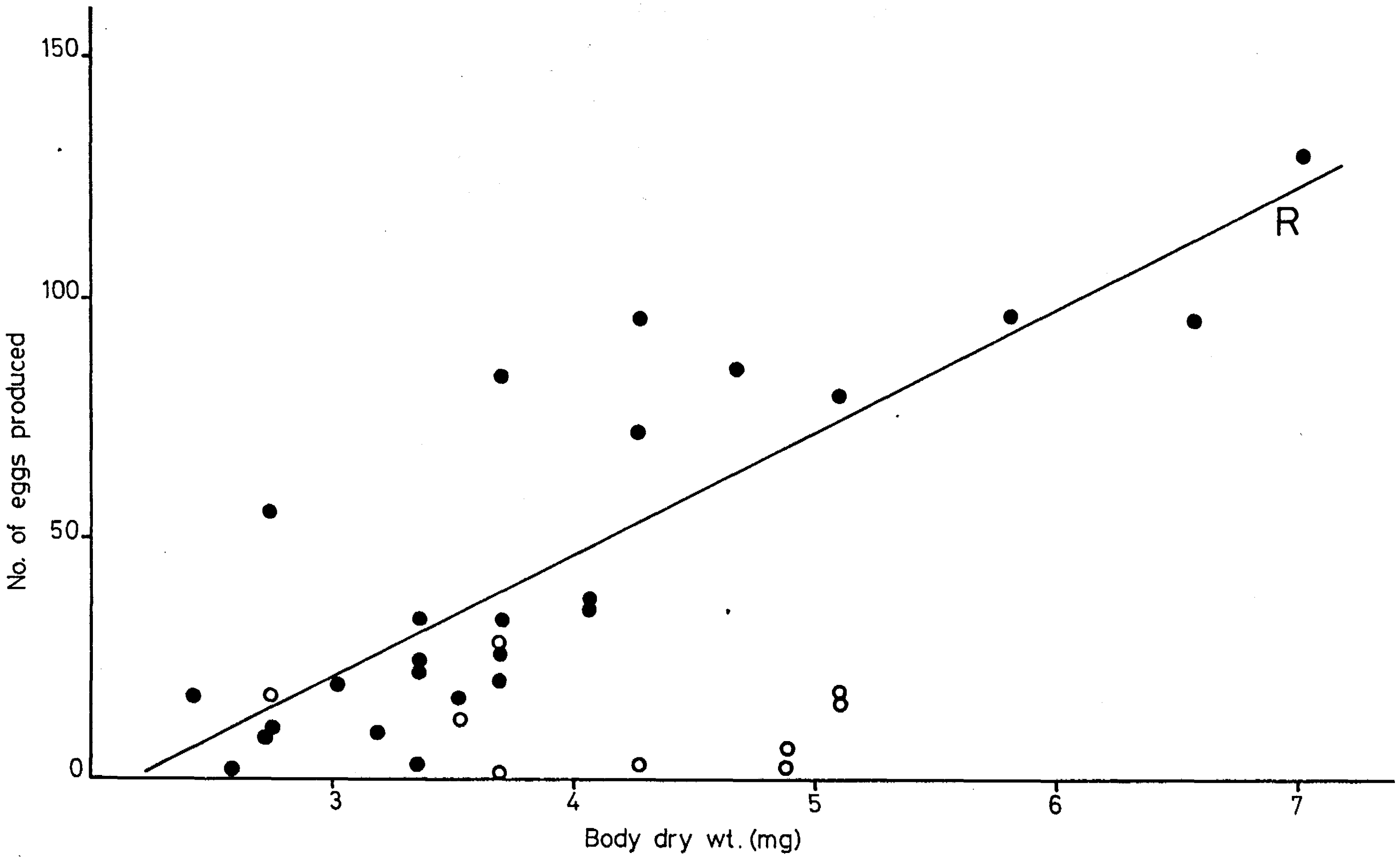
Paremeter	Fresh	Rotting
Length of coupling time	2.8 days	2.7 days
(range)	(1-6 days)	(1-10 days)
Total number of copulations	30	47
% brood failure	70	47
Number of females dying during copulation	6	0
Length of time for eggs to hatch (mean)	6.3 days	7.7 days
(range)	(4-8 days)	(4-10 days)
Length of time for juveniles to leave brood pouch (mean)	3 days	3 days
(range)	(1-5 days)	(1-6 days)

Fig. 35

Numbers of young produced by Gammarus locusta related to body dry weight of female feeding either on rotting weed (●) or fresh weed (o).

Equation of line of best fit for females feeding on rotting weed:

$$y = 25.37x - 56.27$$


150
100
50
0
No. of eggs produced
3
4
5
6
7
Body dry wt. (mg)
R

df. 23, $P < 0.001$). This relationship was compared with B_R (see section 2 - the relationship between numbers of eggs produced and dry weight for similar females feeding on rotting weed). Although these two regression lines did not differ significantly in slope ($F_1 = 2.30$, df. 1, 47, $P > 0.05$), B_R had a significantly higher elevation ($F_2 = 7.57$, df. 1,48, $P < 0.01$). Thus 100% fertility was not achieved even by females feeding on rotting weed.

4) The overall effect of *G. locusta* on decomposition

Figure 36 (a,b) shows the changes in ciliate numbers with time on *L. saccharina* when: (A)*Platynereis dumerilii* and *Psammechinus miliaris* were present, (B) when *G. locusta* was present in addition to the two above animals and (C) the weed alone was present. Initially, the ciliate numbers in A rose at a similar (Fig. 36b) or faster rate (Fig. 36a) than C. Later, however, the ciliate population in C overtook that found in A. The ciliate populations in B remained well below those found on the weed in either A or C.

Figure 37 (a,b) shows the changes in ciliate numbers found in association with the *Platynereis* and *Psammechinus* faeces when: (A) they remained undisturbed and (B) *Gammarus* was present. Consistently, with *Gammarus* present, a smaller ciliate population resulted. The amphipods showed an apparent preference for this material ($\chi^2 = 6.4$, df.1, $P < 0.05$), although geotactic responses could complicate interpretation.

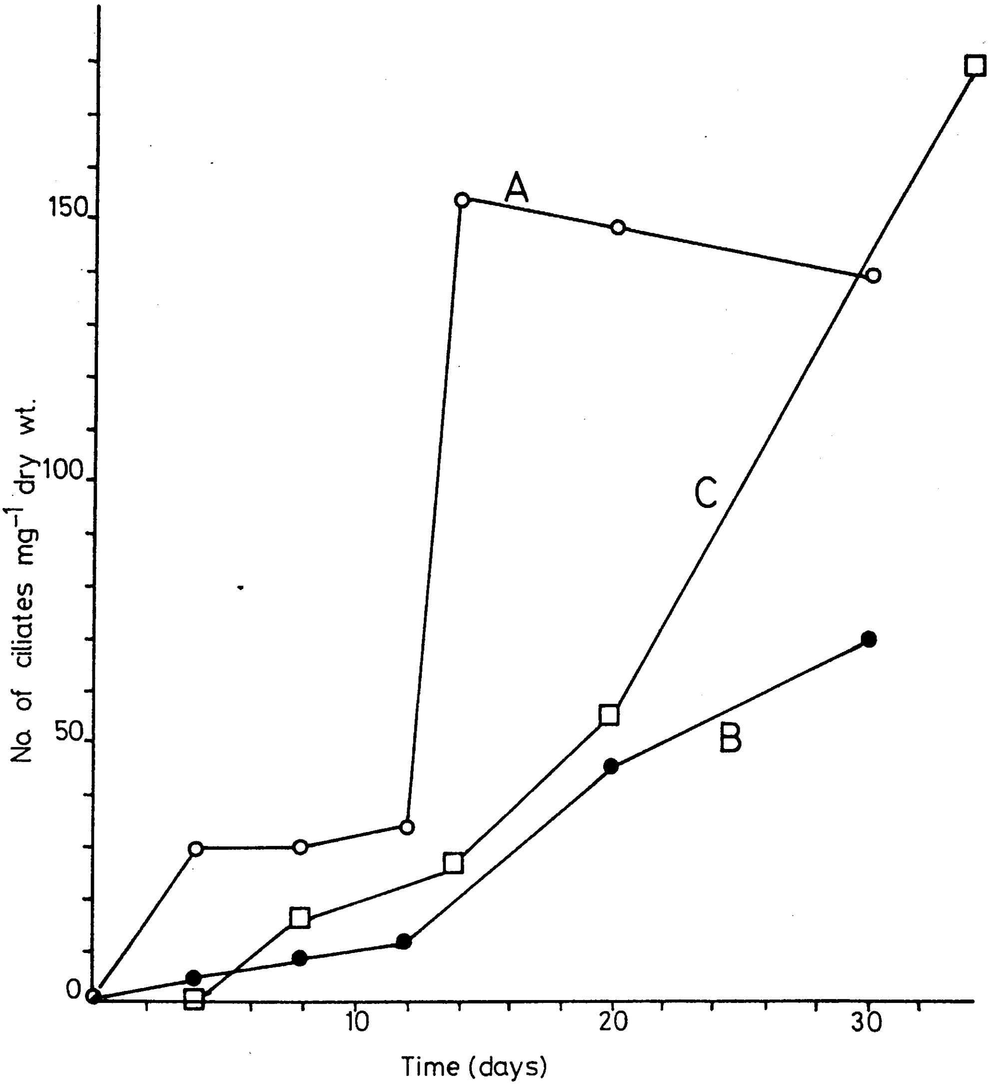
5) Choice experiment

Here, *Gammarus* showed a highly significant preference for rotting weed ($\chi^2 = 117.8$, df. 1, $P < 0.001$) and geotactic responses were not involved.

Fig. 36

Changes in ciliate numbers with time on Laminaria saccharina in the top chamber of cage (Fig. 29) in two experimental runs (a,b) when (A) Platynereis and Psammechinus were present, (B) when Gammarus locusta was present in addition to the above species and (C) when no animals were present.

(a)



(b)

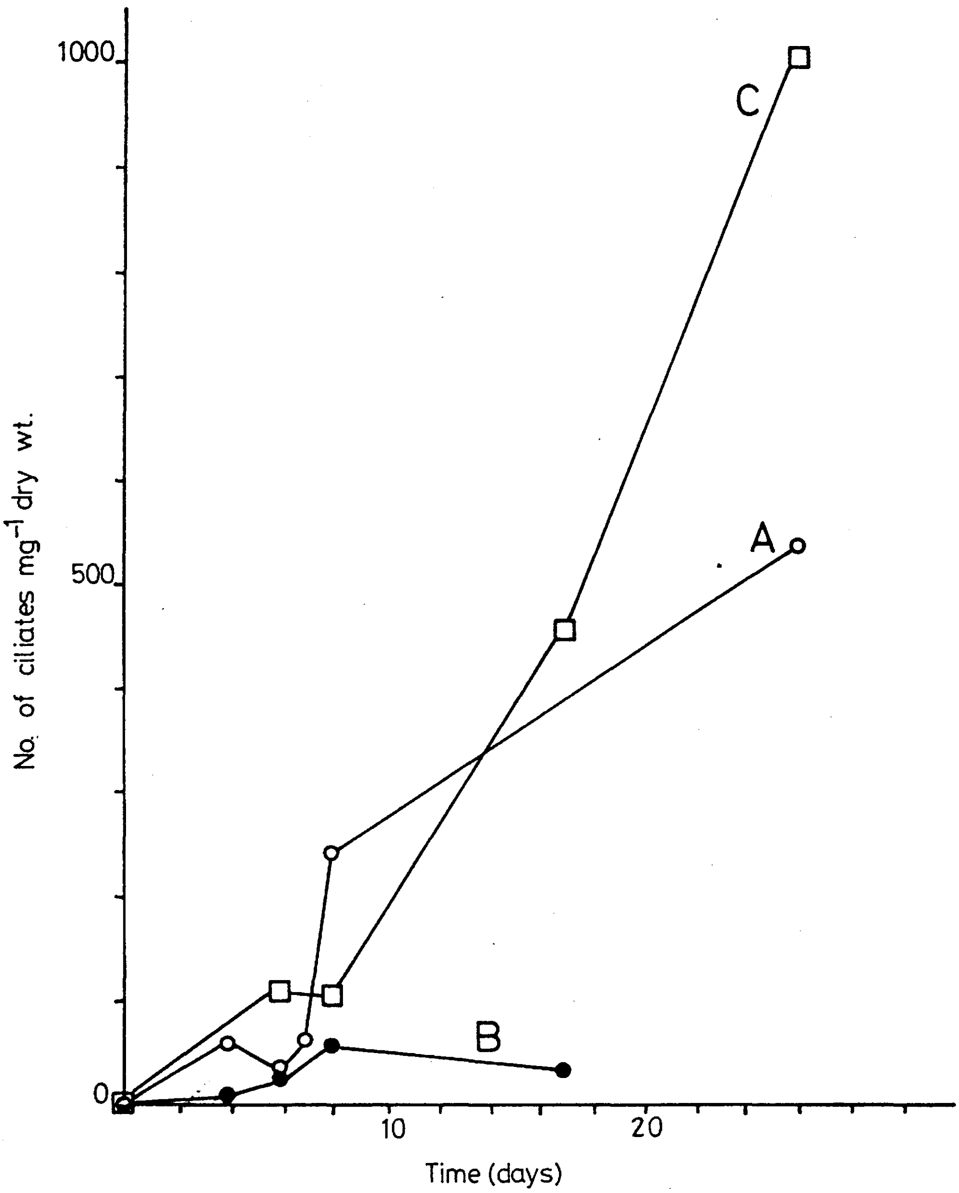
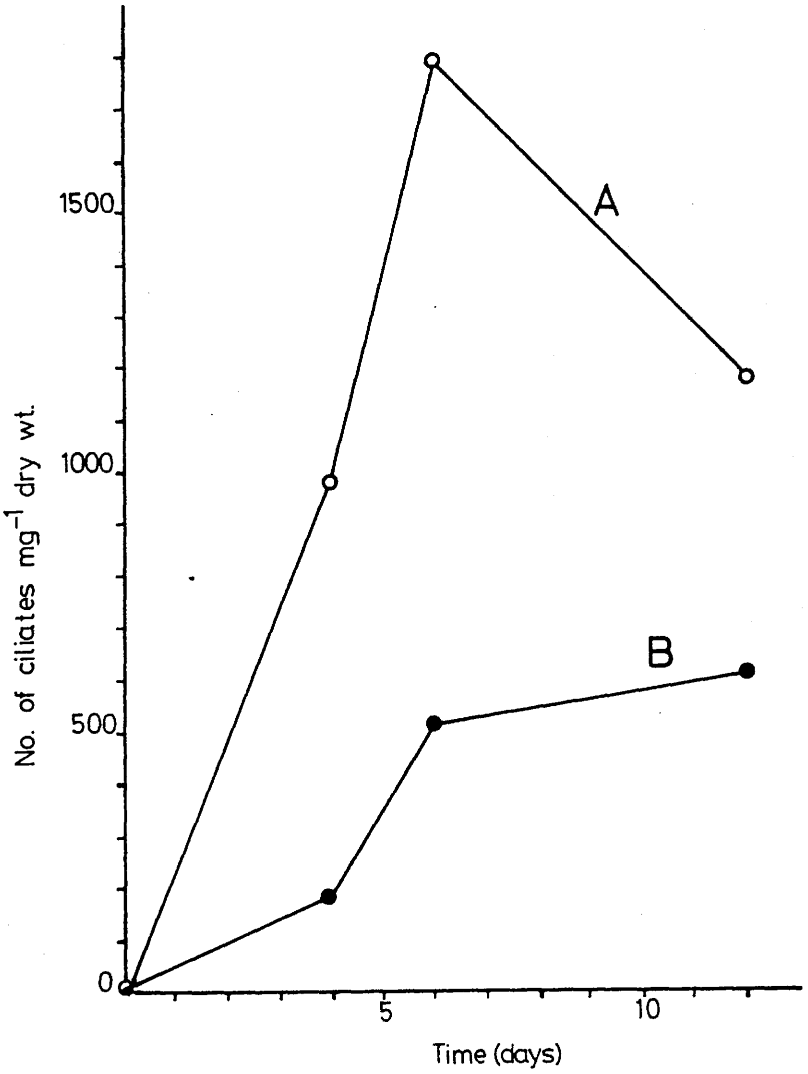


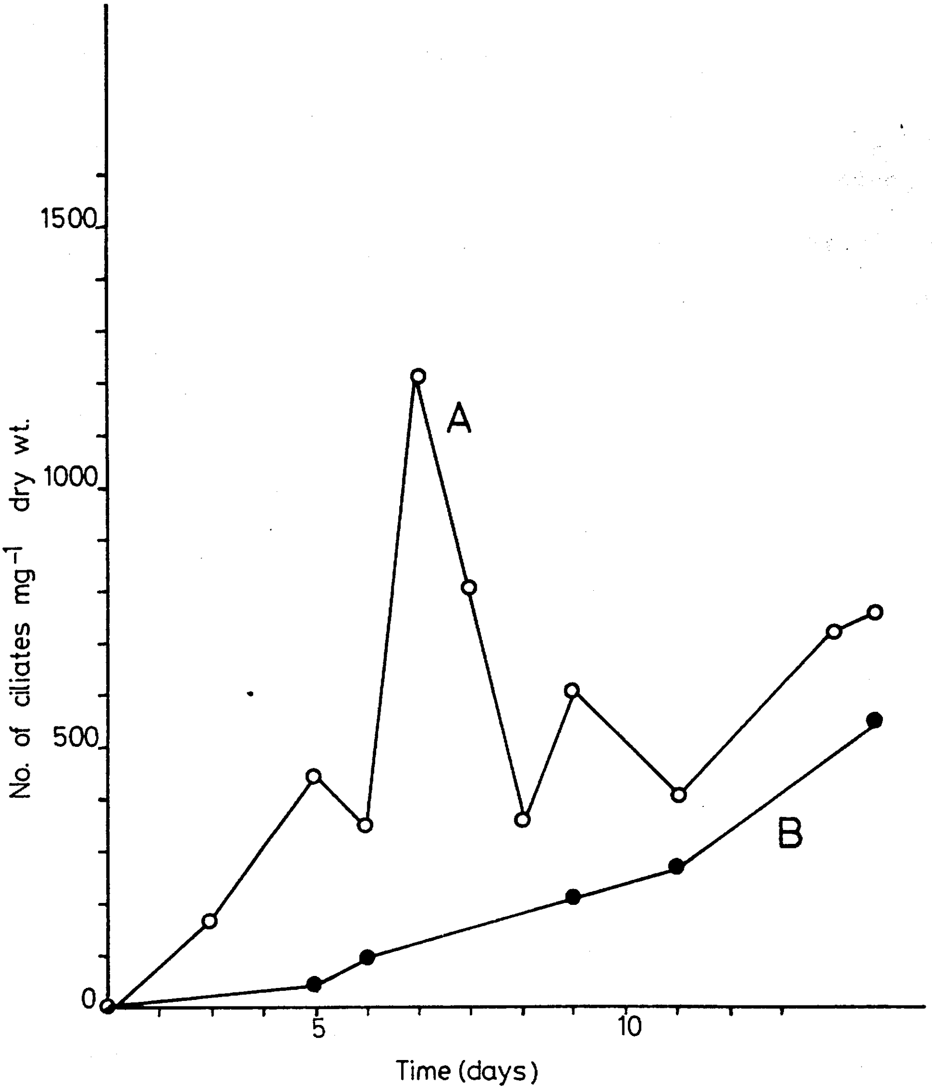
Fig. 37

Changes in ciliate numbers with time on Platynereis and Psammechinus faeces in the bottom chamber of cage in two experimental runs (a,b) with no Gammarus locusta (A) or with G. locusta present(B).

(a)



(b)



DISCUSSION

Homogenized fresh weed promoted greater survival and faster growth in juvenile *G. locusta* than intact kelp tissue. Martin (1966) noted the importance of food texture to its palatability for gammarids. Use of homogenized material eliminated any inhibitory effect of texture and allowed the nutritive value of the frond to be compared with other diets. The ability of juvenile *Gammarus* to develop on a diet of fresh kelp indicates that substratum digestion was occurring to some degree (see Sutcliffe *et al.*, 1981). The greater survival and faster growth of juveniles fed rotting kelp however, indicated the nutritional superiority of this diet. Nilsson (1974) reported increasing absorption efficiency in *G. pulex* with the advancing decay of beech leaves and Sutcliffe *et al.* (1981) found increased specific growth rates of young *G. pulex* when fed on decaying elm leaves with a well developed microbial community. The large numbers of saprophagous micro-organisms present on the decaying plant substratum are presumably digested by juvenile amphipods.

The slower growth and poor survival of juvenile *Gammarus* fed fresh faeces of *Platynereis* (especially) and *Psammechinus* (compared with homogenized fresh weed) was to be expected. Such faeces, being already partially digested, have a relatively low nutritional value with little remaining algal protein. Strangely, however, they did promote faster growth than otherwise similar, but aged, material which would have had protein available in the form of saprophagous microbes. Various authors have oonsidered that ageing increases the palatability (Valeila *et al.*, 1979; Harrison, 1982) and enhances the food value of faecal pellets (Newell, 1965; Fenchel, 1970, 1972; Mann, 1972) and, with rotting kelp inducing faster growth of juvenile *Gammarus* than fresh weed, aged faeces might have been expected to produce better results than fresh faeces. Fresh faeces of *Platynereis* and *Psammechinus* however, are enclosed in a peritrophic membrane (Fretter and Graham, 1976; Buchanan, 1969) which itself has a protein component. This membrane is quickly broken down with age. The aged faeces are then capable of supporting only a very reduced micro-organism population (see Chapters 1 and 2). Possibly then, in aged faeces, the peritrophic membrane provides more protein than do the saprophagous micro-organisms, accounting for the difference in amphipod growth cf. fresh faeces (with smaller differences being attributable to differences in membrane composition in urchins and worms). Some growth occurred in the starved control group, no doubt caused by cannibolism of dead individuals. Total eradication of cannibolism could have been achieved only by keeping juveniles separately, but the extra amount of work involved would have limited the scope for experimentation and the results would have been little affected.

The survival of different broods of juvenile Gammarus reared on the same diet varied greatly. Where sufficient data were available, relationships between temperature and survival were sought, but none was found. This variation presumably resulted from intrinsic differences between broods, possibly related to the mother's previous diet (discussed later) or to differences in genetic constitution. Such differences did not appear to affect juvenile growth. Had they, there presumably would have been no significant positive relationship between rearing temperature and the mean daily increases in amphipod dry weight which were found for animals feeding on both the fresh and rotting weed.

Variations in fecundity can be used as an index of stress on amphipods (Kinne, 1961; Odum, 1971; Steele and Steele, 1975; Moore, 1978). Here, fecundity has been used to indicate the relative quality of fresh and rotting kelp to adult Gammarus. Similar studies have been reported by Vassallo and Steele (1980) on

G. lawrencianus Bousfield. In laboratory experiments, all other conditions can be kept constant. As found by Cheng (1942), Hynes (1954), Kinne (1961), Greze (1972), Steele and Steele (1975) and Moore (1978) for other species, the number of eggs produced by G. locusta varied with body size. Steele and Steele (1975) and Moore (1978) reported a curvilinear relationship between fecundity and female length, but Moore (1981) later explained this in terms of sequential periods of length independence and dependence over the reproductive span of individuals. In the present work, a linear relationship between fecundity and amphipod dry weight was found in all categories examined. Body dry weight is a more satisfactory measure of animal size since, in older individuals, small increases in body length conceal substantial increases in the animals bulk. This effect would also account for the curvilinear relationship recorded by the above authors, though as Moore (1981) pointed out, all ultimately depends on the geometry of the ovary in particular species. Moore (1978) described three processes which can result in inaccurate estimates of egg numbers, (i) loss of eggs resulting from handling, (ii) loss of eggs during movements of the female and (iii) retention of infertile eggs by females following release of the hatched juveniles, resulting in these being mistaken for whole broods. In laboratory experiments, females were killed and examined individually immediately following copulation. Thus, none of these errors was operative. When examining gravid females taken directly from the field, all of these considerations could impinge. When egg loss was observed in the laboratory, a number of eggs were usually lost together and their absence from the brood was clearly visible. All of the field collected amphipods examined had markedly distended brood pouches and there was no obvious egg loss.

The fecundity results for the two categories of amphipods with different dietary histories, ie. (i) animals fed both as juveniles and adults on either the fresh or rotting weed (Fig. 31, A_F and A_R respectively) and (ii) field animals isolated only as adults on one of the two diets (Fig. 32, B_F and B_R) illustrated the nutritional superiority of rotting weed for adult G. locusta. The significant differences between the fecundity relationships for the two groups A_R and B_R illustrate the importance of the female's diet immediately before and during brooding. The results for both categories (i) and (ii) combined also illustrate that juvenile diet can significantly affect future fecundity. It is also clear that the field-collected Gammarus do not feed exclusively on rotting weed (or material of similar nutritional value). From B_F and B_R, it seems likely that fresh algal material plays an important part in Gammarus nutrition at some stage of its life. Comparison of fecundity of wild females (Fig. 33, C) with the other groups showed that these animals had been existing on a diet equivalent to that of B_R. Animals of both categories are known to have been feeding on rotting weed as adults and so these animals could have fed on fresh weed as juveniles. Further work is needed to follow changes in the biochemistry of females fed on different diets to assess the somatic v. gonadal apportionment of energy in situations of nutritional stress.

Watkin (1941a) found that juvenile G. locusta were tidal migrants in Kames Bay, being found in water less than 1 metre deep. An abundance of juvenile Gammarus (but very few adults) has been seen (pers. obs.) in association with filamentous algae bordering Kames Bay(cf. Steele and Steele, 1975; Vassallo and Steele, 1980). These algae presumably provide good anchorages for small amphipods, compared with the Laminarians where G. locusta is rarely, if ever found (Steen, 1951; Moore, 1973; pers. obs.). On the detached weed beds offshore in Kames Bay (17 - 25 metres depth range), an abundance of adult Gammarus can be found. Few juveniles were ever found there, but more could easily have been lost through the trawl mesh. Blegvad (1922) found that juvenile and adult Gammarus spp. existed in different habitats and Watkin (1941b) found a similar situation with Corophium volutator (Pallas). In fact, this may be generally true of littoral amphipods (Moore, 1977), though it is less usual in sublittoral species (see Moore, 1981). Immature G. locusta may then be reared in shallow waters, feeding on fresh filamentous weeds. Once mature, these amphipods may migrate to deeper waters where they find decaying, detached weed in abundance. This explanation would certainly account for the fecundity relationships found for the field amphipods (B_F, B_R and C). Incidentally, the largest brood encountered (145 eggs) is almost identical to the maximum of 143 recorded by Sexton (1924).

Females fed fresh kelp produced fewer fertile broods and copulated less frequently than females fed rotting weed. In addition, a number of females fed fresh weed died. This mortality generally occurred when the females were moulting prior to laying the next brood of eggs and these females were sometimes eaten by their male partner. Sexton (1928) noted male G. chevreuxi eating females exhausted by moulting. Barratt (1966) described a similar situation in Ampithoe valida Smith. Sexton (1928) also noted that such males continued as cannibals following their first indulgence. For this reason, cannibalistic male G. locusta were immediately replaced in these experiments. Female G. locusta fed rotting weed are thus generally fitter. Sexton (1924) found that broods in G. locusta took 9-10 days to hatch at summer temperatures (unspecified). In the present work, however, hatching took anything from 4-10 days (7 days, 15°C). Sexton (1924) also reported that juveniles were extruded from the brood pouch almost immediately following hatching. Here however, juveniles were released spasmodically over a period of up to 6 days following hatching. In many instances, the juveniles fed on algal material whilst still in the brood pouch. Barratt (1966) noted that juvenile *Ampithoe valida* would feed on adult faeces whilst still in the brood pouch and Kinne (1959) recorded freshly hatched *G. duebeni* eating small remnant particles of their mother's meal. Borowsky (1980) found that juvenile emergence in *G. palustris* was stimulated by the mother's feeding and by aerial exposure.

The poor success of females feeding on fresh weed resulted in insufficient data becoming available for comparison between the two diets relating to the number of young hatching. The significant difference between the two relationships for dry body weight and (i) number of eggs produced (Fig. 32, B_R) and (ii) number of young hatching (Fig. 35) for field animals fed rotting weed illustrated that 100% fertility was not achieved even on this diet. Comparing these two relationships, there is some indication that older females are the more fertile.

The results obtained consistently indicated the nutritional superiority of rotting weed, with adult *G. locusta* moving preferentially towards it. Wallace *et al.* (1975) reported increased activity in *G. pseudolimnaeus* Bousfield in the absence of food. Harrison (1982) noted that phenolic exudates of young leaves of *Zostera* inhibited grazing in *Eogammarus confervicolus* (Stimpson) and Kostalos and Seymour (1976) found that *G. minus* moved preferentially towards those foods that promoted greatest survival. Fenchel and Kolding (1979) however, noted that *Gammarus* spp. will feed and grow on a wide variety of food items, eg. decaying plant material, fresh or decaying meat, commercial fish food etc. That some substratum digestion does occur in *G. locusta* was illustrated both by the survival and growth of juvenile amphipods and the limited production of viable broods by adults fed fresh weed. The main structural polysaccharides in *Laminaria* spp. are alginic acid (13-21% of dry solids - Black, 1950) and cellulose (approx. 5% dry solids - Percival, 1968). Kristensen

(1972) failed to find alginase or cellulase activity in *Lagunogammarus zaddachi* although Halcrow (1971), Wildish and Poole (1970) and Monk (1977) did find cellulase activity in *G. oceanicus*, *Orchestia gammarellus* (Pallas) and *G. pulex* (L.) respectively. The capacity of the mysid *Mysis stenolepis* to digest raw cellulose (Foulds and Mann, 1978) may rest with its gut microflora (Wainwright and Mann, 1982). Since Wildish and Poole (1970) and Halcrow (1971)also reported a reduction in cellulase activity after amphipods had been exposed to antimicrobial solutions, bacteriological investigations of the gut of *G. locusta* would clearly be of great interest.

Harrison (1977) considered that, in *G. oceanicus*, mastication of plant material resulted in cell rupture and the release of cell contents to digestion. Examination of the faeces of *G. locusta* fed fresh weed revealed very small fragments of alga with almost all of the cell walls ruptured. Cell contents thus play an important part in sustaining amphipods feeding on fresh weed. The rupturing of cell walls (with leaching of cell contents) by saprophagous micro-organisms during decomposition means that cell contents are of less importance (*cf.* microbes themselves) to animals feeding on rotting weed. Zimmerman *et al.* (1979) found that *Gammarus mucronatus* (Say) fed heavily on seagrass epiphytes and seagrass debris and to a lesser degree on macroalgae (see also Howard, 1982). More recently, Smith *et al.* (1982) working on the same species showed that it fed less specifically (than *Melita appendiculata* (Say)) on bacteria and photosynthetic microeukaryotes and that the numbers of these organisms and detritus decreased significantly during feeding by *Gammarus*.

Probably all *Gammarus* spp. fulfil the 'classical' microbe-stripping, detritivore role described by Fenchel (1977) and selection for particular microbes (White *et al.*, 1979) would be one route to niche separation in co-existing gammarid species flocks (but note Morrison and White, 1980). Another would ensue from selective digestion after indiscriminate ingestion. Thus, Benwell (1980) showed the potential for growth of certain bacterial strains after passage through the guts of nematodes. Studies of this type in amphipods would be rewarding (Lopez and Levinton, 1978). The reduction of ciliate numbers associated with both Platynereis and Psammechinus faeces in the presence of G. locusta suggests that amphipod coprophagy is not restricted to particular donors. Certain amphipods have been recorded consuming their own freshly-produced faeces (summarized by Shillaker, 1977). The latter practice would lead to a more efficient assimilation of energy in organisms with short gut residence times (note Johannes, 1964; Sutcliffe et al., 1981) but this aspect has not been investigated further.

It is clear that Gammarus is inhibiting and controlling weed decay. Being more motile, it effects this control more efficiently than either Platynereis and Psammechinus. Uncontrolled, rapid decay rates, in conjunction with pulsed benthic inputs of debris (due to storms) would result in "boom and bust" cycles in energy availability. G. locusta's feeding tends to stabilize the input of organic material to the sediments, ensuring a more parsimonious distribution of energy. The main input of organic material to the sediments around seabed accumulations of algal drift is in the form of detritivore faecal pellets. Levinton et al. (1976) considered that the breakdown rate of faecal pellets and their recolonization by microbes are rate-limiting steps in detrital availability. In detached weed beds, Platynereis and Psammechinus faeces will accumulate and will be ingested and reworked by G. locusta, increasing the surface area available to, and enhancing the growth of, micro-organisms (Fenchel, 1970, 1972; Hargrave, 1975). Being so mobile, Gammarus also encourages water movement through the weed pile and disturbs the underlying sediments. In this way, it helps prevent the development of anaerobic conditions which might otherwise seriously affect weed decomposition (Hanson and Tenore, 1981). Hargrave (1975) described a number of examples illustrating the importance of sediment disturbance in allowing the cycling of material which would otherwise remain buried. G. locusta clearly plays a very significant role in the sublittoral decomposition of L. saccharina in the sheltered waters of the Clyde Sea area.

CHAPTER 4

MACROFAUNAL INVOLVEMENT IN THE SUBLITTORAL DECAY OF KELP DEBRIS.

INTRODUCTION

The investigations concerning the three detritivores *Platynereis dumerilii*, *Psammechinus miliaris* and *Gammarus locusta* have been described in the previous chapters. Work on these three detritivores was carried out mainly in the laboratory and with the individual species kept in isolation. They are however, part of a complex macrofaunal community and pressures exerted by other members of that community may influence their behaviour in the field. A field sampling programme was therefore undertaken to establish the composition of the total macrofaunal community associated with sublittoral beds of detached *L.saccharina*. The impact of this fauna on weed decomposition was examined experimntally using litter bags. Experiments to compare the relative effects of various combinations of *Platynereis*, *Psammechinus* and *Gammarus* on the rate of weed decay *in situ* were also carried out. These experiments would indicate both the mechanism by which the weed macrofauna effects decomposition and also test the validity of conclusions drawn previously from laboratory experiments concerning the above three species.

MATERIALS AND METHODS

1) Sampling programme

Sublittoral beds of storm detached L. saccharina are found at a number of sites in the Clyde Sea area. Chumley (1918) recorded large quantities of detached Laminaria in Loch Goil and Loch Fyne. Sizeable accumulations were found at the following sites (Fig. 1) and depths: Kames Bay, Great Cumbrae (30m), Irvine Bay (50m), Tomont End, Great Cumbrae (18m), Loch Ranza (16m), Fairlie Channel (50m) and Loch Riddon (40m). The weed beds at Tomont End and Loch Ranza were selected for routine sampling since, being in relatively shallow water, they could be sampled regularly by SCUBA diving. Being at the northern tips of the Isles of Cumbrae and Arran respectively and thus sheltered from prevailing southwesterly winds, these sites suffered relatively infrequently from severe winter storms, further facilitating access. At both sites, detached weed was collected by diving at irregular intervals between Nov. 1976 and March 1978. The weed was collected quickly in strong polythene bags (45 x 30 cm) and the neck of the bag sealed with a rubber band. Six bags of weed were collected on each occassion. The bags were brought to the surface immediately and treated with 5% formalin. Rapid treatment prevented significant predation occurring within the bag. The formalin also served to extract the majority of animals from both the blades and the holdfasts. Holdfasts were dissected to remove any individuals remaining. The Laminaria was then washed in fresh water, oven dried at 60°C for 3 days and weighed. After identifying the macrofauna, the densities of the various species were expressed as mean numbers per 100g dry weight of weed.

2) Deficiencies of sampling technique

The sampling method was not without its drawbacks. Firstly, the quantitative data relate solely to animals returned in the bags. Many larger animals, e.g. large decapods and echinoderms, living under and around the detached weed, were left undisturbed. In the tangle of detached kelp, their exact relationship to particular fronds being collected and hence their densities could not be determined. Their presence was recorded however, and a number of such species are discussed below which do not appear in the quantitative list.

Secondly, natant species may be lost during weed collection. SCUBA sampling is more precise than unselective trawling but with the normally poor visibility of British coastal waters and the speed at which some species escape, the diver may be unaware of such losses. Thus, the densities of certain crustaceans (including the amphipod Gammarus locusta) and fishes are likely to have been underestimated.

Thirdly, the detached weed beds contain some fronds which have retained their holdfasts whilst others have only the stipe and blade present. With many animals living in the holdfast, differences in the proportions of these two weed types collected could significantly alter the recorded density for a number of species.

Finally, though monthly sampling was planned for both Tomont End and Loch Ranza, this was never achieved in practice. Subtle changes in the detached weed fauna may easily have gone unnoticed. Although some of the density data are likely to be underestimates, it is unlikely that any important species actually avoided detection during the sampling programme.

3) Litter bag experiments

Various authors have studied plant litter decomposition in the field by means of litter bag experiments (Odum and de la Cruz, 1967; Burkholder and Doheny, 1968; Heald, 1969; Odum,Heald and Zieman, 1971; Odum and Heald, 1972; Hunter, 1974). Enclosing the plant material in bags of differing mesh sizes restricts the access of various size groups of animals. By comparing the loss of weed from these bags, the importance of various animal groups in the degradation of plant litter can be assessed.

Here, Laminaria was enclosed in bags (25 x 35 cm) of two mesh sizes - 1mm and 50mm. The 1mm mesh excluded all macrofaunal animals. The 50mm mesh served mainly to prevent the weed from being carried away by tidal currents and almost all of the fauna of the detached Laminaria beds could gain access to it. Although the 50mm mesh prevented the larger animals from actually entering the bag, the weed could still be attacked through the meshes. Adult Echinus esculentus L. were observed feeding in such a manner. The 1mm mesh bags were machine-sewn using 4kg breaking strain fishing line. Nylon twine was used to hand sew the 50mm mesh bags. For each experimental run, six bags of both meshes were used. The bags were loosely filled with freshly detached Laminaria saccharina and secured on the sea bed in 20 metres of water at the Wishing Well, Great Cumbrae (see Fig. 1). At regular intervals, two bags (one of each mesh size) were retrieved and the amount of weed lost determined. Altogether, four experimental runs were executed at four different times of year (see Fig. 39 for details)

In order to estimate the loss of weed over the experimental period, it was necessary to know the quantity of weed at the beginning. Detached Laminaria from sublittoral accumulations has never been exposed to the air. Laminaria which has been dried and rehydrated however, loses its rigidity rapidly and shows a tendancy to laminate. If once dried material had been used in these experiments, it would have blocked the meshes in the 1mm mesh bags and prevented water flow. It would also have been washed through the meshes of the 50mm bags. Further, both the palatability of the weed to various invertebrates and its rate of decomposition would have been affected. Thus, it was impossible to determine the dry weight of the actual weed used in these experiments directly. Reliance on changes in wet weight would also have been contentious. For instance, identical conditions of handling, temperature and humidity would have been necessary when weighing the weed at the beginning and the end of all experiments. Consequently, the following procedure was used to estimate the dry weight of the weed used at the beginning of the experiments.

Whole Laminaria fronds were collected and, following the removal of attached macro-invertebrates, hung up by the holdfast. When the excess surface water had drained off the frond, the holdfast, meristem region and all blade tissue beyond the first 60-80cm were removed. The weed remaining was free from epibionts. A specimen of this weed was cut from the middle of the remaining kelp. This specimen included the whole width of the frond so that lateral variations in weed density were included. This specimen section and the remaining experimental weed were wet weighed separately. The specimen was then washed in fresh water, oven dried at 60°C for three days and re-weighed. The percentage dry weight of the weed was then calculated. Assuming that the section of the frond selected was representative, the percentage dry weight of the experimental weed should be the same as the specimen. Hence an estimate of the dry weight of the experimental weed at the beginning of the experiment could be achieved. This procedure was employed for each frond used in these experiments. Excluding the meristem and distal regions, there is a general increase in density distally along the frond. Thus, the specimen section taken from the middle of selected weeds represented the average density of this material.

The experimental weed, following wet weighing, was placed in one of the mesh bags. Several fronds were generally used for each bag.

Approximately the same amount of weed was used in each bag (100±10g). The complete set of experimental bags was then placed on the sea bed. When the individual bags were retrieved, the remaining weed was washed in fresh water, oven dried at 60°C for three days and weighed. Using the estimated initial dry weight, the percentage loss of weed was then determined for the experimental period.

The Wishing Well was not initially a site with accumulated detached weed. It was selected as a good site for positioning field experiments primarily because of its accessibility in all weathers, its sharply sloping bottom (allowing the required depth to be reached quickly from the shore), its proximity to the laboratory and its lack of disturbance by fishing vessels. A rope line was laid on the sea bottom running perpendicular to the shore, spanning a depth range of 2 - 35m C.D. This line, together with other items of debris, trapped drift Laminaria carried by bottom currents and quickly formed an artificial weed bed at 20 metres depth. The first litter bag experiments were positioned more than one year (1977) after this artificial weed bed had been formed. By this time, the fauna of the weed bed was similar to that found within natural detached kelp accumulations at other sites.

4) Combination experiment

Mesh bags (1mm mesh, measuring 20 x 30 cm) were filled with equivalent known weights (100±10g) of fresh L. saccharina. The dry weight of this weed was estimated as in the previous experiment (see above). The following groups of animals were put into six separate bags:

1) 6 Platynereis dumerilii
2) 6 Gammarus locusta
3) 4 Psammechinus miliaris
4) 6 Platynereis + 6 Gammarus

5) 4 Psammechinus + 6 Gammarus

6) 6 Platynereis + 6 Gammarus + 4 Psammechinus

The six bags were secured at the Wishing Well at a depth of 20 metres. At the end of each experimental run, the remaining weed was washed (in fresh water), oven dried at 60°C for 3 days and re-weighed. The loss of weed from each bag could then be determined. A comparison of these "kept together" and "kept separately" weed losses for particular combinations of the three species indicated the relative importance of interactive cropping in weed decomposition. A control with no animals was deliberately not included, since to derive the absolute impact of this combination of species, experiments would need to be conducted at ecologically realistic population densities (rather than at the artificially high levels presently used).

It was essential that the individuals of each species in different trials were of the same size. The size of the individual Psammechinus and Gammarus could be compared quickly by measuring repectively their test diameters (see chapter 1) and head length (see chapter 3). Comparing individual Platynereis by measuring the bite size (see chapter 2) would have been an elaborate and time-consuming procedure. To circumvent this problem, for each complete experiment run, the same individual animals were used for each of the separate trials (lasting for different time periods). This work was carried out in January - February, 1977. The sea temperature was 5-6°C. Two complete experiments(1 and 2) were completed.

RESULTS

1) Sampling programme

Table 9 records the data from the sampling programmes at both Loch Ranza and Tomont End. The densities of the various species found in association with the detached weed at these two sites are shown for different periods of the year. Altogether, sixty-four macrofaunal species were recorded. Fig. 38 illustrates changes in the densities of the important species *Galathea intermedia* Lilljeborg, *Aora gracilis* (Bate), *Platynereis dumerilii*, *Psammechinus miliaris*, *Gibbula cineraria* (L) and *Rissoa lilacina* Recluz throughout the sampling period. All these species showed a marked peak in density in the late autumn-early winter period with a subsequent decline to a minimum the following summer.

Polychaeta

Of the eleven polychaete species collected with the detached kelp at Tomont End and Loch Ranza, all have been recorded as part of the attached *Laminaria* (Fauvel, 1923; Clark, 1960; Scarratt, 1961; Pettibone, 1963; Moore, 1971, 1973; Rasmussen, 1973) or *Saccorhiza* fauna (McKenzie and Moore, 1981). *Ephesia*, however, is mostly associated with *Lithothamnium* spp. gravels (Fauvel, 1923; Pettibone, 1963) and is often found in dredged mud (Pettibone, 1963). It may have been derived from maerl grounds. The majority of the polychaetes were probably carried down with the weed following detachment. Only rare specimens of *Platynereis dumerilii*, however, are found in attached *Laminaria* holdfasts (Scarratt, 1961; Moore, 1971, 1973), certainly insufficient to account for the large numbers recorded in the sampling programme. This species colonises the weed beds following larval settlement (see chapter 2) and feeds on the algal substratum itself. Apart from consuming the weed, the membranous tubes of this worm serve to bind the kelp together.

Table 9. Mean density/100g dry weight of animals associated with sea-bed accumulations of detached *Laminaria saccharina* at two sites in the Firth of Clyde

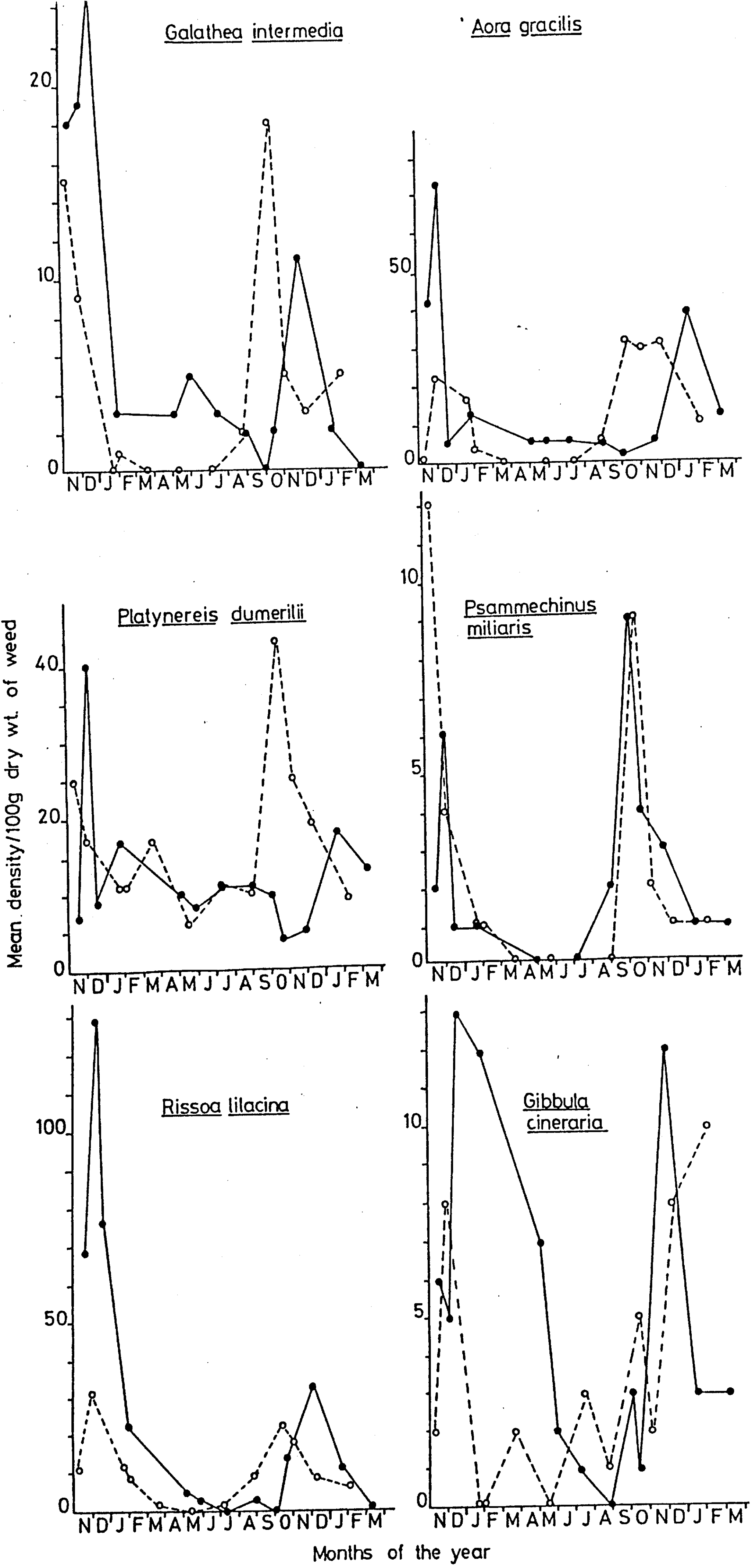
Species / Dates	Loch Ranza, Arran													Tomont End, Gt. Cumbrae											
	17.11.76	3.12.76	17.12.76	27. 1.77	4. 5.77	31. 5.77	14. 7.77	2. 9.77	5.10.77	21.10.77	30.11.77	20. 1.78	10. 3.78	11.11.76	2.12.76	26. 1.77	3. 2.77	24. 3.77	18. 5.77	13. 7.77	31. 8.77	12.10.77	7.11.77	9.12.77	8. 2.78
Polychaeta																									
Ephesia gracilis	-	-	-	-	-	-	-	-	2	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Harmothoe imbricata	10	5	2	3	-	4	6	3	2	4	5	8	-	2	2	2	4	-	-	-	3	8	9	6	4
Lepidonotus squamatus	-	-	-	-	-	-	-	1	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-
Halosydna gelatinosa	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Platynereis dumerilii	7	40	9	17	10	8	11	11	10	4	5	18	13	25	17	11	11	17	6	11	10	43	25	19	9
Nereis pelagica	-	-	-	-	-	1	-	-	-	1	3	2	-	-	-	-	-	-	6	-	-	-	-	-	-
Phyllodoce maculata	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	2	5	-
Eulalia sanguinea	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eulalia viridis	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Magalia peramata	3	6	1	-	-	4	2	3	1	-	-	5	-	-	-	-	-	-	-	-	5	3	2	1	9
Eunice pennata	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mollusca																									
Lepidochitona cinereus	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Patina pellucida	-	1	-	1	-	-	-	-	-	-	-	1	1	1	1	-	-	-	-	-	-	-	1	-	-
Acmaea tessulata	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	2	-	-	1	1	-
Gibbula cineraria	6	5	13	12	7	2	1	-	3	1	12	3	3	2	8	-	-	2	-	3	1	5	2	8	10
Littorina obtusata	5	10	3	3	-	-	-	-	-	-	1	2	-	-	-	-	-	-	-	2	-	-	2	3	1
Lacuna vincta	8	10	1	5	-	-	1	-	-	2	2	1	-	2	2	-	2	-	-	8	14	14	8	12	1
Rissoa lilacina	69	119	77	23	5	3	-	3	-	14	33	11	1	11	32	12	9	2	-	2	10	23	19	9	7
Rissoa parva	3	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Philbertia linearis	-	-	-	-	-	-	-	1	1	3	-	-	-	-	1	-	-	-	-	2	-	-	1	1	-
Nassarius incrassatus	-	1	-	1	-	1	-	-	-	1	3	2	-	-	1	-	-	-	-	6	-	-	-	-	-
Trivia arctica	1	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Odostomia unidentata	12	24	43	20	8	4	1	1	-	-	1	-	-	-	3	6	-	-	-	-	1	-	2	4	1
Onchidoris muricata	36	49	31	18	1	-	-	-	6	9	34	-	-	-	-	-	-	-	-	-	-	-	-	5	-
Chlamys opercularis	-	-	-	-	-	-	-	59	3	-	-	-	1	1	1	-	-	-	-	-	60	-	3	1	1
Amphipoda																									
Lysianassa sp.	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	2
Iphimedia minuta	4	2	2	-	1	1	3	3	1	-	9	8	-	-	-	-	-	-	-	-	-	2	-	2	3
Gammarus locusta	7	-	-	1	-	-	-	-	-	-	-	-	-	2	1	-	-	-	-	-	-	3	1	-	2
Dexamine spinosa	3	-	3	-	-	1	3	2	-	3	10	3	-	3	-	-	-	-	-	-	-	3	2	3	1
Aora gracilis	42	73	5	13	6	6	6	5	2	6	39	12	-	1	23	17	4	-	-	-	6	32	30	31	11
Corophium bonnellii	1	6	2	2	2	16	-	5	1	-	3	3	1	-	8	9	2	-	-	-	1	1	7	6	5
Ericthonius ? brasiliensis	17	5	2	-	4	4	1	-	-	4	-	-	-	-	2	4	1	-	-	-	-	1	2	2	11
Caprella acanthifera	1	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Phtisica marina	1	-	-	-	-	-	-	1	-	-	-	3	-	-	-	-	-	-	-	-	2	18	2	4	-

cont.

Decapoda																									
Eulus pusiolus	7	-	2	-	-	1	1	1	-	1	-	2	-	5	5	-	-	-	-	-	-	-	2	-	-
Thoralus cranchii	4	4	5	2	-	-	-	-	-	-	-	-	-	2	1	-	-	-	-	-	-	-	-	-	-
Hippolyte varians	1	1	-	1	-	-	-	-	-	-	2	1	1	2	-	-	1	-	-	-	-	-	-	-	-
Caridion gordoni	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Pandalus montagui	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Galathea squamifera	1	-	2	-	-	-	-	-	-	-	1	-	-	1	1	-	-	-	-	-	-	-	-	1	-
G. strigosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-
G. intermedia	18	19	25	3	3	5	3	2	-	2	11	2	-	15	9	-	1	-	-	-	2	18	5	3	5
Pisidia longicornis	2	-	9	-	1	1	-	-	-	-	1	2	-	2	16	5	7	-	-	-	2	5	2	5	5
Pagurus bernhardus	-	-	1	-	-	-	-	-	-	1	1	-	-	1	-	-	-	-	-	-	2	-	1	1	1
Cancer pagurus	1	-	1	-	-	1	-	-	-	-	-	1	-	-	1	-	-	-	-	-	1	-	-	-	-
Liocarcinus pusillus	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
L. puber	-	1	-	-	1	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-
Carcinus maenas	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Hyas araneus	1	-	-	-	-	-	-	-	1	-	4	-	-	-	-	-	-	-	-	-	-	2	1	2	1
H. cearctatus	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	1	-	-	-
Eurynome ? aspera	-	-	-	-	-	-	1	-	1	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-
Echinodermata																									
Ophiocomina nigra	-	3	4	6	3	2	-	5	169	44	40	24	294	7	-	-	62	-	52	-	-	-	-	-	-
Ophiothrix fragilis	-	-	-	-	-	-	-	3	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Ophiopholis aculeata	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Amphipholis squamata	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Asterias rubens	2	5	4	3	1	-	-	4	1	1	-	1	1	4	3	1	1	-	6	2	-	1	3	-	1
Solaster papposus	-	-	-	-	-	-	-	-	2	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Psammechinus miliaris	2	6	1	1	-	-	-	2	9	4	3	1	1	13	4	1	1	-	-	-	-	9	2	1	1
Echinus esculentus	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	2	-	-	-	-
Pisces																									
Zeus faber	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Centronotus gunnellus	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	1
Ctenolabrus rupestris	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cyclopterus lumpus	-	-	-	-	-	-	1	-	-	-	1	1	-	1	1	-	-	-	-	-	-	-	-	1	-
Zeugopterus punctatus	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-

Fig. 38

Seasonal changes in population density of important species associated with detached accumulations of Laminaria saccharina on the sea-bed at Loch Ranza, Arran (solid line) and Tomont End, Cumbrae (dashed line). For actual dates see Table 9.


Galathea intermedia
Aora gracilis
Platynereis dumerilii
Psammechinus miliaris
Rissoa lilacina
Gibbula cineraria
20
10
0
50
0
10
5
0
40
20
0
100
50
0
10
5
0
N D J F M A M J J A S O N D J F M
Mean density/100g dry wt. of weed
Months of the year

There is an interesting association between the scaleworm *Harmothöe imbricata* (L) and *Platynereis*. In the detached kelp beds, *Harmothöe* is found lying on occupied *Platynereis* tubes. Pettibone (1963) noted that *Harmothöe* lives commensally with other polychaetes and Sarvala (1971) considered *Harmothöe sarsi* (Malmgrem) to be a carnivore. Sarvala found amphipod and copepod remains in the gut of *H. sarsi* and such remains were also found in the gut of *H. imbricata* caught at Tomont End and Loch Ranza. In addition, bundles of setae and occassionally whole body sections of *Platynereis* were also found. When kept together in the laboratory *Harmothöe* resides on *Platynereis* tubes as described above. No *Platynereis* were killed by *Harmothöe* but those dying from natural causes were quickly consumed. It was noticed, however, both in the field and the laboratory, that *Platynereis* individuals with *Harmothoe* in attendance rarely had any anal segments. Could *Harmothöe* be 'cropping' live *Platynereis*?

Lepidonotus squamatus (L), *Phyllodoce maculata* (L) and *Magalia perarmata* Marian and Bobretzky are all predators (Pettibone, 1963; Rasmussen, 1973). Only occassional specimens of *Halosydna gelatinosa* (M. Sars), *Eulalia sanguinea* Oersted, *E. viridis* (O.F. Müller), *Ephesia gracilis* Rathke and *Nereis pelagica* (L) were found.

The omnivorous *Nereis pelagica* is the commonest polychaete in attached *Laminaria* holdfasts (Moore, 1971, 1973). Its absence from detached kelp which has retained its holdfast is surprising. It was noted however, whilst collecting attached weed underwater, that flexing the holdfast during detachment resulted in this polychaete immediately and violently vacating its tube. A similar reaction is presumably evoked when the weed is detached by storm action. Such a violent exit by *Nereis* may also stimulate other members of the holdfast fauna to leave.

The suspension-feeding *Spirorbis borealis* Daudin has not been included in the data. The calcareous tubes of this sedentary polychaete are found in profusion on the mature tissue of the attached and hence detached weed.

Decapoda

Altogether, seventeen different decapod crustacean species were found. *Pisidia longicornis* (L), *Galathea squamifera* Leach and juvenile *Cancer pagurus* (L) have all been recorded in *Laminaria* (Scarratt, 1961; Moore, 1971, 1973) and/or *Saccorhiza* holdfasts (McKenzie and Moore, 1981) and thus the recorded individuals, most of which were very small, may have been brought down with the weed following detachment. Most of the other species recorded however, occur within a wide depth range, including the *Laminaria* zone. Consequently their mode of colonization of detached weed is unknown. *Galathea intermedia* Lilljeborg was the commonest decapod recorded, with densities of up to 25 adults per 100g dry weight of weed. Examination of gut contents revealed large quantities of bottom silt and decomposing fragments of *Laminaria*. Similar material was also found in the guts of juvenile *G. squamifera* and *Eualus pusiolus* (Krøyer). On two occassions, the buccal cavity of *Eualus* was found to be filled exclusively with *Loxoconcha impressa* (Baird), an ostrocod commonly found in the sediment which settles onto the detached kelp.

Pisidia longicornis was represented mainly by juveniles which were generally found in the holdfasts of detached weed. On one occassion, forty-two individuals were recorded in a single holdfast. Occassional adults were found moving freely amongst the weed. *Pisidia* is a suspension feeder (Nicol, 1932; Warner, 1977). Both adult and juvenile *Cancer pagurus*, *Hyas araneus* (L) and *Liocarcinus puber* (L) were found amongst detached kelp. The density data in Table 9 however, relate only to juveniles. These decapods are all omnivores and may include algal material in their diet. Kikuchi and Pérès (1977) noted that portunid crabs consume large quantities of decaying plant material. The older individuals of these four species are commonly found on open muddy bottoms in the Clyde Sea area. Such individuals may migrate onto the weed, in search of cover as much as for food.

Amphipoda

All the amphipod species recorded with the detached weed are also found amongst attached kelp (Chevreux and Fage, 1925; Scarratt, 1961; Moore, 1971, 1973, 1978; Rasmussen, 1973; McKenzie and Moore, 1981). Thus, transportation with the weed following detachment could account for the presence of the many individuals recorded.

Gammarus locusta (L), which was found in such large numbers in Kames Bay (see chapter 3) was rarely found with the detached weed at either Loch Ranza or Tomont End. Aora gracilis (Bate) was the dominant amphipod at these two sites; seventy-three individuals per 100g dry weight of weed having been recorded. Examination of their guts showed that, like Gammarus locusta, Aora ingests decaying L. saccharina. Ericthonius brasiliensis (Dana) and Dexamine spinosa (Montagu) have both been recorded eating algal material and detritus (Hagermann, 1966; Greze, 1968, 1971). Corophium bonnellii Milne Edwards also feeds on detritus which it either filters from suspension or collects from the vicinity of its tube entrance (Moore, 1978, 1981).

The two caprellids Phtisica marina Slabber and Caprella acanthifera Leach were recorded with the detached weed. P. marina commonly lives in association with Asterias rubens L (McCain, 1968; Rasmussen, 1973). It also predates on C. acanthifera (Costa, 1960).

Mollusca

All of the prosobranch molluscs found with detached kelp (excepting Philbertia linearis (Montagu) which McKenzie and Moore (1981) reported as rare in Saccorhiza holdfasts) are commonly found with attached Laminaria (Scarratt, 1961; Allen, 1962; Graham, 1971; Moore, 1971, 1973) and are almost certainly all transported down with the weed following detachment. Philbertia is a predator found on soft, muddy substrata, it probably feeds on errant polychaetes (Fretter and Graham, 1962; Graham, 1971).

Gibbula cineraria (L), Lacuna vincta (Montagu), Patina pellucida (L), Littorina obtusata (L) and Rissoa lilacina Recluz are all herbivores. They feed either on the algal tissue itself or on its covering layer of diatoms. Either way, the surface tissues of the frond are rasped away by their radulae. Gibbula, Lacuna and Patina are frequently observed at the edge of large areas of exposed weed damaged in this fashion. Littorina may also include decaying algae in its diet (Rasmussen, 1973).

Odostomia unidentata (Montagu) feeds on Pomatoceros triqueter (L). Pomatoceros is sometimes found on the stones carried down with the holdfasts of detached kelp. Nassarius incrassatus (Ström) is a scavenger, favouring silty places where organic debris accumulates (Fretter and Graham, 1962). It is found in the silt that collects on the surface of the detached Laminaria fronds.

The nudibranch Onchidoris muricata (Müller) presumably continues to feed on the bryozoan Membranipora membranacea (L) which is its normal food (Graham, 1971) and which, like Onchidoris, is carried down with the kelp following detachment.

Large numbers of Chlamys opercularis (L) were found attached by byssal threads to the detached kelp in late August/early September (up to 60 individuals per 100g dry weight of weed). These animals have settled selectively from the plankton. Chumley

(1918) recorded a similar association between detached Laminaria and juvenile Pecten maximus (L) and Kikuchi and Pérès (1973) described large numbers of juvenile Musculus senhousia attached to Zostera sp. leaves.

Echinodermata

All of the quantitative data concerning echinoderms in Table 9, excepting that for Ophiocomina nigra (Abildgaard), relate to juveniles. Adults of these and other species are, however, also found with the weed.

Asterias rubens (L) is the commonest of the Asteroidea found with the detached weed. Juvenile Asterias are found in the holdfast of attached Laminaria (Moore, 1971) and presumably again, these are transported down with the weed following detachment. Adult Asterias also move onto the weed from the surrounding substratum. Asterias is a general carnivore and scavenger, eating not only bivalves but also gastropods, echinoderms (including other Asterias), crustaceans and any dead tissue (Clark,1968; Feder and Christensen, 1966). Occasional Solaster papposus (L) juveniles were also found with the detached weed. Adults of this species and Marthasterias glacialis (L) and Luidia sarsi Duben and Koren, like Asterias, move onto the weed from the surrounding benthic sediments. These three species are mainly predatory, feeding on other echinoderms, molluscs, crustaceans and polychaetes (Mortensen, 1927; Clark, 1968; Fenchel, 1965; Feder and Christensen, 1966). Luidia however will also feed on algal material (Clark, 1968).

On occasions, Ophiocomina nigra was found in very large numbers on detached kelp, eg. 640 individuals (of all ages) on a single frond (pers. obs.). Ophiocomina is a polyphagous feeder (Fontaine, 1965) and has been recorded including algal material in its diet (Vevers, 1956). O. nigra kept in the laboratory never ingested any *Laminaria* and the above-mentioned frond supporting 640 individuals had not been attacked. In both these instances, the *Ophiocomina* showed the special raised-arm feeding posture employed when using the mucus-net suspension feeding mechanism (Fontaine, 1965). Fontaine considered that this method was only used when other food sources, such as sessile algae, were not available. Clearly this is not so. Moore (in press) has photographed *O. nigra* suspension feeding *in situ* while clinging to kelp fronds and has criticized Norton and Milburn's (1972) contention that *O. nigra* is herbivorous on these grounds. *Ophiocomina* will also feed on both sedentary and actively swimming invertebrates (Vevers, 1956; Gorzula, 1976a). *Ophiocomina* is found locally in dense, discrete beds below the *Laminaria* zone (Gorzula, 1976a) but scattered individuals are present in deeper water (Gorzula, 1976b). Individuals from the dense beds have obviously "spilled over" onto the detached weed, accounting for the large densities recorded. Juveniles of the other ophiuroid species - *Ophiothrix fragilis* (Abildgaard), *Ophiopholis aculeata* (O.F.Müller) and *Amphipholis squamata* (Delle Chiaje) have all been recorded with attached *Laminaria* (Scarratt, 1961; Moore, 1971) and *Saccorhiza* holdfasts (McKenzie and Moore, 1981). The few individuals of these species recorded were presumably carried down with the weed following detachment.

Psammechinus, like the polychaete *Platynereis dumerilii*, was found at all the sublittoral sites where detached *Laminaria* accumulated. At Tomont End and Loch Ranza, all *Psammechinus* were less than one year old. At other sites, such as Kames Bay and Irvine Bay, individuals of all ages were found (see chapter 1). Adult *Echinus esculentus* (L) were found in large numbers at Tomont End and Irnine Bay. *Echinus* ingest large quantities of weed, producing extensive holes in fronds. Large quantities of *Echinus* faecal pellets were also found in the sediment underlying the detached weed at Tomont End. A few juvenile Echinus were also found at Tomont End and Loch Ranza. These, like Psammechinus, settle onto the kelp from the plankton.

Pisces

The three species Ctenolabrus rupestris (L), Zeugopterus punctatus (Bloch) and Pholis gunnellus (L) are all found associated with attached Laminaria (Bagenal,1973) and could possibly have been carried down with the weed following detachment. When large quantities of attached kelp were collected underwater for experimental work Ctenolabrus and Pholis were frequently found trapped in bundles of weed. All three species are predators, feeding on crustaceans, polychaetes and molluscs (Bagenal, 1973; Norman and Greenwood, 1975). A few very young Cyclopterus lumpus L. were also found attached to the weed by their ventral suckers. Wheeler (1969) has also noted the presence of juvenile Cyclopterus with drift weed.

Only a single juvenile Zeus faber L. was found.

2) Litter bag experiment

The percentage loss of weed dry weight with time in bags of both mesh sizes (1mm and 50mm) are illustrated in Fig. 39 for the four separate experimental runs. In all cases, significant positive relationships were found. For each experimental period, the regression lines fitted to the data were compared (Table 10) using covariance analysis (Snedecor and Cochran, 1967). For the December-March, September-November and February-May periods, the "A" regression lines (1mm mesh bags) had significantly higher elevations than the corresponding "B" lines. In September-November, the slope of the "A" line was also significantly greater. Thus, in all but the June-August period, weed was lost at a significantly faster rate from the 1mm mesh bags.

Fig. 39

Rate of weed loss in litter bags of mesh size 1mm (A, solid symbols) and 50mm (B, open symbols) secured on the sea-bed (20m depth) at the Wishing Well, Cumbrae, at different seasons of the year.

Equations for lines of best fit:

Sept. - Nov.

(A) $y = 1.37x + 9.40$ ($r = 0.92$, df. 4, $P < 0.01$),

(B) $y = 0.59x + 1.24$ ($r = 0.84$, df. 4, $P < 0.05$).

Dec. - Mar.

(A) $y = 0.73x - 6.20$ ($r = 0.91$, df. 4, $P < 0.05$),

(B) $y = 0.55x - 11.0$ ($r = 0.85$, df. 4, $P < 0.05$).

Feb. - May

(A) $y = 1.36x + 4.87$ ($r = 0.93$, df. 3, $P < 0.05$),

(B) $y = 0.82x + 6.34$ ($r = 0.96$, df. 4, $P < 0.01$).

June - Aug.

(A) $y = 1.61x - 37.0$ ($r = 0.97$, df. 4, $P < 0.01$),

(B) $y = 1.15x + 1.81$ ($r = 0.90$, df. 4, $P < 0.05$).

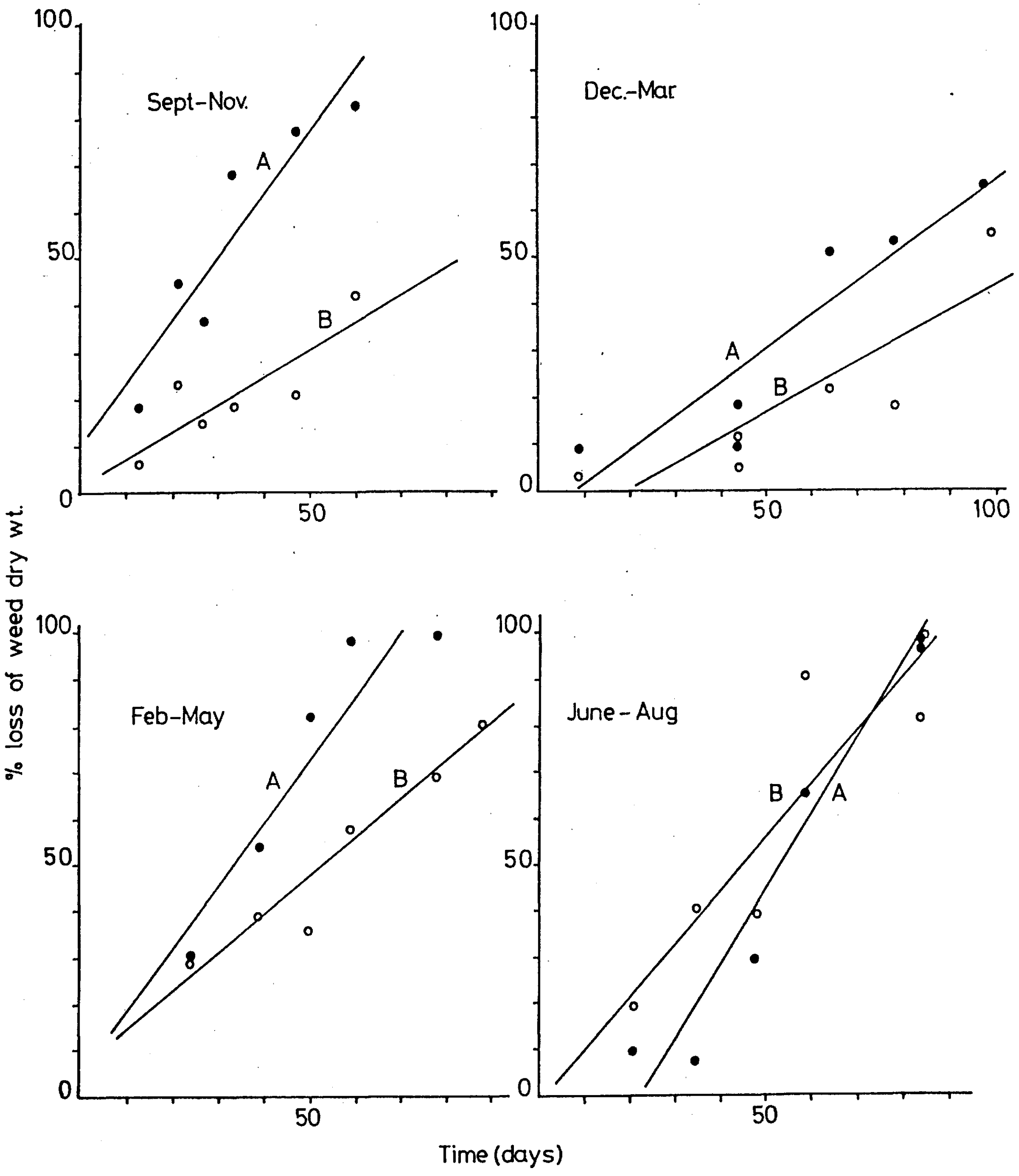

Sept-Nov.
Dec.-Mar
Feb-May
June - Aug
A
B
100
50
0
50
100
% loss of weed dry wt.
Time (days)

Table 10

Covariance analysis of regression lines fitted to data for weed loss with time for litter bags of two mesh sizes, A. v. B (see Fig. 39):

ns = not significant $P > 0.05$;

* = 0.05 $P \leqslant 0.01$;

** = 0.01 $P \leqslant 0.001$

Time of year	Slope		Elevation	
	F_1	df.	F_2	df.
Sept. - Nov.	5.02*	8	27.0**	9
Dec. - Mar.	0.56^{ns}	8	7.0*	9
Feb. - May	3.31^{ns}	7	16.01**	8
June - Aug.	1.93^{ns}	8	1.37^{ns}	9

3) Combination experiment

The results obtained from the two trials of the combination experiment are shown in Figs. 40 (a-c) and 41 (a-c). Each pair of graphs illustrates the loss in dry weight of weed over the experimental period when the species in question were either (i) kept in the same experimental bag (solid line) or (ii) kept in separate experimental bags and individual weed losses combined (broken line). Figures 40a and 41a show the combined effects of Gammarus and Platynereis. Little difference was found between the amount of weed lost whether these animals were kept singly or together. With Psammechinus and Gammarus (Figs. 40b and 41b) however, more weed was lost when the animals were kept separately than together. Initially, little difference was observable. After 2-3 weeks however, the rate of weed loss for animals kept separately increased rapidly. Weed was lost at a fairly constant rate when these two animals were kept together. Similar results were found with the combination of all three species (Figs. 40c and 41c); less weed being lost when the animals were kept together rather than singly. There is little evidence that accompanied Psammechinus is feeding on rotting weed, despite its preference for this diet (see chapter 1). Presumably , the highly motile Gammarus consumes this material before it is located by Psammechinus. Geometric rates of tissue loss in summated trials (Figs. 40c and 41c) result from the rapid onset of microbial decomposition of weed in sub-cultures with no microbe-stripping gammarid and/or "cut edge-recropping" nereid.

Fig. 40

Combination Experiment 1. Reduction in dry weight of weed (g) with time when different combinations of species were kept together (solid line), compared with the combined effect of the same species kept individually (dashed line);

(a) Platynereis and Gammarus,

(b) Psammechinus and Gammarus

(c) Platynereis, Psammechinus and Gammarus.

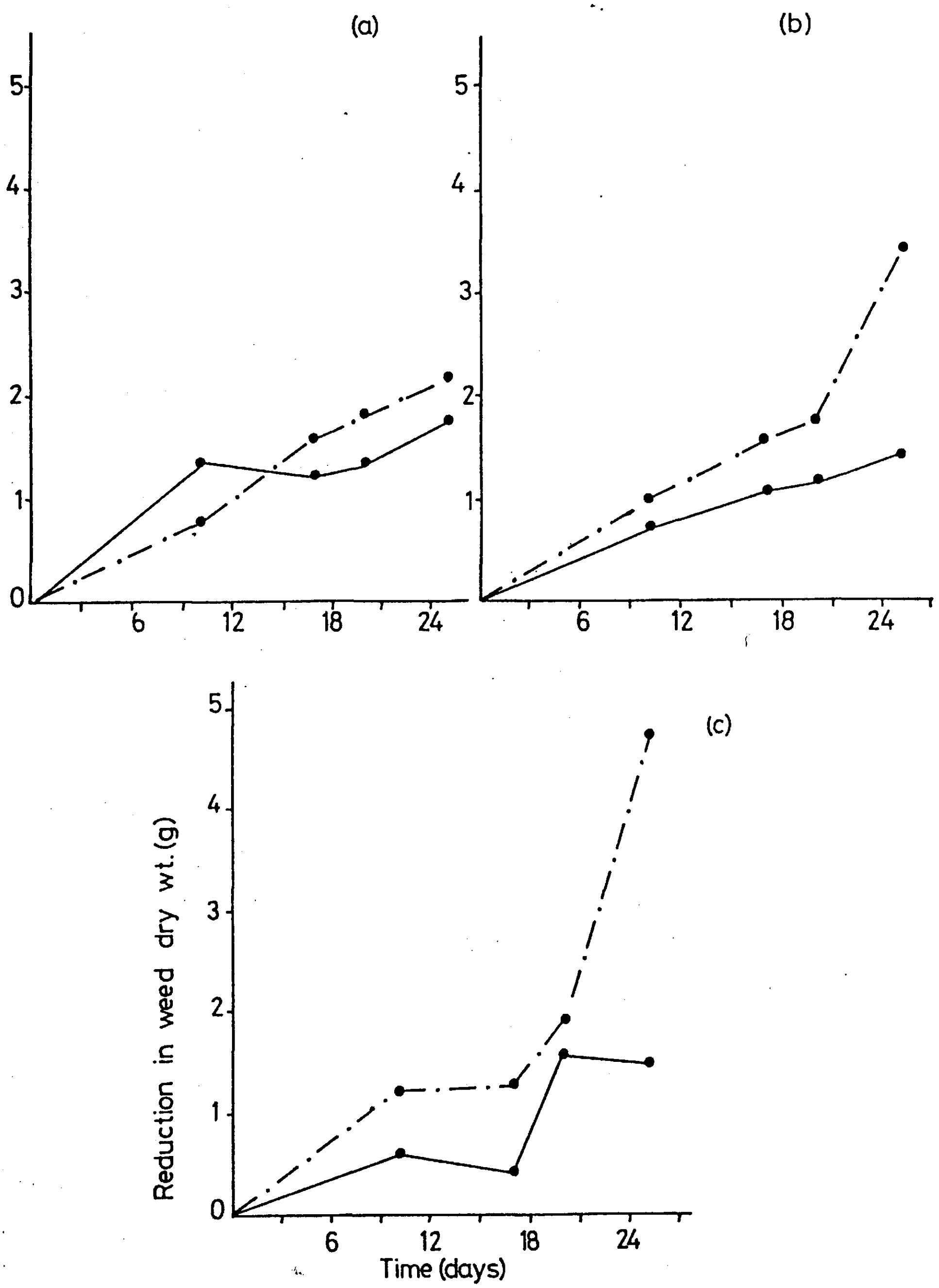

(a)
(b)
(c)
0
1
2
3
4
5
6
12
18
24
Reduction in weed dry wt. (g)
Time (days)

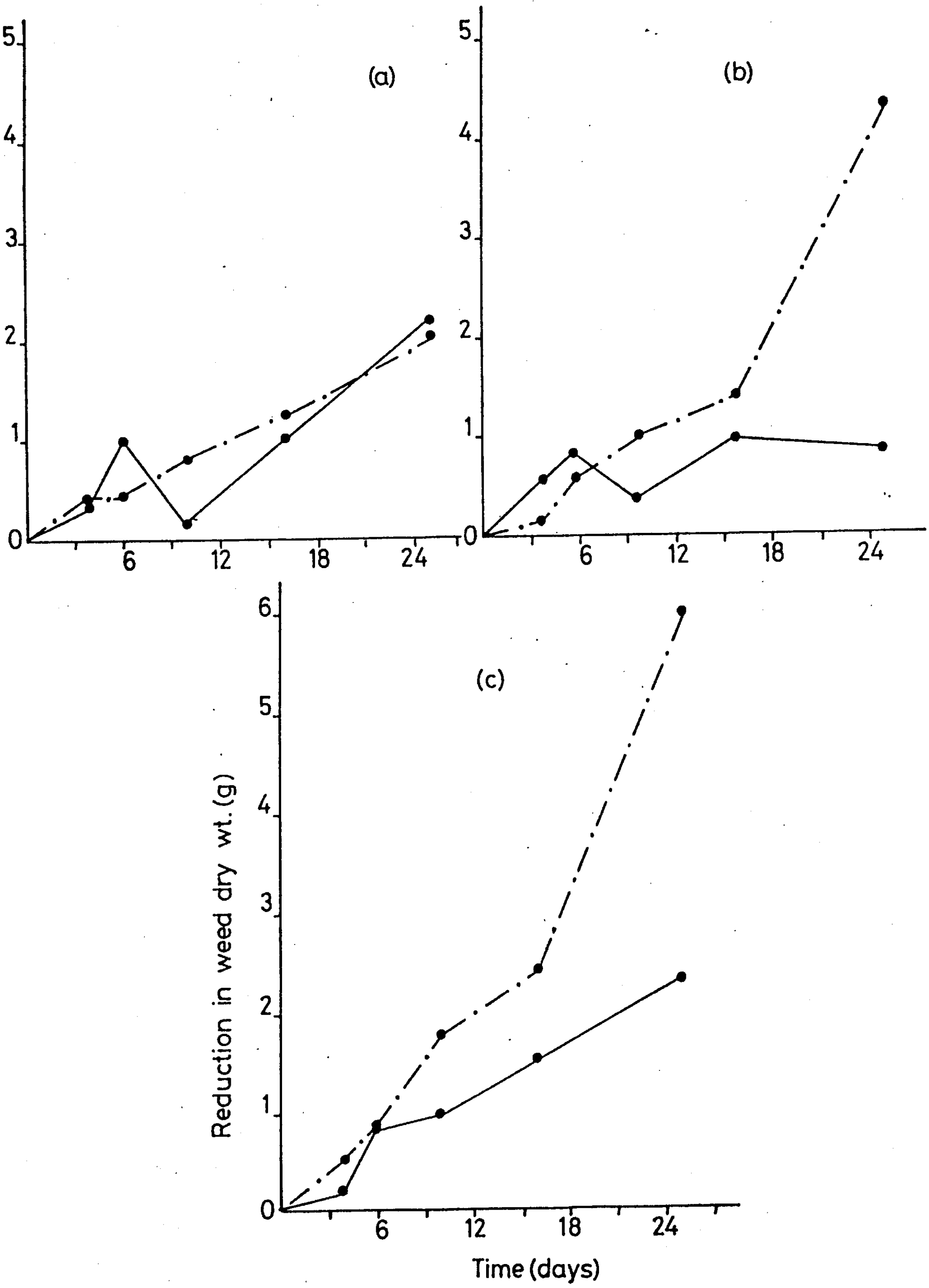
Fig. 41

Combination Experiment 2. Reduction in dry weight of weed (g) with time when different combinations of species were kept together (solid line), compared with the combined effect of the same species kept individually (dashed line);

(a) *Platynereis* and *Gammarus*,

(b) *Psammechinus* and *Gammarus*,

(c) *Platynereis*, *Psammechinus* and *Gammarus*.


(a)
(b)
(c)
0
1
2
3
4
5
6
6
12
18
24
Reduction in weed dry wt. (g)
Time (days)

DISCUSSION

The fauna of detached weed is derived from three sources. Firstly, many animals are transported into deeper water with the weed itself following detachment by storm action. Secondly, some animals migrate onto the detached weed from the surrounding sediment. Thirdly, some animals settle onto the weed from the plankton. To consider their role within the detached kelp community, the fauna is best divided into the following categories:

a) animals ingesting the intact algal substratum, eg. many gastropods, the polychaete Platynereis and the echinoids Psammechinus and Echinus.

b) animals feeding on the decaying frond material and digesting mainly the saprophagous micro-organisms. This material constitutes the main food of many of the amphipods. Some decapods and echinoderms also include this material in their diet.

c) animals feeding on the bottom sediments (and sediment and detritus collecting on the fronds). Incorporated in the sediment are decaying algal fragments and the faecal pellets of animals in the two groups above. The decapods Galathea intermedia and Eualus pusiolus are included within this group.

d) animals that are carnivorous and/or scavengers, eg. certain polychaetes, some decapods, gastropods such as Nassarius and Philbertia, echinoderms such as Asterias rubens and some of the fishes.

e) animals that use the weed as suitable cover or substratum for attachment, eg. Porcellana longicornis and Chlamys opercularis.

This classification is obviously not rigid, the feeding repertoire of some species covering several classes. The majority of species, however, fit this system reasonably well.

In the sampling programme, only the macrofauna intimately associated with the Laminaria fronds was captured. No attempt was made to examine the infauna of the underlying substratum. Kikuchi and Pérès (1977) considered, when discussing the fauna of sea-grass meadows, that the sediment infauna was simply an extension of the surrounding benthic community. This is most likely to be true here. Nevertheless, the underlying infauna will be modified by overlying kelp since the sediments will be showered with highly nutritious decomposing algal fragments and detritivore faecal pellets. The sediments will thus be able to support larger densities of infaunal detritivores. Overlying weed reduces the water flow over the sediment. This, coupled with the oxygen demand of the aerobically decomposing detritus can lead to reduced oxygen tensions at the benthic interface. Both these factors affect the densities of the normal sediment infauna (Pearson and Rosenberg, 1978).

It is clear from the litter bag experiments that except during the summer, weed is lost from sea-bed accumulations at a faster rate when macrofaunal animals are excluded. The macrofauna thus inhibits decomposition. In the autumn, large quantities of weed are detached by storms. This weed carries down with it to the sea-bed a large part of its normal fauna. Additional species settle onto the weed from the plankton, whilst others migrate onto the weed from the surrounding sea bed. Autumn corresponds with the time of peak density of all these species (Fig. 38). Macrofaunal densities then decline, reaching minimum levels in summer. Mesh bag experiments set up in September, December and February, had a detached weed fauna available to colonize the kelp in the 50 mm mesh bags and this fauna seems to have controlled decomposition effectively. In the June experiment, however, few macrofaunal individuals were available locally to colonize the weed and decomposition continued at approximately the same rate in bags of both mesh sizes.

Comparing rates of decomposition in the 1 mm mesh bags, weed decomposed at a slower rate in December-March compared with similar material in the September-November experiment. This would be an expected consequence of lowered seawater temperature. There was little difference in the water temperature between the December-March and February-May periods. In February-May, however, weed decomposed at a significantly faster rate than in December-March. In February, Laminaria undergoes a period of rapid growth (Johnston et al., 1977). The resulting kelp tissue is more flimsy in structure, illustrated by its lower density at this period (Johnston et al., 1977). Thus weed used to set up the February experiment would be less resistant to decay than the tougher material used in December.

Using litter bags to study sea-grass decomposition, Burkholder and Doheny (1968), Heald (1969) and Odum, Heald and Zieman (1971) all found that macro-invertebrates, particularly amphipods, speeded up the rate of decomposition. Marine angiosperms have a large proportion of structural polysaccharides and coverings of waxes etc. which make them relatively unpalatable (Odum, Zieman and Heald, 1971). Very few animals naturally graze this material (Odum et al., 1971; Kikuchi and Pérès, 1973; Fenchel, 1977, but note Cammen, 1980). With macro-invertebrate involvement, sea-grass litter would decompose very slowly, taking somewhere in the region of 6-12 months (Odum and de la Cruz, 1967; Wood et al., 1969; Odum et al., 1971; Tenore, 1977). Following a period of autolysis, during which soluble materials leach out (Valeila et al., 1979), the plant detritus is attacked by saprophagous micro-organisms (Mann, 1972). The decaying material is then consumed by various detritivores, such as amphipods, which digest only the micro-organisms. Passage through the gut of the detritivore results simply in mechanical breakdown of the plant substratum. This fragmentation increases the surface:volume ratio of the substratum, encouraging bacterial lysis of the material and hence enhancing decomposition (Fenchel, 1970, 1972; Mann, 1972; Hargrave, 1970, 1975). These faecal pellets, following colonization by micro-organisms, constitute a rich food source for other detritivores (Newell, 1965; Fenchel, 1970, 1977; Mann, 1972; Hargrave, 1975). Sea-grass detritus thus represents a "bottle-neck" to energy flow (Macfadyen, 1961) due to nitrogen limitation (Findlay, 1982), but reworking of the plant substratum by successive detritivores, and interactions between meiofauna and macrofauna (Tenore, Tietjen and Lee, 1977), speeds up the intrinsically slow decomposition of marine angiosperms and encourages leaching of secondary plant substances which otherwise inhibit detrital utilization. Compared with algal detritus, the degradation of sea-grass litter, even with macro-invertebrate involvement, is still slow. In temperate climates, this slow decomposition assures a relatively constant source of energy for heterotrophic organisms throughout the year, in contrast to autotrophs which are subject to seasonality due to variations in photosynthesis (Fenchel,1977).

The results from the combination experiment give some indication of the mechanism of macrofaunal control over weed decomposition. The presence of Gammarus with Psammechinus resulted in less weed being lost than when Psammechinus was isolated. Psammechinus is a browsing feeder. Moving over the frond, its feeding exposes the delicate internal kelp tissues to saprophagous micro-organisms when feeding alone. Weed is lost therefore both from the urchin's activities and from microbial decomposition. This effect is particularly noticeable after a period of time, when large areas of underlying tissue have been exposed and the saprophagous microbial community has become well established. Once established, microbial and meiofaunal elements (particularly nematodes , see Benwell, 1980; Findlay, 1982; Findlay and Tenore, 1982) break down the weed rapidly. The violent body movements of nematodes fragment tissue which has been weakened by bacterial lysis and aid water movements within it, ensuring that aerobic decomposition continues. Nematodes do not colonize the weed immediately, but follow the establishment of bacterial and ciliate populations. Gammarus feeds preferentially on decomposing algal tissue. When Gammarus is present with Psammechinus, it "crops" the rotting weed, effectively preventing the establishment of the saprophagous community, particularly of nematodes. Thus with Psammechinus and Gammarus together, weed loss is due solely to the feeding requirements of these two animals.

When feeding, Platynereis also exposes algal tissue in the same fashion as Psammechinus. With its tendency to crop the same region of the frond repeatedly (see Chapter 2), however, Platynereis itself prevents any substantial colonization of the weed by saprophagous micro-organisms. Thus, whether kept together or separately, the loss of weed with Platynereis and Gammarus simply reflects the food requirements of these two animals.

Confirmation of earlier conclusions (Chapters 1,2 and 3) can be drawn from these combination experiments. There is little evidence that Psammechinus is feeding on rotting weed despite its preference for this diet (see Chapter 1). Presumably, the highly motile Gammarus consumes this material before it can be located by Psammechinus (cf. Traer, 1980).

Rates of tissue loss followed a geometric curve. This was particularly the case with Psammechinus kept in isolation (Figs 40b,c; 41b,c). Curvi-linear responses result from the rapid onset of weed decomposition resulting from the action of saprophagous micro-organisms. Ciliate populations (used here as an index of decomposition rate) on both weed and faecal pellets expand geometrically with time (see Chapters 1-3). The data from the litter bag experiments are of the same basic type as those from the combination experiment. With the controlling effect of the macrofauna, the relationship between weed loss and time in the 50mm. mesh litter bags would be expected to be linear. In the 1mm mesh bags, which exclude macrofauna however, a curvi-linear relationship would be expected, with a period of slow colonization by saprobes being followed by rapid weed decomposition. The litter bag experiments, however, were conducted for much longer periods than the combination experiments, so little data were collected during the "colonization period". Almost all the data then relate to the later period of rapid weed decomposition which can be considered a linear response.

Algal detritus, by contrast with sea-grass detritus, has a much lower level of tough, structural polysaccharides (Tenore, 1977) and the distal region of the frond is already decaying when the weed is detached (Johnston, 1971; Johnston et al., 1977; Mann, 1972). As shown by the litter bag experiments, the detached weed will decompose very quickly without the aid of macro-invertebrates. In addition, however, there are a number of species such as Psammechinus, Echinus, Platynereis and various gastropods which ingest large quantities of the weed. These animals digest the algal substratum itself and this constitiutes their main food source. Thus, as soon as the detached kelp accumulates on the sea bed it is attacked by these animals, Saprophagous micro-organisms tackling an intact frond first have to penetrate the tough outer tissues. This barrier, combined with the leaching of various antibacterial exudates (Sieburth, 1968; Valeila et al.,1979; Tenore and Rice, 1980), results in an initial period during which little microbial decomposition occurs. The feeding of the above macro-invertebrates gives micro-organisms immediate access to the less resistant internal frond tissues. These macro-detritivores are also showering sediments inderlying the weed with faecal pellets, Once the saprophagous micro-organisms are well established on the kelp, the whole frond will decompose very quickly. As described earlier, decomposition is greatly assisted by the action of ciliates

(Briggs et al., 1979) and nematodes (Tenore, Tietjen and Lee, 1977; Benwell, 1980; Findlay, 1982; Findlay and Tenore, 1982). As with the sea-grass litter, these meiofaunal detritivores enhance weed decomposition. Detached Laminaria, however, does not represent a "bottle-neck" to energy flow; quite the reverse. With the input of weed to sublittoral accumulations being pulsed in synchrony with storm action, microbial decomposition of this material would be similarly pulsed. Left alone, decomposing Laminaria fronds lose rigidity and would tend to blanket the underlying substratum. Synchronized decomposition would, at best, result in irregular, massive inputs of fine detritus to the sediment. At worst, it would result in severe anaerobic conditions suffocating both the fauna associated with the fronds themselves and also the infauna of the underlying sediments. Such a situation often occurs on the sea bed in areas in receipt of organic pollutants, eg. wood pulp (reviewed by Pearson and Rosenberg, 1978).

The highly motile amphipods however actively seek out and crop the decaying algal material, which may also be included as part of the diet of other invertebrates, eg. certain decapods. As with the sea-grass litter, the amphipods digest only the saprophagous micro-organisms. Cropping the rotting weed prevents the saprophagous micro-community gaining the upper hand. Since the weed would decompose very quickly if undisturbed by macrofaunal croppers, the effect of the amphipods in this instance is to seriously retard weed decomposition. The action of the amphipods thus ensures that the kelp macro-fauna (not saprobic micro-organisms) controls frond degradation. The rate of degradation is governed mainly by the rate of feeding of macro-detritivores such as Platynereis and Psammechinus. Thus, almost all of the kelp tissue initially passes though the gut of macro-detritivores feeding on the algal substratum. Their faecal pellets will be colonized by micro-organisms and will be re-ingested by sediment feeding detritivores

Eualus pusiolus, Galathea intermedia and various amphipods, including Gammarus (see Chapter 3). The algal substratum will be re-worked by these macrofaunal and other meiofaunal detritivores as described above for sea-grass litter. Levinton et al., (1976) considered that the rates of faecal pellet breakdown and of microbial recolonization are the rate-limiting steps in detrital energy availability. As the kelp egested by detritivores such as Psammechinus is partially digested, the resulting faecal pellets offer a less nutritious substratum for micro-decomposers than fresh algal fragments (see Chapters 1,2 and 3). This results in the slower colonization of their faeces by the microbial community, presumably resulting in a longer period elapsing before they are re-ingested. This process also helps to prolong the decomposition of the algal substratum.

The active scavenging by amphipods and other detritivores for the faecal pellets of larger organisms aids water circulation around and amongst the weed and in the surface floc of the sediment. Hargrave (1975) described a number of examples illustrating the importance of sediment disturbance in allowing cycling of material which would otherwise remain buried (see also Briggs et al., 1979). Locomotory activity by swarms of these animals then, helps to prevent the onset of anaerobic conditions. Ultimately, algal detritus is incorporated into the tissues of infaunal deposit feeding invertebrates found abundantly in fine, muddy sediments (Newell, 1965; Levinton et al., 1976). These, and the detritivores already mentioned eventually fall prey to the various carnivores associated with the detached weed. Detritus in the water column, produced from the erosion of either attached or detached kelp fronds, is exploited by suspension feeders (Lenz, 1977; Foulds and Mann, 1978; Newell, 1980; Stuart, Newell and Lucas, 1982).

Macrofaunal involvement with the decomposition of macro-algal detritus then differs in two important ways from sea-grass litter (but note Cammen, 1980). Firstly, with detached Laminaria, a considerable number of detritivores probably digest the detrital substratum. In the light of these and Cammen's (1980) findings, the general conclusion of Fenchel (1977, see also Fenchel and Jørgensen, 1977) that detrital matter derived from macrophytes and the energy contained in it has to pass through a bacterial or fungal link before it can be utilized will have to be modified not only to distinguish macro-algal from vascular plant debris (see also Tenore, 1977, 1981, 1982) but also to take into account Christian and Wetzel's (1978) point about low microbial densities on detritus particles in many situations. Secondly, the detritivores associated with Laminaria detritus act together to inhibit rather than to enhance decomposition. The effect of the orchestrated action of the great variety of detritivores associated with detached weed is then to stabilize both their own food supply (cf. Gore et al., 1981) and the supply of fine detritus to sediment-living heterotrophs.

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