Some aspects of fielding ecology and phosphorus bedgeting in the mussel, mytilus edulis (l.)

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SOME ASPECTS OF FEEDING ECOLOGY AND PHOSPHORUS BUDGETING IN THE MUSSEL, MYTILUS EDULIS (L).

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INTRODUCTION

Phosphorus is immensely important to living organisms as it plays a fundemental role in the metabolic processes of energy transfer. Hutchinson (1957) suggests that phosphorus is likely to be the most important element in ecological situations as organisms tend to accumulate phosphorus more actively than other biologically useful elements. Thus a deficiency of phosphorus is more likely to limit productivity on the earth's surface than is the deficiency of any other material, excluding water. The biogeochemistry of phosphate and compounds of phosphorus with respect to freshwater ecosystems has been extensively reviewed (Hutchinson, 1952, 1957).

In marine systems most interest has centered around the interrelationships between phytoplankton and zooplankton, and the resultant effects on the nutrient cycle (Corner and Davies, 1971; Corner, 1973). A simplified version of the marine phosphorus cycle is presented in FIG. 1. One of the most important features of this cycle in the conversion of dissolved phosphorus into particulate phosphorus either in living organisms or detritus. The process of conversion of dissolved phosphorus is mainly undertaken by plants and bacteria, although Kobayashi _et al._ (1972) have shown that _Artemia_ is able to utilize phosphorus. Ronkin (1950) was also able to show the uptake of dissolved phosphorus by excised gills of _Mytilus edulis_. However, the uptake of dissolved phosphorus by animals is unlikely to be of great significance in the marine cycle. They are thought to derive the majority of their dietary phosphorus from phytoplankton and bacteria. There is also some evidence that marine animals are able to utilize non-living particulate matter. These particles are derived from organic particles becoming absorbed into bubbles. These aggregates may become large enough to be retained by filter-feeding animals. Baylor and Sutcliffe (1963), who have shown that these particles may

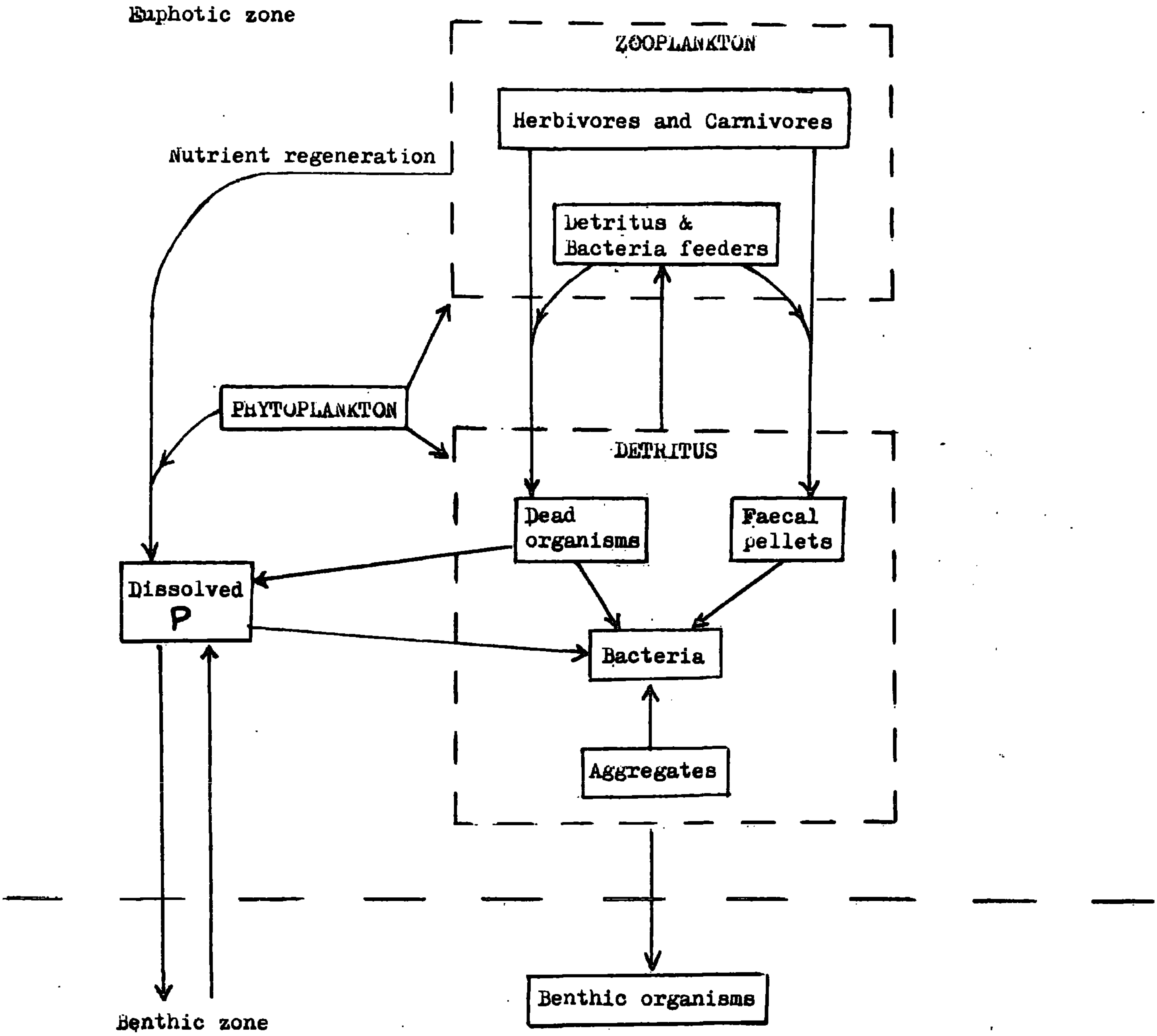


FIG. 1 : Aspects of the marine phosphorus cycle.
Adapted from Corner (1973).

be of significant nutritive value for *Artemia salina*, speculated on their importance to intertidal communities.

Clearly there are many facets of the marine phosphorus cycle but, at present, there is a lack of information inter-relating the mechanisms and importance of the cycle in the Bathypelagic, Epipelgic and Littoral zones of the marine environment. There is limited information on phosphorus in the littoral - for example: Kuenzler (1961) on *Modiolus* and McRoy *et al.* (1972) on *Zostera*. As the mussel, *Mytilus edulis*, is one of the major components of the fauna in the British rocky shore intertidal a study of phosphorus budgeting and its inter-relationships with feeding and the energetics in *Mytilus* populations is fundemental to our understanding of the ecosystem.

The mussel, *Mytilus edulis*, is a filter-feeder selectively collecting particulate matter from water that is passed through filibranch gill structures. Jørgensen (1966) points out that filter-feeding is not synonymous with suspension feeding. The term suspension feeder was originally exclusive to benthic animals (Hunt, 1925) but its present usage embraces benthic, planktonic and nectonic organisms. One should therefore restrict filter-feeding to denote a mode of feeding where water is passed through structures that retain particulate matter, often selectively.

The gill systems of many bivalves are well-developed sorting mechanisms (Atkins, 1936, 1937), with frontal ciliary tracts beating both dorsally and ventrally. In many species particles are sorted by size and weight. Light particles are carried dorsally to the mouth palps while heavy particles are moved ventrally and eventually fall off the gills to be ejected as pseudofaeces. Among the filibranchs the Mytilacea are one of the families to have en-latero-frontal cilia (Atkins, 1938). Ansell's observations on *Mytilus* indicate that resting latero-frontal cilia act as a sieve, straining particles from the passing current. As the particles are removed from the water active cilia throw them onto the frontal tracts of adjecent gill filements where they are sorted and conveyed to the two pairs of mouth palps (Ansell, 1961). Other research (Tammes and Dral, 1955) has described particles adhering to latero-frontal cilia which seemed to be sticky. These particles were then wiped off onto the frontal ciliary tracts.

The results obtained by MacGintie (1941) contrast strongly with the sorting mechanism suggested above. He removed sections of the shell and underlying mantle tissue in a number of species of bivalve; including *Mytilus californianus* and inserted glass windows. Once the animals had recovered he was able to observe the feeding process directly, without disturbing or further mutilating the animals. In this situation the entire gill surfaces were covered with a mucus sheet which was ingested periodically. The gill cilia had no selective function and the palps were only partially selective.

An attempt has bean made to unify the two contrasting views on the feeding mechanism in filter-feeding bivalves by suggesting that the mode of feeding in waters with a low concentration of suspension is by mucus sheets. The sorting abilities of the gill system are thought to be utilized in the presence of excessive quantities of material in the water. Selection of particles which are light and small is very important to filter-feeding bivalves as digestion is mainly intra-cellular (Yonge, 1937). Most workers suggest that the ciliary tracts are capable of sorting particles according to size and weight but not with respect to food quality. However Bu ley (1936) found that *Mytilus californianus* is able to select in a qualitative fashion. Over a seven month period the phytoplankton in the water had an advantage composition of 2.4% dinoflagellate and 97.6% diatom, while the stomach content of the mussels contained 97.4% and 2.6 % respectively. Foster-Smith (1975 a) showed that differential selection by the pallial organs does not occur in Mytilus edulis when the animal is offered a choice between Phaeodactylum and inorganic particulate matter; although the inorganic material is selectively rejected in the gut.

While the role of food quality is not completely documented it seems that the physical characteristics of the particles are of importance in determining the degree of retention by the animals. Mytilus edulis is able to completely retain particles of greater than 30 µm (Tammes and Dral, 1955). The gill system is capable of efficiently retaining particles of sizes down to about 1 µm but the lower limit of retention appears to be related to the degree of disturbance and the experimental conditions to which the animals are subjected (Jørgensen, 1966). It appears that in extremely artificial situations the porosity of the gills increases.

The food intake of the animal is therefore a function of the product of cell concentration, the efficiency of cell retention of the gill system and the filtration rate.

Filtration rates in bivalves have been studied using a number of methods. These methods fall into two classes; direct methods in which the rate of pumping water is measured and indirect methods in which the pumping rate is directly proportional to the rate of removal of suspended particulate matter. Direct methods require either physical separation of the inhalent and exhalent siphons or techniques which make the flow of water visible (Hersh, 1960; Coughlan and Ansell, 1964). Physical separation of the siphons is often difficult and the method adopted must ensure that the animal is not pumping against pressure. A number of major modifications have been made to the original techniques of Wallengren (1905) and Moore (1910), and the method has been successfully employed by a number of workers. (Loosanoff and Nomejko, 1946; Loosanoff and Engle, 1947; Tammes and Dral, 1955; Davids, 1964; Hiddreth, 1976).

Indirect methods of estimating filtration rates require the measurement of the concentration of suspended particles at discrete time intervals. Some authors have used suspensions of artificial materials. For example, Damas (1935) worked on mud deposition by *Cardium edule*; Fox *et al*. (1937) used calcium carbonate to determine water propulsion rates in *Mytilus californianus*. A number of workers have used colloidal graphite to determine filtration rates: Jørgensen (1952) in *Crassostrea virginica*; Rao (1953) and Segal *et al*. (1953) in *Mytilus californianus*; Jørgensen (1960) and Theede (1963) in *Mytilus edulis*.

As an alternative to inorganic particulate matter a number of workers have determined filtration rates using suspension of micro-algal cells. Jørgensen (1949) used *Dierateria inornate* and *Isochrysis galbana* in estimating filtration rates in *Mytilus edulis*; Loosanoff and Engle (1947) working on *Ostrea virginica* used *Chlorella* sp, *Nitzchia closterium* and *Euglena viridis*. More recently Ali (1970), working with *Hiatella arctica*, determined filtration rates using *Phaeodactylum tricornutum* and *Isochrysis galbana*, while Hildreth and Crisp (1976), using a flow system, estimated the filtration rate of *Mytilus edulis* feeding on *Isochrysis galbana*.

A number of authors have determined filtration rates using radio-actively labelled algal suspensions. Chipman and Hopkins (1953) used *Nitzchia* on *Pecten irradians*; Rice and Smith (1958) used a range of P^{32} labelled algae in studying the filtration rate of *Venus mercenaria*; Allen (1962) used *Phaeodactylum* labelled with P^{32} in his work and most recently Foster-Smith (1975 b) used *Phaeodactylum tricornutum*, *Isochrysis galbana* and *Platymonas* labelled with P^{32} in his study of filtration rates of *Mytilus edulis*, *Cerastoderma edule* and *Venerupis pullastra*.

Whichever method is employed to determine the filtration rate it is of great importance that the procedure and the materials used should have no direct influence on the results. There are only a few instances in the literature where workers have considered the importance of cell concentration. *Ostrea virginica* has a reduced filtration rate when feeding on cell concentrations of *Nitzchia closterium* in excess of 80 X 10^3 cells ml^{-1}, but inhibition of filtration does not occur until the suspension concentration is 5400 X 10^3 cells ml^{-1} for the smaller alga *Chlorella* (Loosanoff and Engle, 1947). These results contrast with those given for the mussel, *Mytilus edulis*, where all concentrations of *Chlorella* exceeding 40 X 10^3 ml^{-1} cause a marked reduction in filtration rate; while *Nitzchia* has no effect on filtration until a concentration of 3000 X 10^3 cells ml^{-1} is reached (Davids, 1964). Chiba and Oshima (1957), feeding *Mytilus* with suspensions of Bentonite, showed the filtration rate to be a constant up to 3700 X 10^3 particles ml^{-1}. Davids (1964) reported a reduction in filtration rate in *Mytilus* in the presence of *Isochrysis* suspensions with concentrations greater than 200 X 10^3 cells ml^{-1}; while Foster-Smith (1975 b) found the rate to be fairly constant for cell concentrations between 50 - 800 cells ml^{-1}. Jørgensen (1966), using the alga *Phaeodactylum tricornutum*, suggested that the filtration rate of *Mytilus edulis* is a constant between 30 - 60 X 10^3 cells ml^{-1}. This has been confirmed by Foster-Smith (1975 b), who found filtration to be a constant until about 650 X 10^3 cells ml^{-1} and to be reduced by around 30% at a concentration of 900 X 10^3 cells ml^{-1}.

The production of pseudofaeces is dependent on the cell concentration offered. Arctica islandia and Modiolus modiolus produced pseudofaeces when fed with Clamydomanas sp at a cell concentration of 600 X 10^3 cells ml^{-1} (Winter, 1969). Foster-Smith (1975 b), working on Mytilus, showed that the proportion of material rejected as pseudofaeces is dependent on the concentration of the suspension offered and that the minimum concentration causing pseudofaecal production varied with the material used.

The assimilation efficiency of Mytilus is also related to food availability. It is reported to be a inverse linear function of food concentration (Thompson and Bayne, 1972, 1974). They suggest that once the digestive tubules become full of algae and the animals continue feeding, a greater proportion of ingested material is able to bypass the digestive process.

The effect of cell concentration on the feeding ecology of Mytilus edulis must be a major factor in determining the productivity of mussel populations. On shores with large areas of mussel clumps the community structure of the associated fauna living in the clumps may also be determined by the amount of material rejected by the mussels; although there is no quantitative data on this subject at the present time.

Comparison of the published data on Mytilus edulis feeding ecology is at present very difficult as the size and the pre-feeding histories of the animals used is often omited from the literature. In this dissertation I undertook a study of feeding ecology using Mytilus edulis with a defined pre-feeding history. The animals were starved for two weeks and then fed on a low level diet of the alga Phaeodactylum tricornutum. Animals with this pre-history were fed under three food regimes and a number of feeding parameters were studied - filtration rate, pseudofaecal production, egestion, excretion and assimilation efficiency. Total phosphorus contents of the same sized animals were also determined in order to estimate the ecological and physiological turnover time of Mytilus edulis collected in June.

MATERIALS AND METHODS

INTRODUCTION

The mussels were collected from Holy Island, Northumberland (Nat. Grid. NU 04 124427) in June. The animals were from the same population as that used by Foster-Smith (1975 a, b) in his experiments on the feeding ecology of Mytilus edulis.

In the laboratory the animals were washed and cleaned of any epibiotic growth. They were then maintained in aerated, artificial seawater (SeAquarium/Waterlife, England) under a light regime of sixteen hours light and eight hours darkness at a constant temperature of 15 ± 2°c until required for feeding experiments. The mussels were kept on a low level diet, after two weeks without food, prior to feeding experiments to minimise the effects of variation in pre-feeding history.

While the animals were in the laboratory they were fed with the alga Phaeodactylum tricornutum (Bohlin) which is relatively large (24.3 ± 4.0 µm) and should be completely retained by the feeding apparatus of the mussel.

PART I

RADIO-TRACER EXPERIMENTS

1.1 CULTURE METHODS FOR *Phaeodactylum tricornutum*

Stock cultures of the alga *Phaeodactylum tricornutum* were prepared using a modified Erb-Schreiber medium (Provasoli et al, 1957). The method was as follows:-

1.1.1 To one litre of artificial seawater, soil extract (50 ml), $NaNO_3$ (0.2 g) and $Na_2HPO_4 \, 12H_2O$ (0.03 g) were added.

1.1.2 The soil extract was made by adding water to garden loam until the volume of the supernatant water was twice that of the soil used. This mixture was then heated in a steamer for three hours and allowed to settle. The supernatant liquid was then filtered off. The final soil extract added to the seawater was a ten per cent extract solution, made up in distilled water; autoclaved at 15 lb. for 15 mins.

NOTE: If the soil extract is required for a period of several months a preservative of 1 part chlorobenzene, 1 part 1:2 dichloro-ethane, 2 parts 1 chlor-butane may be added. All traces of this are removed by further autoclaving.

1.1.3 The medium was filtered and shaken before inoculating with the alga. Miguel-Allen solutions (Galtsoff, 1959) have also frequently been used to maintain cultures of this alga. (Foster-Smith, 1975 a, b; Walne, 1966). The initial culture was inoculated from a pure sample of the alga (N.E.R.C. Culture of Algae and Protozoa). Once this culture approached a high density (over 500 X 10^3 cells ml^{-1}) sub-cultures were taken. These sub-cultures were inoculated to give an initial cell concentration of about 5 - 10 X 10^3 cells ml^{-1}. Stock cultures were kept at room temperature in 250 ml volumes in 1 litre culture flasks and continually agitated using an aerator block and a high air flow rate.

Radioactively labelled alga were prepared using mature cultures to which 0.267 mCi of carrier-free orthophosphate P^{32} were added per litre of solution. Algal suspensions were kept for at least one week before being used in feeding experiments to allow for the P^{32} label to be almost totally incorporated into the alga (Rice, 1958).

1.2 *Mytilus edulis* FEEDING EXPERIMENTS

Healthy individuals of *Mytilus edulis*, size range 45 - 55 mm, were selected for the P^{32} uptake experiments. Each animal was placed in 1 litre of aerated *Phaeodactylum* suspension of known concentration.

To provide a particular concentration of suspension, the cell density of the radioactive stock was determined using a haemocytometer. A suitable volume of this stock was then taken and made up to one litre with artificial seawater. The algal suspension was aerated for 10 minutes prior to introduction of the experimental animal and during the whole of the feeding experiment. This served two functions: to prevent deoxygenation of the suspension and to prevent settling out of the algal cells.

Feeding experiments were run at three different suspension densities: 20, 250, 750 X 10^3 cells ml^{-1}.

An initial 0.2 ml suspension sample was taken at the start of each feeding experiment. The animal was then introduced and allowed to feed for two hours. At 15 minute intervals during this feeding period 10 - ml aliquots of the suspension were removed and 0.2 ml placed on a planchet for counting. At each of these 15 minute intervals the suspension concentration was adjusted to approximately that of the initial cell density by adding an appropriate volume of stock solution and the total volume was made up to 1 litre by adding seawater. A further 0.2 ml sample was removed once the cell density had been re-equilibrated so that filtration rates could be determined and from these values the number of cells removed during the course of the experiment was calculated.

At the end of the feeding experiment the animal was removed and the surfaces of the shell were wiped to remove excess P^{32} solution. The animal was then introduced into 1 litre of freshly filtered aerated seawater and pseudofaeces, faeces and 0.2 ml water samples were removed at intervals over the course of the next 48 hours.

1.3 COUNTING TECHNIQUES

All samples were assayed using a Geiger-Muller tube mounted in a lead castle connected to a decade counter (Labgear, England). Samples were places on 25 RA planchets (Gallenkamp, England) and dried under Infra-Red lamps before counting. The activity of samples was then determined. A number of corrections were applied to the activity level (counts per second) recorded by each sample:-

1.3.1 The background was subtracted from the gross sample count to give the nett activity of the sample. The background radiation level was recorded by using a clean planchet in the counting apparatus.

1.3.2 The actual activity level was then corrected for radioactive decay since the time of issue of the P^{32} solution. This correction was required because P^{32} has a fairly short half life of 14.3 days.

1.3.3 The time standardised activity was then corrected to account for the efficiency of the counter. Due to the design of the counting apparatus only a fraction of the disintegrations given by a sample are recorded. As this is a constant it is possible to estimate counter efficiency by counting a sample of known activity. The counter efficiency is then given by:

$$\frac{\text{Nett recorded c.p.s. from sample}}{\text{Actual disintegrations per second in sample}} \times 100$$

The counting efficiency of the apparatus used was found to be about 7%

1.4 STATISTICAL CONSIDERATIONS

The accuracy of an observed count rate is dependent on the number of counts recorded and the time taken over the observation. This is due to the stochastic nature of the events being recorded, i.e. a number of determinations of the count rate made under the same conditions will produce a range of values around a mean count.

In all cases the time for a standard number of counts (at least 400) given by a sample was recorded. The standard error of the sample was then calculated as:

$$S.E. = \sqrt{\text{Total number of counts recorded}}$$

The standard error of the nett count rate was calculated as:

$$S.E. = \sqrt{S.E._{B}^{2} + S.E._{S}^{2}}$$

where B is the background count
and S is the gross sample count.

1.5 RADIOLOGICAL SAFETY TECHNIQUES

All types of radiation produced by radioactive material have the potential for damaging living tissues. The extent to which special precautions are required in the handling of isotopes on the amount used, the characteristics of the emissions and the radioactivity of the material. P^{32} is only moderately hazardous and as such does not require many of the stringent precautions demanded when using isotopes as Sr^{90} and high mass number radioactive elements.

The total amount of P^{32} used in the feeding experiments was relatively small: this along with the fact that P^{32} has a comparatively short life and is a pure β emitter meant that it could be used in safety; providing that a number of elementary precautions were adopted.

These were as follows:-

1.5.1 Acid digestion of active material wascarried out in a fume cupboard.

1.5.2 All working surfaces were covered with thick absorbent material - "Benchcoat".

1.5.3 Disposable gloves and syringes were used when removing radioactive samples.

1.5.4 Waste contaminated with P^{32} was confined to one bin for separate disposal.

1.5.5 Stock radioactive algal culture flasks were stored in enamel trays in order to contain any accidental spillages.

1.5.6 All glassware was thoroughly washed before reuse to reduce contamination of later experiments.

1.5.7 Active material was always transferred using a rubber bulb pipette in order to eliminate the possibility of oral contact with P^{32}.

PART II

PHOSPHORUS DETERMINATIONS

Phosphorus estimates were carried out on samples of *Phaeodactylum tricornutum* and individuals of *Mytilus edulis*.

2.1 *Phaeodactylum tricornutum*

The cell density of a mature culture of the alga was determined using a haemocytometer. 10 - ml aliquots of the culture were then centrifuged for 15 minutes and the supernatant removed. The algal cells were then resuspended in 1 ml of distilled water and transferred to a pre-weighed aluminium foil container. The algal were over-dried at 40°c to constant weight. The dry weight of the samples were then determined and a weighed proportion of the materialwas transferred to a 50 ml Erlenmeyer flask for acid digestion and phosphorus estimation.

2.2 *Mytilus edulis*

Individual animals, size range 45 - 55 mm, were dissected and the tissues were separated into a number of categories - shell, gills, mantle and gonads, adductors, foot, digestive system (Schulz-Baldes, 1974). Wet weights were determined and the tissues were then over-dried at 40°c to constant weight.

Dry weights were determined and weighed portions of the tissues were transferred to a 50 ml Erlenmeyer flask for acid digestion and phosphorus estimations.

2.3 ACID DIGESTION TECHNIQUES

Reagents : a) Concentrated sulphuric acid
b) 30% Hydrogen peroxide

Procedure:

2.3.1 About 20 mg of dried material was transferred to a 50 ml Erlenmeyer flask.

2.3.2 0.4 ml conc H_2SO_4 were added and heated gently, in a fume cupboard. The solution was then cooled.

2.3.3 3 drops of peroxide were then added and the solution reheated. If the solution remained colourless on cooling the digestion was regarded as being complete. The hydrogen peroxide digest was repeated until the final mixture remained colourless.

It was found that excess oxidising reagents left after the completion of digestion caused the formation of a stable yellow complex during the phosphorus determination and prevented the formation of molybdenum blue. It is therefore important not to add excess oxidising reagent to the digest.

2.3.4 On completion of the acid digest the material was transferred with washings to a 100 ml volumetric flask and made up to volume.

2.3.5 Digested portionsof <u>Mytilus edulis</u> shell failed to become clear at the end of the digestion due to the production of insoluble Calcium sulphate precipitate. This precipitate was filtered off before the digest was made up to volume.

2.4 PHOSPHORUS ESTIMATIONS

The method used in the determination of phosphorus was adapted from a standard colourimetric method based upon the formation of molybdenum blue (Linder, 1944). The molybdenum blue complex is produced on the reduction of molybdophosphoric acid by stannous chloride. This heteropoly acid is itself produced by the reaction of dilute phosphate solution and ammonium molybdate in acid medium.

Reagents: a) 2.5 N Sodium reagent

b) Molybdate reagent

2.5% Ammonium molybdate in 28% sulphuric acid

c) Stannous chloride

2.5% $SnCl_2 . H_2O$
10 ml conc HCl
90 ml H_2O

Reagent b) and c) were freshly prepared before each set of phosphorus determinations.

Procedure:

2.4.1 A 10 - ml aliquot of the peroxide-digested material was transferred to a 50 ml volumetric flask.

2.4.2 2.5 ml of 2.5N Na OH was added to neutralize excess acid.

2.4.3 2 ml of the molybdate reagent was then introduced and the solution was made up to volume.

2.4.4 2 drops of Stannous chloride reagent were then added and the solution was shaken thoroughly. The mixture was then left for 5 minutes to allow maximum colour development.

2.4.5 A portion of the solution was then transferred to a 40 mm optical cell and a spectrophotometer reading at 610 μm was teken on a H 700 Uvispeck spectrophotometer (Hilger and Watts, England) against a distilled water blank.

The amount of phosphorus in the original dried material was then estimated from a di-Sodium hydrogen orthophosphate standard curve, range 0.025 to 0.2 mg P. Beer's law is valid in this range.

RESULTS AND ANALYSIS

PART I

RADIO-TRACER EXPERIMENTS

1.1 FILTRATION RATE

The filtration rate of Mytilus edulis was calculated from the difference in activity levels of the labelled cell suspensions at successive fifteen minute intervals. Five assumptions are fundamental to these calculations. All are believed to be reasonable, and any errors involved to be quantitatively negligible. The assumptions are as follows:

1.1.1 All P^{32} in the cell suspensions was incorporated into the algal tissue.

1.1.2 The reduction in activity level of the suspension was due to filtration of the cells by the animal.

1.1.3 The animals pumping rate was constant in each fifteen minute interval.

1.1.4 The particle retention by the gills was 100% efficient.

1.1.5 The cell suspension was at all times homogeneous.

If this set of conditions is met, the calculated filtration rate would be equal to the pumping rate of the animal.

A number of equations have been published since Dodgson (1928) attempted to calculate filtration rate from the rate of removal of particles from suspension. These have been reviewed and shown to be identical by Coughlan (1969).

I calculated the filtration rate from the formula derived by Jørgensen (1943):

$$F = \frac{v. (\log Co - \log Ct)}{\log e \; . \; t}$$

where F is the filtration rate ($ml\ h^{-1}$)
v is the volume of suspension (ml)
t is the time interval between samples (h)
Co is the initial concentration/activity of the suspension.
Ct is the final concentration/activity of the suspension.

The weight-specific filtration rates summarized in Table 1 and FIG. 2, and detailed in Appendix I were based on the wet tissue weights of the individual animals.

Table 1 : Filtration rate (± 1 S.E.) and Weight specific filtration rate (± 1 S.E.) of *Mytilus edulis* at a range of food concentrations

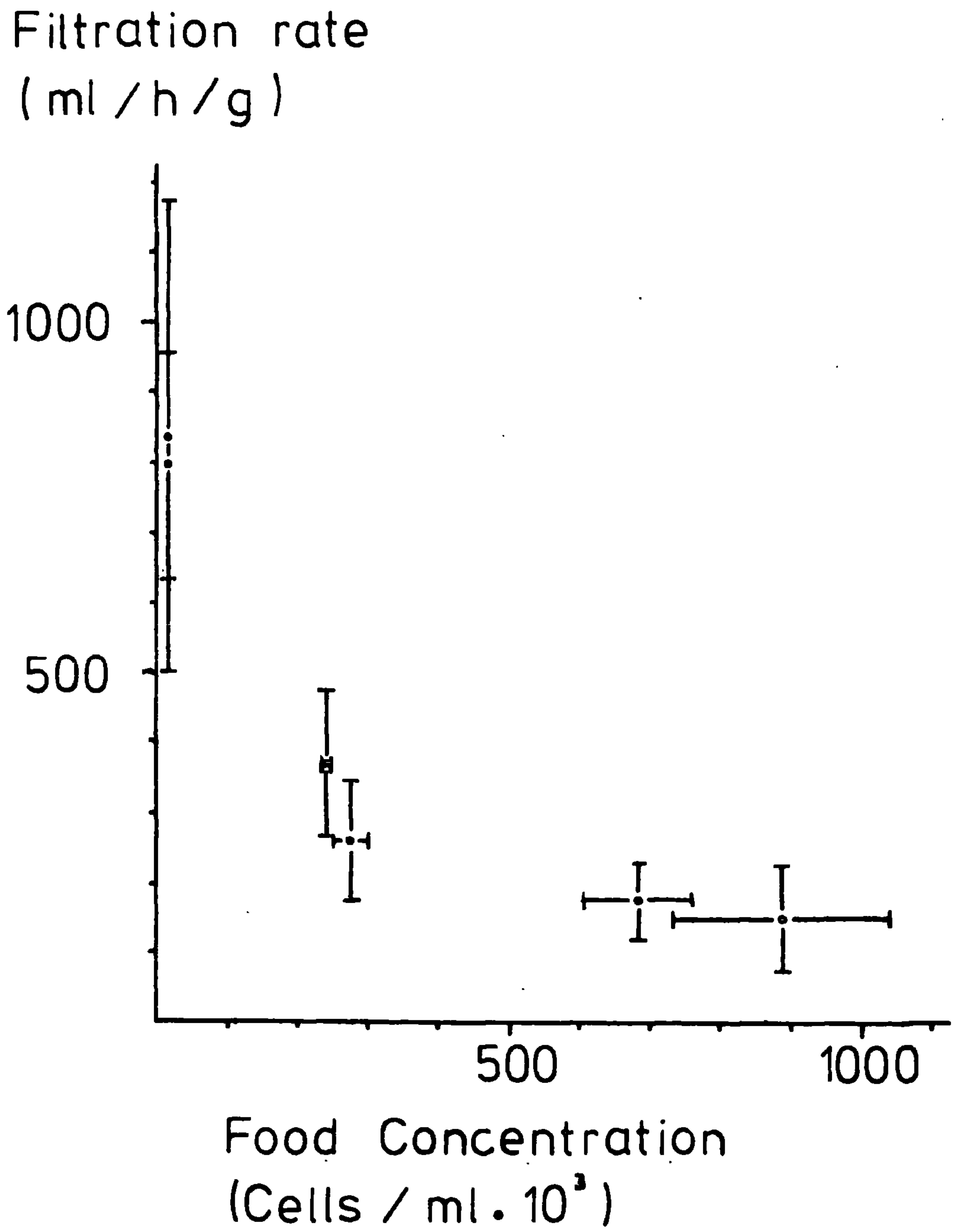
food concentration (cells ml^{-1}. 10^3)	filtration rate ($ml\ h^{-1}$)	Wt. specific filtration rate ($ml\ h^{-1}\ g^{-1}$)
17.9 ± 1.1	1217 ± 324	842 ± 171
17.3 ± 1.9	1762 ± 176	796 ± 79
237.2 ± 5.3	562 ± 91	368 ± 59
275.9 ±14.7	485 ± 85	259 ± 46
685.6 ±43.4	323 ± 60	175 ± 33
892.4 ±81.0	236 ± 64	151 ± 41

Table 2 : t - values derived from comparisons of pairs of filtration rates

($^{*}P<0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.)

Food conc.	17.3					
17.3		17.9				
17.9	0.23		237.2			
237.2	4.04^{***}	2.46^{*}		275.9		
275.9	5.49^{***}	3.08^{**}	1.32		685.6	
685.6	6.78^{***}	3.59^{**}	2.60^{*}	1.41		892.4
892.4	6.73^{***}	3.67^{**}	2.72^{*}	1.62	0.40	

Figure 2 : The relationship between weight specific filtration rate (± 2 S.E.) and food concentration (± 2 S.E.) in Mytilus edulis



The weight-specific filtration rates recorded at the two lowest food concentrations (17×10^3 cells ml^{-1}) were significantly higher than those recorded at all higher food levels; while the weight-specific filtration rates measured at food concentrations greater than 275×10^3 cells ml^{-1} were not significantly different from each other (Table 2). These results indicate that with increasing food availability the weight-specific filtration rate is starved Mytilus edulis falls to a steady level reached at cell concentrations above about 250×10^3 cells ml^{-1}.

The present literature states that Mytilus edulis does not filter in very dilute suspensions and that filtration is initiated at a critical threshold particle concentration (Theede, 1963; Thompson and Bayne, 1972; Bayne, 1976). Thompson and Bayne (1974) found that, once the threshold was passed, the filtration rate was unaffected by the cell concentration; but these authors used concentrations of only $2 - 25 \times 10^3$ cells ml^{-1}. Winter (1969) observed a decrease in the filtration rate of Modiolus with an increase of Dunatiella cell concentrations from 20 to 40×10^3 cells ml^{-1}. More recently Foster-Smith (1975 b) has reported that the filtration rate of Mytilus edulis is fairly constant at Phaeodactylum concentrations of between 50 and 800×10^3 cells ml^{-1}. He quoted the weight-specific filtration rate at a concentration of 200×10^3 cells ml^{-1} as 390 ml h^{-1} g^{-1}; at about 900×10^3 cells ml^{-1} this rate was reduced by about 30%. This contrasts with the results presented here which recorded a weight-specific filtration rate of 366 ml h^{-1} g^{-1} at 237×10^3 cells ml^{-1} and a reduction of about 60% at just less than 900×10^3 cells ml^{-1}.

1.2 INTAKE AND INGESTION RATES

The intake of particles into the mantle cavity is the rate at which particles are filtered from suspension and is the product of filtration rate and the suspension concentration.

Table 3 : Synopsis of data from Mytilus edulis feeding experiments. Feeding time in each experiment - 2 hrs.

Food concentration (cells ml^{-1} . 10^3)	Total phosphorus in suspension (µg P)	Phosphorus intake (µg P)	Phosphorus rejected in pseudo- (µg P)	pseudofaeces %	Phosphorus ingested (µg P)	Phosphorus egested (µg P)	Assimilation efficiency %
17.9	93.2	70.6a)	4.2	6	66.4	1.5	98
		63.6b)		7	59.4		97
17.3	102.5	91.1a)	27.7	30	63.4	12.4	80
		62.3b)		44	34.6		64
237.2	701.8	419.1a)	273.9	65	145.2	82.2	43
		529.9b)		52	252		67
275.9	871.9	413.7a)	223.2	54	190.5	17.4	91
		151.0b)					
685.6	1902.5	683.3a)	329.3	50	329.0	41.4	87
		477.5b)		69	148.2		72
892.4	2404.2	574.2a)		74	147.0	70.2	52
		591.6b)		72	164.0		57

a) calculated by iteration (Appendix II).

b) calculated by the difference between the total phosphorus content of the suspension at the start of feeding and the phosphorus content after two hours (Appendix III).

Particle intake rates were calculated by the formula: $I = \Sigma\, C.V$
where C is the initial cell concentration
and V is the volume (ml) filtered in each fifteen minute interval.
The rates were calculated for each hour of feeding (FIG. 3). The total phosphorus intake in each feeding experiment was also estimated. Two methods of estimation were used (Table 3). The first is based on the total number of cells removed in two hours of filtering (Appendix II). The second figure was estimated from the difference between the initial and final total phosphorus contents of the suspension. This second figure was derived from the activity level of a sample of the suspension (Appendix III). In each feeding experiment it was assumed, as before, that all the P^{32} had been incorporated into the algal tissue and therefore that activity level bore a fixed relationship to the total phosphorus content in a known volume of the algal culture.

My results indicate that intake rate increases with an increase in food concentration towards a plateau rate. However Foster-Smith (1975 b) states that intake rate increases linearly with cell concentrations up to 650×10^3 cells ml^{-1}. The difference between our results arises from the significantly greater reduction in filtration rates with increasing cell concentration found in my study.

Time ingestion rates were determined by subtracting the rate of production of pseudofaeces from the intake rate (Table 3; FIG. 4).

Ingestion rates at the lowest food concentrations were about 20×10^6 cells h^{-1} rising to a maximum of 78×10^6 cells h^{-1} at 685×10^3 cells ml^{-1}. These results differ from the pattern which Foster-Smith (1975 b) observed. He found that ingestion increased gradually up to a concentration of 300×10^3 cells ml^{-1} and remained fairly constant to 800×10^3 cells ml^{-1}. Between these cell densities ingestion reached a maximum of 108×10^6 cells h^{-1} at $500 - 700 \times 10^3$ cells ml^{-1}. A comparison of the ingestion rates I measured for

Figure 3 : Rate of intake by *Mytilus edulis* at increasing concentrations of *Phaeodactylum tricornutum*.

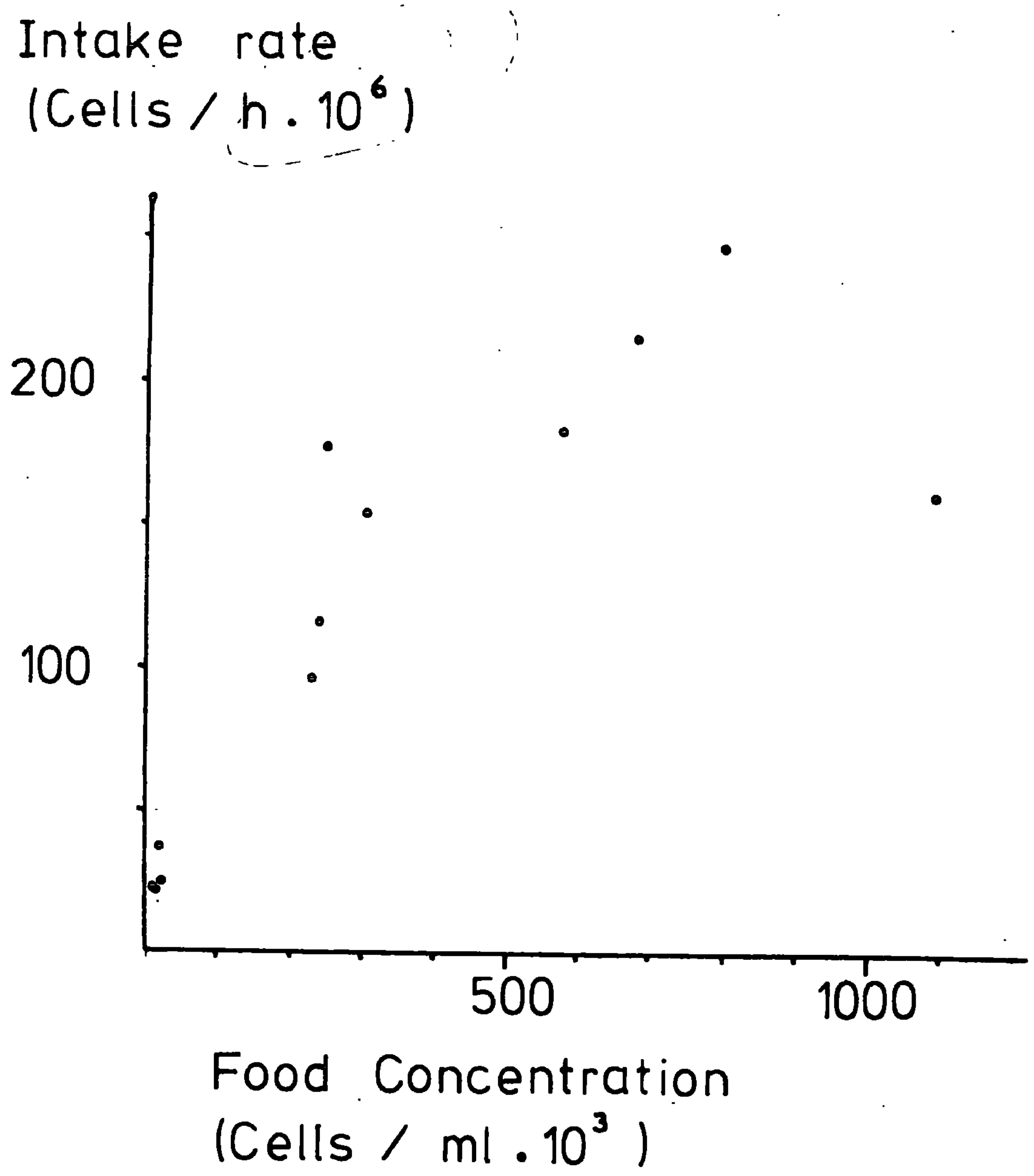
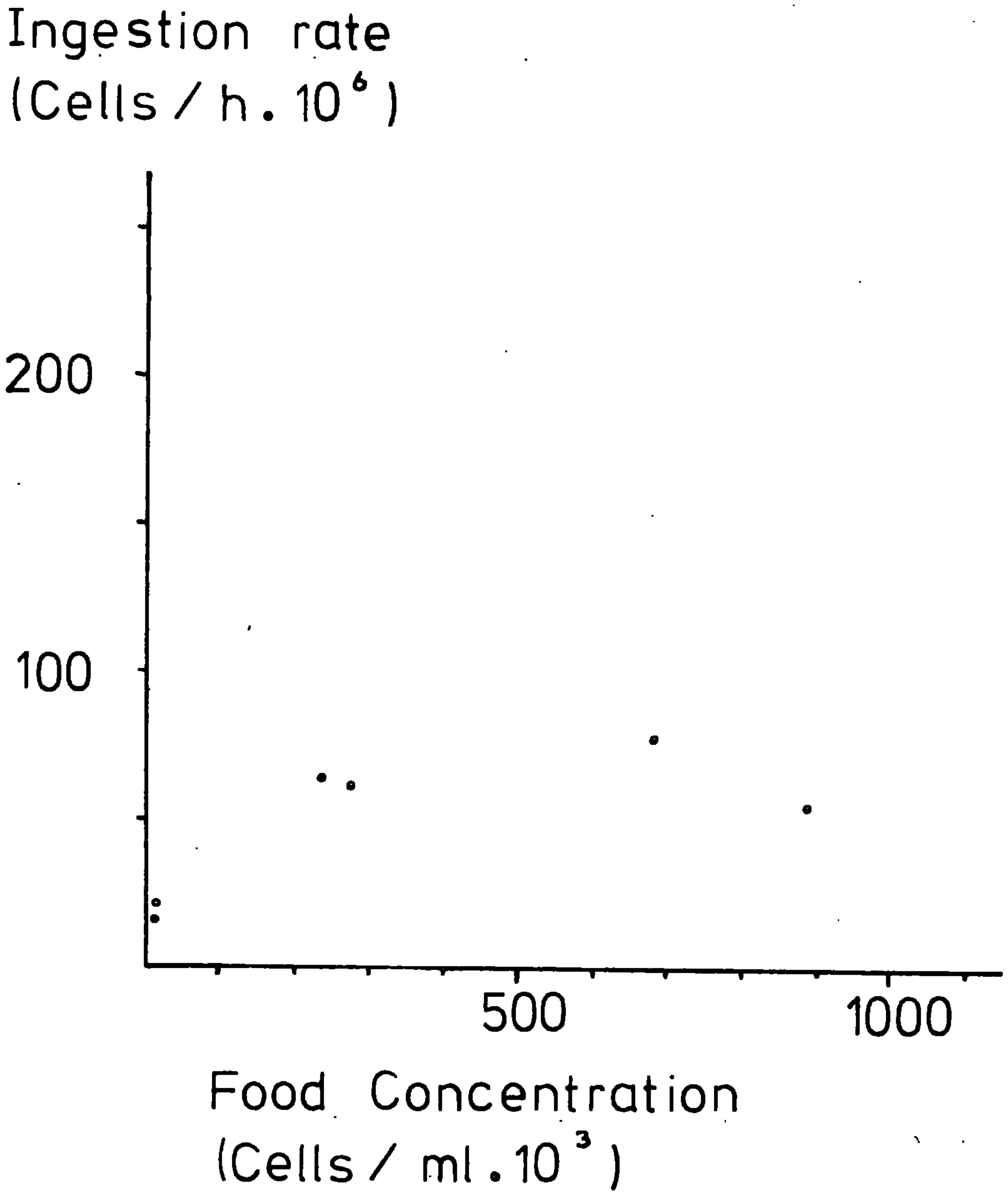


Figure 4 : Rates of ingestion by *Mytilus edulis* at increasing concentrations of *Phaeodactylum tricornutum*



starved animals with those recorded by Foster-Smith shows, at food concentrations greater than 200 X 10^3 cells ml^{-1}, that after a period of starvation a significant reduction in the rate occurs (Wilcoxon test $P < 0.05$). A comparison of maximum ingestion rates suggests that the reduction associated with starvation is about 25%.

However at the lowest food densities, the ingestion rates I measured were about 20 X 10^6 cells h^{-1}, much greater than the figure of 5 X 10^6 cells h^{-1} given by Foster-Smith (1975 b).

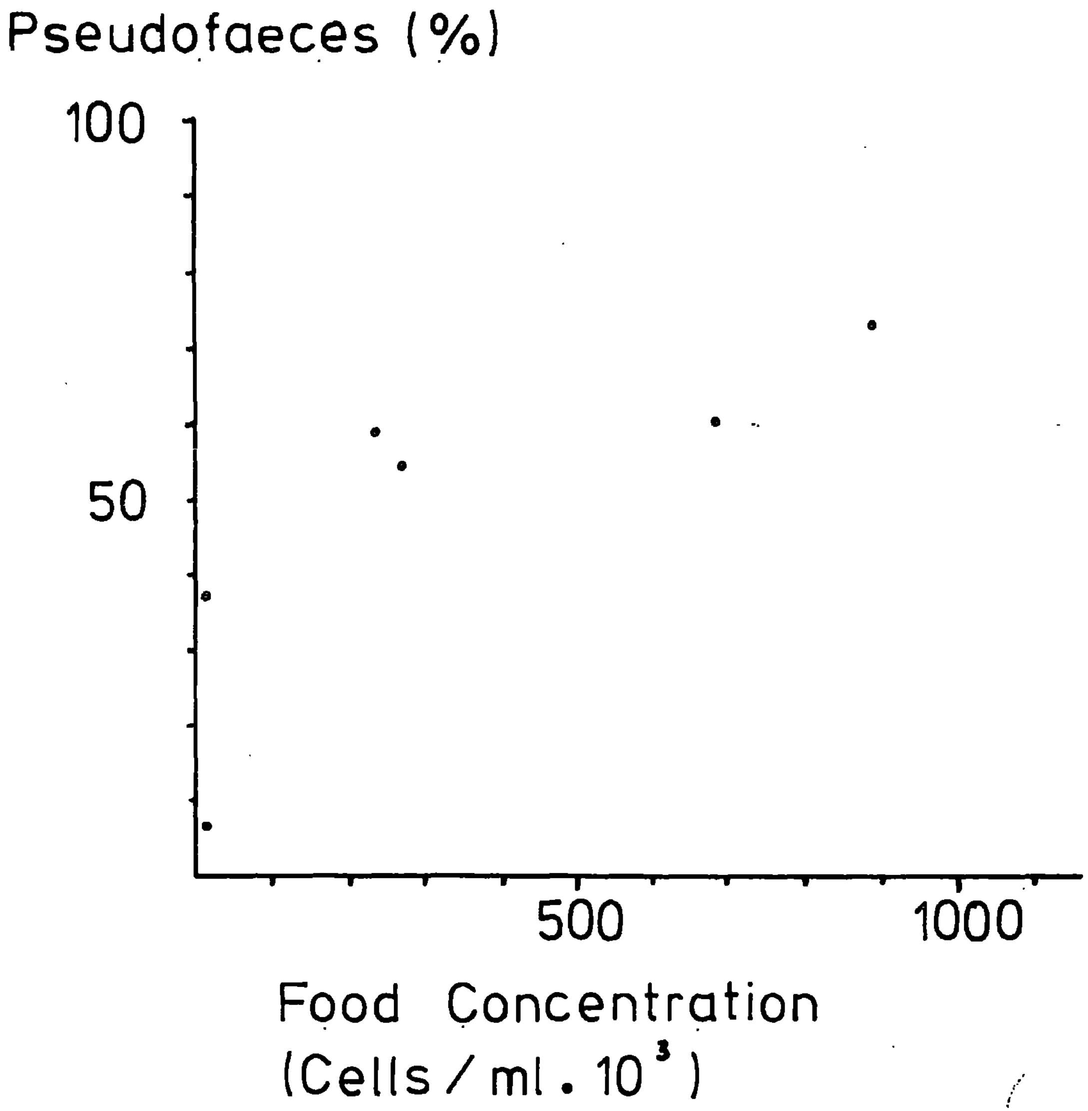
In summary, over the whole range of food concentrations studied, my results indicate that a starved Mytilus edulis ingests a greater proportion of the cells filtered from suspension than does Mytilus edulis which has been maintained on normal rations. Although the proportion of the food ingested is increased following starvation, the maximum rate of ingestion at higher food concentrations is significantly reduced.

1.3 PSEUDOFAECAL MATERIAL

The amount of material rejected as pseudofaeces was estimated by resuspending the rejected material in the feeding suspension at the end of the two hour feeding period. The increase in total activity of the feeding suspension was calculated by summing the activities of a series of 0.2 ml samples, and was then converted to an estimate of the weight of phosphorus rejected. The proportion of the phosphorus filtered from suspension which was rejected as pseudofaeces was estimated at each suspension concentration (FIG. 5; Appendix III).

The results indicate that a greater proportion of cells filtered from solution were rejected with an increase in food concentration, and that, at the highest concentration studied, over 70% of the filtered material was rejected. Pseudofaeces were produced at all cell concentrations and by comparison with the results of Foster-Smith

Figure 5 : Percentage of material rejected before ingestion, by *Mytilus edulis*, with increasing concentrations of *Phaeodactylum tricornutum*



(1975 b) it seems that the threshold cell concentration inducing the production of pseudofaeces is not significantly altered by starvation. Foster-Smith (1975 b) demonstrated that the particle concentration inducing pseudofaecal production varied with the material used:

Phaeodactylum	(size : 29.0 µm)	- 10 - 20 X 10^3 cells ml^{-1}
Isochrysis	(size : 5.3 µm)	- 17 - 25 X 10^3 cells ml^{-1}
Alumina	(size : 8.0 µm)	-150 -200 X 10^3 particles ml^{-1}
Alumina	(size : 17.5 µm)	- 20 - 25 X 10^3 particles ml^{-1}

Thompson and Bayne (1972, 1974), working with *Mytilus edulis*, observed no production of pseudofaeces at *Tetraselmis* cell concentrations of 25 X 10^3 cells ml^{-1}.

At cell concentrations greater than 200 X 10^3 cells ml^{-1} the proportion of material rejected as pseudofaeces rose from about 50% to about 70% at the higher cell concentrations studied (Table 3). These values are less than those reported for *Mytilus edulis* which had not been subjected to starvation. Foster-Smith (1975 b) recorded the proportion of material rejected as about 70% at 200 X 10^3 cells ml^{-1} rising gradually to about 90% at 850 X 10^3 cells ml^{-1}. The difference between our results is a reflection of the increase in the proportion of food ingested by starved *Mytilus edulis*.

1.4 EGESTION

Faecal material egested by *Mytilus edulis* was collected at intervals over the 48-hour period following the start of the feeding experiments. The total phosphorus content of the faecal material was estimated from the P^{32} levels in each sample. Two components could be identified in the faeces, the glandular fraction (brown and apparently digested) and the intestinal fraction (green and containing many undamaged cells) (Van Weel, 1961). These components were not separated.

Results are presented in FIGS. 6, 7 and 8 as the phosphorus egested in each 30 minute period as a percentage of the total egested during the first 24 hours after the start of feeding. Details of the measurements are given in Appendix III.

Figure 6 : Time course of phosphorus egestion in *Mytilus edulis*, fed at 20 cells ml^{-1}. 10^3. Plotted as a fraction of the total phosphorus egested in the 24 h from the initiation of feeding

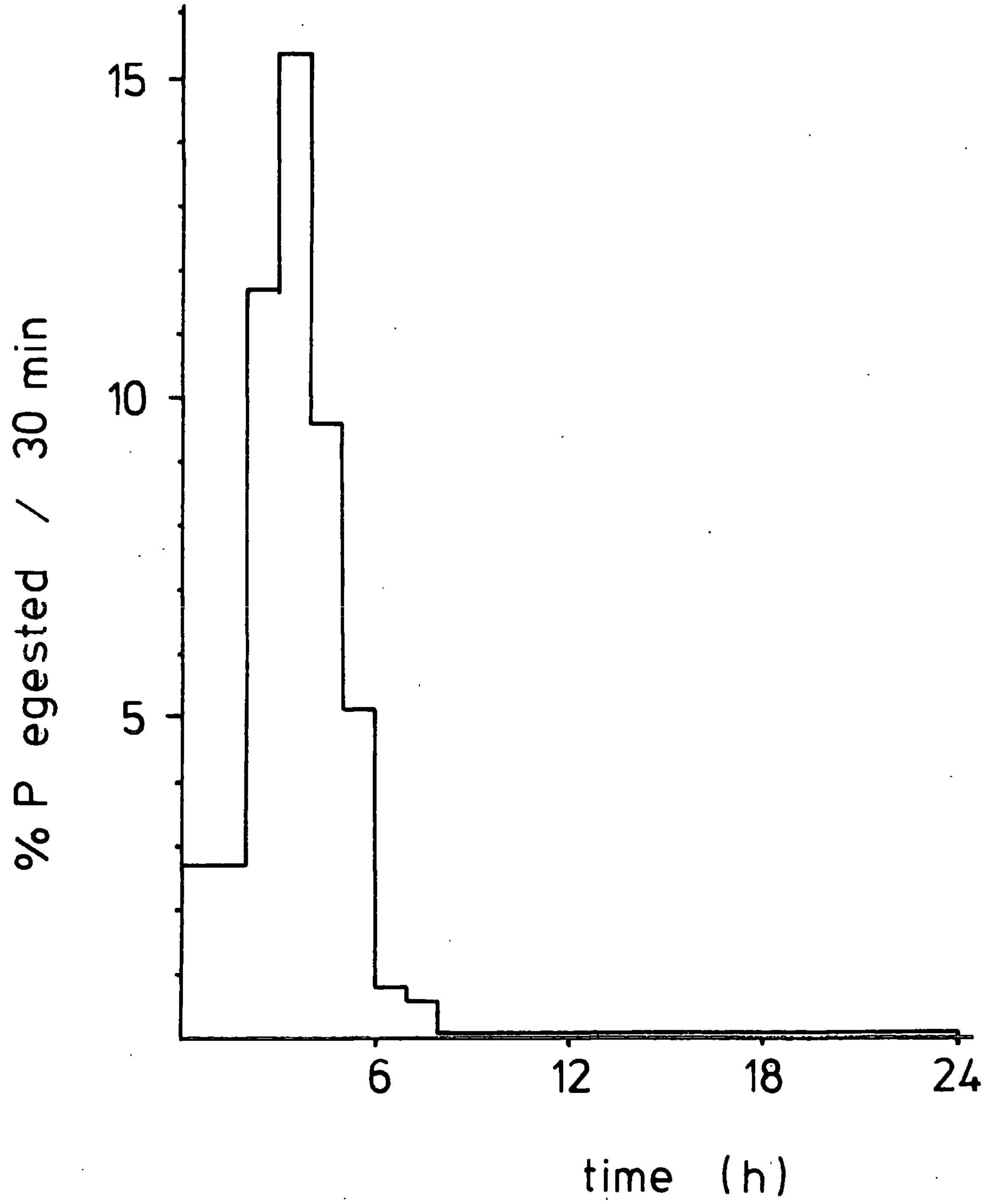


Figure 7 : Time course of phosphorus egestion in *Mytilus edulis*, fed at 250 cells ml^{-1}. 10^{3}. Plotted as a fraction of the total phosphorus egested in the 24 h from from the initiation of feeding

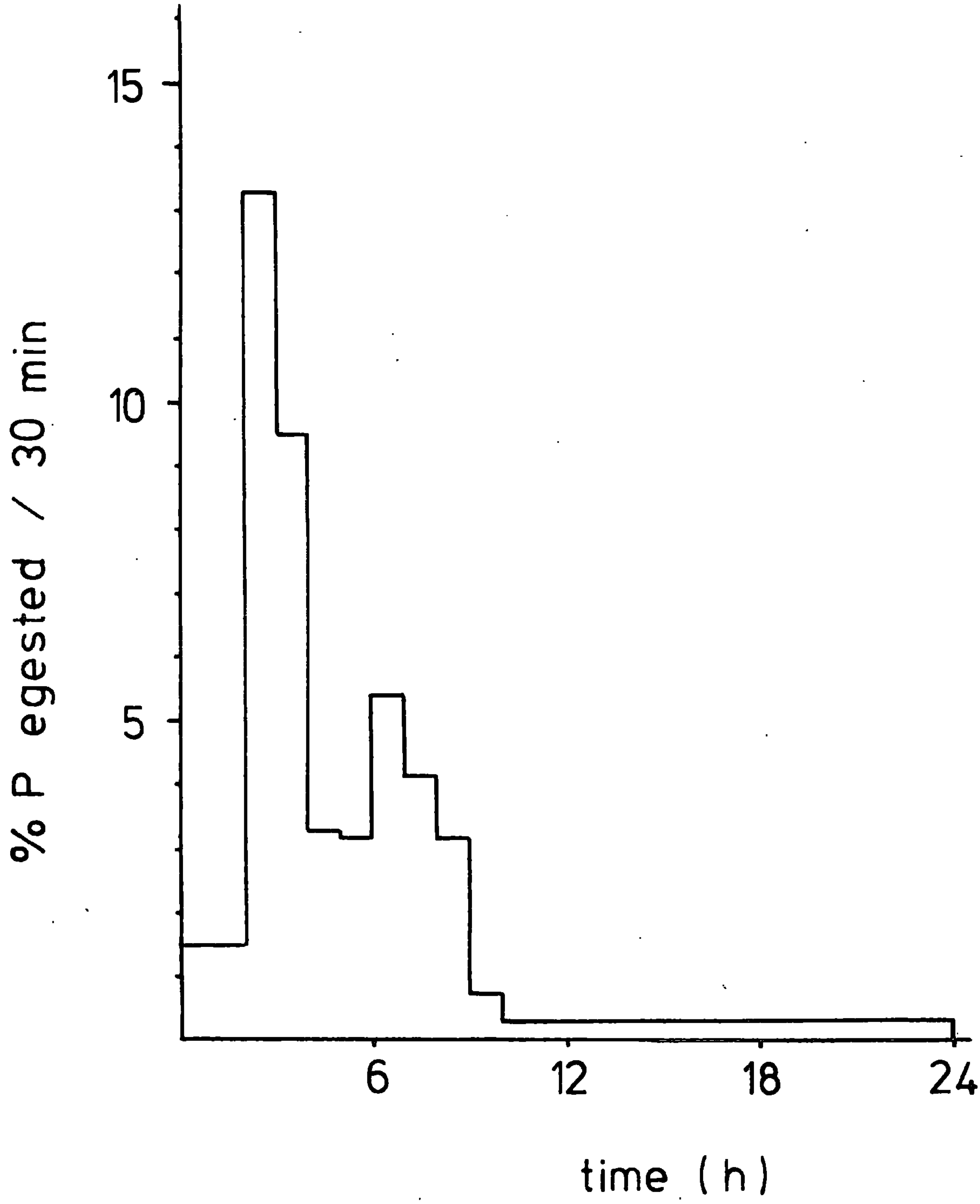
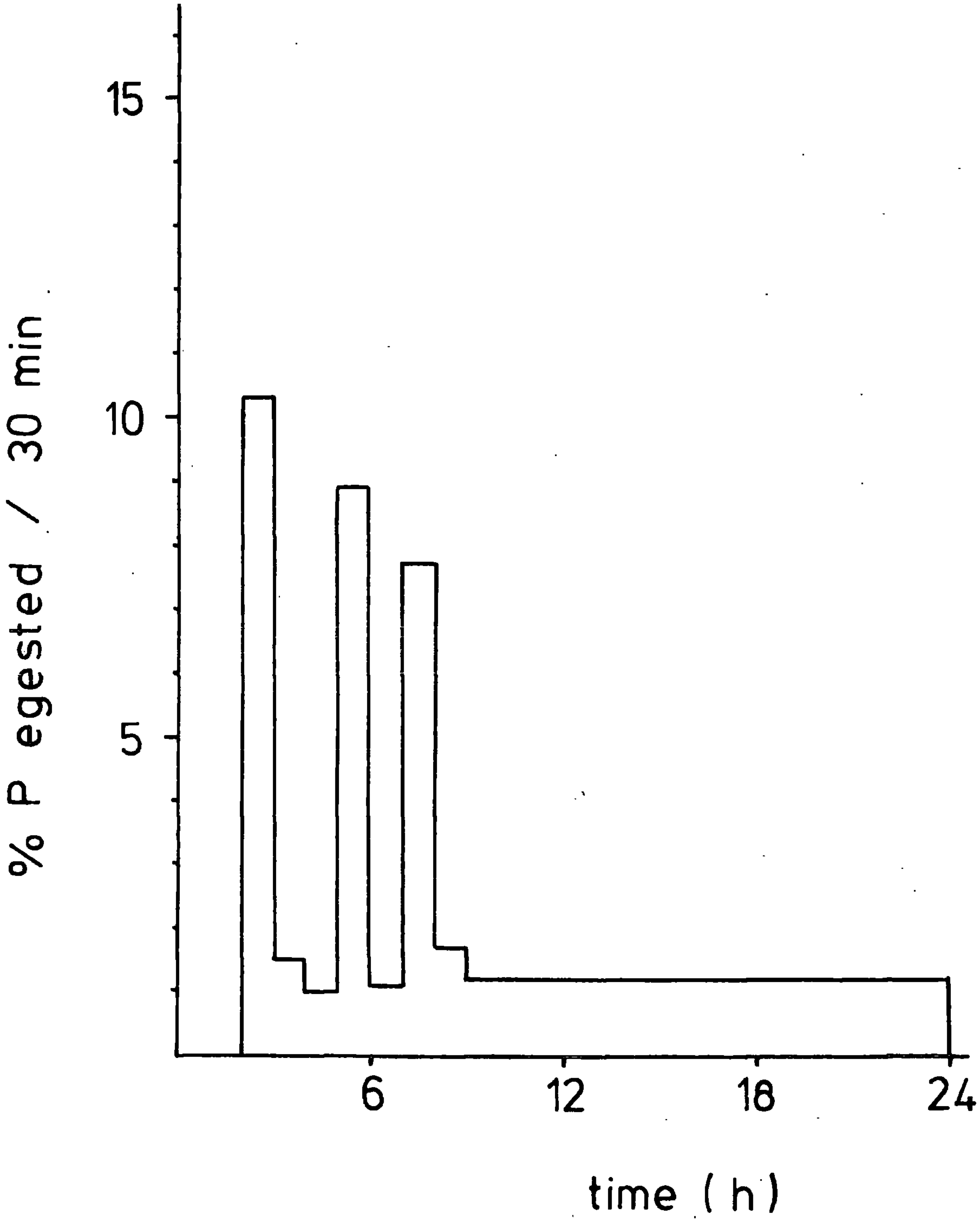


Figure 8 : Time course of phosphorus egestion in *Mytilus edulis*, fed at 7.50 cells ml^{-1} . 10^3. Plotted as a fraction of the total phosphorus egested in the 24 h from the initiation of feeding



The results indicate that at the lowest food levels the egestion rate reached a maximum in the fourth hour after the start of feeding; the median egestion time was about 3½ hours. With an increase in food concentration the time course of egestion is extended and at the highest food concentrations the median egestion time rose to just less than 8 hours, although the highest egestion rate occured in the third hour after the start of feeding. At the intermediate food concentrations the median egestion time was about 4½ hours.

The increase in median egestion time with increasing food concentration suggests that Mytilus is able to retain considerable amounts of material in the stomach. This will maximize the amount of material digested rather than passed straight into the intestine.

1.5 ASSIMILATION EFFICIENCY

The assimilation efficiency of an animal is the proportion of ingested food which is passed into the tissues and is expressed as a percentage. Assimilation efficiencies were calculated for Mytilus edulis at each food concentration and were based on the amount of P^{32} assimilated. At the lowest concentration studied the assimilation efficiency was about 85%. This was reduced to 55% at high cell concentrations of about 900 X 10^3 cells ml^{-1} (Table 3).

In unstarved Mytilus a large proportion of the egested material is in the form of the intestinal component, i.e. the material which has not entered the digestive gland but has been chanelled directly in the intestine (Van Weel, 1961). However, at the lowest food concentration used in my experiments the faecal strip consisted of a large glandular component, suggesting that most of the ingested cells were being digested. In contrast, at higher food concentrations, the intestinal component was large and this may account for the fall in assimilation efficiency.

The assimilation efficiencies recorded in my experiments are at variance with those given by previous workers. Thompson and Bayne (1972) and Foster-Smith (1975 a) concluded that the assimilation efficiency of unstarved Mytilus edulis was inversely related to food concentration. Both sets of data record assimilation efficiencies of greater than 80% at 1000 cells ml^{-1}, falling to 40% at 15 X 10^3 cells ml^{-1}. Thompson and Bayne (1972) also recorded an assimilation efficiency of 0% at 25 X 10^3 cells ml^{-1}.

PART II

PHOSPHORUS ESTIMATIONS

2.1 PHOSPHORUS CONTENT OF Phaeodactylum tricornutum

Phosphorus estimations were carried out on dried 10 - ml samples of Phaeodactylum tricornutum culture (Table 4). The mean phosphorus content of the dried samples was 0.132 mg, about 3%.

The cell density of the culture was estimated using a haemocytometer and the number of cells in 1.0 mg dry tissue was calculated. This figure was then used in all calculations of Phaeodactylum phosphorus content:

19 500 000 cells = 1.0 mg dry wt. = 0.03 mg P

Table 4 : Phosphorus content of *Phaeodactylum tricornutum*

	Dry wt. of 10 - ml Algal sample (mg.)	Estimated phosphorus content (mg)	% P
	3.8	0.108	2.84
	4.2	0.128	3.05
	4.5	0.129	2.87
	5.1	0.164	3.21
$\bar{x}$ ± S.E.	4.4 ± 0.3	0.132 ± 0.012	3.00

Cell density of culture (cells/ml) ± S.E.	8 590 000 ± 380 000
Cells/mg. dry wt.	19 500 000

2.2 PHOSPHORUS CONTENT OF *Mytilus edulis*

The dry weights and phosphorus contents of the body components of fourteen individuals, length 47 - 55 mm, were estimated (Appendix IV).

The dry weights and phosphorus contents were then calculated for a "standardized" 50 mm animal, using the regression lives calculated for shell length against weight of dry tissue (FIG. 9), dry body component weight against weight of dry tissue (FIGS. 10, 11, 12, 13, 14) and phosphorus content against dry body component weight (FIGS. 15, 16, 17, 18, 19). The estimations for the "standardized" 50 mm animal are given in Table 5.

The phosphorus concentration in the soft tissues of *Mytilus edulis* was estimated as c. 6000 p.p.m dry weight. The distribution of phosphorus levels in the various body components was not uniform (Table 6). The gill tissues had a phosphorus concentration of c.13000 p.p.m whereas the pedal tissue held only c. 4300 p.p.m. The other soft tissues had intermediate values. The phosphorus levels in the different tissues may reflect the nutrient needs and metabolic activity of the tissues.

The shell material had a more variable, though lower, phosphorus content per unit weight than the other tissues. Phosphorus present in the shell is likely to have remained there since shell calcification.

Ecological and physiological turnover times of phosphorus can be estimated for *Mytilus edulis* based on the uptake of particulate phosphate. A more accurate estimate of these turnover times should include uptake of dissolved organic and inorganic phosphate.

Johannes (1964) gives two classes of turnover time:-

(i) the physiological turnover time, i.e. the time it takes an amount of phosphorus equal to that in each tissue of the animal to pass through that tissue. (This has also been expressed as the Body Equivalent Excretion Time - Corner (1973).)

(ii) the ecological turnover time, i.e. the time it takes an amount of phosphorus equal to that in all the tissues to be ingested by the animal, whether it is assimilated or not.

Figure 9 : Dry flesh weight related to shell length in *Mytilus edulis*

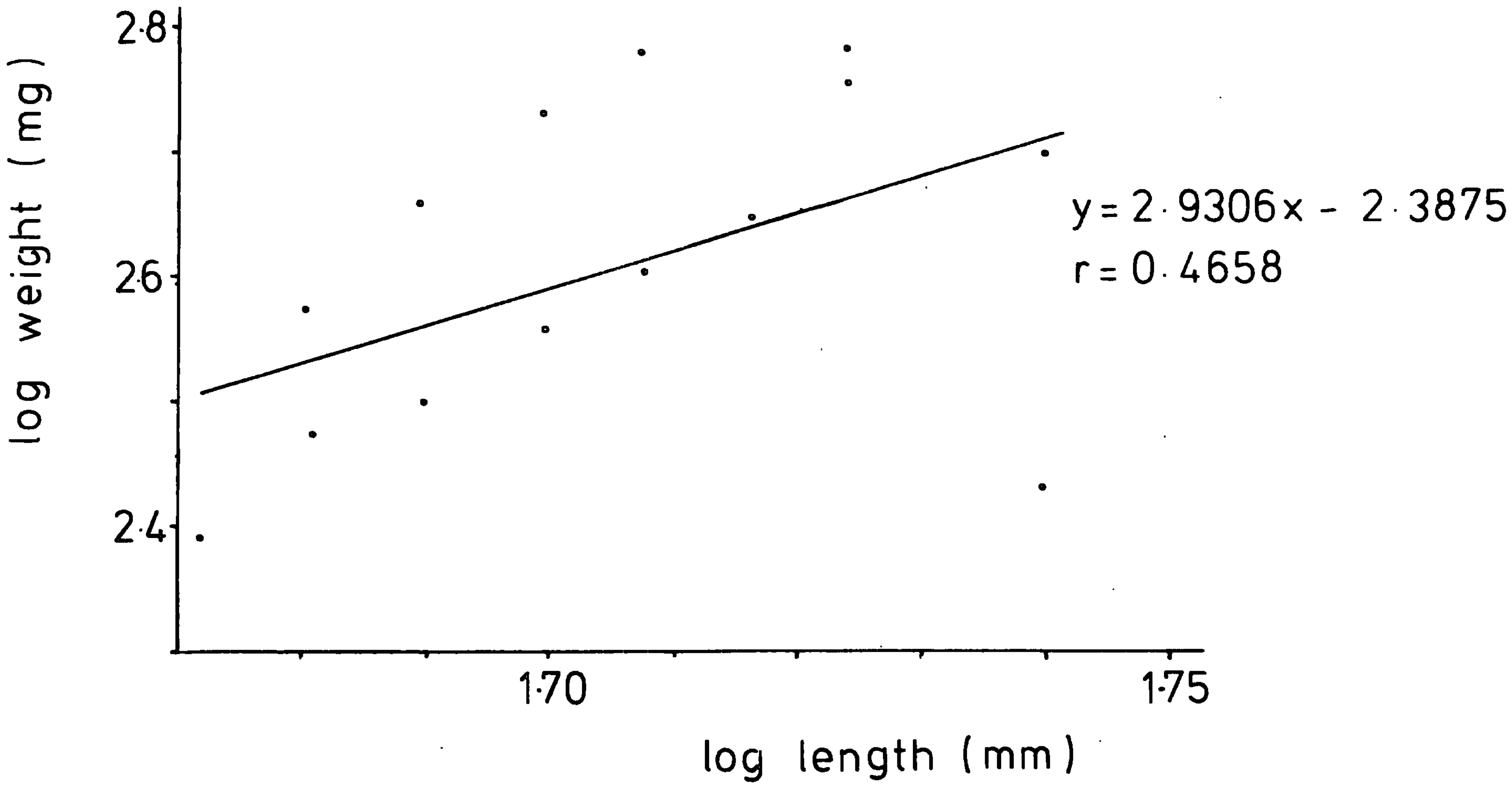


Figure 10 : Dry weight of Gill related to Dry flesh weight in *Mytilus edulis*

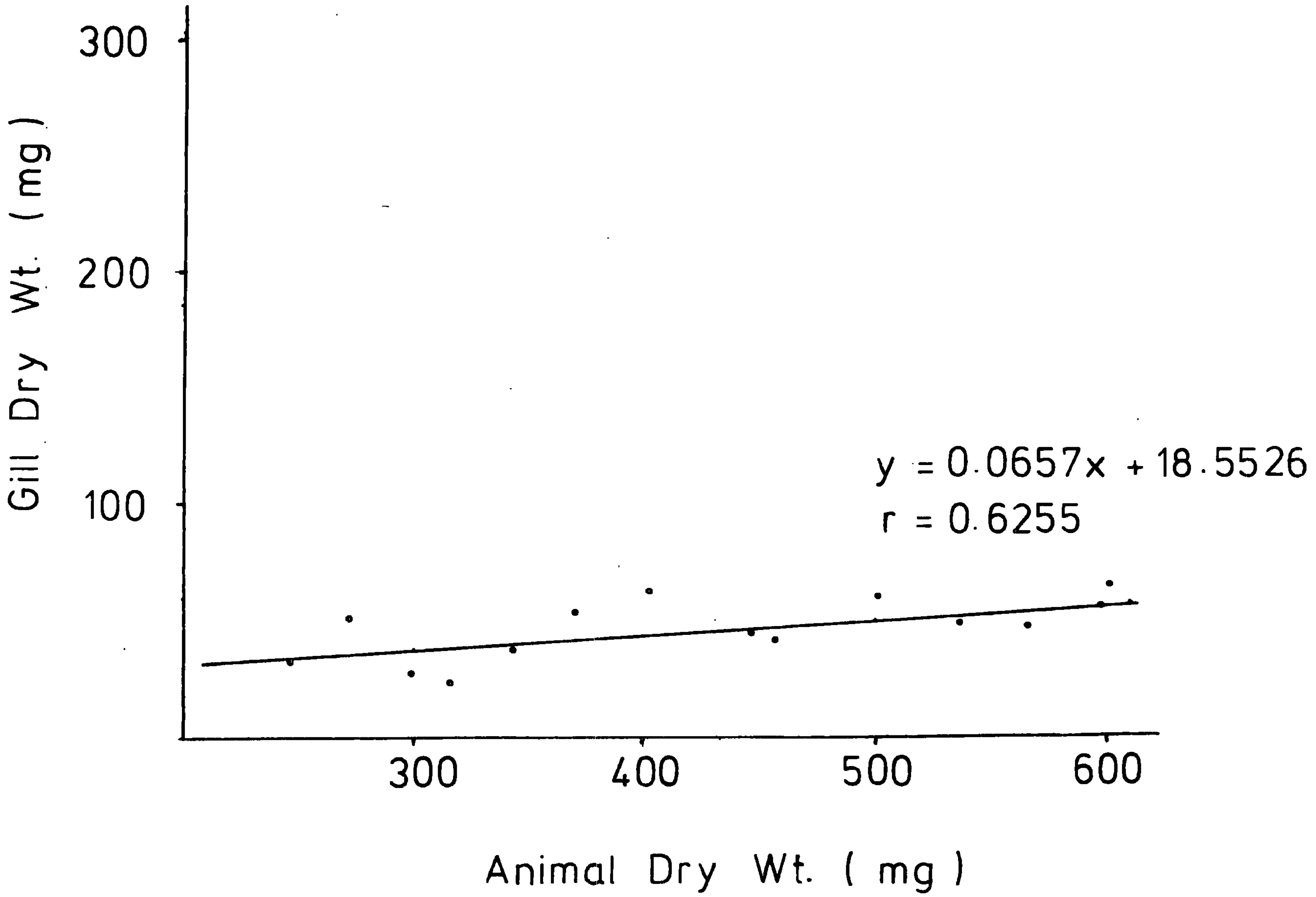


Figure 11 : Dry weight of Mantle and Gonads related to Dry flesh weight in *Mytilus edulis*

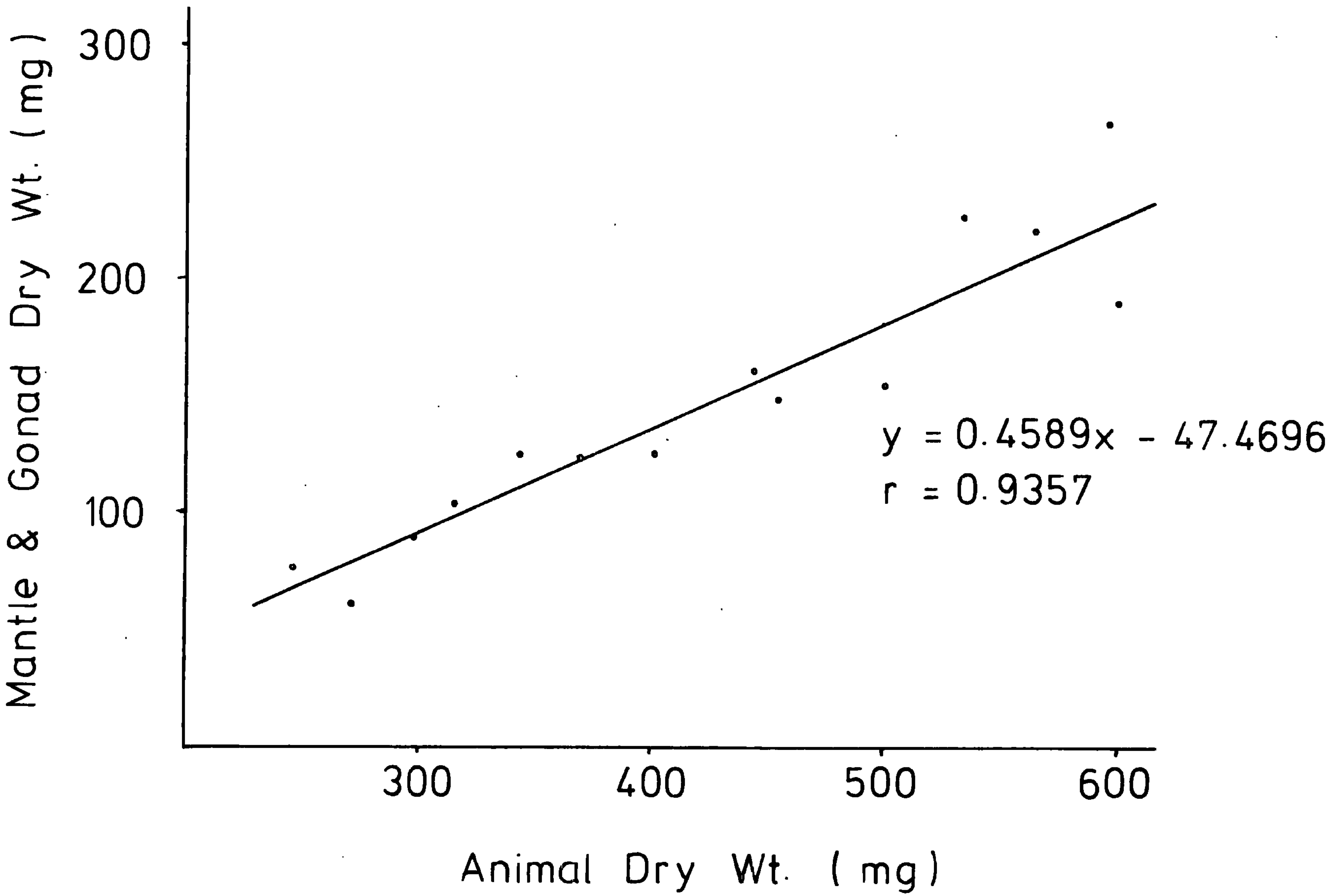


Figure 12 : Dry weight of Adductor muscles related to Dry flesh weight in Mytilus edulis

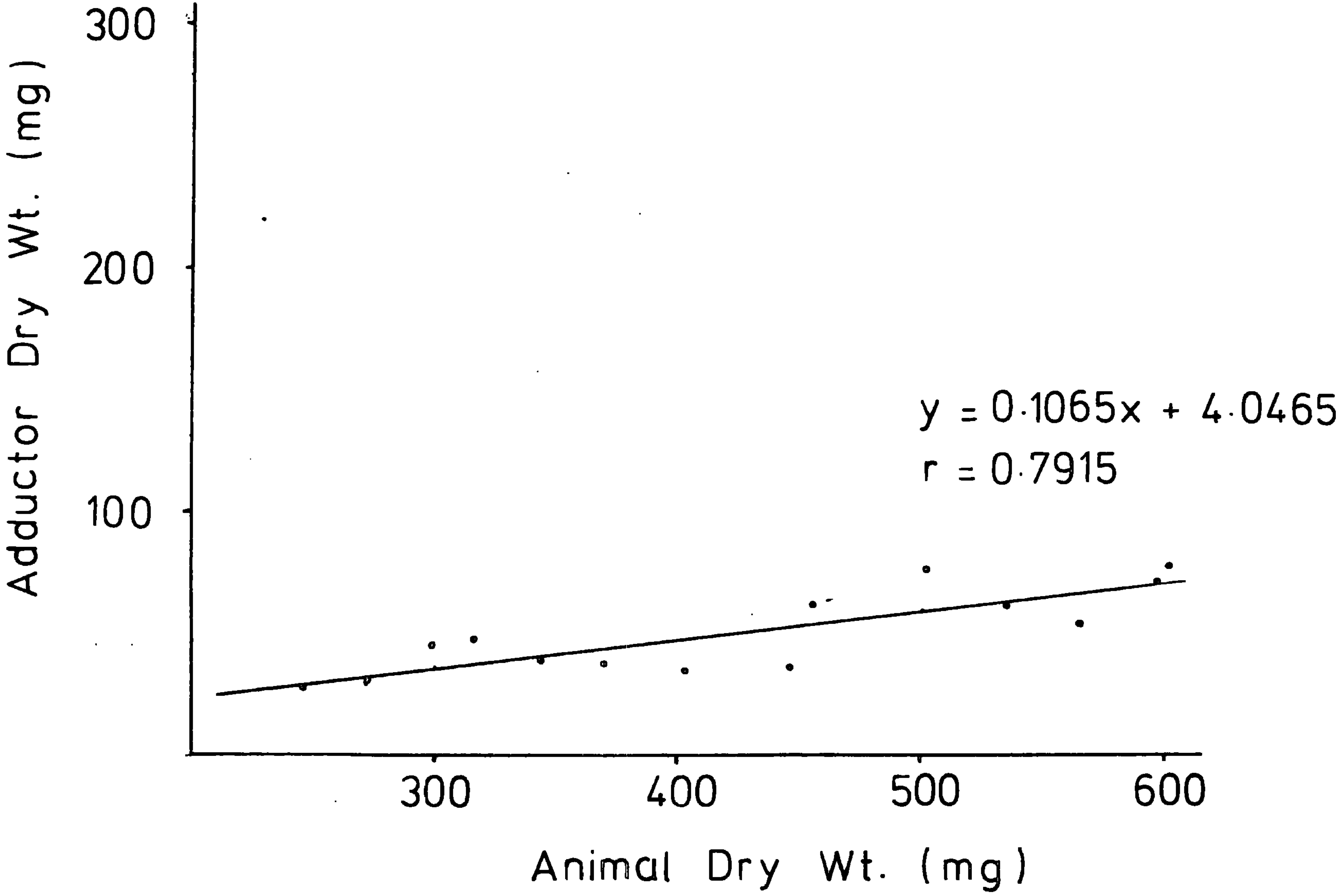


Figure 13 : Dry weight of Foot related to Dry flesh weight in *Mytilus edulis*

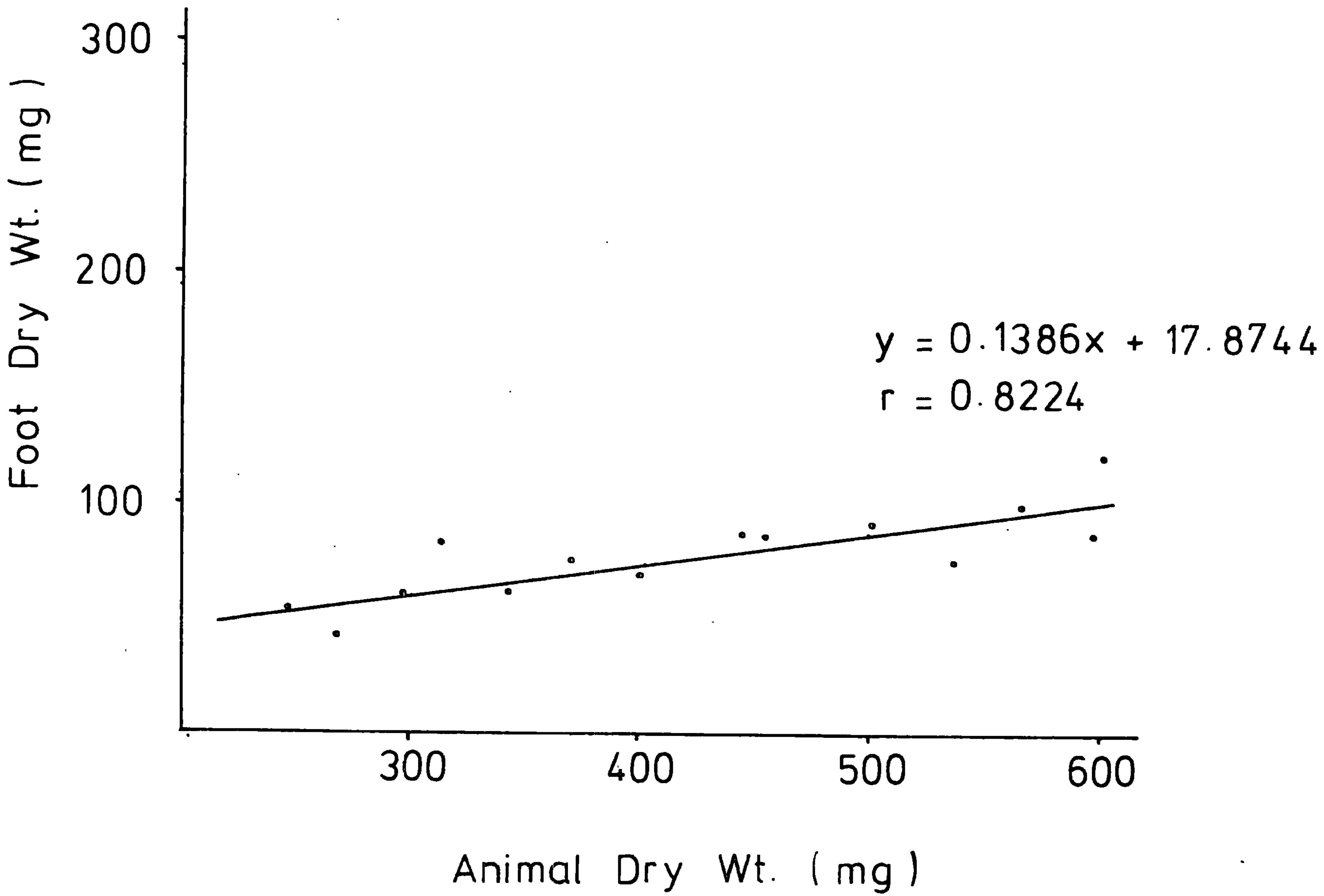


Figure 14 : Dry weight of Digestive system related to Dry flesh weight in *Mytilus edulis*

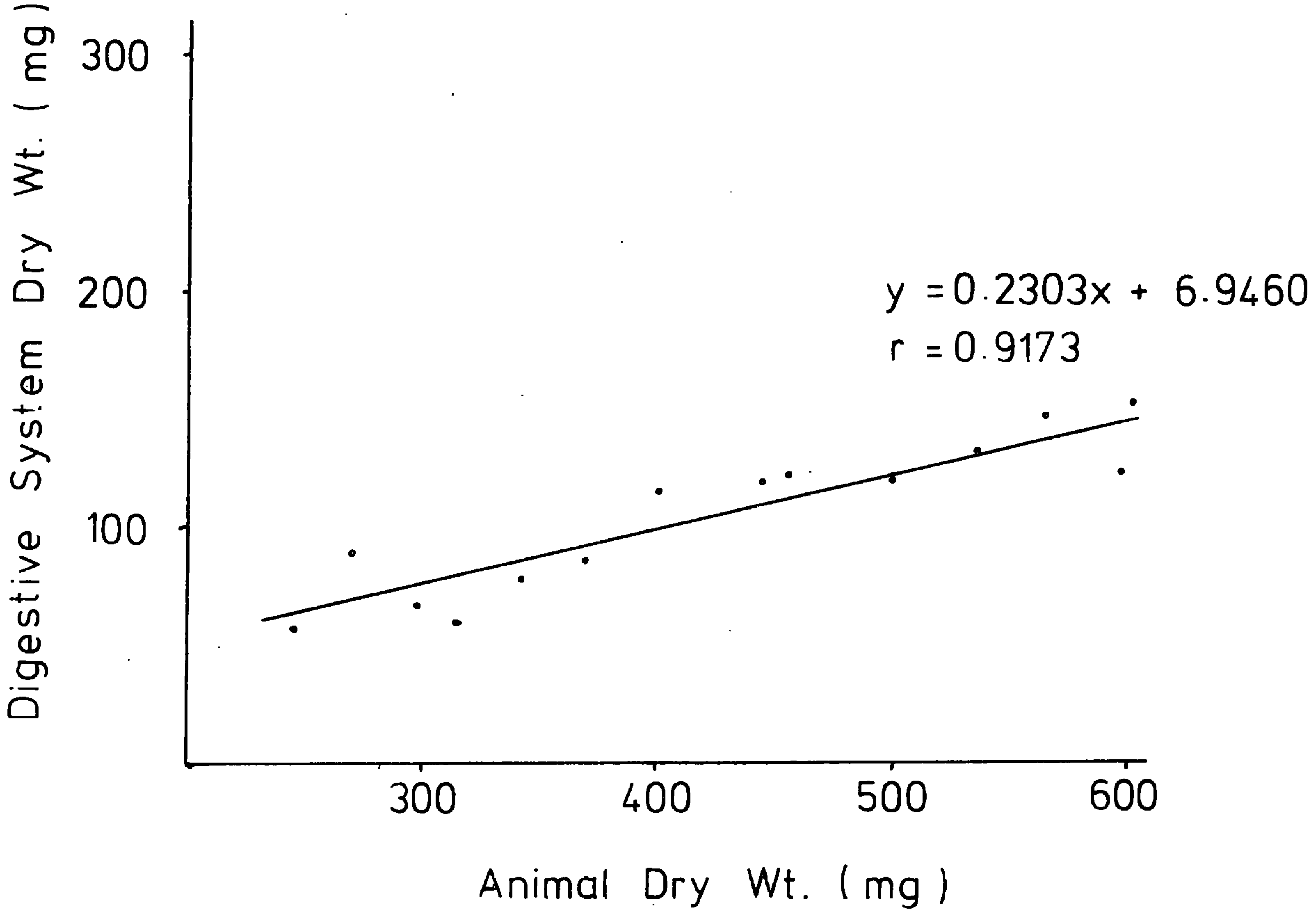


Figure 15 : The relationship between total phosphorus content and dry weight in *Mytilus edulis* Gill tissue

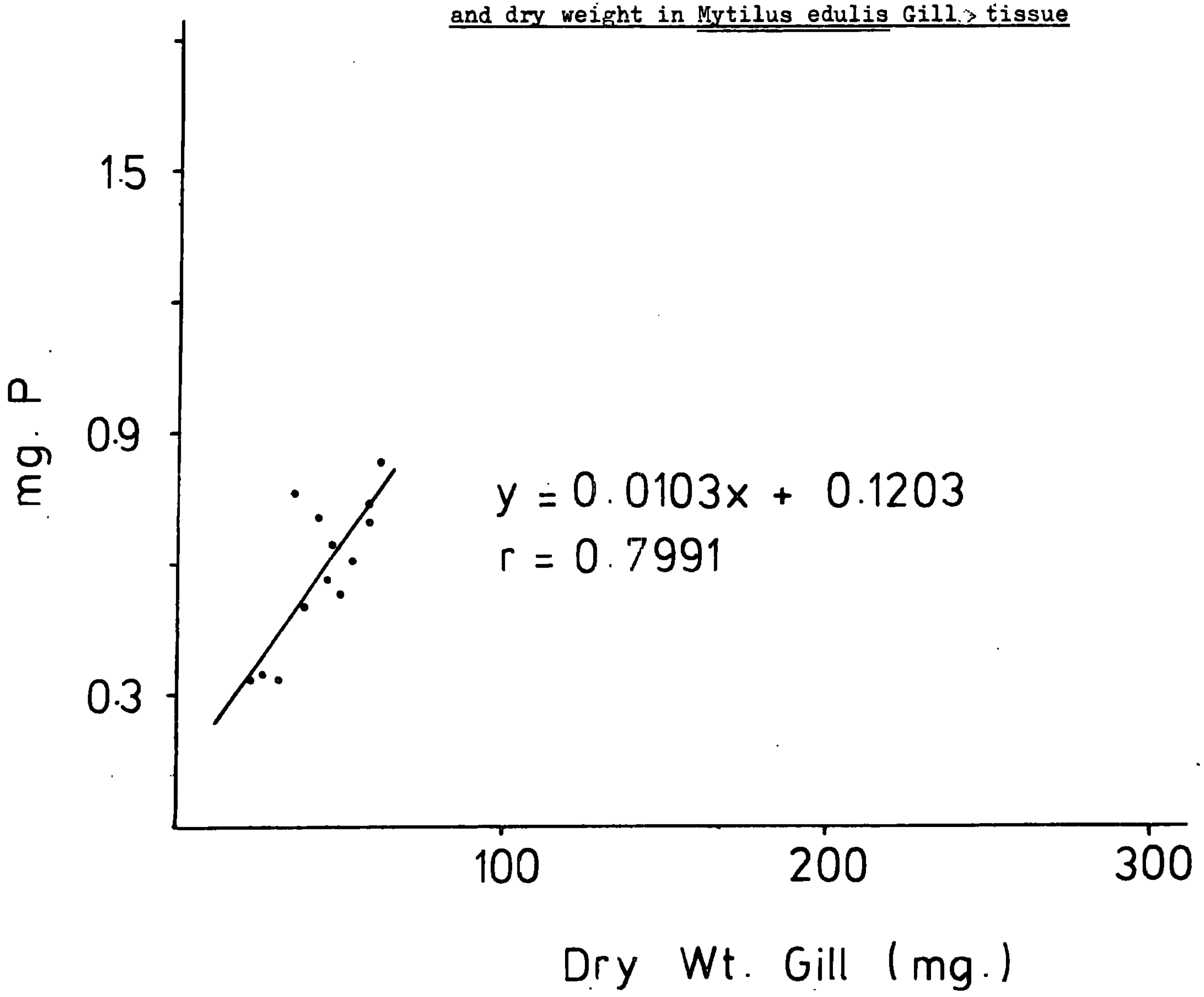


Figure 16 : The relationship between total phosphorus content and dry weight in *Mytilus edulis* Mantle and Gonad tissue

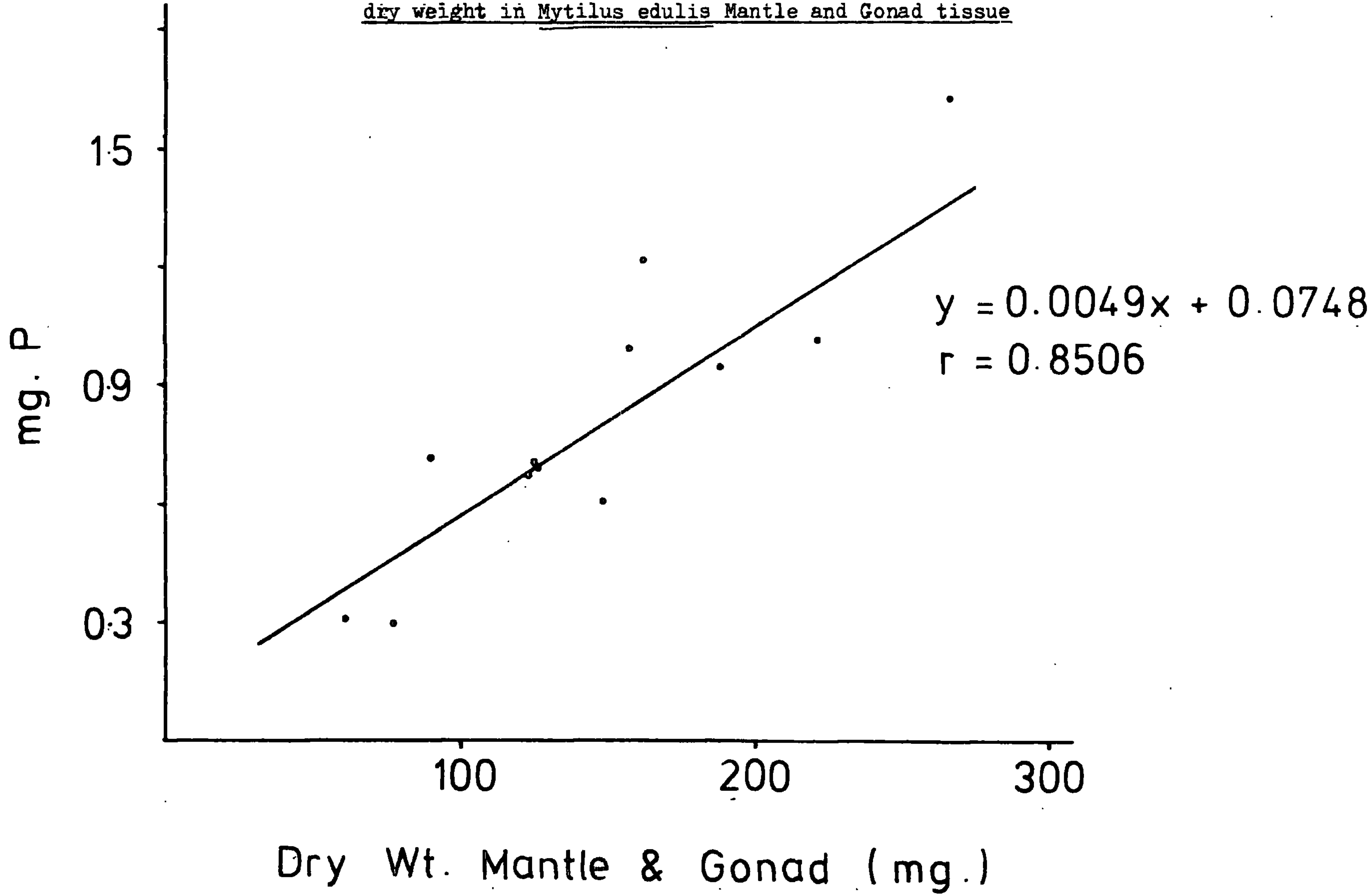


Figure 17 : The relationship between total phosphorus content and dry weight in *Mytilus edulis* Adductor tissue

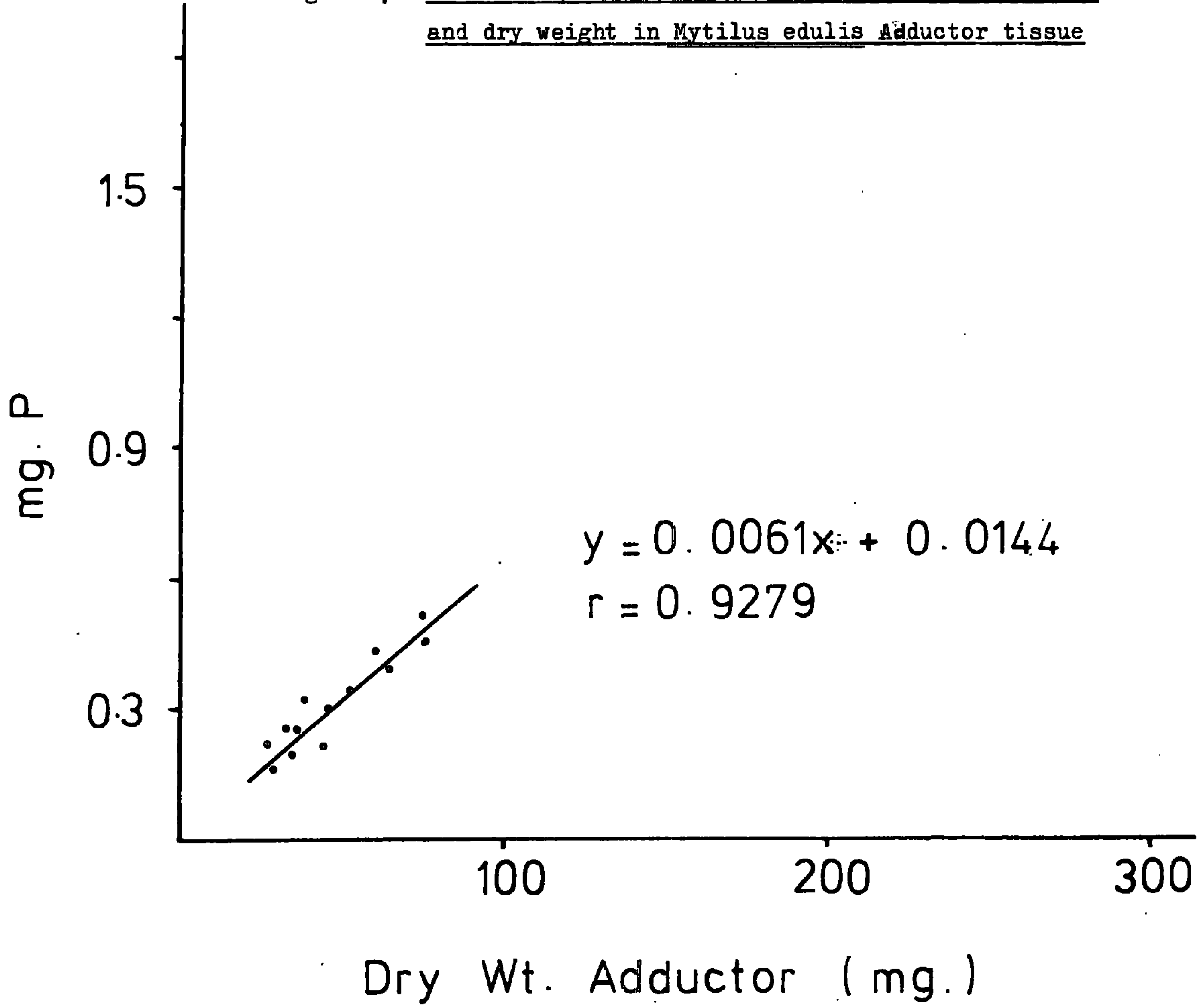


Figure 18 : The relationship between total phosphorus content and dry weight in *Mytilus edulis* Foot tissue

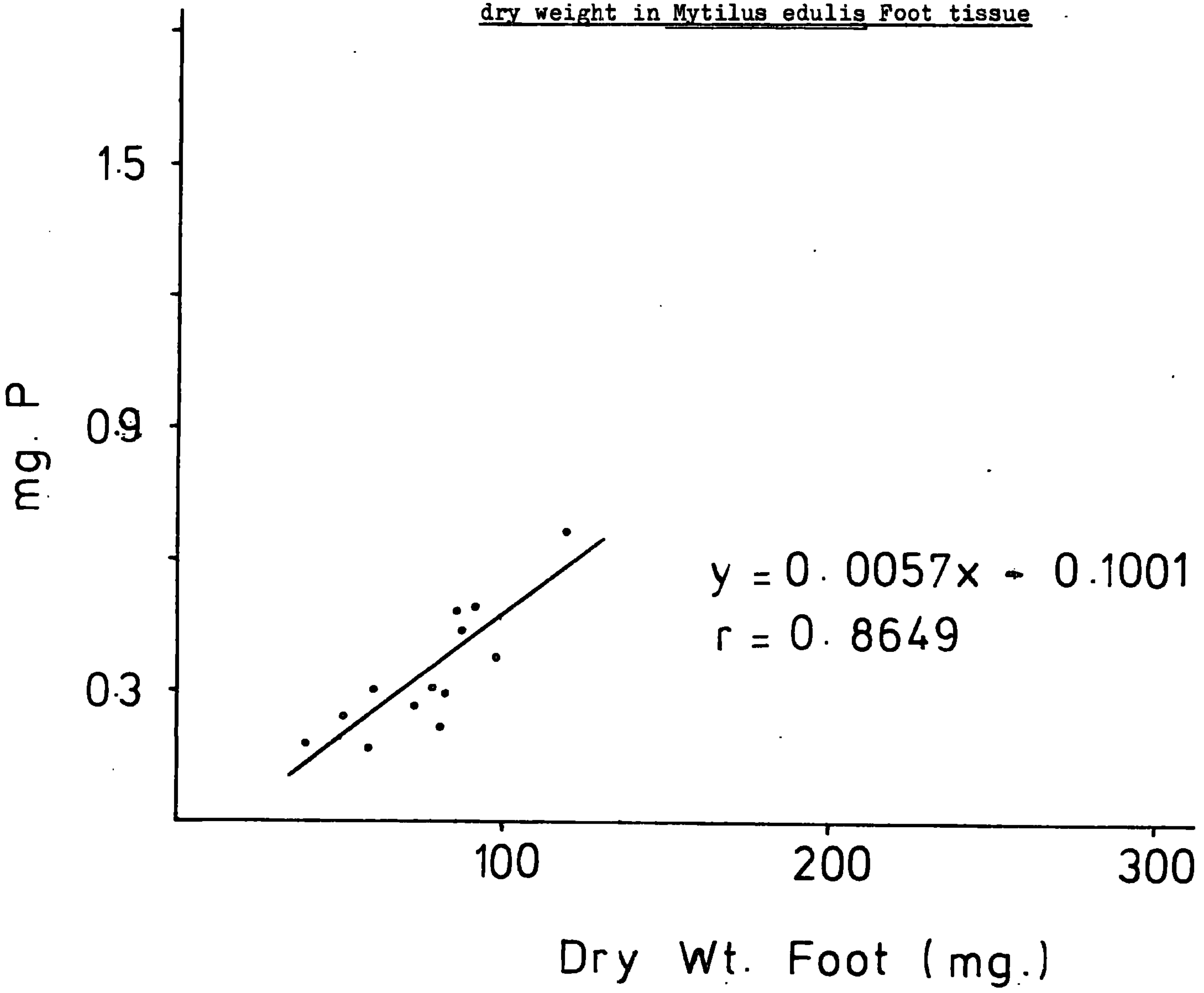


Figure 19 : The relationship between total phosphorus content and dry weight in Mytilus edulis Digestive system

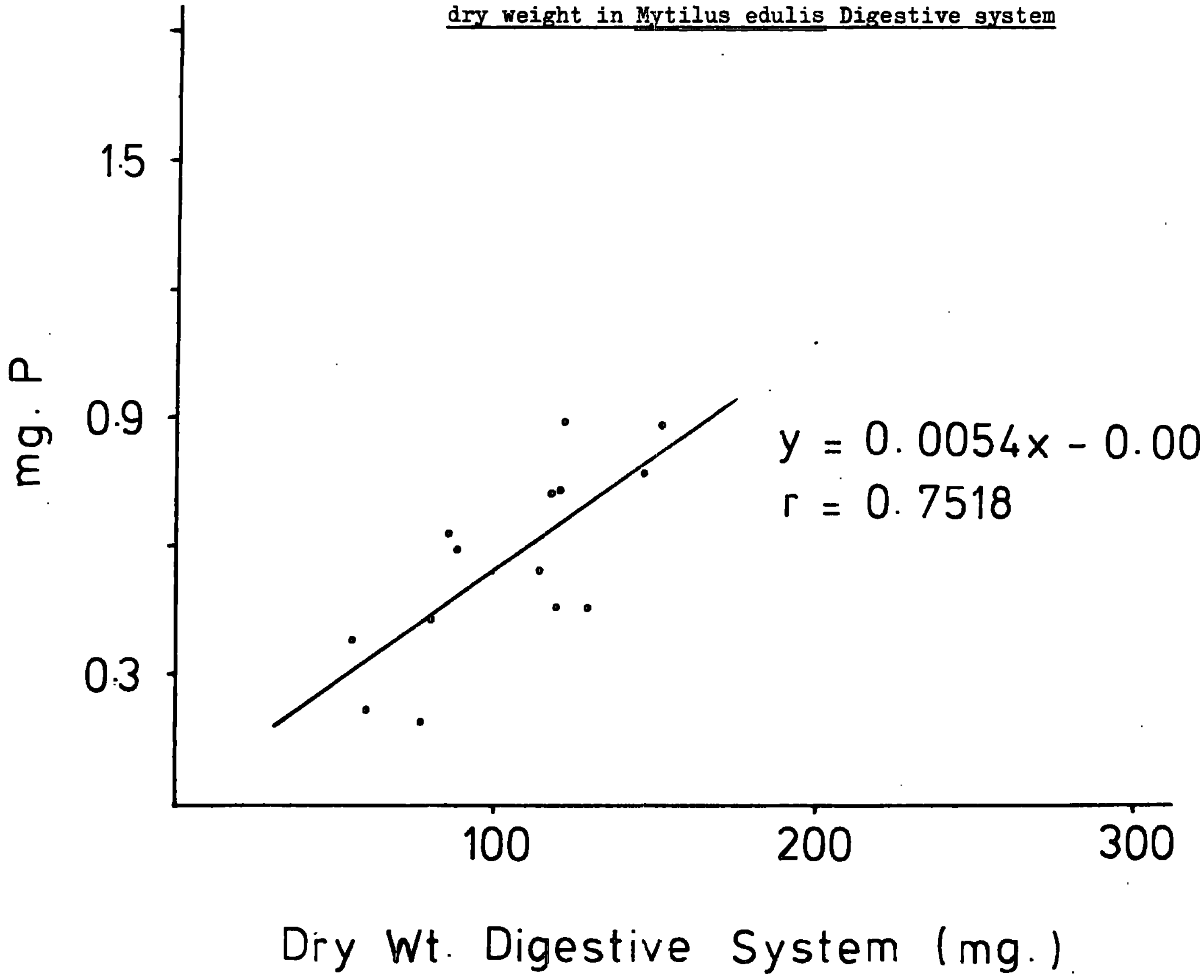


Table 5: Dry weights and Phosphorus content of body components of a "standardized" 50 mm *Mytilus edulis*

Body component	Dry wt. (mg)	Total phosphorus (mg)	mg P/ g. dry tissue
Gill	44.2	.576	13.0
Mantle and gonads	131.7	.720	5.5
Adductors	45.6	.293	6.4
Foot	72.0	.310	4.3
Digestive system	96.9	.521	5.4
Whole animal soft parts	390.4	2.420	6.2

Table 6 : t - values derived from comparisons of mg P/g. dry wt. results of the *Mytilus* body components

(* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$)

	shell	gill	mantle & gonads	adductor	foot	digestive system
shell	-					
gill	15.20*** 23 d.f.	-				
mantle & gonads	9.91 *** 23 d.f.	9.55 *** 24 d.f.	-			
adductor	14.71 *** 23 d.f.	8.62 *** 24 d.f.	2.20 * 24 d.f.	-		
foot	9.07 *** 23 d.f.	11.42 *** 24 d.f.	2.48 * 24 d.f.	5.42*** 24 d.f.	-	
digestive system	8.69*** 24 d.f.	9.47 *** 25 d.f.	0 25 d.f.	2.00 25 d.f.	2.24* 25 d.f.	-

Both classes of turnover time were based on the figure of 4 µg phosphorus/litre of seawater (Jørgensen, 1966). The ecological turnover time for a "standardized" 50 mm _Mytilus_ filtering 10 litres of seawater a day was estimated as 60 days. The physiological turnover time is dependent on the assimilation efficiency but will be in the region of 120 days.

DISCUSSION

1. THE EFFECT OF STARVATION ON Mytilus edulis FEEDING ECOLOGY

A number of parameters are known to effect filtration rates in Mytilus edulis; the size of the animal, temperature, salinity, oxygen tension, position in the intertidal zone, and the concentration and the size of particles in suspension (Bayne, 1976). To this list may now be added starvation, the effects of which have not previously been measured in Mytilus edulis. However, Bayne et al (1976) recorded a reduction in filtration rate in starved Mytilus californianus. They suggested that this arose in the following way. Upon starvation, oxygen uptake is reduced to a standard metabolic rate, associated with a reduction in ventilation rate (Theede, 1963). If the ventilation rate is reduced then the amount of food reaching the gills must also be lower, causing a reduction in filtration rate. A reduction in the metabolic rate of Mytilus edulis after prolonged starvation to a standard level was recorded by Bayne et al (1973), and this may account for the significant reduction in filtration rate observed in my experiments.

Lowered filtration rates decrease the amount of food available for ingestion, as the intake rate is directly proportional to the filtration rate. This is one of the methods which may be available to restrict the amount of material a mussel ingests (Foster-Smith, 1975 b). The second method he suggested was a high degree of selection by the mouth palps. Comparison of the intake and ingestion rates I measured with those measured by Foster-Smith indicates that, after a period of starvation, the proportion of material rejected by Mytilus is decreased at all food concentrations. However, animals still exerted a high degree of quantitative selection. The ingestion rates themselves are also significantly less in starved than unstarved animals, at cell concentrations greater than 200 X 10^3 cells ml^{-1}.

Although the animals filtered sufficient material from suspension to allow the normal higher levels of ingestion to be reached. Starvation, which leads to increased ingestion efficiency and lower ingestion rates thus affects post-starvation feeding so as to maximize energy gain. This will allow the animals to return to a state of positive energy balance. at a faster rate.

This argument is supported by the finding that higher assimilation efficiencies occured in starved rather than unstarved animals at all food concentrations I studied. Thompson and Bayne (1972) recorded a negligable assimilation efficiency at cell concentrations greater than 25 X 10^3 cells ml^{-1} while the data presented here recorded efficiencies of more than 50% at all concentrations greater than 600 X 10^3 cells ml^{-1}.

Langton (1975) reported that changes in the structure of the digestive tubules of mussels were related to the period of exposure and submersion on the shore, and that this pattern was altered by starvation. Four types of tubules were recognised, characterized by the condition of the digestive cells. Cytological techniques showed three stages in digestive cell condition:

i absorption.

ii digestion.

iii fragmentation and excretion.

Starvation leads to a marked increase in the proportion of tubules in the holding phase, from 25% in unstarved animals to 67% in animals after two weeks of starvation. Digestion in <u>Mytilus edulis</u> has an intracellular component (Yonge, 1937; Bayne, 1976) and the increased proportion of tubules in the holding phase may allow an increase in the proportion of material undergoing intracellular digestion. This could account in part for the higher assimilation efficiencies I recorded. Subsequent feeding by the starved animals should lead to a rapid decrease in assimilation efficiency as the digestive diverticula revert to their more normal condition.

It should be noted that the assimilation efficiencies are based on the amount of phosphorus assimilated rather than on the organic matter assimilated. It is possible that the protein, carbohydrate and lipid fractions of the ingested material may not be assimilated in the same proportions, and that the increased assimilation efficiency is due to specific selection of nutrients, in this case phosphorus, by Mytilus edulis after a period of starvation.

Bayne (1973) found that seasonal changes in the atomic ratio of oxygen consumed to nitrogen excreted indicated a decline in the use of protein, relative to carbohydrate and lipids, as an energy substrate during the summer. He also noted that, during nutritive stress, there was a decline both in oxygen consumption and in the ratio of oxygen consumed to nitrogen excreted. This indicates a relative increase in the use of protein as an energy yeilding substrate. Gabbott and Bayne (1973) reported that effects of nutritive stress in Mytilus edulis varied with its reproductive condition. Over winter, when the gonad index is very low, Mytilus is able to continue to maintain the somatic tissues, while nutritive stress in early summer results in the recession of the gonads and a rapid loss of protein from the mantle tissue.

The mantle tissue is thought to be used for the storage of nutritive reserves along with the digestive gland. Gabbott and Bayne (1973) suggest that the digestive gland serves both as a nutrient storage organ and also in the regulation of the distribution of nutrients to the body tissues. Starved mussels were found to be capable of storing nutrients, such as phosphorus, in the digestive glands for long periods. The rate of transfer of nutrients to other body components was found to be lower in the winter months than in the summer. This suggests that starvation may lead to a reduction in the rate of transfer of nutrients and an increased demand for such nutrients should they become available. There is also some evidence which suggests that nutrients from ingested food are directly channelled into the somatic tissues and used in gametogenesis. The higher assimilation of phosphorus after starvation may be linked to an increase in nutrient demand by the somatic tissues and the necessity of completing the reproductive cycle, which will be considerably delayed after recession of the gonads.

The results from the experiments presented here and from the previous work on pseudofaecal production in Mytilus edulis(Foster-Smith, 1975 b) show that a large proportion of filtered material is rejected by the mouth palps, especially at high food concentrations. In both studies, the animals were allowed to feed for only a short time and the results can be interpreted only in terms of the proportion of the material rejected with respect to the food concentration. There is a possibility that the length of feeding time could affect the proportion rejected, especially at low food concentrations. If the animal's ingestion rate is sometimes greater than the rate at which the digestive glands are able to deal with the food, than a progressively greater proportion of the material will by-pass the diverticula during the course of feeding, and be egested as the intestinal component of the faeces. As Mytilus is thought to feed for almost all its period of submersion (Jørgensen, 1966) the digestive diverticula are likely to be filled during the feeding period, and the assimilation efficiency will decrease as the intestinal component of the faeces increases. An alternative tactic, allowing the animal to maintain a high efficiency of assimilation throughout the feeding period would be the rejection of a progressively greater proportion of the filtered material to control the balance between ingestion rate and the rate at which the diverticula can digest the food.

2. TURNOVER OF PHOSPHORUS IN Mytilus edulis.

The distribution of phosphorus in Mytilus edulis is uneven and may reflect the relative nutrient requirements and the various metabolic demands of the different tissues. The gill tissue had the highest level of phosphorus per unit dry weight and this tissue is continually active during submersion, in food collection and oxygen uptake. In contrast, the relatively inactive pedal tissues had a phosphorus content per unit weight of about a third of that of the gill tissues.

The somatic tissues of the mussels contained the largest proportion of the tissue phosphorus, about 30% in the animals I examined in June and July. This figure should show some variation during the reproductive cycle, reflecting the development, maturation and release of gamets. Gabbott and Bayne (1973) reported a maximum gonad index in June which suggests that the figure of 30% tissue phosphorus is likely to be a maximum for the mantle and gonads.

The greatest part of the total weight phosphorus in Mytilus was found in the shell, although the results obtained were very variable. Phosphate is activelly used in the initial stages of shell deposition and the phosphorus estimates (Appendix IV) include phosphate remaining in the shell matrix after calcification. Bevelander and Benzer (1948) suggested that calcification of mollusc shells begins with the deposition of calcium phosphate, which is converted into calcium carbonate in the presence of a phosphatase. Shell deposition in Crassostrea virginica has been shown to be associated with phosphatase activity (Pomeroy and Hoskin, 1954).

The estimated physiological turnover time of phosphorus in the whole animal is likely to be of little significance as the distribution of the tissue phosphorus is uneven. The rate of exchange of phosphorus between tissues and the condition of the animal will be important in determining the mean turnover time of phosphorus in the whole animal. This will be substantially altered if one body component contains a large proportion of the tissue phosphorus and has a high standard level of metabolic cost.

The ecological turnover time will also be influenced by a number of parameters. Wave action is likely to increase the suspension load of the water. Foster-Smith (1975 a) showed that inorganic material was not selectively rejected by the mouth-palps. The absence of qualitative selection by the palps would lead to a decrease in the amount of phosphorus ingested due to the relative dilution of phosphorus rich particles. The size of the animal may also influence the turnover time. Kuenzler (1961) showed that small individuals of Modiolus (0 - 25 mg dry flesh) contained c. 9000 p.p.m. phosphorus while the largest animals (1000+ mg dry flesh) contained c. 6500 p.p.m. phosphorus. However the higher filtration rates reported in smaller individuals (Walne, 1972; Bayne, 1976) may cause the estimate of ecological turnover time of phosphorus to be similar to that of the largest animals.

The estimated ecological turnover time will be altered by the numerous requirements of the different size classes within a population. The nutritional condition of the animals and the availability of particulate material will also have a bearing on the rate of movement of the nutrient through the animal. However, Mytilus edulis has a relatively long ecological turnover time of about 60 days and it is unlikely that phosphorus is limiting. Both starved and unstarved Mytilus exert a high degree of quantitative selection before filtered material is ingested and a large proportion is rejected as pseudofaeces. It seems that Mytilus edulis is likely to be of major importance as a depositional agent in the intertidal zone. Kuenzler (1961) suggested that Modiolus modiolus played a similar role in a salt marsh ecosystem. The large amount of material rejected and deposited on the shore may be a major factor in determining the structure of the communities living within the mussel clumps.

ACKNOWLEDGEMENTS

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Appendix I : Filtration rate of *Mytilus edulis*.

Cell concentration about 20 cells ml^{-1} . 10^3.

Experiment A

time interval (min)	nett. c.p.s. Co	nett. c.p.s. Ct	decay corrected Co*	c.p.s. Ct*	filtration rate ml/h	wt. specific ml/h/g
0 - 15	0.056	0.027	0.316	0.153	1515.8	1049.5
15 - 30	0.430	0.116	2.429	0.655	2739.0	1896.4
30 - 45	0.201	0.152	1.136	0.859	584.1	404.4
45 - 60	0.271	0.217	1.531	1.226	464.3	321.5
60 - 75	0.301	0.192	1.701	1.085	939.7	650.6
75 - 90	0.353	0.174	1.994	0.893	1478.2	1023.5
90 - 105	0.225	0.116	1.271	0.655	1385.5	959.3
105 - 120	0.239	0.177	1.350	1.000	627.2	434.3
				Σ	9733.8	6739.5
				$\bar{x}$	1216.7	842.4
				S.E.	±324.4	±170.8

Experiment B

time interval (min)	nett. c.p.s. Co	nett. c.p.s. Ct	decay corrected Co*	c.p.s. Ct*	filtration rate ml/h	wt. specific ml/h/g
0 - 15	0.074	0.050	0.622	0.420	820.7	370.8
15 - 30	0.173	0.076	1.454	0.639	1718.2	776.2
30 - 45	0.121	0.042	1.017	0.353	2211.4	999.0
45 - 60	0.256	0.080	2.151	0.672	2431.4	1098.4
60 - 75	0.096	0.053	0.807	0.445	1244.0	562.0
75 - 90	0.256	0.096	2.151	0.807	2048.9	925.6
90 - 105	0.217	0.083	1.824	0.697	2010.5	908.2
105 - 120	0.240	0.111	2.017	0.933	1611.2	727.9
				Σ	14096.3	6368.1
				$\bar{x}$	1762.0	796.0
				S.E.	±175.9	±79.3

Appendix I : Filtration rate of *Mytilus edulis*

Cell concentration about 250 cells $ml^{-1} . 10^{3}$.

Experiment A

time interval (min)	nett. c.p.s. Co	nett. c.p.s. Ct	decay corrected Co*	c.p.s. Ct*	filtration rate ml/h	wt. specific ml/h/g
0 - 15	1.215	1.145	7.547	7.112	124.1	80.8
15 - 30	1.313	1.087	8.155	6.752	394.5	256.8
30 - 45	1.263	0.936	7.845	5.814	626.1	407.5
45 - 60	1.122	0.892	6.969	5.540	473.6	308.2
60 - 75	1.098	0.735	6.820	4.565	838.9	546.0
75 - 90	1.012	0.859	6.286	5.335	342.8	223.1
90 - 105	1.018	0.700	6.323	4.348	782.6	509.3
105 - 120	1.122	0.725	6.969	4.503	912.7	594.0
				Σ	4495.3	2925.7
				$\bar{x}$	561.9	365.7
				S.E.	± 91.0	± 59.1

Experiment B

time interval (min)	nett. c.p.s. Co	nett. c.p.s. Ct	decay corrected Co*	c.p.s. Ct*	filtration rate ml/h	wt. specific ml/h/g
0 - 15	0.450	0.316	6.818	4.788	738.7	394.6
15 - 30	0.582	0.487	8.818	7.379	372.3	198.9
30 - 45	0.536	0.498	8.121	7.545	153.7	82.1
45 - 60	0.657	0.480	9.955	7.273	656.0	350.5
60 - 75	0.573	0.487	8.682	7.379	339.8	181.5
75 - 90	0.852	0.560	12.909	8.485	877.2	468.6
90 - 105	0.694	0.540	10.515	8.182	523.3	279.6
105 - 120	0.954	0.859	14.455	13.015	219.2	116.7
				Σ	3880.2	2072.5
				$\bar{x}$	485.0	259.1
				S.E.	± 85.2	± 45.5

Appendix I : Filtration rate of *Mytilus edulis*.

Cell concentration about 750 cells $ml^{-1} . 10^3$.

Experiment A

time interval (min)	nett. c.p.s. Co	nett. c.p.s. Ct	decay corrected Co*	c.p.s. Ct*	filtration rate ml/h	wt. specific ml/h/g
0 - 15	1.190	0.902	23.107	17.515	578.8	313.6
15 - 30	1.391	1.091	27.010	21.184	508.1	275.3
30 - 45	1.190	1.060	23.107	20.583	242.3	131.3
45 - 60	1.252	1.239	24.311	24.058	21.6	11.7
60 - 75	1.672	1.454	32.466	28.233	292.4	158.4
75 - 90	2.005	1.613	38.932	31.320	454.6	246.3
90 - 105	1.780	1.557	34.563	30.233	279.7	151.5
105 - 120	1.826	1.652	35.456	32.078	209.4	113.5
				Σ	2586.9	1401.6
				$\bar{x}$	323.4	175.2
				S.E.	± 60.1	± 32.5

Experiment B

time interval (min)	nett. c.p.s. Co	nett. c.p.s. Ct	decay corrected Co*	c.p.s. Ct*	filtration rate ml/h	wt. specific ml/h/g
0 - 15	0.706	0.515	16.810	12.262	659.6	426.1
15 - 30	0.883	0.752	21.024	17.905	335.8	216.9
30 - 45	0.955	0.892	22.738	21.238	142.7	92.2
45 - 60	1.091	0.994	26.976	23.667	194.7	125.8
60 - 75	1.362	1.285	31.071	30.595	32.2	20.8
75 - 90	1.315	1.229	31.310	29.262	141.4	91.3
90 - 105	1.518	1.346	36.143	32.048	251.3	162.3
105 - 120	1.617	1.518	38.500	36.143	132.0	85.3
				Σ	1889.7	1220.7
				$\bar{x}$	236.2	152.6
				S.E.	± 63.9	± 41.3

Appendix II: Phosphorus intake, estimated by iteration

Cell concentration about 20 cells ml^{-1}. 10^3. Experiment A

Time interval	Number of cells introduced	Number of cells in solution	ml. filtered	Number of cells removed	Number of cells remaining	µg P removed
0 - 15	22 041 600	22 041 600	378.95	8 353 664	13 688 936	12.844
15 - 30	5 510 400	19 199 338	684.75	13 146 747	6 052 591	20.216
30 - 45	5 510 400	11 562 991	146.03	1 688 486	9 874 505	2.596
45 - 60	5 510 400	15 384 905	116.08	1 785 803	13 599 102	2.746
60 - 75	5 510 400	19 109 502	124.93	4 489 299	14 620 203	6.903
75 - 90	5 510 400	20 130 603	369.55	7 439 262	12 691 339	11.440
90 - 105	5 510 400	18 201 739	346.38	6 304 627	11 897 112	4.197
105 - 120	5 510 400	17 407 512	156.80	2 729 498	14 678 014	4.197

Σ:143 038 190

$\bar{x}$: 17 879 773 ± 1 060 000

Σ:70.637

Appendix 14 : Phosphorus intake, estimated by iteration.

Cell concentration about 20 cells $ml^{-1} . 10^3$. Experiment B

Time interval	Number of cells introduced	Number of cells in suspension	ml. filtered	Number of cells removed	Number of cells remaining	µg P removed
0 - 15	24 875 000	24 875 000	205.18	4 898 533	19 976 467	7.533
15 - 30	5 970 000	25 946 467	429.55	11 145 305	14 801 162	17.139
30 - 45	5 970 000	20 771 162	552.85	11 483 337	9 287 825	17.658
45 - 60	5 970 000	15 257 825	607.85	9 274 469	5 983 356	14.262
60 - 75	5 970 000	11 953 356	311.00	3 717 494	8 235 862	5.717
75 - 90	5 970 000	14 205 862	512.23	7 276 598	6 929 264	11.190
90 - 105	5 970 000	12 899 264	502.63	6 483 493	6 415 771	9.970
105 - 120	5 970 000	12 385 771	402.80	4 988 989	7 396 782	7.672

Σ : 138 294 707

$\bar{x}$: 17 286 836 ± 1 895 000

Σ : 91·141

Appendix II : Phosphorus intake, estimated by iteration.

Cell concentration about 250 cells ml^{-1} . 10^3. Experiment A.

Time interval	Number of cells introduced	Number of cells in solution	ml. filtered	Number of cells removed	Number of cells remaining	µg P removed
0 - 15	201 924 250	201 924 250	31.03	6 264 700	195 659 550	9.634
15 - 30	36 352 000	232 011 550	98.63	22 882 139	209 129 411	35.187
30 - 45	36 352 000	245 481 411	156.53	38 423 978	207 057 433	59.086
45 - 60	36 352 000	243 409 433	118.40	28 819 677	214 589 756	44.317
60 - 75	36 352 000	250 941 756	209.73	52 630 014	198 311 742	80.932
75 - 90	36 352 000	234 663 742	85.70	20 110 683	214 553 059	30.925
90 - 105	36 352 000	250 905 059	195.65	49 089 575	201 815 575	75 487
105 - 120	36 352 000	238 167 484	228.18	54 345 056	183 822 428	83.569

Σ:1897 504 685

$\bar{x}$: 237 188 085 ± 5 246 700

Σ:419.137

Appendix II : Phosphorus intake, estimated by iteration.

Cell concentration about 250 cells ml^{-1} . 10^3. Experiment B

Time interval	Number of cells introduced	Number of cells in solution	ml. filtered	Number of cells removed	Number of cells remaining	μg P removed
0 - 15	206 200 000	206 200 000	184.68	38 079 985	168 120 015	58.557
15 - 30	51 550 000	219 670 015	93.08	20 445 787	199 224 228	31.440
30 - 45	51 550 000	250 774 228	38.43	9 636 000	241 138 228	14.818
45 - 60	51 550 000	292 688 228	164.00	48 000 869	244 687 359	73.813
60 - 75	51 550 000	296 237 359	84.95	25 165 364	271 071 995	38.698
75 - 90	51 550 000	322 621 995	219.30	70 751 004	251 870 991	108.797
90 - 105	51 550 000	303 420 991	130.83	39 696 568	263 724 423	61.043
105 - 120	51 550 000	315 274 423	54.80	17 277 038	297 997 385	26.568

Σ:2206 887 239

$\bar{x}$:275 860 904 ± 14 700 000

Σ:413.734

Appendix II : Phosphorus intake, estimated by iteration.

Cell concentration about 750 cells ml^{-1} . 10^3. Experiment A.

Time interval	Number of cells introduced	Number of cells in solution	ml. filtered	Number of cells removed	Number of cells remaining	µg P removed
0 - 15	515 500 000	515 500 000	144.70	74 592 850	440 907 150	114.705
15 - 30	103 100 000	544 007 150	127.03	69 102 508	474 904 642	106.262
30 ÷ 45	103 100 000	578 004 642	60.58	35 012 631	542 992 011	53.840
45 - 60	103 100 000	646 092 011	5.40	30 488 897	642 603 114	5.365
60 - 75	103 100 000	745 703 114	73.10	54 510 898	691 192 216	83.824
75 - 90	103 100 000	794 292 216	113.65	90 271 310	704 020 906	138.814
90 - 105	103 100 000	807 120 906	69.93	56 437 929	750 682 977	86.787
105 - 120	103 100 000	853 782 977	52.35	44 695 539	809 087 438	68.730

Σ:5484 503 016

$\bar{x}$: 685 562 877 ± 43 409 000

Σ:658.327

Appendix II : Phosphorus intake, estimated by iteration.

Cell concentration about 750 cells ml^{-1} . 10^3. Experiment B.

Time interval	Number of cells introduced	Number of cells in solution	ml. filtered	Number of cells removed	Number of cells remaining	µg P removed
0 - 15	583 400 000	583 400 000	164.90	96 202 660	487 197 340	147.935
15 - 30	140 016 000	627 213 334	83.95	52 654 560	574 558 774	80.969
30 - 45	140 016 000	714 574 774	35.68	25 492 455	689 082 319	39.201
45 - 60	140 016 000	829 098 319	48.68	40 356 361	788 741 958	62.058
60 - 75	140 016 000	928 757 958	8.05	70 476 502	921 281 456	11.497
75 - 90	140 016 000	1061 297 456	35.35	37 516 865	1023 780 591	57.691
90 - 105	140 016 000	1163 796 591	62.83	73 115 521	1090 681 070	112. 433
105 - 120	140 016 000	1230 697 070	33.00	40 613 003	1190 084 067	62.452

Σ:7138 835 502

$\bar{x}$: 892 354 437 ± 80 950 000

Σ:574.236

Appendix III : Faecal and Pseudofaecal material egested by Mytilus edulis, fed at 20×10^3 cells ml^{-1}

Experiment A.

Faecal material:

Time interval (mins)	Disintegrations per sec.	µg P	µg P egested/ 30 mins.	µg P egested 30 mins/ µg P egested over 24 h (%)
0 - 120	338.1	0.145	0.036	2.50
120 - 150	328.2	0.141	0.141	9.81
150 - 180	76.2	0.033	0.033	2.29
180 - 210	468.7	0.201	0.201	13.98
210 - 240	753.2	0.324	0.324	22.53
240 - 270	204.9	0.088	0.088	6.12
270 - 300	439.2	0.189	0.189	13.14
300 - 360	453.5	0.195	0.098	6.82
360 - 420	62.6	0.027	0.014	0.97
420 - 480	83.7	0.036	0.018	1.25
480 - 1440	136.3	0.059	0.002	0.14
1440 - 3120	35.9	0.015		

µg P egested in 24 h. 1.438

	Disintegrations per sec.	µg P
Material rejected as Pseudofaeces.	9754.1	4.191
Activity of final feeding solution.	69000	29.624

Appendix III: Faecal and Pseudofaecal material egested by *Mytilus edulis*, fed at 20×10^3 cells ml^{-1}

Experiment B

Faecal material:

Time interval (mins)	Disintegrations per sec.	µg P	µg P egested/ 30 mins.	µg P egested 30 mins/ µg P egested over 24 h (%)
0 - 120	2227.1	1.382	0.346	2.80
120 - 250	405.8	0.252	0.252	2.04
150 - 180	6483.5	4.024	4.024	32.54
180 - 210	3985.7	2.474	2.474	20.01
210 - 240	989.6	0.614	0.614	4.97
240 - 270	1634.4	1.014	1.014	8.20
270 - 300	2183.5	1.355	1.355	10.96
300 - 360	1318.3	0.818	0.409	3.31
360 - 420	266.1	0.162	0.081	0.66
420 - 480	38.6	0.024	0.012	0.10
480 - 1440	396.4	0.246	0.008	0.06
1440 - 3120	89.7	0.056		
µg P egested in 24 h		12.365		

	Disintegrations per sec	µg P
Material rejected as Pseudofaeces	44611	27.671
Activity of final feeding solution	64330	39.925

Appendix III: Faecal and Pseudofaecal material egested by Mytilus edulis, fed at 250×10^3 cells ml^{-1}.

Experiment A

Faecal material:

Time interval (mins)	Disintegrations per sec.	µg P	µg P egested/ 30 mins	µg P egested 30 mins/ µg P egested over 24 h (%)
0 - 120	17095.2	9.690	2.423	2.96
120 - 150	6817.0	3.864	3.864	4.72
150 - 180	6656.4	3.773	3.773	4.61
180 - 210	9809.9	5.561	5.561	6.80
210 - 240	19431.2	11.014	11.014	13.46
240 - 270	4915.7	2.786	2.786	3.41
270 - 300	10284.3	5.829	5.829	7.13
300 - 360	16759.3	9.500	4.750	5.81
360 - 420	18998.6	10.769	5.385	6.58
420 - 480	14240.2	8.072	4.036	4.93
480 - 540	9809.9	5.561	2.781	3.40
540 - 600	2949.2	1.672	0.836	1.02
600 - 1320	6553.4	3.715	1.858	2.27
1320 - 1620	729.6	0.414	0.207	0.253
µg P egested in 24 h		81.806		

	Disintegrations per sec.	µg P
Material rejected as Pseudofaeces	483546.3	273.9
Activity of final feeding solution	310481.9	175.9

Appendix III: Faecal and Pseudofaecal material egested by Mytilus edulis, fed at 250 x 10^3 cells ml^{-1}.

Experiment B

Faecal material:

Time interval (mins)	Disintegrations per sec.	μg P	μg P egested/ 30 mins.	μg P egested 30 mins/ μg P egested over 24 h (%)
0 - 120	-	-	-	-
120 - 250	2413.7	1.940	1.940	12.15
150 - 180	6257.7	5.030	5.030	31.50
180 - 210	-	-	-	-
210 - 240	3528.6	2.836	2.836	17.76
240 - 270	-	-	-	-
270 - 300	502.7	0.404	0.404	2.53
300 - 360	216.5	0.174	0.087	0.54
360 - 420	1712.1	1.376	0.688	4.31
420 - 480	1347.7	1.083	0.542	3.39
480 - 540	1141.0	0.917	0.459	2.87
540 - 1440	2749.9	2.210	0.074	0.46
1440 - 2880	1791.8	1.440		
μg P egested in 24 h.			15.970	

	Disintegrations per sec.	μg P
Material rejected as Pseudofaeces	277868.4	223.238
Activity of final feeding solution	897384.3	720.954

Appendix III: Faecal and Pseudofaecal material egested by *Mytilus edulis*, fed at 750×10^3 cells ml^{-1}.

Experiment A

Faecal material:

Time interval (mins)	Disintegrations per sec.	μg P	μg P egested/ 30 mins.	μg P egested 30 mins/ μg P egested over 24 h (%)
0 - 120	-	-	-	-
120 - 150	-	-	-	-
150 - 180	2319.1	1.864	1.864	5.36
180 - 210	2.7	0.002	0.002	0.01
210 - 240	95.3	0.077	0.077	0.22
240 - 270	157.2	0.126	0.126	0.36
270 - 300	501.8	0.403	0.403	1.16
300 - 360	14225.9	11.436	5.718	16.45
360 - 420	638.4	0.513	0.257	0.74
420 - 480	12842.2	10.323	5.162	14.85
480 - 540	917.4	0.737	0.369	1.06
540 - 1440	11548.8	9.284	0.309	0.89
1440 - 2880	8327.3	6.694		
μg P egested in 24 h.			34.770	

	Disintegrations per sec.	μg P
Material rejected as Pseudofaeces	409888.5	329.3
Activity of final feeding solution	1773722.4	1425.0

Appendix III : Faecal and Pseudofaecal material egested by Mytilus edulis, fed at 750 x 10^3 cells ml^{-1}.

Experiment B

Faecal material:

Time interval (mins)	Disintegrations per sec.	µg P	µg P egested/ 30 mins.	µg P egested 30 mins/ µg P egested over 24 h (%)
0 - 120	-	-	-	-
120 - 250	26995.9	19.647	19.647	30.77
150 - 180	4421.0	3.217	3.217	5.04
180 - 210	4238.5	3.085	3.085	4.83
210 - 240	819.5	0.596	0.596	0.93
240 - 270	2125.3	1.547	1.547	2.42
270 - 300	-	-	-	-
300 - 360	2348.2	1.709	0.855	1.34
360 - 420	2544.6	1.852	0.926	1.45
420 - 480	1099.9	0.800	0.400	0.63
480 - 540	4173.1	3.037	1.519	2.38
540 - 1440	38948.2	28.345	0.945	1.48
1440 - 2880	8734.7	6.357		
µg P egested in 24 h.		63.835		

	Disintegrations per sec.	µg P
Material rejected as Pseudofaeces	587342.7	427.2
Activity of final feeding solution	2492059.8	1812.6

Appendix IV : *Mytilus edulis* organ weights and Phosphorus content.

	Size (mm)	47	48	48	49	49	50	50
	Wet wt (mg)	1547.9	1444.3	1868.8	1536.5	2213.6	1871.8	3279.9
	Dry wt (mg)	246.4	298.3	375.2	315.6	456.2	343.7	536.0
shell	(Wet wt (mg)	7535.9	7885.3	7663.7	8716.2	8831.4	10911.9	9157.5
	(Dry wt (mg)	7399.6	7706.4	7460.9	8542.5	8530.5	10672.0	9043.5
	(mgP	16.3	1.5	6.7	12.8		12.8	16.3
gill	(Wet wt (mg)	229.0	154.6	336.8	128.0	380.4	389.1	285.9
	(Dry wt (mg)	32.9	27.0	54.4	23.4	40.3	38.1	48.2
	(mg P	0.349	0.351	0.604	0.344	0.508	0.771	0.651
mantle and gonads	(Wet wt (mg)	571.1	495.0	641.9	587.1	990.0	956.8	1165.2
	(Dry wt (mg)	77.0	90.0	123.6	104.1	147.9	125.3	225.8
	(mg P	0.293	0.711	0.655		0.606	0.689	1.016
adductor	(Wet wt (mg)	135.9	202.8	174.4	184.3	408.8	335.0	297.4
	(Dry wt (mg)	28.7	45.3	37.1	46.7	62.0	39.5	61.2
	(mg P	0.218	0.213	0.252	0.299		0.320	0.435
foot	(Wet wt (mg)	295.4	264.8	357.3	368.2	525.3	486.1	310.3
	(Dry wt (mg)	51.7	59.9	74.6	81.8	85.4	60.2	70.3
	(mg P	0.243	0.162	0.261	0.286		0.301	0.204
digestive system	(Wet wt (mg)	316.5	327.1	358.4	268.9	666.9	543.4	521.1
	(Dry wt (mg	56.1	76.1	85.5	59.6	120.6	79.9	130.5
	(mg P	0.381	0.190	0.633	0.226	0.736	0.423	0.457
Total tissue P (mg)		1.484	1.627	2.405			2.504	2.763
% P		0.602	0.545	0.641			0.729	0.515

Appendix IV : Mytilus edulis organ weights and Phosphorus content.

	Size (mm)	51	52	52	53	53	55	55
	Wet wt (mg)	2237.2	2250.7	3007.0	2717.0	2730	1845.7	2426.8
	Dry wt (mg)	403.0	447.1	598.1	567.1	603.1	271.3	501.8
shell	(Wet wt (mg)	12142.3	11309.1	13477.4	8987.7	12848.5	13551.5	12903.4
	(Dry wt (mg)	11859.1	11044.0	13277.6	8875.9	12680.0	13278.0	12710.6
	(mg P	5.9	15.5		16.6	19.0	5.3	21.6
gill	(Wet wt (mg)	368.3	260.5	365.2	308.1	361.5	345.5	356.9
	(Dry wt (mg)	61.4	45.4	56.2	47.4	65.1	51.3	60.4
	(mg P	0.761	0.713		0.569	0.840	0.534	0.701
mantle and gonads	(Wet wt (mg)	783.6	928.5	1428.2	1108.3	920.4	509.3	913.5
	(Dry wt (mg)	124.2	161.6	266.7	220.4	188.6	61.1	155.5
	(mg P	0.696	1.212	1.627	0.860	0.943	0.312	0.995
adductor	(Wet wt (mg)	143.4	154.8	298.4	247.4	321.8	161.7	296.4
	(Dry wt (mg)	33.9	35.7	65.4	52.6	76.7	30.5	76.4
	(mg P	0.254	0.182	0.392	0.337	0.453	0.162	0.512
foot	(Wet wt (mg)	400.1	420.0	408.3	458.1	517.6	263.3	340.7
	(Dry wt (mg)	68.3	86.2	87.7	99.8	120.0	40.3	90.5
	(mg P	0.301	0.457	0.430	0.369	0.660	0.185	0.489
digestive system	(Wet wt (mg)	541.8	486.9	506.9	595.8	608.9	565.9	519.3
	(Dry wt (mg)	115.2	118.2	122.1	146.9	152.7	88.1	119.0
	(mg P	0.541	0.721	0.891	0.764	0.886	0.590	0.464
Total tissue P (mg)		2.553	3.285		2.899	3.782	1.783	3.161
% P		0.633	0.735		0.511	0.627	0.657	0.630