ENERGETICS OF THE FRESHWATER MUSSEL
HYRIDELLA MENZIESI GRAY

A Thesis
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of the requirements for the degree
of
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at the
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by

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This work is dedicated to

George Aaron Nobes

died

6th January

1980.

ABSTRACT

Various aspects of the biology of *Hyridella menziesi* were studied to obtain an energy budget so that its role in the Waikato River could be elucidated.

Respiration rates were found to increase with both temperature and animal size. The Q_{10} ranged from 1.1 to 8°C to 2.6 at 27.5°C. Weight dependent respiration increased exponentially with weight (in g. dry weight), the relationship being $R = 417\ W^{0.410}$ $\mu g\ O_2.hr^{-1}$ at ambient temperatures (18.5 to 24.6°C).

The water pumping rate (P) increased with animal size ($P = 3.8\ W^{0.27}$ $\ell.hr^{-1}$), but filtering rates were variable, being affected by the particle retention efficiency of the gill. Retention efficiencies decreased in larger animals, a result of increasing interfilament distances which were evident from electron micrographs.

Filtration rates using *Chlorella* showed no variation with animal size or food concentration (FC $cells.ml^{-1}$), the mean being 1.02 $\ell.hr^{-1}$, but the proportion of food ingested did depend on the amount available (ingestion ratio $= 2.20\ FC^{-0.22}$) and assimilation efficiencies (AE %), obtained by the dual isotope method of Calow and Fletcher, decreased as the feeding rate increased ($AE\ \ 272\ FR^{-0.128}$, FR $cells.hr^{-1}$).

Calculated energy budgets were positive but cell numbers in the Waikato River fell below that required for maintenance by animals of 0.05 g dry weight and larger during the winter months of July through September. The expected energy fluxes derived from river-bed transect and budget data were higher than those for other bivalves, but similar to that of *Potamopyrgus antipodarum* which is also found in the Waikato River, and is indicative of the intermediary role played by *Hyridella* of providing detritus for the benthos and speeding nutrient cycling.

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CONTENTS

LIST OF FIGURES

LIST OF PLATES

LIST OF TABLES

INTRODUCTION

The Waikato River is the longest in New Zealand and is greatly modified by man. There are now eight hydrodams in its middle reaches. 250,000 people live in the catchment area, 160,000 of them urban dwellers contributing domestic sewage to the river's pollution load. There are also industrial pollutants and farm waste discharges. Concern has been felt for many years over the deterioration of the country's water resources, yet until recently, there has been no information on the rivers communities and biological parameters.

A report has been recently published collating surveys done during the period 1972 and 1978 (Strachan 1979). Others have worked on *Paratya curvirostrus* and *Potamopyrgus antipodarum* (Wash 1974), *Potamopyrgus* sp. (West 1975), *Mugil cephalus* (Wells 1977), *Anguilla* sp. (Jellyman 1977) and *Ictalurus nebulosus* (Patchell 1977). Boubée (1977) studied the benthos of the river, and recognised 44 taxa, dominated numerically by Oligocheata, Nematoda, Nemertea and *Potamopyrgus antipodarum*. Bivalve molluscs were found at five of his six sampling sites, and the fresh water mussel *Hyridella menziesi* (Gray) was present at three of them.

Of the six limnetic bivalve molluses in New Zealand, *Hyridella menziesi* is the most abundant and wide spread (Ponder 1964). Nevertheless, the only studies done are by Percival (1931) on the life cycle of *H. menziesi* and that of Grimmond (1968) who established the age structure and migration patterns of the population of *H. menziesi* in Tomahawk Lagoon (Otago).

In fact little is known about the role of mussels in fresh water, even though much work has been done on marine bivalve molluscs, especially those of economic significance, in relation to feeding, metabolism, growth and energy flow (e.g. Kuenzler 1961, Hughes 1970, Widdows and

Bayne 1971, Bayne *et al.* 1976a, Dame 1976). The population dynamics of unionid mussels in the River Thames have been determined and the annual production of the populations calculated.

A similar study, also determining annual production, was done on gastropod and bivalve molluscs in the Madison River (Gillespe 1969). The suggested role of bivalves in fresh water systems in that of removing suspended particulate matter (Hinz and Scheil 1972) and cycling material by providing detritus for the benthos (Stańczykowska *et al.* 1975). I have made a study of *Hyridella menziesi* from the Waikato River to determine parameters necessary for the estimation of an energy budget. It was hoped that the role of *H. menziesi* in the community would be elucidated and contributions made to an understanding of the animal itself, fresh water mussels in general and the Waikato River as a whole.

The trophic dynamic model of ecosystems is now well established as a basis for ecological studies. The ecosystem is divided into trophic levels, the energy content of each being in a state of flux, receiving energy from the previous trophic level and losing it by passing it to the next level and dissapating it in metabolism and decomposition. Increased understanding of ecosystem dynamics has come through considerations of the concept of production and factors controlling food uptake, assimilation and metabolism (Mann 1969). Studies can be approached from the view of the energetics of whole populations, such as Hughes' (1970) work on the tidal flat bivalve *Scrobicularia plana*, or of individuals and small groups from the population as did Stańczykowska *et al.* (1975) with *Dreissena polymorpha* in Mikolayskie Lake. However, controlling factors and energy fluxes are more readily recognised when the energetics of single animals are determined. This heuristic approach not only allows the role of particular organisms to be elucidated but also the effects of the manipulation of ecosystem components to be predicted.

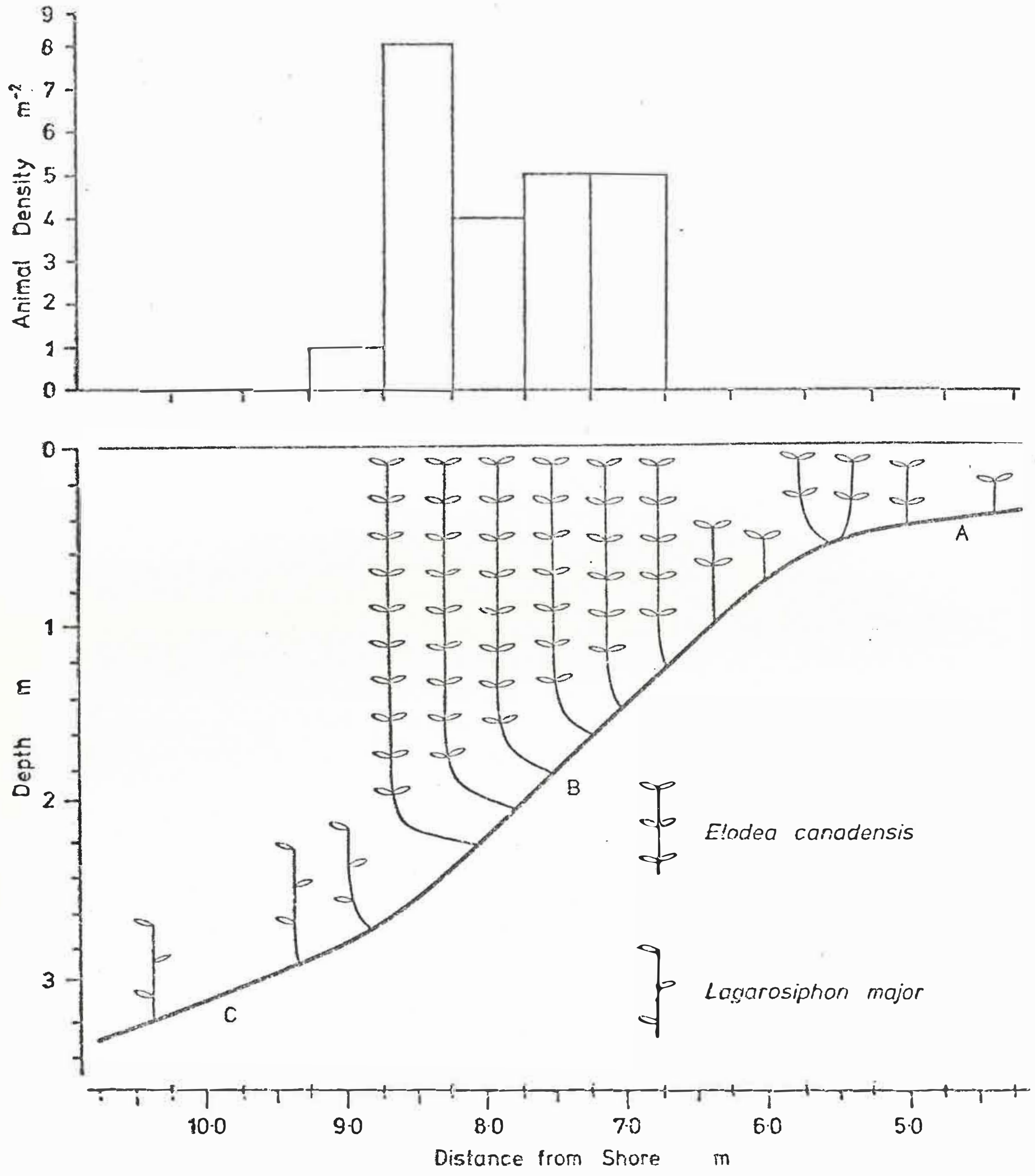

Fig. 1. Longitudinal transect of the Waikato River bed at sampling site showing animal density and macrophyte distribution and composition. Substrate textures were: at A, slightly gravelly sand; B, sand and C, gravel.

Collection and Storage of Animals

Mussels were taken from a weed bed on the west bank of the Waikato River 200 m downstream from Cobham Bridge (NZMS 1 N65 800448). During times of low flow the animals could be collected with a long handled rake with ten cm long tines, but usually they were gathered by a SCUBA diver. The animals were placed in plastic containers nearly filled with river water for transport to the laboratory.

In the laboratory each animal was marked for future identification by engraving through the periostracum into the prismatic layer, measured for overall length, cleaned to remove any adhering substrate and put in an aquarium.

River Bed Transect

A 2 m wide transect through a weed bed at the collection site was used to establish the density and distribution of *Hyridella menziesi* in the river. The transect, which began 4.25 m from the water's edge and extended 5 m perpendicularly out from the water's edge, was divided into sections 0.5 m long. Weed was removed by clipping and sediment samples taken from the transect were analysed for particle distribution by standard petrological techniques (Folk 1968).

The pertinent features of the transect are shown in Fig. 1. From outside the weed bed the substrate was predominantly gravel which shows the high sediment carrying ability of the river. Within the bed, the substrate texture was sandy, the small amount of mud present being made up predominantly of silt sized particles, indicating the retarding effect by the weeds on the current, allowing sedimentation of finer particles. Inshore of the bed, the very low mud content results from wave action (Davies 1970).

Mussels were found within the weed bed where the substrate is stabilized by macrophyte roots and particle reentrainment much reduced. The absence of *Hyridella menziesi* inshore from the weed bed where the water is shallow could be due to predation by birds or death by dessication since these areas are also exposed during periods of low river flow. The denisty of *H. menziesi* in each section of the transect is given in Fig. 1 and the mean density in the weed bed was 4.6 animals m^{-2} (S.D. 1.2 animals. m^{-2}). An analysis of variance showed no significant difference of animal size between section locations.

Acclimatization of Animals

Lomte and Nagabhushanah (1971), have shown that the oxygen uptake of bivalve molluscs decreases with time when the animals are removed from the field and kept in experimental conditions. The decrease in oxygen uptake is most marked during the first three days after collection and is caused by starvation. Consequently, one week prior to experimentation, the required animals were removed from their holding aquarium and placed in a small covered aquarium containing filtered river water to ensure that all animals were in a comparable metabolic condition.

The filtered river water was obtained from the Hamilton City Council Water Treatment Station and had been through the flocculation tanks and sand filters, but no lime, excess chlorine or fluorine compounds had been added. The pH of the filtered river water after aeration was 7.3. That of the river water varies from 7.0 to 7.5 throughout the year (Hamilton City Council, Engineering Department, pers. comm.) as measured at the intake of the Water Treatment Station.

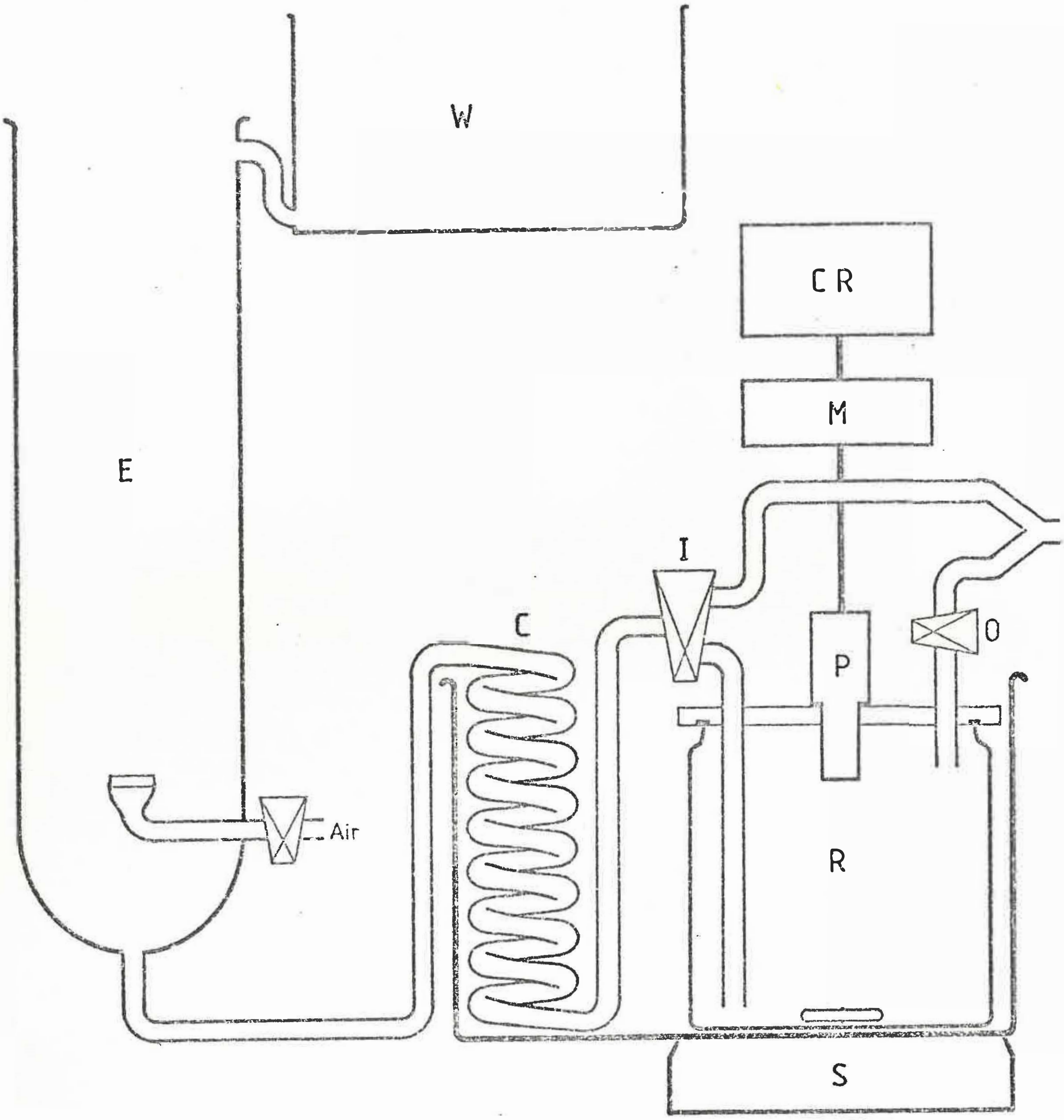

Fig. 2. Diagram of the respirometer. Letters represent: W, water reservoir; E, gas exchange column; P, polarographic oxygen probe; M, oxygen meter; CR, chart recorder and S, the magnetic stirrer. The heat exchange coil, C and respiration chamber R were submerged in a temperature controlled water bath.

METHODS

Respiration

The apparatus (Fig. 2) used was similar to that described by Bayne (1971). Water from a 25ℓ. resevoir was held in a water-gas exchange column of 2ℓ. capacity through which air or oxygen free nitrogen could be bubbled for adjustment of the water oxygen concentration. The water outlet was connected to a glass coil for temperature equilibration by an 8 mm. diameter plastic tube. The glass coil was connected to the inlet of the respiration chamber by a similar piece of plastic tubing. The respiration chamber of 0.55ℓ. capacity was provided with four ports. The inlet port contained a two-way tap so that water from the exchange column could be directed to the chamber or to waste. The outlet port contained a one-way tap, which could be used to control the flow of water through the chamber. A Yellow Springs Instrument polarographic oxygen electrode was inserted into the chamber through the third port and the fourth port was closed with a serum bottle top so samples could be taken from or added to the chamber with a syringe and hypodermic needle.

The current of polarographic electrodes at constant oxygen tensions is dependant on the water velocity past the membrane (Müller 1947, Carrit *et al.* 1959, Carey *et al.* 1965) so the water in the respiration chamber was circulated with a magnetic stirrer. A stand was used to support the animal in the chamber in an inverted position with the hingeline horizontal, and to keep it clear of the stirrer.

The water current produced by the stirrer did not seem to affect the animals normal activity since most resumed filtering activity soon after being placed in the respiration chamber.

A preliminary experiment in which the valve activity of a single animal was monitored over a five day period showed that it was sensitive to mechanical disturbance and was most active in the early evenings. The respiration determinations were therefore carried out in the evenings when the laboratory was quiet, and the animals handled as carefully as possible. The activity followed a diurnal pattern and the valves were open 45% of the time.

For each experimental run, an animal was placed on the stand in the respirometer and the chamber flooded with water. The top was fastened down, excluding all air. Then the chamber and heat exchange coil were placed in the temperature controlled water bath with the respirometer over the magnetic stirrer. With the stirrer turned on, the respirometer was slowly flushed with 1.5ℓ. of water from the exchange column. Constant pressure conditions within the chamber, necessary because the oxygen probe was sensitive to variations in hydrostatic pressure, were attained by closing the outlet tap, leaving the inlet tap open and refilling the exchange column. If by this time the siphons were extended, respiration measurements were made, otherwise the experiment was abandoned and another animal used. Oxygen concentrations in the chamber were monitored for 30 to 60 minutes and recorded on a chart recorder (Fig. 2). When the animals were mobile, the experiment was repeated the following evening. This ensured that all animals were in a similar activity state, and following Newell and Pye (1970) were defined to be non-feeding, so giving the standard respiration.

After the respiration experiments animal weights were determined. The mussels were left to drain for 15 minutes after cutting their adductor muscles, then weighed. They were then dried to constant weight at 75°C and after removing the dried flesh, the shell reweighed. From these measurements wet and dry flesh weights were calculated.

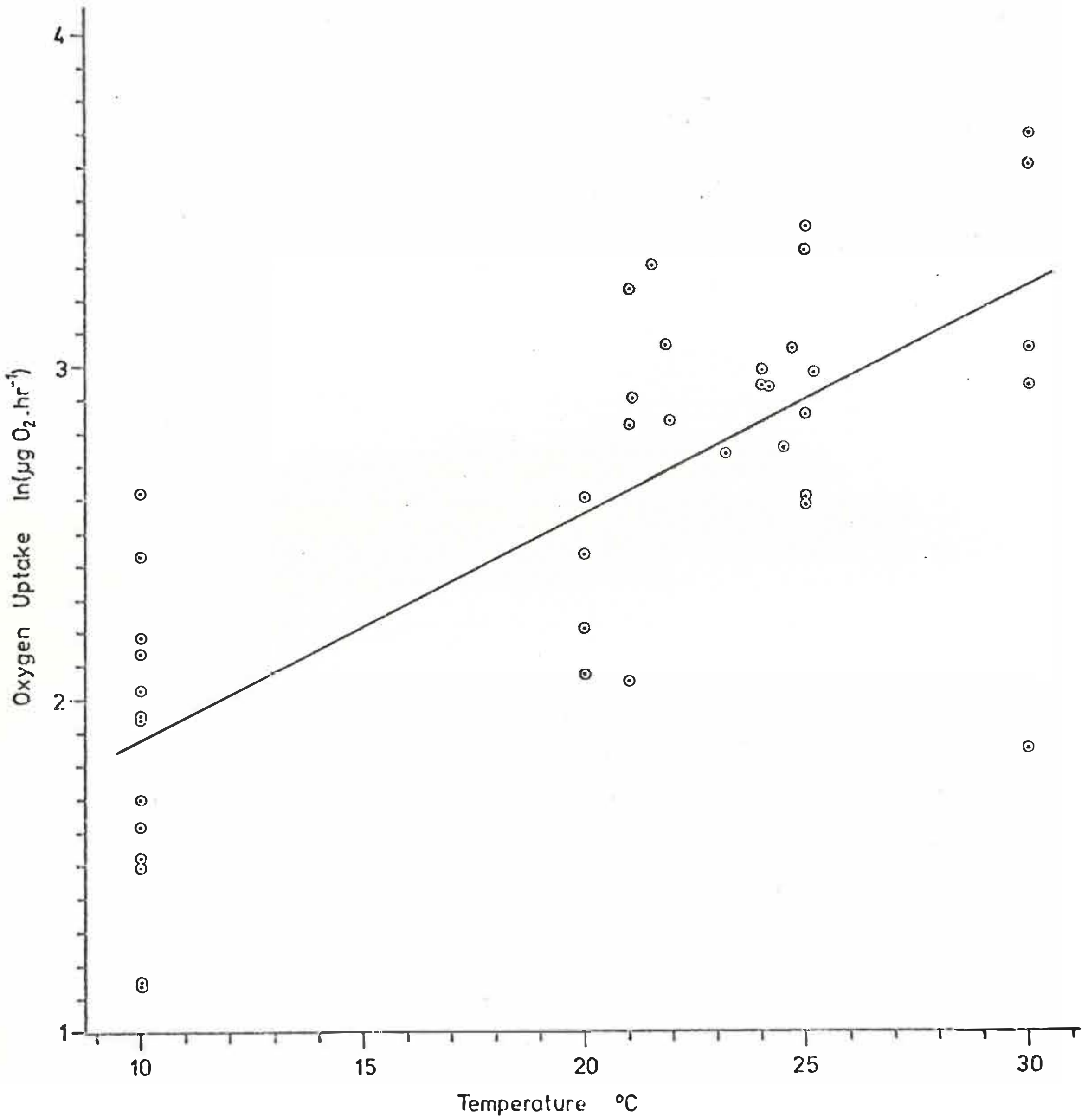

Fig. 3. Oxygen uptake in the respirometer, without animals, at various temperatures.

Two sets of experiments were carried out; the first to establish the dependence of respiration rates on animal size at ambient temperatures (range 18.5 to 24.6°C), the second to establish the dependence of respiration rate on temperature. The second set was done using two groups of animals, both ranging in size from 49.9 to 59.9 mm in length. One group of animals was used to determine the respiration rate at 6, 10, 15 and 20°C and the other at 10, 20, 25 and 30°C. Each group of animals was acclimatized for one week at the required temperature before any respiration determinations were made. This range of temperatures was chosen because it included the seasonal variation of 10°C to 23°C (Hamilton City Council, Engineering Division, pers. comm.) experienced by *Hyridella* in their natural habitat.

Control experiments with no animal in the chamber were run overnight to determine the oxygen uptake by the apparatus, which was found to be temperature dependent (Fig. 3), the relationship being

$$U = 3.310\ e^{0.0682T} \qquad (p\ ***)^{\dagger} \qquad \text{(I)}$$

where U is the oxygen uptake of the apparatus in $\mu g.O_2.hr^{-1}$

T is the experimental temperature.

The oxygen uptake for any experimental temperature was calculated from the regression equation and subtracted from the observed animal respiration to give the true respiration.

A single experiment with a group of 14 animals in a large respiration chamber was done to observe the effect of oxygen concentration on the respiration rate.

Pumping Rates and Particle Retention

Measurements of particle retention ability were made during the respiration experiments by adding known concentrations of different

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† Throughout this thesis * $0.05>p>0.01$, ** $0.01>p>0.001$, *** $0.001>p$.

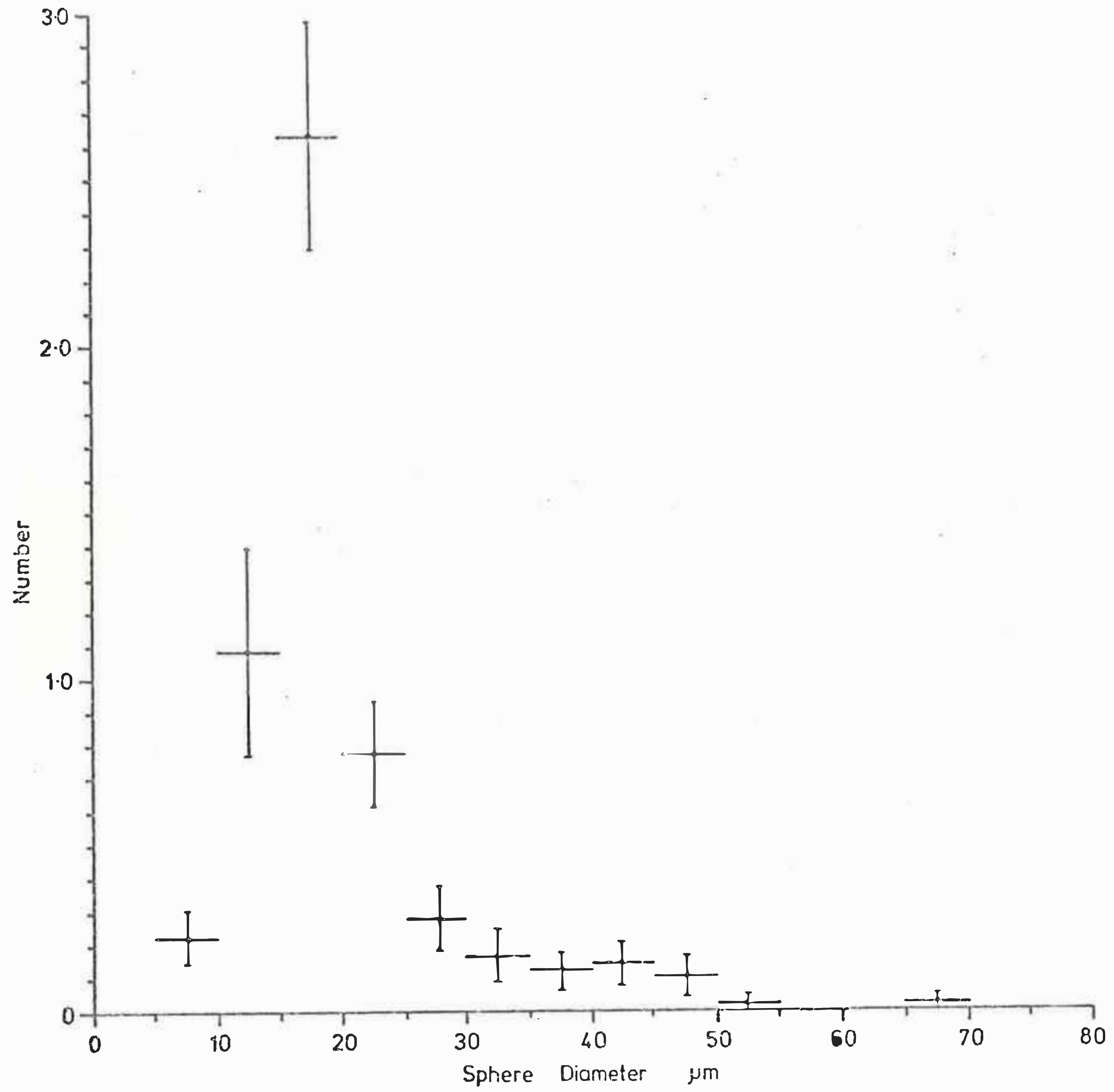


Fig. 4. Size frequency of Micronic beads in the stock suspension. Counts were made of 40 microscopic fields. The horizontal bar shows the size range and the vertical bar the standard error of the mean.

sized particles and determining changes in their concentration in suspension after a known period of time.

The particles used were plastic 'Micronic' spheres which range in diameter from about 5μm to 80μm. They have been previously used in feeding experiments (Burns 1968, Green 1973) in preference to algal cultures because they are available in a wide size range and are of uniform shape and a single stock suspension of beads is required instead of the preparation and maintenance of many algal cultures to give the required size range. Although different in shape and texture to most phytoplankton species, it was hoped that the beads would give a good indication of what size range is retained by *Hyridella*, and, as shown later (p. 38) their response to both beads and algae are the same.

Fig. 4 gives the size-frequency distribution of the beads. Because of the peaked distribution, three sphere-size classes were considered; 5.1 to 15.0μm, 15.1 to 30.0μm, 30.1 to 80.0μm in diameter.

After the start of a respiration run, 2 ml of sphere suspension was put through the serum cap into the respiration chamber using a syringe and hypodermic needle. No disturbance to the animal was observed. Initial sphere concentrations in the chamber ranged from 1000 to 3500 particles.ml^{-1}. For determination of pumping rates, 1.99 ml samples were taken after 5 and c. 15 minutes and filtered through a Millipore membrane filter (0.45μm pore size, 25 mm in diameter) and the retained spheres counted. To ensure a random distribution of spheres on the membrane, about 10 ml of water was first put into the filter unit. The resulting suspension filtered at a rate of 5 to 10 ml min^{-1}. This low filtering rate prevented large areas of surface film from developing which would have entrapped the smaller spheres and the movement of the spheres on the membrane when the last of the water was being removed.

Turbulence produced in the filter tube by the sample leaving the syringe was sufficient to produce complete mixing.

Forty random fields of view from each sample were counted at a magnification of 400x and the mean and standard error of the concentration for each size class calculated. A control experiment, made with an empty shell with the valves glued together in the chamber was used to estimate the rate at which spheres settled out of suspension in the absence of filtration (Table 1). The high concentrations obtained in the initial sample taken immediately after the stock suspension was added, may be due to the suspension in the chamber not being homogeneous as the remaining values indicate that the sphere concentration did not change with time. An analysis of variance between these means for each size class showed no significant difference ($p = 0.05$) so no correction for particle settling was applied to the data.

TABLE 1. Micronic sphere concentrations (particles.ml^{-1}) in the respirometer during a control experiment. Data are mean ± standard error; $n = 40$.

Time	Sphere size µm			
min.	0.1 - 15.0	15.1 - 30.0	30.1 - 70.0	0.1 - 70.0
0	1226 ± 162	3700 ± 278	540 ± 102	5466 ± 337
5	235 ± 74	632 ± 78	54 ± 31	921 ± 112
10	361 ± 84	830 ± 121	72 ± 45	1261 ± 154
15	469 ± 96	740 ± 124	72 ± 36	1281 ± 161
20	180 ± 53	921 ± 129	72 ± 37	1173 ± 144
25	343 ± 69	595 ± 105	18 ± 18	956 ± 127

The filtration rate, as measured by the indirect method of Coughlan (1969) enables the clearance rate of suspensions to be determined. If all the particles are retained, then the observed filtering rate is also the water pumping rate. The retention efficiency for each sphere size class, which is calculated by the ratio of the maximum filtering rate found in each animal size group to their filtering rate for each sphere size class, is expressed as a percentage, in which it is assumed that:

(i) the pumping rate of the animals is constant

(ii) the test suspension is at all times homogeneous

(iii) that particle retention by the animal is 100% efficient or that a known constant percentage is retained.

The filtration rate was calculated by using the equation:

$$m = \frac{M}{n} \left(\frac{\ln C_o - \ln C_t}{t}\right)$$

where m is the filtration rate of each animal

M is the volume of suspension

n is the number of animals

C_o is the mean initial particle concentration

C_t is the mean particle concentration after time T.

Formulae used to determine particle concentrations are given in Appendix 1.

The Determination of Gill Area

A group of 22 animals ranging in length from 33.4 mm to 70.2 mm was used to determine the relationship between animal length and gill area. The length of each animal was measured and the valve and mantle removed to expose the left gill. After washing, the animal was placed under a thin sheet of glass and the area of the outer lamella of both demibranchs was obtained using a polar compensating planimeter. Total gill area was taken to be four times the sum of the two areas. The flesh dry weight of each animal was determined by the known relationship between length and body weight (Fig. 23, Appendix 1).

Assimilation Efficiencies

The assimilation efficiency of an animal may be determined either by finding the weight of food ingested and that egested, or by using an isotopic label in the food. Both these methods require quantitative collection of faeces, which can be difficult. An alternative is to examine the ratios of some absorbed component to some non-absorbed one in the food and in the faeces, of which only a qualitative sample need be collected. These latter methods involve determining the increase in concentration of an inert, non-absorbed substance after passage through the gut, which may be part of the food, e.g. ash (Conover 1966) or may be added by the experimenter, e.g. chronium trioxide (Corbet *et al.* 1960).

Calow and Fletcher (1972) developed such an indicator technqiue using two radioisotopes. Food was labelled with ^{14}C, which is absorbed across the gut, and with ^{51}Cr, which is not absorbed to any great extent. Assimilation efficiencies can then be calculated from the ratios of the two isotopes in the food and in the faeces. The assimilation efficiency is calculated by the equation

$$A = \left\{ 1 \quad \frac{\text{isotope ratio in the food}}{\text{isotope ratio in the faeces}} \right\} \times 100\%$$

The calculation is dependant on the following assumptions:

(i) The ^{14}C and ^{51}Cr are uniformly distributed throughout the food.

(ii) That ^{14}C and ^{51}Cr move along the gut at similar rates.

(iii) That ^{51}Cr is not absorbed by the animal to any significant extent.

(iv) The non-absorbed indicator is all present in the faeces, i.e. is not readily leached out.

These assumptions were tested experimentally by Calow and Fletcher and when the conditions were not met, corrections were applied. In establishing this technique they used two species of gastropods; one a microherbivore, and the other a bacterial feeder. The technique was tested using different foods and as well the findings were compared with results obtained from the more usual techniques which involve ^{14}C only. They found that the assimilation efficiencies estimated from the ratio of ^{14}C : ^{51}Cr in food and faeces are directly comparable with assimilation efficiencies estimated from the difference between ^{14}C lost from the food discs and ^{14}C appearing in the faeces irrespective of the food used.

Calow and Fletcher suggested that other isotopes could be used for the non-absorbed indicator and Nash (1974) in determining the assimilation efficiencies of *Paratya curvirostrus* (Heller) and *Potamopyrgus antipodarum* (Gray), used ^{144}Ce for the following reasons:

(i) It has a longer half-life (285 d.) than ^{51}Cr (28 d.) and is suitable for use over a longer time period.

(ii) As ^{144}Ce is a β-emitter the samples could be counted for both isotopes simultaneously, eliminating the need for counting the samples twice.

An aspect of the technique not considered by Nash was that decay of ^{144}Ce results in a daughter product ^{144}Pr which has a half-life (H_d) of 17 minutes, the predominant emission being β- particles at 2.98 Mev. ^{144}Ce has a half-life of 285 days (H_p) and is a β-emitter with a predominant emission energy of 0.32 Mev (Wilson 1966). When the parent is longer lived than the daughter, H_p being 10 to 100 times greater than H_d, transient equilibrium is established, and if H_p is more than

100 times greater than H_d, as for ^{144}Ce and ^{144}Pr, then secular equilibrium is established. This effectively widens the energy spectrum of the non-absorbed indicator enabling an easier separation between it and the absorbed isotope.

The chemical properties of cerium and praesodynium, when both are in the 3+ oxidation state are very similar (Moeller 1973). Thus the uptake rates of these two isotopes from solution by algae, and also transport across the gut, is expected to be the same. However, if separation of the isotopes had occurred, the time for which the samples were stored between collecting and counting was sufficient for the equilibrium to be re-established. Calculations showed that equilibrium would be established within two hours for the extreme cases of either only cerium or praesodynium being absorbed, the criterion being when the change in number of radionuclii over a one hour period was less than one per cent.

In this study, the method of Calow and Fletcher, using ^{144}Ce as the non-absorbed indicator instead of ^{51}Cr, was used, allowing mussels to feed for a known time on labelled algae, after which samples of faeces were collected for liquid scintillation counting.

(a) Food Preparation

Attempts to culture two species of algae from the Waikato River in Modified Chu 10 medium were of limited success. *Melosira granulata*, the predominant species, did not grow, and although *Ankistrodesmus fusiformis* grew, it did not become labelled with ^{14}C when isotopes were added to the culture. Thus *Chlorella vulgaris* was used as food for *Hyridella*. This alga was grown in a mineral salt solution spiked with 0.5% glucose as the carbon source (Appendix 4) and the cultures agitated by continuous shaking and maintained at 20°C by a water bath. Standard culture techniques were used throughout (Stein 1973).

For labelling with isotopes, ^{14}C glucose and ^{144}Ce as cerous chloride were added so that the final isotope concentration in the culture was about 0.2 μCi. ml^{-1} for ^{14}C and 0.08 μCi. ml^{-1} for ^{144}Ce. The isotopes were added to cultures which were dense green in colour, containing approximately 50 x 10^6 cells. ml^{-1}. Maximum isotope uptake by *Chlorella* occurred after about 20 hours and the cells remained adequately labelled for at least ten days (Appendix 4).

For feeding experiments, a 5 to 10 ml sample of a labelled culture was centrifuged to separate out the cells, and the supernatant discarded. The pellet of cells was washed by resuspending in nutrient medium, centrifuging (1760g for 10 min.) and discarding the supernatant, a process which was repeated twice. Resuspension of the pellet in nutrient medium gave the prepared food.

(b) Feeding Procedures

A preliminary experiment using yeast cells was carried out to determine the gut clearance time. Two animals were put into a small chamber of about 400 ml capacity. Yeast culture was added to the chamber until a faint cloudiness was observed while the water was being stirred (about 10^3 cells. ml^{-1}) and the animals left to feed under observation. From one of the animals pseudofaeces were collected outside the inhalent siphon after 110 minutes and when examined microscopically were found to contain yeast cells. After 205 minutes faeces were observed leaving the exhalent siphon as short strands of material. These also contained yeast cells. Faeces were also observed leaving the exhalent siphon 320 minutes from the beginning of the experiment.

No pseudofaeces or faeces were observed from the second animal. After 300 minutes it was removed from the chamber and dissected. Samples taken from the palp, oesophagus, stomach, style sac and rectum all had yeast cells present.

For feeding rate determinations, up to four animals of similar size which showed active filtering behaviour were taken from the acclimatization aquarium and placed in a 5 ℓ. feeding chamber. The animals were observed for five minutes and any not resuming active filtering were returned to the aquarium. Labelled algal suspension was added to the feeding chamber and the animals allowed to feed for two and a half to three hours during which the water was aerated to keep the algae in suspension. 10.0 ml samples were taken after 30 and 90 minutes to determine the filtration rate. The animals were then placed in a second chamber with no added food for half an hour to ensure that all pseudofaeces were expelled. They were next individually placed in small chambers (0.4 ℓ. of water) so that faeces could be collected. Care was taken to ensure all faeces produced were collected so ingestion ratios could be calculated.

Experiments were carried out with a group of animals of various sizes at each of the following algal cell concentrations: 0.5×10^4, 1.0×10^4, 2.5×10^4, 5.0×10^4 and 1×10^5 cells. ml^{-1}. The algal content of the Waikato River varies from about 500 to 50,000 cells. ml^{-1} (Coffee *et al.* 1975) and the food concentrations used were a compromise between field conditions and the requirements for adequate radioactivity in the faeces.

(c) Leaching of Isotopes from Food and Faeces

Labelled compounds and ^{144}Ce are soluble in water so the amount of leaching from algae and faeces was determined. A pellet of washed labelled algae (c. 4mg) and faeces collected from an animal fed on radioactive food were put into scintillation vials and covered with 20.0 ml of aerated filtered river water. After centrifugation for 10 minutes at 3130g, 2.0 ml samples of each supernatant were taken 0.25 hours after

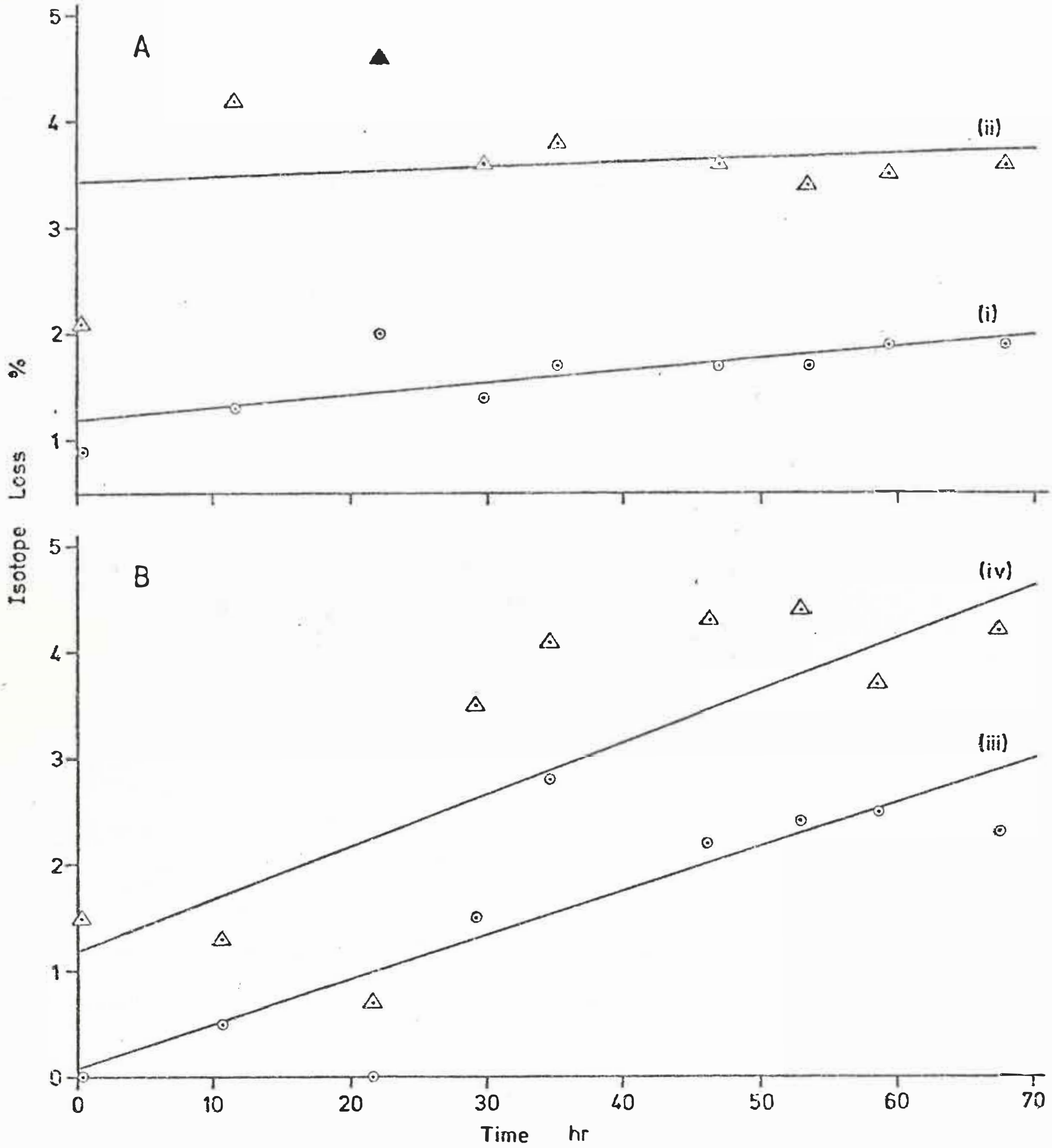


Fig. 5. Leaching of isotopes from *Chlorella* (A) and faeces of *Hyridella* (B). Each point is the mean of two determinations. ^{14}C (⊙), ^{144}Ce (⊡). The equations for the regression lines are:

(i) $\%^{14}C = 1.19 + 0.012t$ (p *) (II)

(ii) $\%^{144}Ce = 3.44 + 0.0046t$ (p N.S.) (III)

(iii) $\%^{14}C = 0.094 + 0.042t$ (p **) (IV)

(iv) $\%^{144}Ce = 1.18 + 0.053t$ (p **) (V) adding the water, and at various time intervals for the following 70 hours, put into pairs of vials and prepared for counting. The determinations were done in duplicate.

Leaching was found to be minimal (Fig. 5), but appropriate corrections were applied. The isotope ratio of the food was taken to be that calculated at half the feeding time. It was assumed that faecal production occurred at a constant rate and for corrections, the time of contact with water was considered to be half the time the animal was in the defaecating chamber, or in the case of the experiment described below, half the time between sample collections.

(d) Retention of ^{144}Cerium in the Gut

In order to determine the amount of ^{144}Ce retained in the gut, three replicate experiments were carried out with animals fed for 2½ to 3 hours on labelled algae. Faeces were collected at approximately 12 hourly intervals for 85 hours, and their activity measured. The wet and dry flesh weights and the activity remaining in the animal were also determined.

About 13% ^{144}Ce was retained (Fig. 6) so experimental results were corrected for this.

(e) Sample Preparation for Liquid Scintillation Counting

A wet oxidation method using perchloric acid and hydrogen peroxide described by Mahin and Lofberg (1970) was used in the preparation of samples.

(i) Faeces. Faeces were collected with a tube connected to a syringe fitted with a Swinney attachement. The membrane filter and adhering faeces were placed in a scintillation vial and digested by wet oxidation for 30 to 90 minutes. The contents were swirled two or three times during the digestion. Complete digestion of the membrane filter

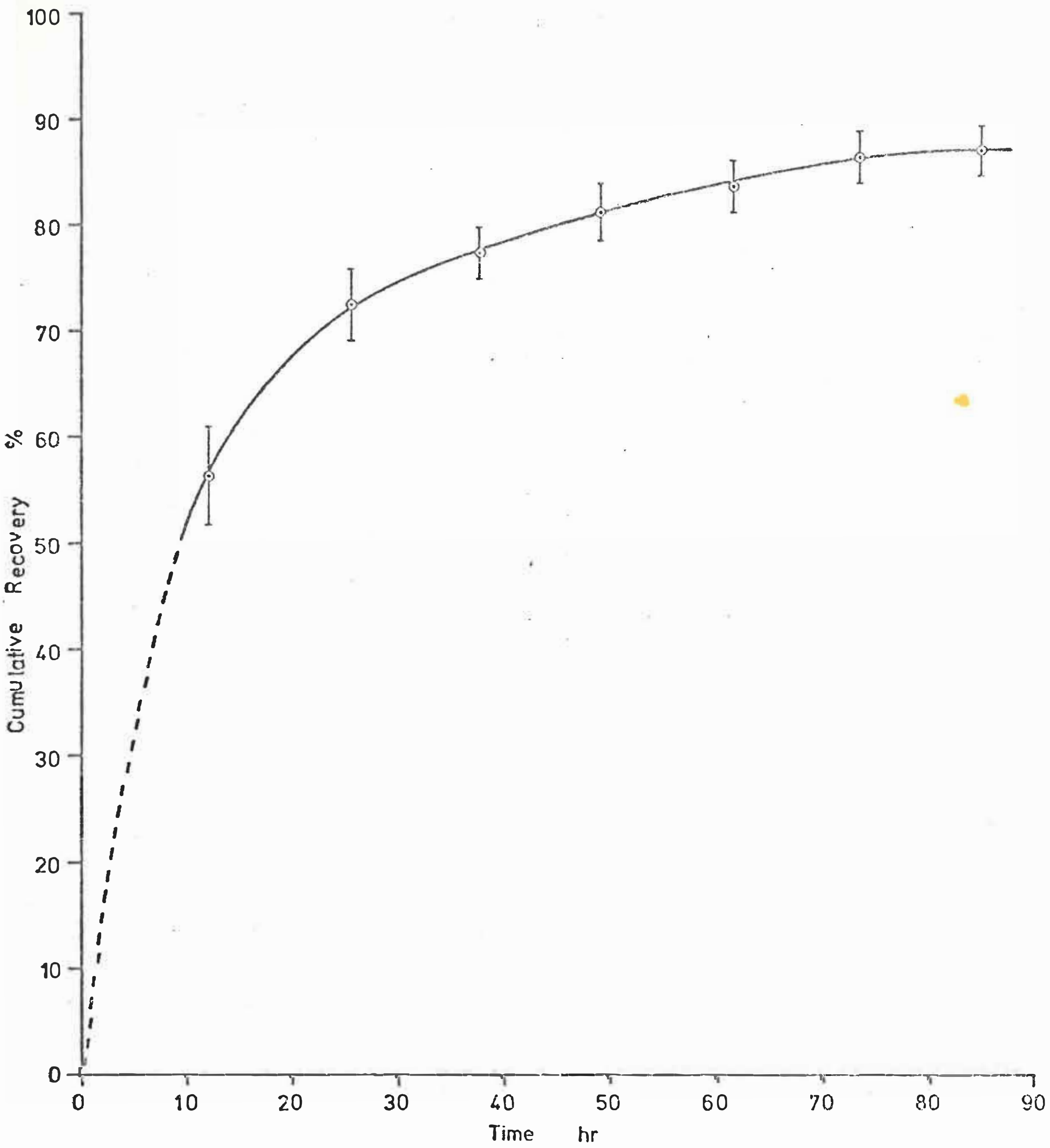


Fig. 6. Percentage cumulative recovery of ^{144}Ce in the faeces of *Hyridella*. Vertical bars show the standard errors of the means. Curve fitted by eye.

was not essential as it was soluble in the scintillator solution.

(ii) Food. Samples of prepared algal suspension (0.20 ml) were digested for 30 to 45 minutes.

Samples (10.0 ml) taken from the feeding chamber were filtered by a Swinney attachment and the membrane filter with collected algae treated in the same way as faecal samples.

(iii) Animal tissue. After drying at 70 - 80°C, tissue was placed in a weighed vial and ground to fine particles with a glass rod. Perchloric acid (60% ww) was added to the macerated flesh in the proportion of 3 ml acid per gram dry flesh, the vial capped and placed in an oven at 70 - 80°C for 60 minutes. The contents were swirled two or three times during digestion. The vial and contents were then weighed, and a 0.2 ml aliquot was removed and put into a scintillation vial with 0.40 ml hydrogen peroxide (30% ww). Bleaching, at 70 - 80°C with the vial capped, was complete in 20 minutes.

(iv) Aqueous samples. The sample was put in a scintillation vial and if more than 0.5 ml, placed on a planchet dryer to reduce the volume to 0.5 ml or less.

Sample preparation was completed by adding 16.0 ml of scintillator solution (1 ℓ toluene, 0.6 ℓ cellosolve (2-ethoxyethanol) and 6 g P.P.O.) and shaking to ensure complete mixing.

Filtration Rates

Filtration rates were determined indirectly from measurements of the radioactivity of the water in the feeding chamber at known intervals during the course of each assimilation experiment. The average number cells.ml^{-1} in the prepared food suspension was determined by haematocytometer counts (Dacie and Lewis 1968), as well as the activity. ml^{-1} (by counting a 0.20 ml sample) so that the activity per algal cell could be estimated.

The formulae used in determining the amount of activity removed from suspension are given in Appendix 1.

Ingestion Ratios

The ingestion ratio is the proportion of the food removed from suspension which is ingested, and can be obtained from a simple budget of activity for the indicator isotope.

Knowing the filtration rate and the radioactivity per cell, the amount of activity removed from suspension is calculated. The amount of activity ingested by the animal is equal to the sum of faecal and remaining body activity.

Organic Content of Food and Mussel Flesh

The organic content of samples was determined by quantitative dichromate oxidation (Maciolek 1962). A known volume of standard dichromate (2N) solution was added to the sample, acidifed with sulphuric acid and put into a water bath (100°C) for three hours for oxidation to occur. The remaining dichromate was titrated against standardized ferrous sulphate solution and the organic content, in energy units, calculated from the amount of oxygen consumed.

Cells were removed from 60.0 ml (c. 5.9×10^6 cells. ml^{-1}) of *Ankistrodesmus* culture by centrifugation and washed with distilled water. The resulting pellet was dried to constant weight at 70 to 80°C and a piece about 1 mg in weight used as the sample.

For *Chlorella*, the procedure was simplified. The energy content of 2.00 ml of culture was determined and the energy content of an equivalent amount of medium from which the cells had been removed by centrifugation subtracted.

The dried flesh of three mussels was ground to a powder with mortar and pestle and dried to constant weight at 70 to 80°C. A sample of about 40 mg was used for analysis.

Each determination was done in triplicate and the average energy contents found were (mean ± standard error):

Ankistrodesmus, $48.3 \pm 0.33 \times 10^{-6}$ cal. cell^{-1};
Chlorella, $3.24 \pm 0.08 \times 10^{-6}$ cal. cell^{-1}; and
Hyridella flesh, 1.83 ± 0.02 kcal. g^{-1}.

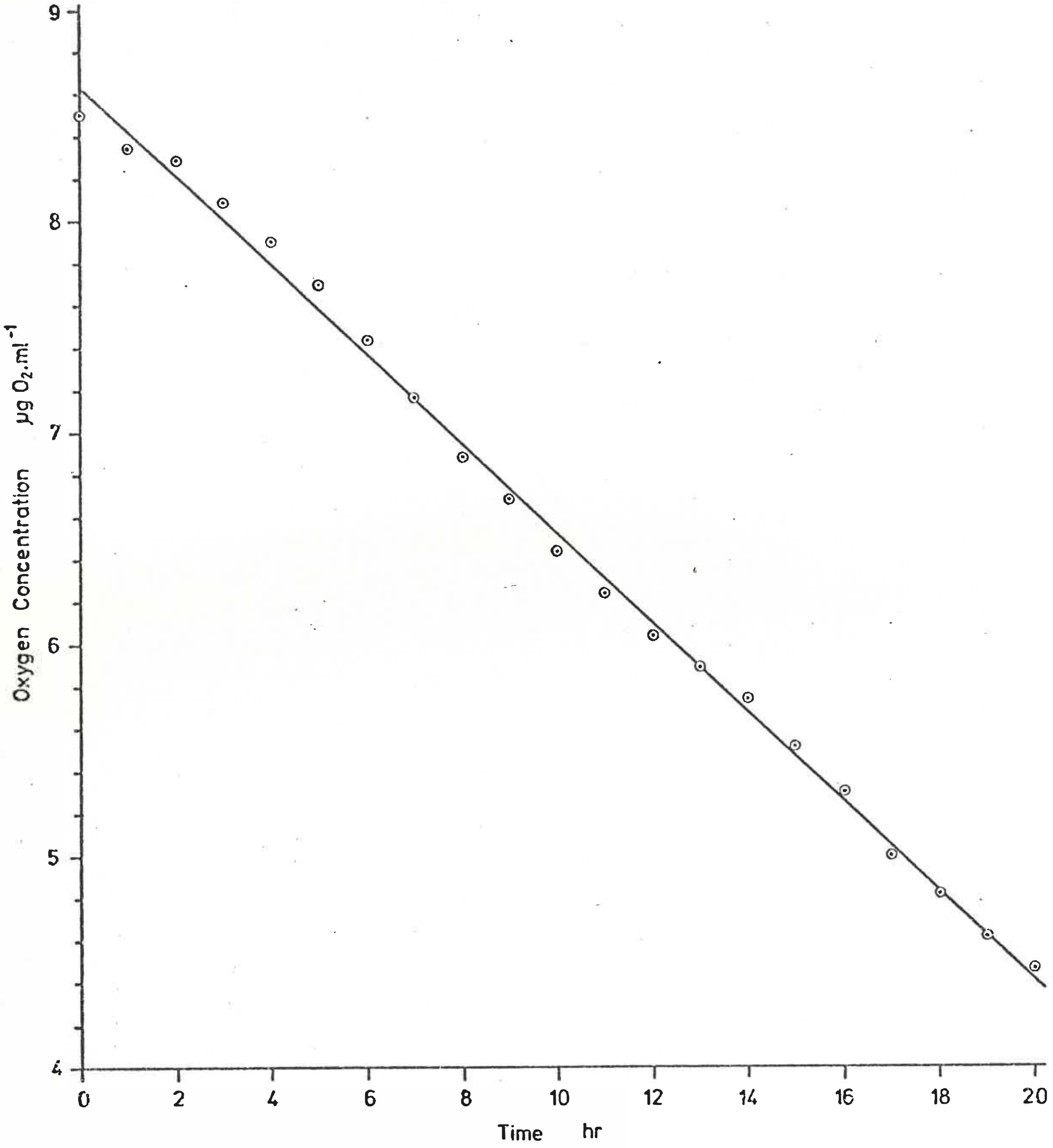


Fig. 7. Change in oxygen tension in a respiration chamber containing 14 mussels over a period of 20 hours. The equation of the regression line is:

$$\emptyset = 8.63 - 0.21t \quad (p\ ***) \qquad (VI)$$

RESULTS AND DISCUSSION

Respiration Rates and Ambient Oxygen Concentration

When the oxygen concentration in a chamber containing 14 mussels was monitered over a 20 hour period, it was found to decrease linearly (Fig. 7) which indicates that at least above 4.4 $\mu g O2.ml^{-1}$, the respiration rate of *Hyridella* is independent of the ambient oxygen concentration. This finding is in agreement with that of McLusky (1973) who showed that the respiration rate of the scallop *Chlamys opercularis* was independent of oxygen tension down to 20% saturation (at $15^{o}C$). However Bayne (1971) in comparing the respiration rates of three species of lamellibranch molluscs found only partial independence, the critical oxygen tension being related to the specific oxygen uptake, a lower critical tension being observed for species with a low respiration rate. In all my further experiments respiration rates were determined when the oxygen tension was between 8.5 and 7.5 $\mu g O_2.ml^{-1}$.

Respiration Rates and Animal Size

The respiration rate was dependent on animal size, increasing with increasing body dry weight (Fig. 8), the relationship being:

$$R = 417.4 \ W^{0.410} \qquad (p \ ***) \qquad (VII)$$

where R is the respiration rate in $\mu g \ O_2.hr^{-1}$
W is flesh dry weight in g.

Thus for an animal of 1g flesh dry weight, the respiration rate would be 417 $\mu g O_2.hr^{-1}$. This value is called the weight independent metabolism and can be used for comparisons with other species.

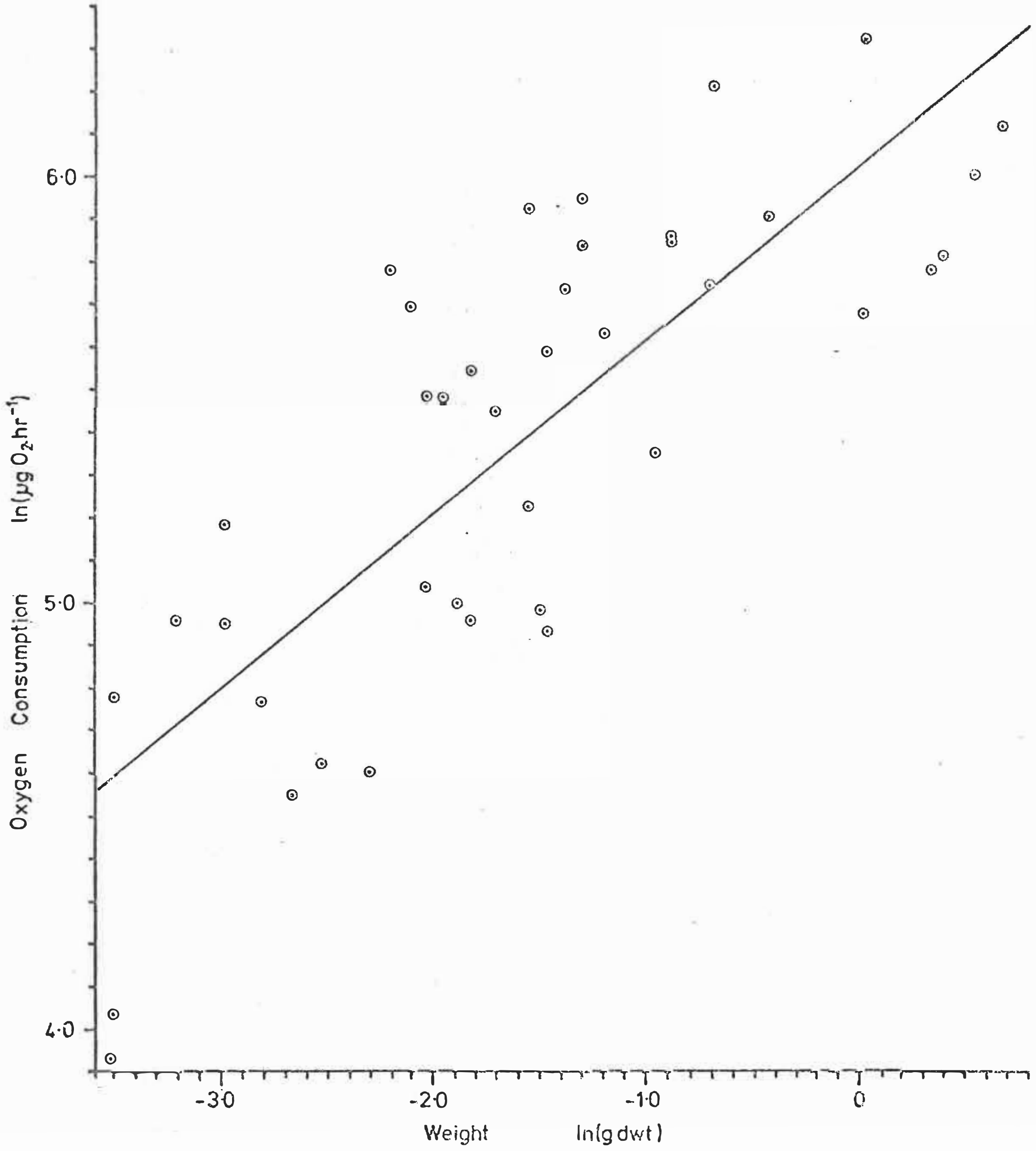


Fig. 8. The relationship between oxygen consumption and size for *Hyridella menziesi*.

TABLE 2. Weight independent respiration for bivalve molluscs at 20°C. Where the respiration was given at temperatures other than 20°C, a Q_{10} of 2.0 was assumed so corrected values could be calculated. These values are marked *

Bivalve	Respiration $\mu g.O_2.hr^{-1}$	Reference
Cardium edule	1056 *	Vahl (1972b)
Artrea islandica	996 *	Bayne (1971)
Donax vittatas	883	Ansell (1973)
Parreysia corrugata	457 *	Lomte & Nagabhushanam (1971)
Hyridella menziesi	417	Present study
Laevicardium crassum	330 *	Bayne (1971)
Chlamys opercularis	327	McLusky (1973)

Table 2 contains the weight independent metabolism obtained by other workers for a range of bivalve molluscs and shows that the respiration of *Hyridella* is comparable.

Ansell (1973) found that b (the weight exponent) varied from 0.097 to 1.654, and since a covariance analysis showed no significant difference in the exponents he used a common weight exponent of 0.865 for his calculations. The weight exponent of cockle (*Cardium edule*) respiration was 0.77 (Vahl 1972) and 0.601 and 0.627 for *Arctica islandica* and *Laevicardium crassum* respectively (Bayne 1971). Hemmingsen (1960) in reviewing the metabolic rates of both protozoan and metazoan organisms, ranging in size from 10^{-12} to 10^{6}g body weight obtained regression lines for the three groups of organisms, unicellular, poikilotherms, and

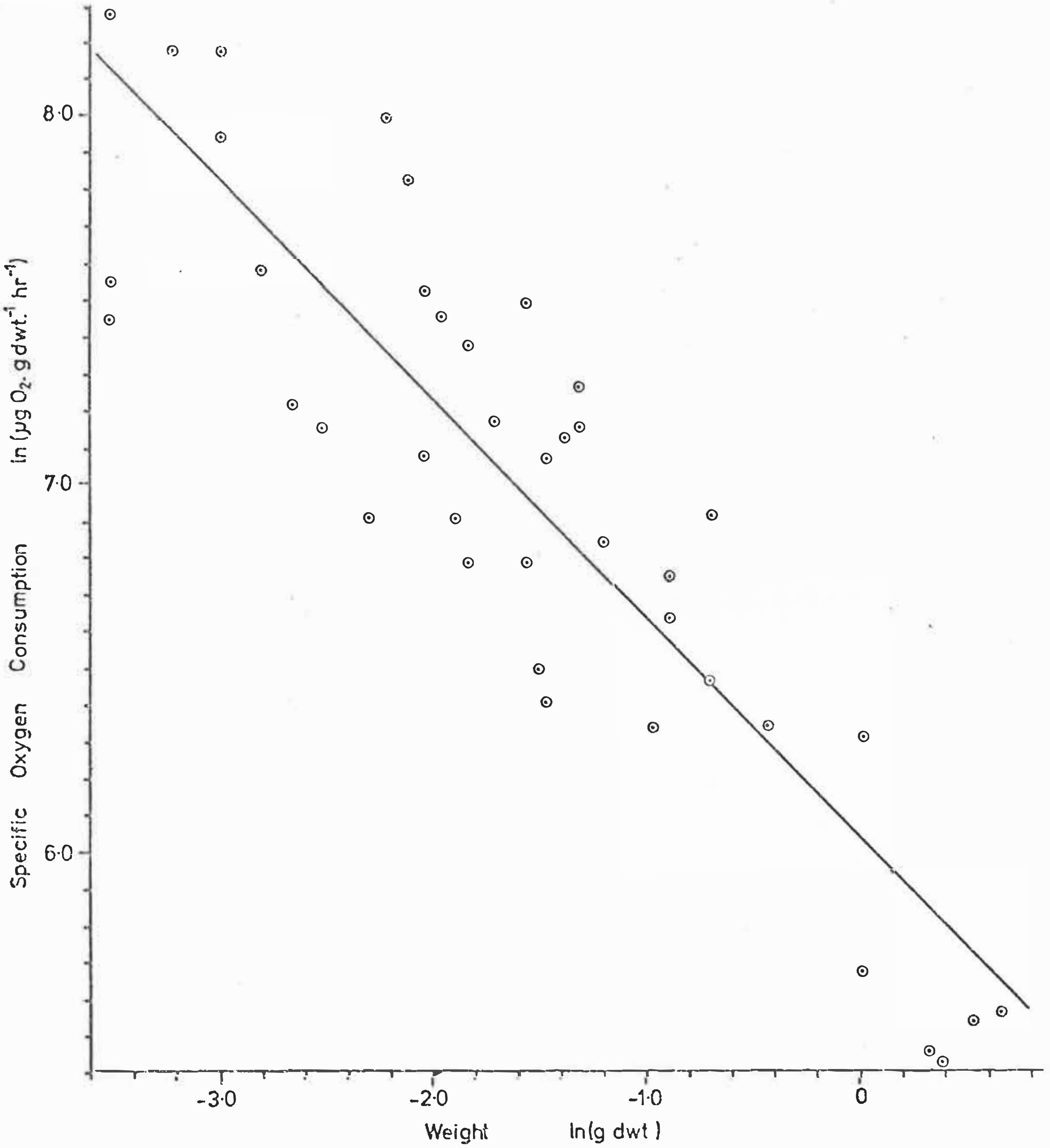


Fig. 9. The relationship between specific respiration rate and body weight for *Hyridella menziesi*.

homeotherms, of slope 0.751. However the weight exponent obtained experimentally for *Hyridella* was 0.410, and although different from that obtained for general poikilotherm respiration, was well within the range of values obtained by Ansell (1973). Kennedy and Mihursky (1972) also found widely varying values of b. Those obtained were: 0.600 to 0.489 for *Mya arenaria*; 0.235 to 0.666 for *Macoma balthica*; and 0.029 to 0.854 for *Mulinia lateralis*.

The specific respiration rate of *Hyridella* decreased with increasing body weight (Fig. 9), the relationship being:

$$RR = 415.3\ W^{-0.592} \qquad (p\ ***) \qquad (VIII)$$

where RR is the specific respiration rate in $\mu g\ O_2.hr^{-1}.gdwt^{-1}$

W is the flesh dry weight in g.

This rapid decrease in the intensity of metabolism may indicate that larger animals have a greater proportion of tissue of low metabolic activity such as fat or gonad.

If two classes of tissue are considered to be present, one of high metabolic rate (HR), and the other of low rate (LR) making no appreciable contribution to the observed metabolism, then the proportion of each can be determined. Assuming that animals of 0.03 gdwt (the smallest used during the respiration experiments) consist entirely of metabolically active tissue and that the weight dependency of respiration is as Hemmingsen (1960) suggests, the relationship between respiration rate (Ra) and metabolically active tissue (only) is:

$$Ra = 1392\ W^{0.751}$$

This relationship, as well as the observed respiration rate of whole animals (equation VII) is shown in Fig. 10, and the difference in slopes gives a measure of the amount of inactive tissue. If P is the proportion of metabolically active tissue to total animal tissue, i.e.

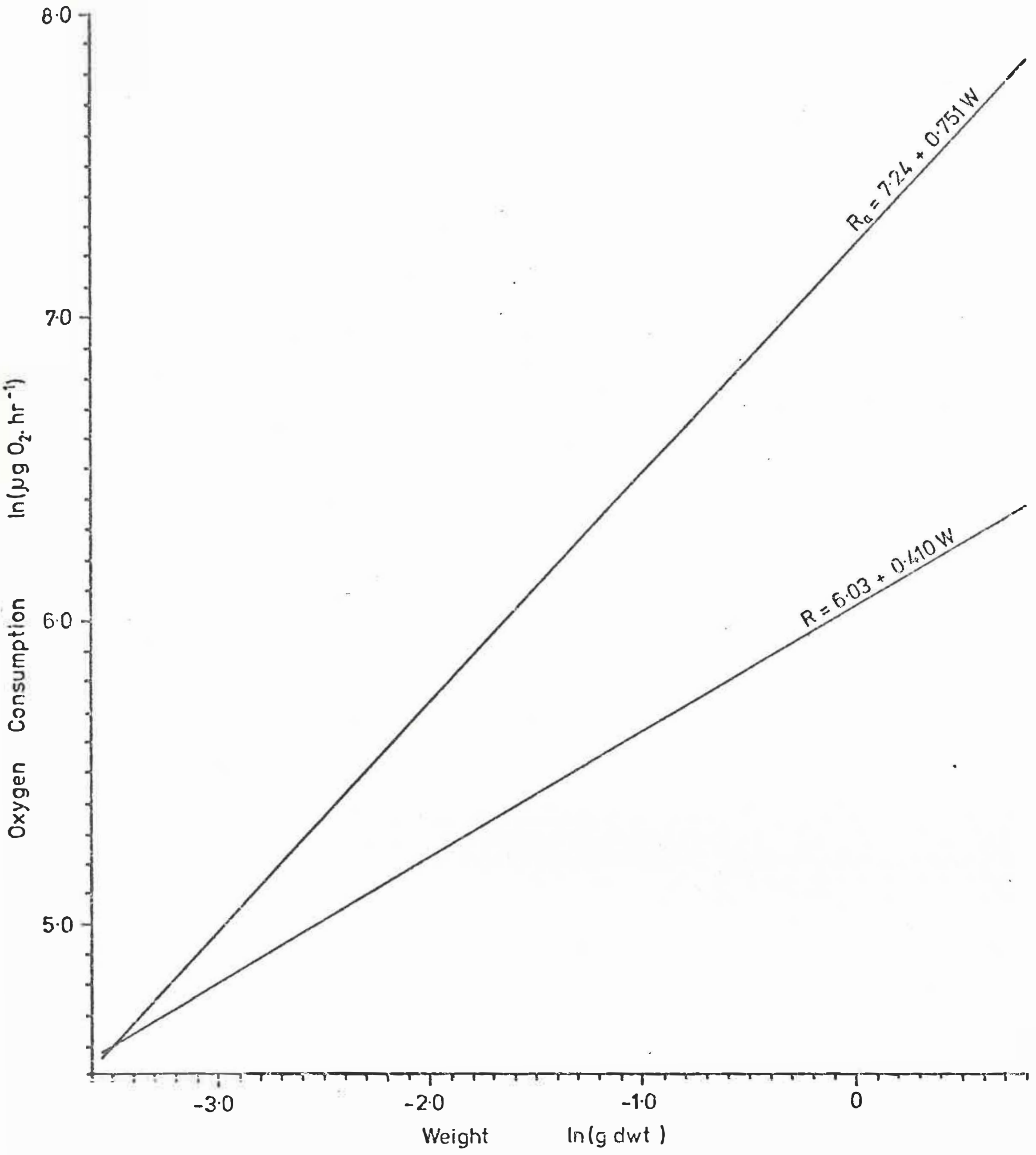


Fig. 10. Comparison of the observed respiration of *Hyridella menziesi* (R) and theoretical respiration (Ra) as proposed by Hemmingsen (1960) for poikilotherms.

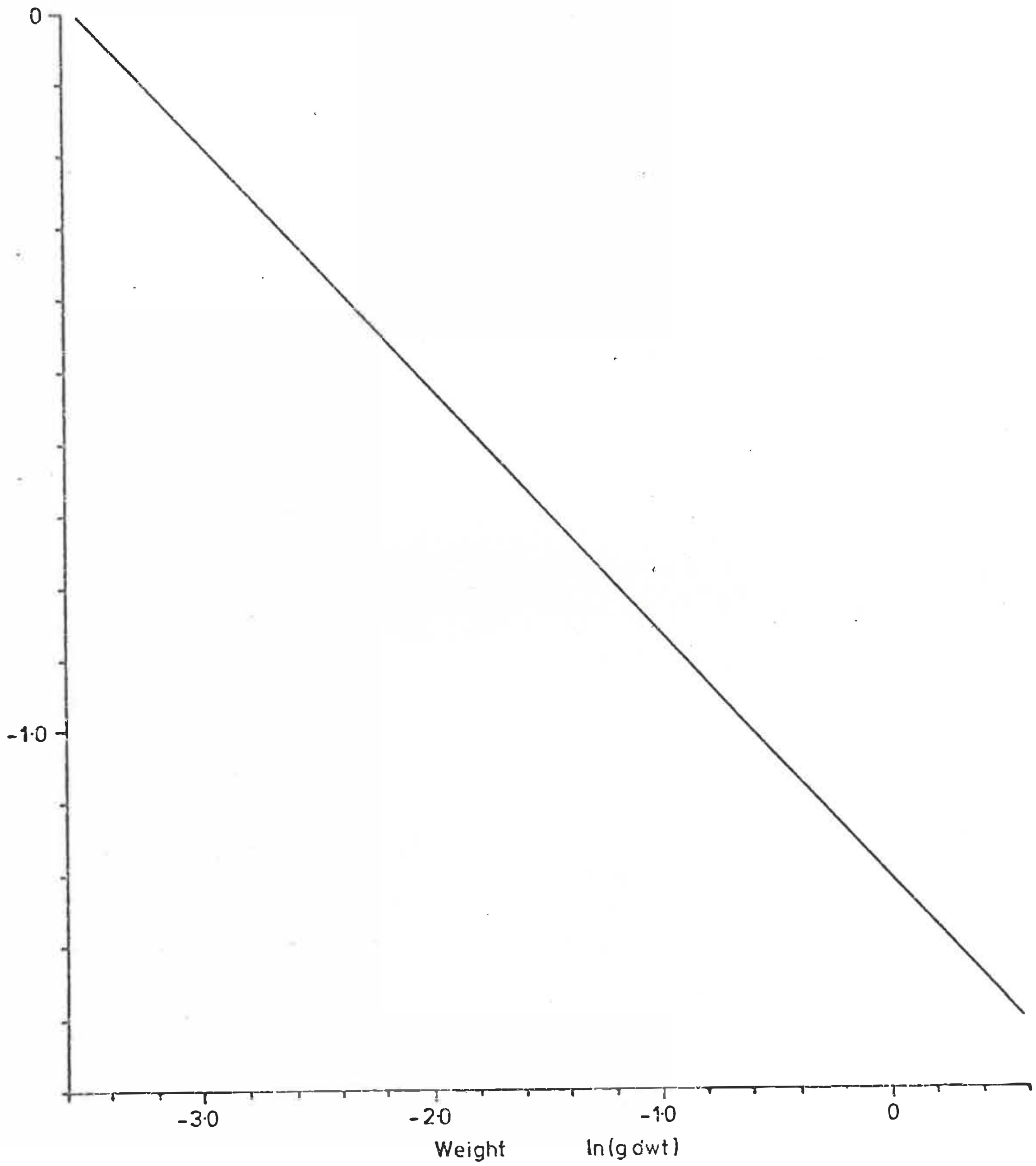


Fig. 11. The proportion of metabolically active tissue in *Hyridella menziesi* between 0.03 g and 1.8 g dry weight, calculated from Fig. 10 as described in the text.

$P = HR/(HR + LR)$, then the observed respiration will be $P \times Ra$; i.e.

$$P \times 1392\ W^{0.751} = 417.4\ W^{0.410}$$

and $$P \quad 0.300\ W^{-0.341}$$

This derivation (Fig. 11) also assumes the ideal condition where metabolic activity is dependent on cell type and not cell age.

However, this relationship may have resulted from aging processes. Most, if not all, metazoans are subject to aging, caused by loss of viability at the cellular level. Although environmental conditions may influence an individuals life span, there appears to be a genetically determined set of factors which act independently, involving changes in the cellular chemical composition giving conditions of rate of synthesis, rate of utilization, rate of transport, rate of storage of depletion of stores, incompatible with continual survival (Strehler 1962). The decrease in specific respiration rate with increasing size (Fig. 9) may be evidence of the aging process rather than an increase of metabolically inactive tissue, or it may be the result of an interaction of the two.

Respiration Rates and Temperature

Specific respiration rates at temperatures between 6° and 30°C were determined using separate groups of mussels for the upper and lower temperature ranges; so as to check their comparability, experiments with both groups were carried out at 10 and 20°C. There were no significant differences between the mean rates of consumption of both groups so the results were pooled (Appendix 1, Tables 17 and 18).

The specific respiration rate increased with temperature in an exponential fashion (Fig. 12), the relationship being:

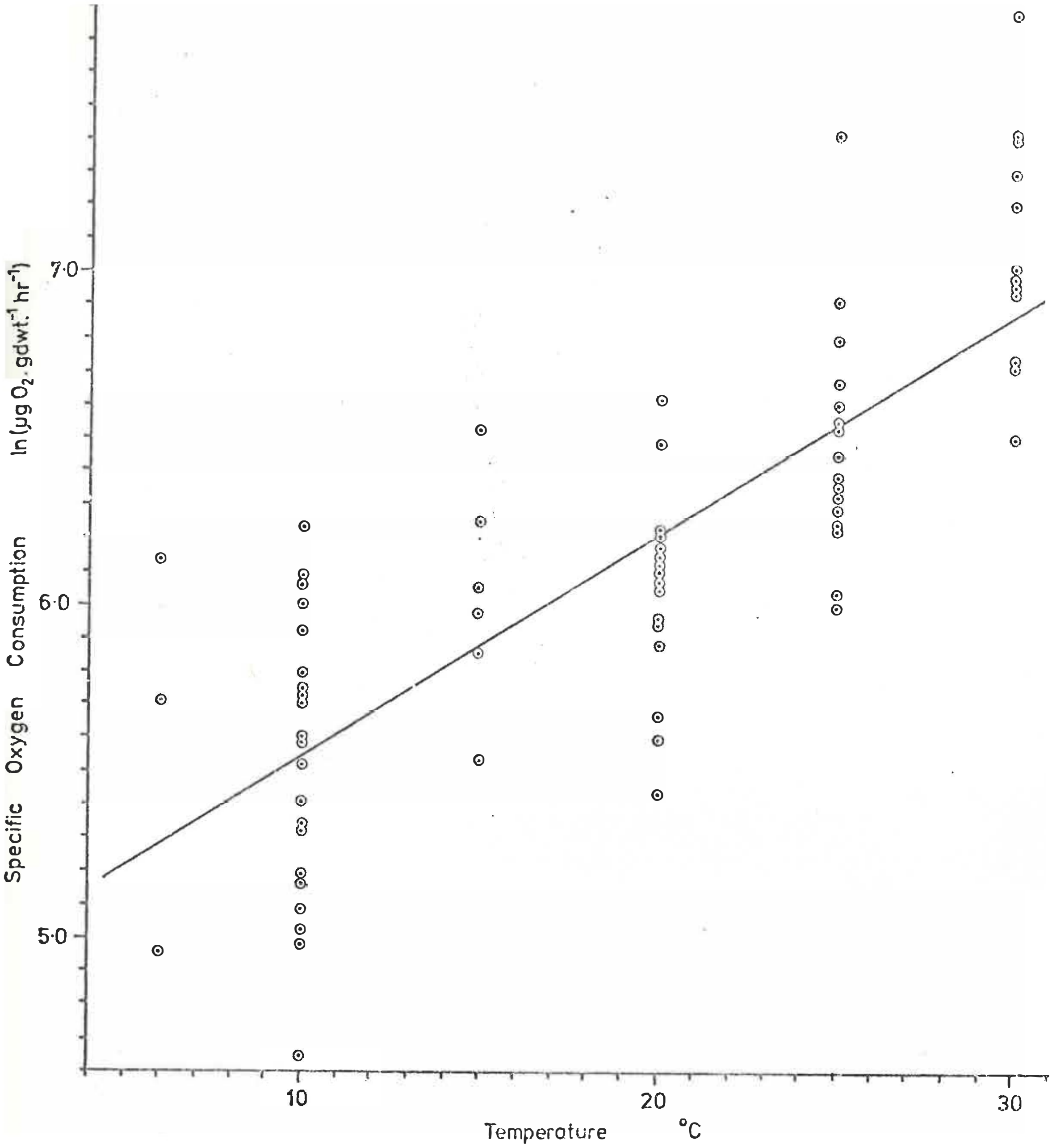


Fig. 12. Specific respiration rate of *Hyridella menziesi* at various temperatures.

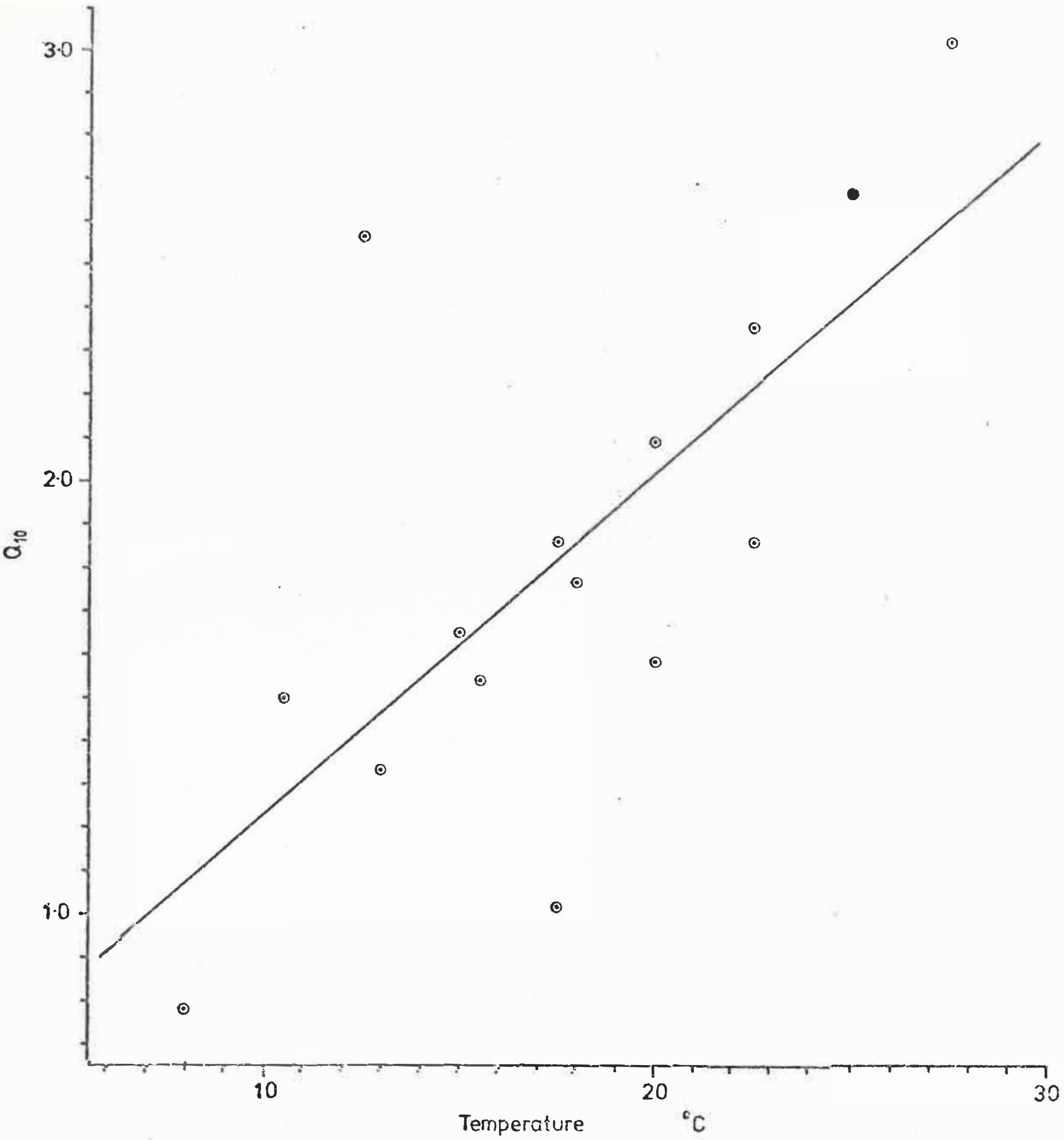


Fig. 13. The variation of Q_{10} with temperature.

TABLE 3. Specific respiration rate of *Hyridella* at various temperatures. Data are mean ± standard error, with n in parenthesis.

Temperature °C	Respiration $\mu g O_2.hr^{-1}.gdwt^{-1}$
6	302 ± 92 (3)
10	277 ± 22 (23)
15	437 ± 60 (6)
20	451 ± 27 (21)
25	685 ± 67 (18)
30	1198 ± 113 (15)

$$RR = 132.5\ e^{0.0662T} \qquad (p\ ***) \qquad (IX)$$

where RR is the specific respiration rate $\mu g\ O_2.hr^{-1}.gdwt^{-1}$

and T is the temperature in °C.

This equation implies a Q_{10} of 1.94 ($Q_{10} = e^{0.0662 \times 10}$). However, if the Q_{10}'s between each of the experimental temperatures are calculated from the respiration rates given in Table 3, Q_{10} is seen to vary with temperature, the relationship being:

$$Q_{10} = 0.439 + 0.079\ T \qquad (p\ **) \qquad (X)$$

where T is the mid-point of the temperature range involved in the Q_{10} measurement (Fig. 13). Since

$$Q_{10} = \frac{R_2}{R_1}^{\frac{10}{T_2 - T_1}}$$

$$R_2 = R_1\ (0.439 + 0.079\ T)^{(T_1 - T_2)/10}$$

where R_1 is the specific respiration rate at 21.5°C (T_1), as determined by equation IX, T_2 is the temperature at which the specific respiration rate is required and $T = (T_1 + T_2)/2$, both specific respiration rate and respiration rate can be calculated for any animal size and temperature within the experimental range.

The standard errors are lower for temperatures between 10° and 25°C than those at 6° and 30°C (Table 3). This greater variability of respiration at the extremes of the experimental temperature range may be an indication of physiological stress when the animals are placed in conditions beyond those normally experienced in their natural habitat (10° to 23°C).

In *Hyridella*, the dependence of respiration on temperature (Fig. 9) is typical of that found in freshwater organisms e.g. *Branchiostoma lanceolatum* (Courtney and Newell 1965) and sockeye salmon (Brett 1971). Most other bivalves studied show independence (Newell and Northcroft 1967, Newell and Pye 1971), but these are intertidal animals, where the temperatures experienced are liable to fluctuate widely. Daily temperature fluctuations in freshwater lakes and rivers are small, and mechanisms to reduce the temperature dependence of metabolsim, such as are found in marine bivalves, are not necessary.

Particle Retention and Pumping Rates

The retention efficiency of different sized particles in relation to animal weight and sphere size is given in Table 4. Small animals retained particles down to 5μm in diameter with almost 100% efficiency. The retention efficiency for small spheres (5.1 to 15.0μm in diameter) is variable, showing a general decrease with increasing animal size. The complete retention of small spheres by mussels of the 0.41 to 0.60 gdwt size range comes from the high filtration rate of these particles (Table 5). The standard error of the filtration rate is large however, and the true value may in fact be much lower. Large spheres are retained with high efficiency by all sized animals so the observed filtration rate for these particles is also the pumping rate.

TABLE 4. Retention efficiency (%) of three sphere size groups by various sized *Hyridella*.

Sphere Size	Weight class gdwt.			
Diameter μm	0.01 - 0.20	0.21 - 0.40	0.41 - 0.60	0.61 - 0.80
5.1 - 15.0	97	30	100	0
15.1 - 30.0	100	37	76	66
30.1 - 80.0	98	100	69	100

Particle retention by lamellibranchs is species specific. The scallop *Chlamys opercularis* generally does retain particles 1.55μm to 1.65μm or less in diameter, and retention efficiency increases progressively to a maximum over the size range 1.65μm to 7.2μm (Vahl 1972a). The value of 2μm is the minimum size for high retention by *Mytilus edulis* (Vahl 1972, cited in Vahl 1972a) and 5μm for *Crassostrea virginica* (Haven and Morales-Alano 1970, cited in Vahl 1972a). Morton (1971) used colloidal graphite particles 0.5μm to 1.5μm in size for his studies of filtration rates by *Dreissena polymorpha* and found them to be lower than

TABLE 5. Filtration rates ($\ell.hr^{-1}$) of Micronic spheres of different sizes by *Hyridella*. Data are mean ± standard error. n in parenthesis.

Sphere Size	Weight class gdwt.			
Diameter μm	0.01 - 0.20	0.21 - 0.40	0.41 - 0.60	0.61 - 0.80
5.1 - 15.0	1.76 ± 0.97 (8)	0.54 ± 0.06 (2)	4.80 ± 2.46 (3)	0.00 (1)
15.1 - 30.0	1.80 ± 0.44 (8)	0.65 ± 0.21 (2)	3.66 ± 1.36 (3)	1.38 (1)
30.1 - 80.0	1.77 ± 0.39 (8)	1.78 ± 1.07 (2)	3.29 ± 0.20 (3)	2.03 (1)

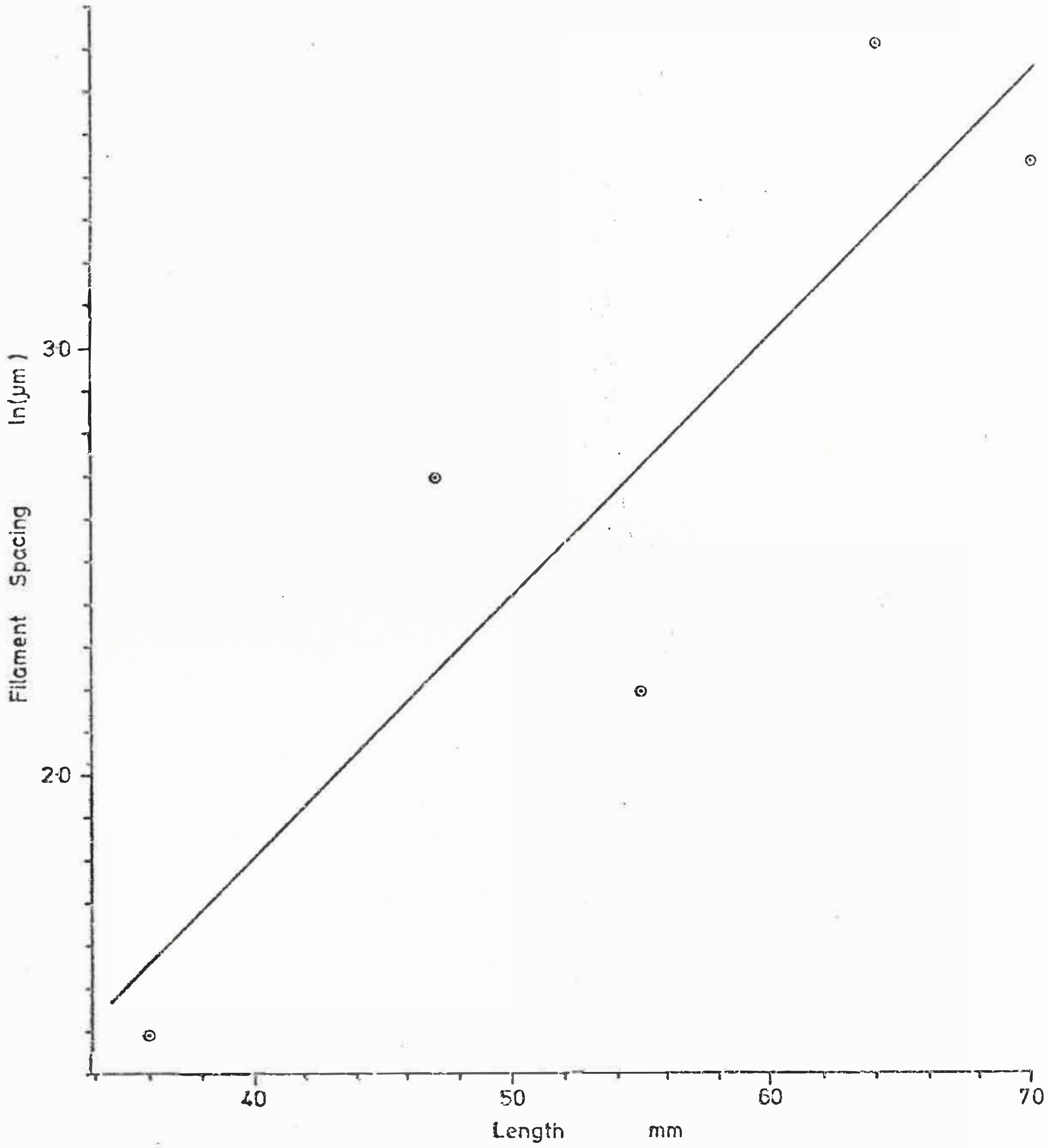


Fig. 14. The relationship between interfilamental distance and animal size.

in other bivalves. He did not attempt to estimate the retention efficiency although it has been shown that *Dreissena* filters bacterial cells 0.4µm to 1.0µm in diameter (Mikhev and Sarakin 1966, cited in Morton 1971).

The mechanism of particle retention has been described for *Mytilus edulis* (Dral 1967). It is not a simple straining of a suspension by the regularly spaced fronto-lateral cilia but dynamic filtering involving interactions between the water moving past the filaments and the relative motion of the cilia. *Mytilus* can decrease its retention efficiency by shifting the range of beat of the fronto-lateral cilia, so that they no longer completely bridge the gap between the gill filaments, allowing particles to pass through. Also adjacent cilia beat in opposite phase presenting mesh sizes of 2 - 3µm and 5 - 6µm. At low pumping rates, the effective mesh size is 2 - 3µm while at high pumping rates it is 5 - 6µm, so retention of particles up to 6µm is highly variable.

Filament width, interfilament distances and ciliation of the gill filaments are probably indentical in animals of different sizes (Dral 1967, Vahl 1973). It is not the dimensions of the gill units which change, but the number of units, and with larger animals, it is the number of gill filaments and their length which is increased.

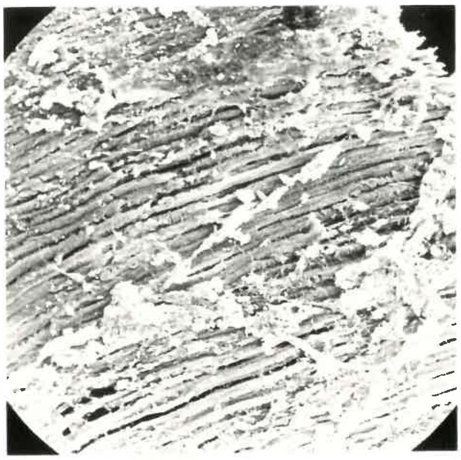
Some principal dimensions obtained from scanning electron micrographs of gills from a size range of *Hyridella* show considerable differences with animal size (Table 6 and Plate 1). Spacing of the fronto-lateral cilia, being independant of mussel size, is 2µm, which with an alternating ciliary beat, presents mesh sizes of 2µm and 4µm. Retention efficiencies of particles 5µm and larger are expected to be high, which was obserced in small mussels. Regression analysis gave the significant relationship (Fig. 14)

$$D = 0.513\ e^{0.062L} \qquad (p\ *) \qquad \text{(XI)}$$

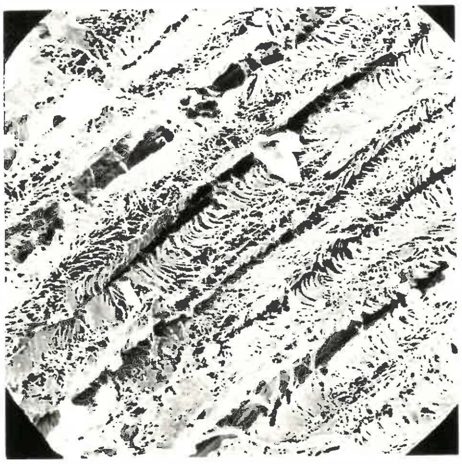
where D is the distance between filaments in µm

L is mussel length in mm

Plate 1. Scanning electron photomicrographs of gills from *Hyridella menziesi* of length 36 mm (a - c) and 64 mm (d - f). Scale in µm.



a



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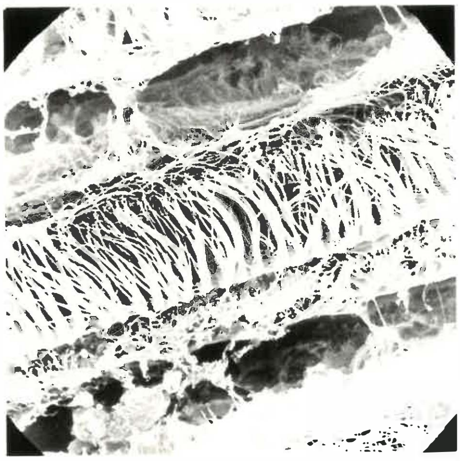

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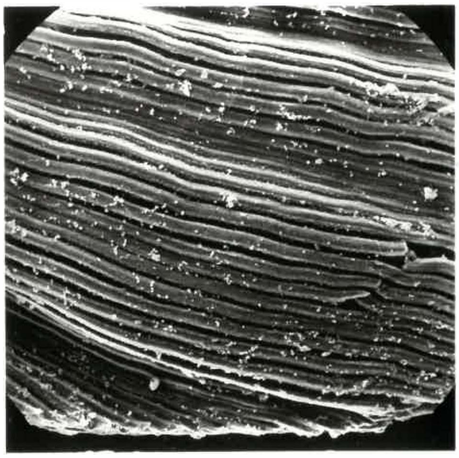
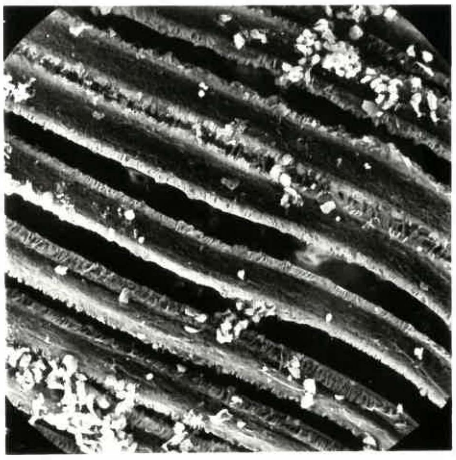


d



e

f

TABLE 6. Gill dimensions of various sized *Hyridella* determined from electron micrographs (e.g. Plate 2).

Animal Length mm	Fronto-lateral Cilia Spacing μm	Fronto-lateral Cilia Length μm	Gill Filament Width μm	Inter-filament Distance μm	Filament Spacing μm
36	2.3	16	22	26	4
47	2.0	17	30	45	15
55	1.9	15	16	25	9
64	2.6	12	30	71	41
70	1.4	15	33	64	31
$\bar{X}$ ± S.E.	2.0 ± 0.2	15 ± 1	26 ± 3	-	-

and explains the decreasing retention efficiency of small spheres by the larger animals, in which the fronto-lateral cilia would no longer bridge the gap between filaments allowing small particles to pass through. If the cilia are regarded as passive strainers and using the above equation with the weight-length regression (Appendix 1), it can be calculated that the cilia of animals 0.66 gdwt just meet. However, with active filtering the distance between filaments would need to be less for effective retention of particles, so the retention efficiency of small spheres by mussels of 0.66 gdwt upwards is expected to be low.

The reduction in the size range of particles retained by the older animals means that a smaller proportion of the energy available as suspended particulate organic matter is removed, thus reducing scope for growth and reproduction. However energy utilization is also dependant on other factors such as pumping rate, ingestion ratio and assimilation efficiency, which need to be known before trends in energy

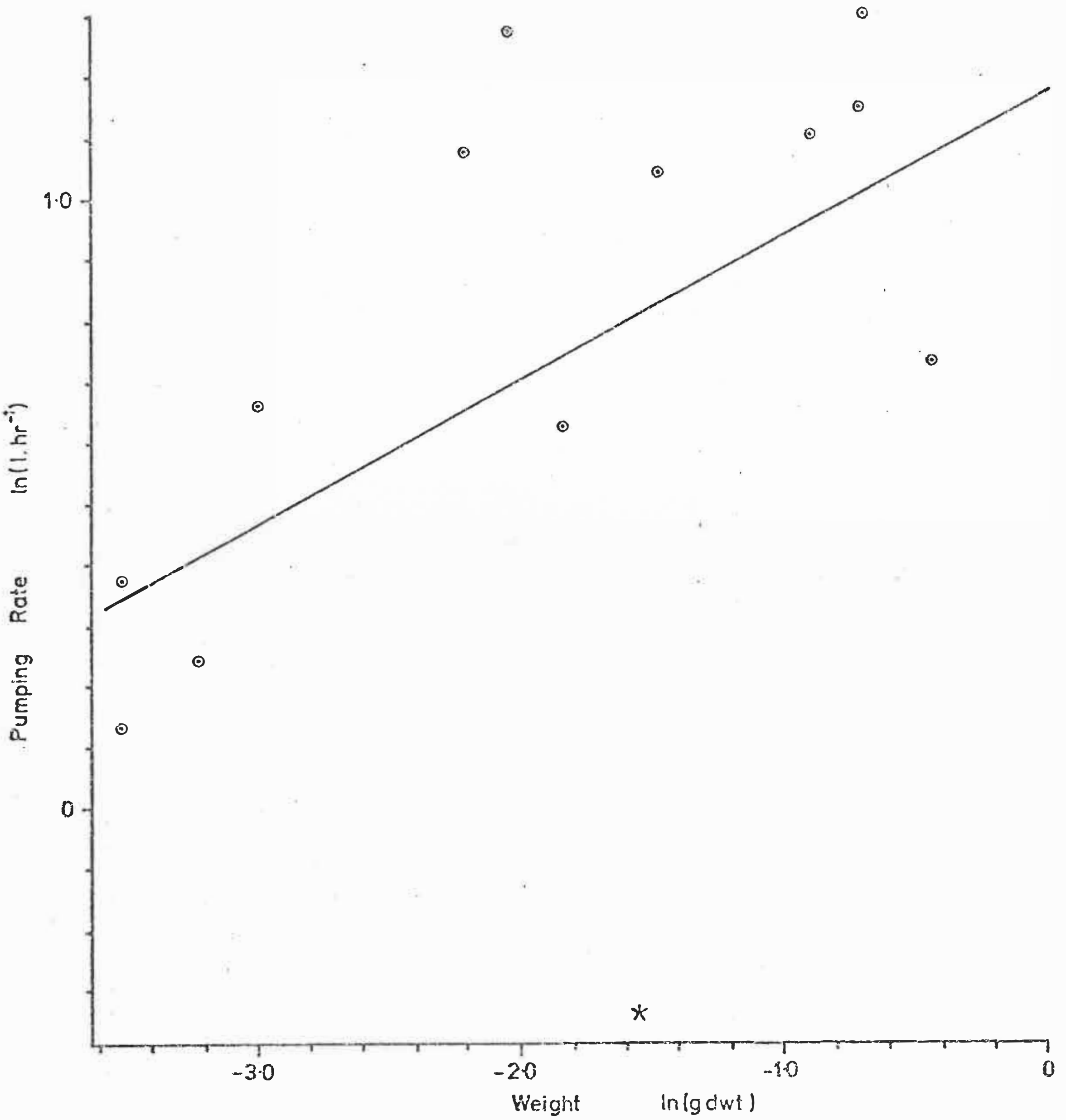


Fig. 15. The relationship between pumping rate (P ℓ.hr^{-1}) and animal size (g. dry weight) in *Hyridella menziesi*. The equation of the regression line is:

$$P = 3.796\ W^{0.269} \qquad (p\ **) \qquad (XII)$$

utilization can be fully elucidated.

The pumping rate increases with animal size (Fig. 15) and the relationship, along with those of other species is given in Table 7. For animals of a standard size (1 gdwt) all species have broadly similar pumping rates (the constant a). However, the weight exponent (b) for *Hyridella* is much lower and while showing a weak dependance of the pumping rate on weight, also indicates a possible limitation in growth by food in older animals.

Table 7. Pumping rates of some bivalve molluscs, expressed in the form $P = a W^b$. P is in $\ell.hr^{-1}$, W gdwt.

Species	a	b	Reference
Chlamys opercularis	-	0.82	McLusky 1973
Mytilus edulis	2.41	0.74	Winter 1973
	3.90	0.60	Vahl 1973
Cardium edule	2.00	0.58	Vahl 1972b
Hyridella menziesi	3.80	0.27	Present study

The mechanism of ciliary action is still being elucidated in bivalves. There is no innervation of the gill but Ghiretti (1966) cites Aiello as finding that the branchial nerve has a facultative role in *Mytilus edulis* by the possible release of 5-hydroxytryptamine or of a similar substance which activates the lateral cilia. Temperature, pH and osmotic pressure also have a profound effect on ciliary activity and consequently the flow of water. Furthermore the gill and mantle edge musculature and the adductor muscles can also control the water flow, and these in turn are influenced by mechanical and chemical factors. Thompson and Bayne (1972) found that the presence of particles, either of food or inert, induced filtration in *Mytilus* and that no filtration activity occurred below a particle concentration of 300 ml^{-1}. The pumping rate and oxygen consumption also increased when particles were present. They also found that the oxygen uptake was directly proportional to the pumping rate. Hoshi and Hoshiyama (1963) found a linear relationship between ciliary activity and respiration rate of isolated *Mytilus* gill and Usuki (1962) concluded from his study of isolated oyster gill that ciliary movement is closely linked with the oxidative metabolism of glycogen.

Hamwi and Haskin (1969) determined the pumping rate and oxygen uptake of the clam *Mercenaria mercenaria* and found a linear relationship between them. They concluded that water transport may at least be partly regulated by oxygen requirements. This may also be the case for *Hyridella* since a significant relationship was found between respiration and pumping rates where

$$R = 9.381 + 97.00\ P \qquad (p\ ^{*}) \qquad\qquad (XIII)$$

and R is the respiration rate in $\mu g O_2 . hr^{-1}$

and P is the pumping rate in $\ell . hr^{-1}$.

The metabolic state of *Mercenaria* was not defined, but that of *Hyridella* was the standard, or resting metabolism. Lamellibranchs are recognised as animals with low respiratory requirements (Ghiretti 1966) and with the large gill area and the animal in the standard metabolic state most of the oxygen requirements are probably for ciliary activity. Pumping is the result of ciliary activity and so it seems likely that oxygen uptake would result from, rather than regulate, water transport.

The ratio of water pumped to oxygen consumed is useful in determining the concentration of organic matter required to meet the energy requirements for maintenance. The relationship between the mean values for various size groups (Table 8) was:

$$B = 0.013 - 0.011\ W \qquad (p\ *) \qquad \text{(XIV)}$$

where B is litres of water pumped per $\mu g O_2$ consumed and W is body weight in gdwt. The decrease in ratio with increasing animal size indicates that food may become a factor in reducing scope for production. Utilization of the available oxygen during respiration experiments varied from 0.5 to 2.3%, which is less than that for all mollusca quoted by Ghiretti (1966), so oxygen is unlikely to be limiting except in conditions where oxygen tension is low. Similar values of the ratio have been obtain for other bivalves (Table 9). Vahl (1972b, 1973) has noted a decrease in the ratio with size, but described it as a power relation as he only compared the regression equations he obtained for the relationships between pumping and respiration rates with animal size, and not the ratio for each animal with animal size.

TABLE 8. Pumping ratios for various sized *Hyridella*. Individual data and mean for size groups 0.01 - 0.20, 0.21 - 0.40, 0.41 - 0.60 and 0.61 - 0.80 gdwt. given.

Flesh Dry Weight gdwt.		Pumping Ratio $\ell.\mu g\ O_2^{-1}$	
x	$\bar{x}$	y	$\bar{y}$
0.03		0.08	
0.03		0.023	
0.04		0.008	
0.05		0.012	
0.11	0.09	0.009	0.012
0.13		0.021	
0.15		0.000	
0.16		0.012	
0.21		0.004	
0.23	0.22	0.019	0.011
0.41		0.008	
0.49	0.47	0.010	0.008
0.50		0.070	
0.65	0.65	0.005	0.005

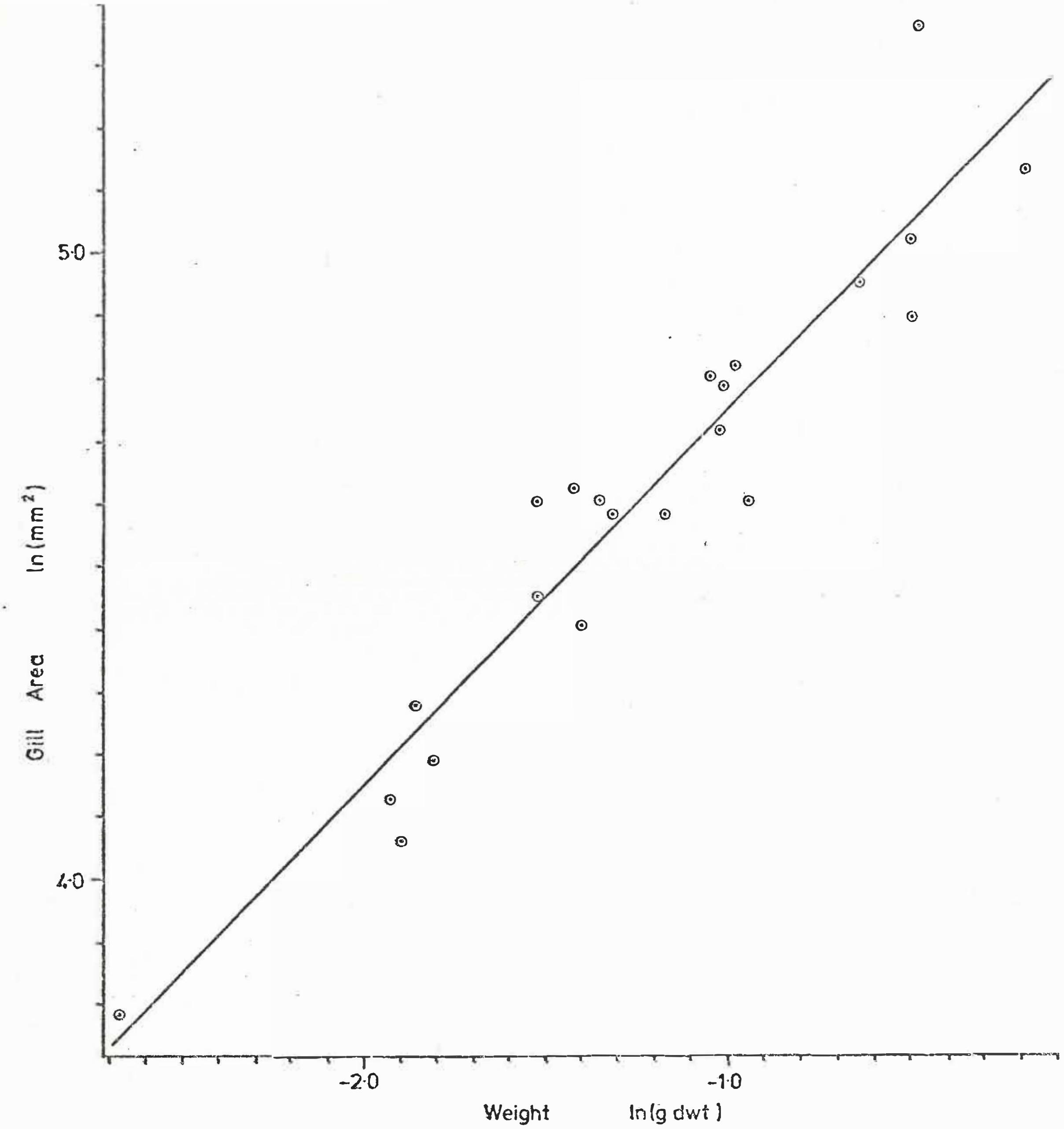


Fig. 16. The relationship between gill area and animal size in *Hyridella menziesi*.

TABLE 9. Pumping ratios of some bivalve molluscs. Data are the range of values observed for each species.

Species	Pumping ratio $\ell.\mu gO_2^{-1}$	Reference
Adult Oysters and Scallops, and Oyster Veligers	0.006 - 0.028	Jorgensen 1966
Chlamys opercularis	0.005 - 0.027	McLusky 1973
Chlamys opercularis	0.044 - 0.068	Vahl 1972a
Cardium edule	0.004 - 0.007	Vahl 1972b
Mytilus edulis	0.007 - 0.017	Vahl 1973
Hyridella menziesi	0.006 - 0.013	Present study

Gill Area

The gill area varied with the size of the animal (Fig. 16), the relationship being:

$$A = 211\ W^{0.601} \qquad (p\ ***) \qquad (XV)$$

where A is the total area in mm^2

and W is flesh dry weight in g.

It is the site of water pumping and respiratory exchange and it might be expected that these parameters would have similar dependencies on body weight. However, an analysis of covariance and multiple range testing between the slopes of the respective regressions (equations VII, XII (Fig. 15), and XV) showed a significant difference between the gill area and pumping rate with size regressions but not between either gill area and respiration or respiration and pumping rates, which may result from a reduction in ciliary activity with age. If there is a linear relationship between ciliary activity and respiration of excised gill tissue (as in *Mytilus edulis*; Hoshi and Hoshiyama 1963), the decreasing respiration rate of isolated gill with body size found by Lukacsovics (1967) in *Anodonta cygnea* can also be attributed to lower ciliary activity, and suggests that for both *Hyridella* and *Anodonta* pumping activity is the major component of the respiration rate.

Filtration Rates

The filtration rate of *Hyridella* showed much variation (Table 10) and as an analysis of variance showed no significant differences with animal size or food concentration a mean value for the filtration rate of 1.02 ± 0.13 $\ell.hr^{-1}$ ($\bar{X}$ ± S.E.) was calculated. This lack of relationship between size and filtering rate is particularly notable. It probably occurs because while large *Hyridella* have low retention efficiencies for small particles between 5 and 15µm dia., and thus might be expected to show lower filtering rates than small animals when fed on *Chlorella* (7µm dia.), this is compensated for by their higher pumping rates.

Walne (1972) has shown that in some bivalves filtering rates are affected by current. Water movement in my respirometer was maintained by a magnetic stirrer and would be faster than that in the feeding chamber. However, a *t* test between the above filtering rate and that for the small sphere size class showed no significant difference and for the purpose of this study the filtration rate was considered to be independent of current.

Ingestion Ratios

The mean ingestion ratios for each size class at each food concentration are given in Table 11. No clear trends were evident and

TABLE 10. Filtration rate in $\ell.\text{hr}^{-1}$ of *Hyridella* when feeding on various densities of *Chlorella*. Data are the mean for each weight class and standard error, with the number of animals in parentheses.

Flesh Dry Weight g	Food Concentration x 10^4 cells.ml^{-1}				
	0.5	1.0	2.5	5.0	10.0
0.01 - 0.20	-	-	1.50 (1)	0.57 ± 0.08 (2)	1.40 (1)
0.21 - 0.40	1.14 ± 0.94 (2)	0.60 ± 0.07 (7)	1.04 ± 0.29 (6)	0.63 ± 0.05 (4)	1.36 ± 0.05 (2)
0.41 - 0.60	0.20 (1)	0.67 ± 0.08 (5)	-	1.25 ± 0.37 (5)	1.58 ± 0.98 (4)
0.61 - 0.80	0.20 (1)	0.55 (1)	-	0.74 (1)	1.31 (1)
0.81 - 1.00	2.08 (1)	1.21 ± 0.93 (2)	-	-	-
>1	-	0.28 (1)	-	-	4.53 (1)
Mean	0.95 ± 0.46 (5)	0.67 ± 0.11 (16)	1.11 ± 0.25 (7)	0.89 ± 0.17 (12)	1.81 ± 0.53 (9)
Overall mean	1.02 ± 0.13 (49)				

TABLE 11. Ingestion ratios of *Hyridella* when feeding on various densities of *Chlorella*. Data presentation as for Table 10.

Flesh Dry Weight g	Food Concentration x 10^4 cells.ml^{-1}				
	0.5	1.0	2.5	5.0	10.0
0.01 - 0.20	-	-	0.06 (1)	0.27 ± 0.10 (2)	0.08 (1)
0.21 - 0.40	0.37 ± 0.24 (2)	0.24 ± 0.06 (7)	0.24 ± 0.12 (6)	0.63 ± 0.05 (4)	0.10 ± 0.07 (2)
0.41 - 0.60	0.18 (1)	0.32 ± 0.08 (5)	-	0.17 ± 0.06 (5)	0.22 ± 0.04 (4)
0.61 - 0.80	0.63 (1)	0.57 (1)	-	0.25 (1)	0.49 (1)
0.81 - 1.00	0.03 (1)	0.24 ± 0.15 (2)	-	-	-
>1	-	0.93 (1)	-	-	0.04 (1)
Mean	0.31 ± 0.13 (5)	0.33 ± 0.06 (16)	0.22 ± 0.14 (7)	0.18 ± 0.03 (12)	0.19 ± 0.05 (9)

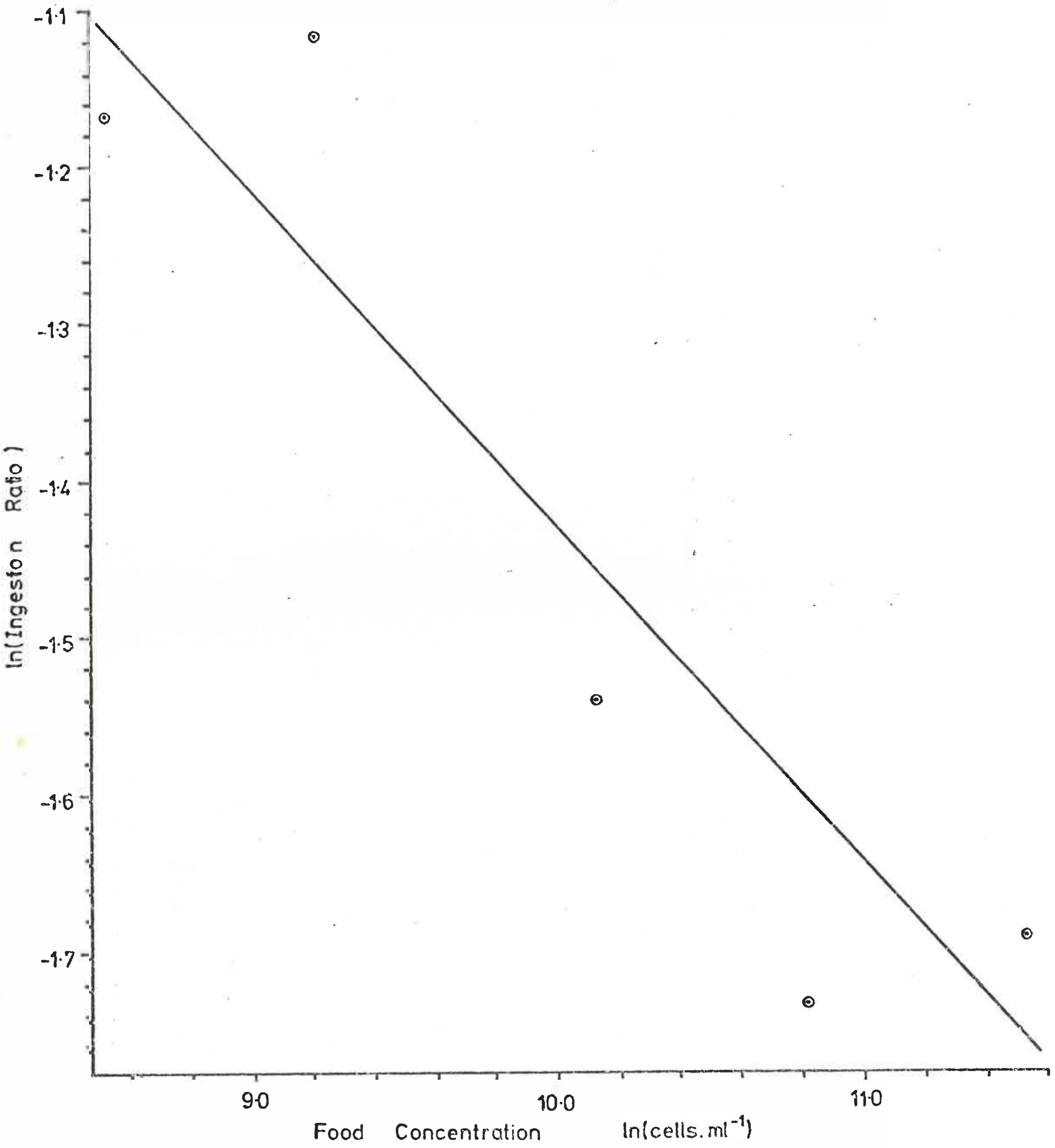


Fig. 17. The relationship between ingestion ratio and food concentration for *Hyridella menziesi* feed on *Chlorella*.

since an analysis of variance showed no significant differences, the mean ingestion ratio at each food concentration was calculated and included in the above table.

The mean ingestion ratio (IR) showed dependence on food concentration (Fig. 17), the relationship being:

$$IR = 2.197\ FC^{-0.223} \qquad (p\ *) \qquad (XVI)$$

This decrease of IR with increasing food concentration results from a rejection mechanism which enables food intake to be controlled.

TABLE 12. Food utilization by *Hyridella* at different food concentrations.

Food Concentration $x10^4$ cells.ml^{-1}	(a) Cells removed $x10^4.hr^{-1}$	(b) Cells ingested $x10^4.hr^{-1}$	(c) Food Used % ($^a/_b$ x 100)
0.5	510	160	31
1.0	1000	280	28
2.5	2600	590	23
5.0	5100	1000	20
10.0	10000	1700	17

The mechanism is probably associated with the production of pseudofaeces which are formed by cilial tracks on the mantle which receive excess food entrapped in mucus from the gills and/or the palps. It is dependent on the food density and the percentage of food ingested decreases with increasing food concentration (Table 12). This is in contrast to *Mytilus edulis* which, up to the food level of 4 x 10^4 cells.ml^{-1}, ingests all the cells removed (Winter 1973), and controls food intake by varying the filtration rate (Winter 1973, Shulte 1975).

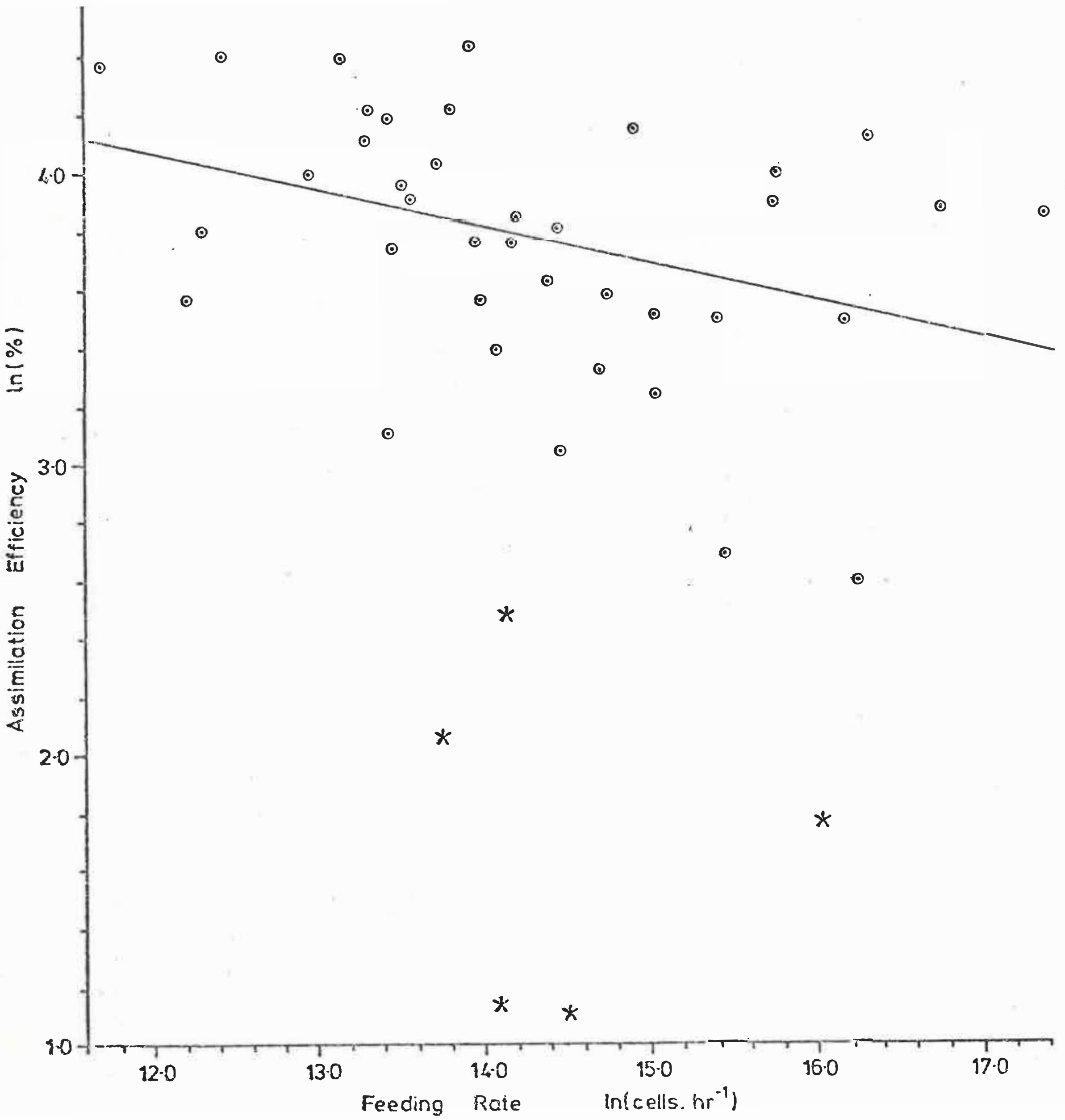


Fig. 18. The relationship between assimilation efficiency and feeding rate of *Hyridella menziesi* fed on *Chlorella*. Data shown as * not used in calculating the regression line.

Assimilation Efficiencies

There was no relationship between assimilation efficiency (being the proportion of the food ingested which is absorbed by digestive processes), and animal size (Table 13). The mean efficiency at each food level shows great variability, the only significant differences being between the extreme values.

However, assimilation efficiency and feeding rate are significantly related (Fig. 18), animal size having no effect at each level:

$$AE = 272.6\ FR^{-0.128} \qquad (p\ *) \qquad (XVII)$$

where AE is assimilation efficiency in %

and FR is feeding rate in cells ingested.hr^{-1}.

Thompson and Bayne (1974) found the assimilation efficiency of *Mytilus* to be independent of weight, but dependent on ration level for food concentrations between 0.05×10^4 cells.ml^{-1} and 2.5×10^4 cells.ml^{-1}. They observed no production of pseudofaeces, and with a constant filtration rate, the amount of food ingested was directly proportional to its concentration. *Dreissena polymorpha* has an overall assimilation efficiency of 40.5% (Stańczykowska *et al.* 1975) which was dependant on food quality, the large algal sizes being unfavourable and reducing it. Changes with food concentration have been observed in *Mytilus edulis* (Widdows and Bayne 1971), apparently due to increasing amounts of undigested and often live algae in the faeces as the consumption rate increases. Thompson and Bayne (1972) observed that the appearance of the faeces varied with the amount of food available. Below 1000 cells.ml^{-1}, the assimilation efficiency being 89%, the faeces appeared as a single brown ribbon, whereas at 25,000 cells.ml^{-1} the assimilation efficiency was zero and the ribbon bright green. At intermediate food levels the two components, one brown and apparently digested, the other green and packed with algal cells, were distinguishable. They concluded

TABLE 13. Assimilation efficiencies (%) of *Hyridella* when feeding on various densities of *Chlorella*. Data presentation as for Table 10.

Flesh Dry Weight g	Food concentration x 10^4 cells.ml^{-1}				
	0.5	1.0	2.5	5.0	10.0
0.01 - 0.20	43.0 (1)	20.9 (1)	81.2 (1)	41.4 ± 7.9	14.7 (1)
0.21 - 0.40	54.4 ± 1.8 (2)	35.7 ± 6.3 (8)	57.6 ± 12.0 (6)	35.0 ± 12.0 (4)	18.0 ± 15.0 (2)
0.41 - 0.60	23.5 ± 22.5 (2)	41.9 ± 4.5 (5)	-	58.3 ± 3.6 (2)	22.4 ± 13.1 (3)
0.61 - 0.80	66.0 (1)	35.9 (1)	-	25.5 (1)	43.7 (1)
0.81 - 1.00	35.4 (1)	33.7 ± 13.0 (3)	-	-	-
>1	-	20.9 (1)	-	-	33.0 (1)
Mean	42.9 ± 7.9 (7)	35.5 ± 4.4 (19)	61.0 ± 10.7 (7)	40.5 ± 6.6 (9)	24.8 ± 6.3 (8)

that proportions of the ingested material could pass through the gut without digestion. Such a mechanism of food bypass in the molluscan gut would explain the dependance of assimilation efficiency on the amount of food consumed shown by *Hyridella*.

An interesting difference is seen in food utilization between the two mussel species. *Hyridella* regulates intake by rejection of food after it has been collected, whereas a reduction in filtering ability at high food concentrations occurs in *Mytilus*. In both cases the assimilation efficiency is influenced by the rate of food ingestion. *Mytilus* makes more efficient use of the available food, but *Hyridella* makes a greater relative contribution of material to detritovores. *Hyridella* may thus play an important role in New Zealand lake ecosystems since apart from sedimentation and the activities of zooplankton, they are probably the only other means of linking algal production with that of the benthos.

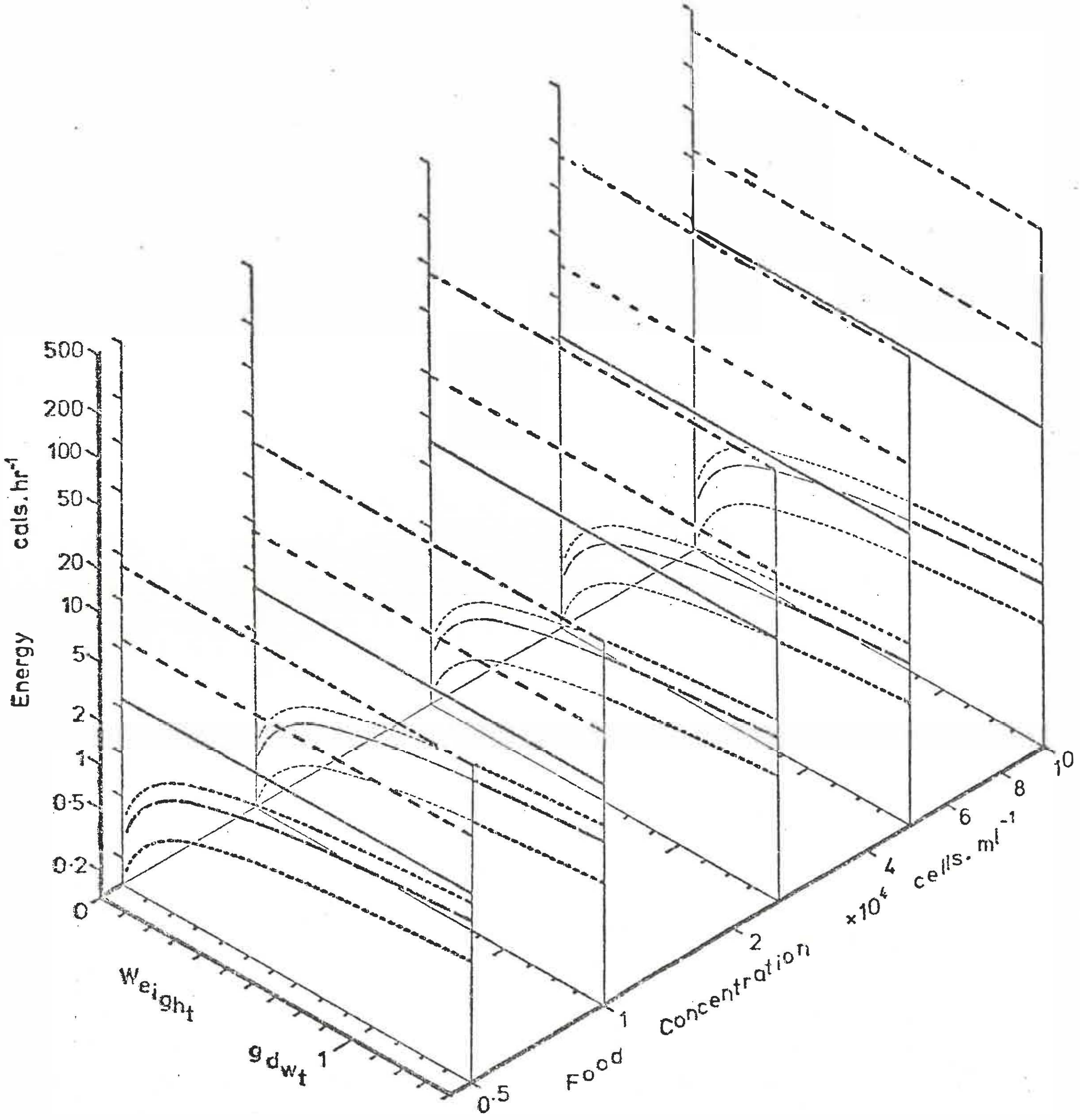


Fig. 19. Energy budgets in cals.hr^{-1} for *Hyridella menziesi* of different sizes at various food concentrations. Material removed -·-·- , material ingested – – – , material assimilated —— , respiration at ambient temperature (20°C) ——— , respiration at 25°C ----- (upper line) and 10°C ----- (lower line).

AN ENERGY BUDGET

Energy budgets of a trophic unit, whether an organism or population, which are the basis of all productivity studies, can be succinctly expressed in three equations (Petrusewicz and Grodziński 1970).

$MR = NU + C$

$C \quad P + R + FC$

$A \quad P + R$

where MR is the material removed
NU material not used
C material consumed
P production due to growth and reproduction
FC material in the excreta
A assimilated material
R respiration

Such budgets were calculated for *Hyridella* feeding on different concentration of *Chlorella*, which has an energy content of 3.24×10^{-6} cal.cell^{-1} (p 20) and taking the energy equivalent of oxygen to be 3.38×10^{3} cal.μgO_2^{-1} (Maciolek 1962).

The budget at each food concentration is shown in Fig. 19, the balance being position (i.e. $A > R$) for all animals. The dashed lines show the upper and lower respiration limits at the respective temperature extremes that would be experienced in the Waikato River. Again the balance is positive, but does come close to zero for the largest animals experiencing the lowest food concentration and maximum temperature.

As a result of constant filtration rate and weight dependent respiration small animals have the highest scope for growth (100(A-R)/body energy content), and thus the highest growth rate (Fig. 20). For

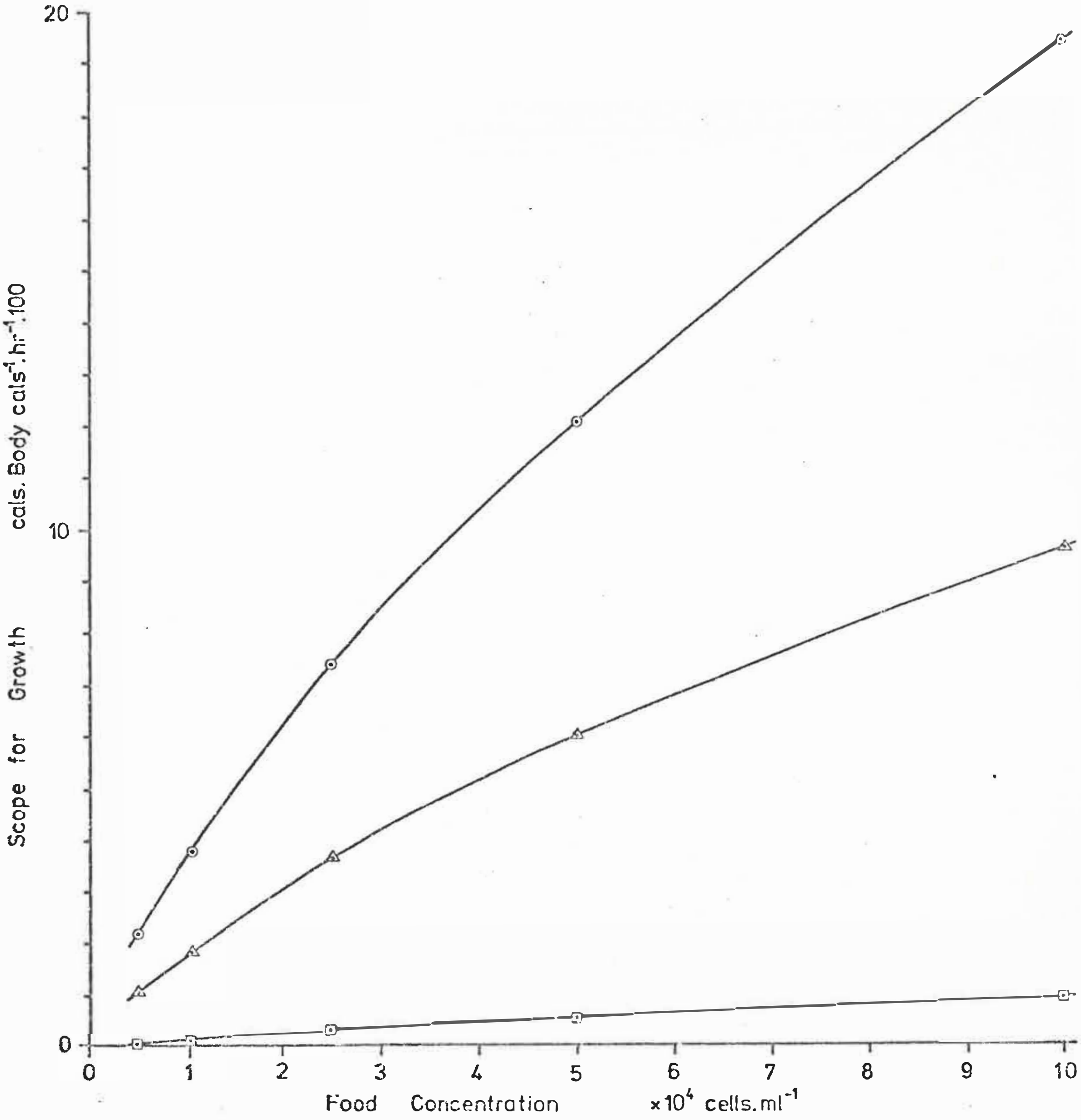


Fig. 20. Scope for growth of different sized *Hyridella menziesi* at 20°C and various food concentrations. 0.01 g dry weight(⊙), 0.1 g. dry weight(⊡)and 1.0 g. dry weight(△).

all animal sizes, scope for growth increases with food concentration. However the effects of temperature are small and masked by changes in food concentration and animal size (Table 14), except for large animals at low food concentrations in which the maintenance ration is being approached and small changes in assimilated energy cause large percentage changes in growth.

TABLE 14. Scope for growth of *Hyridella menziesi* in cals. Body cals^{-1}.hr^{-1}. 100 for two animal sizes at different *Chlorella* cell concentrations and temperatures.

Month (end 1975 and 1976)	Mid month river Temperature °C	Animal Size 0.05 gdwt. Food conc. x 10^4 cells.ml^{-1}		Animal Size 1.0 gdwt. Food conc. x 10^4 cells.ml^{-1}	
		0.5	10.0	0.5	10.0
November	15.8	2.30	19.61	0.08	0.94
December	18.0	2.26	19.57	0.07	0.94
January	20.0	2.21	19.51	0.06	0.93
February	19.5	2.22	19.53	0.06	0.93
March	19.0	2.23	19.54	0.07	0.93
April	16.8	2.28	19.59	0.07	0.94
May	13.2	2.34	19.64	0.08	0.95
June	10.4	2.36	19.67	0.09	0.95
July	10.5	2.36	19.67	0.09	0.95
August	11.4	2.35	19.66	0.09	0.95
September	12.2	2.35	19.65	0.09	0.95
November	15.6	2.31	19.62	0.08	0.94
Mean		2.30	19.61	0.08	0.94
Range		0.15	0.16	0.03	0.02
Range as % of Mean		6.5	0.8	38.7	2.1

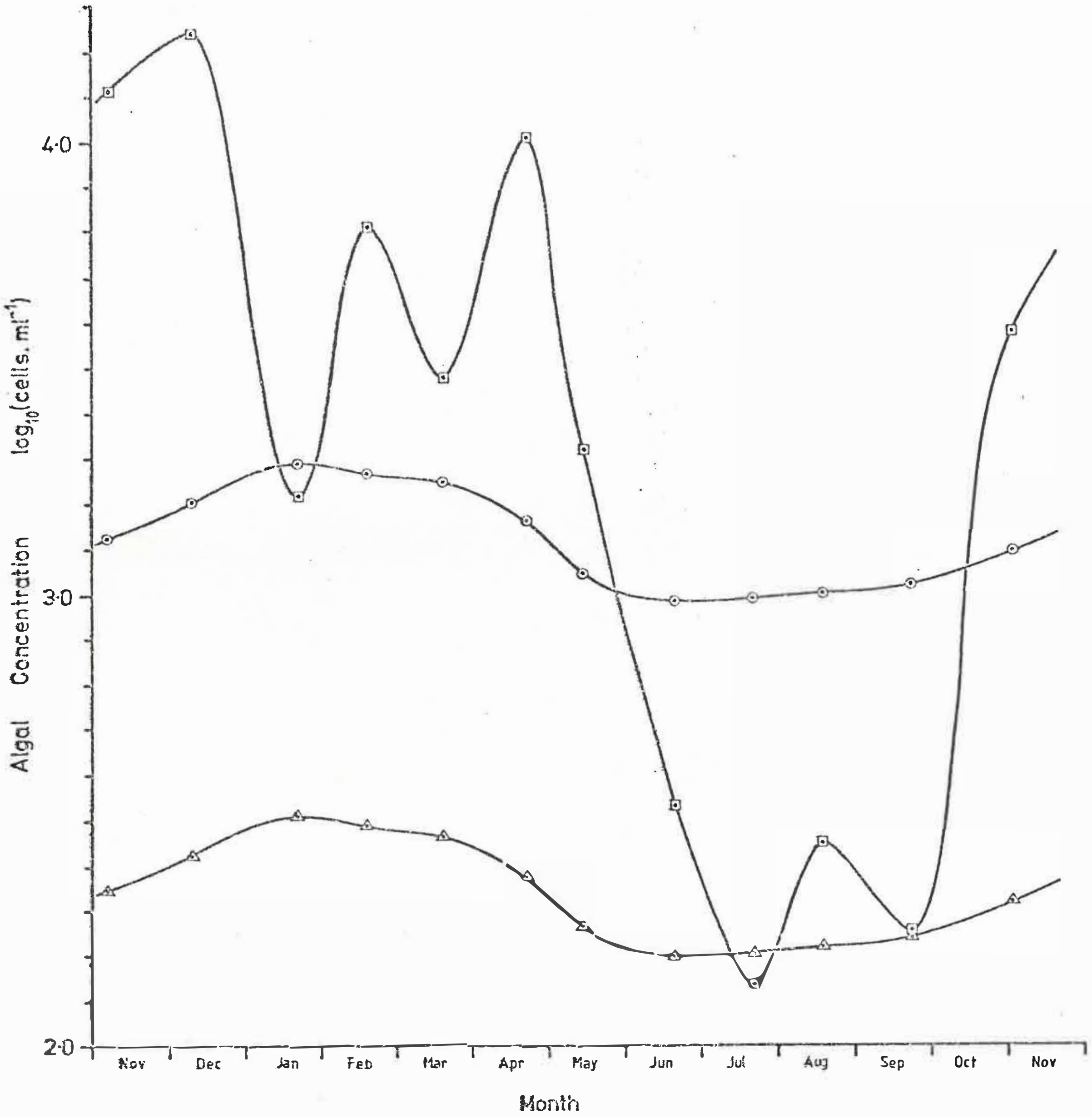


Fig. 21. The numbers of algae in the Waikato River in 1976 (⊡) and the numbers of *Chlorella* required for maintenance by *Hyridella menziesi* of size 0.05 g. dry weight (△) and 1.0 g. dry weight (⊙). (Mussel data from Table 28, algal and temperature data M.W.D. pers. comm.).

The concentration of *Chlorella* cells required for maintenance is compared to the algal concentration in the Waikato River in Fig. 21. During the summer months the concentrations of algae available were more than that required for maintenance, enabling growth to occur, but during the winter months (June through to September) algal numbers were much reduced and, except for the smallest animals, below maintenance level. Growth during these months would cease.

Negus (1966) demonstrated a close relationship between temperature and growth in mussels while others (Thompson and Bayne 1974) have shown the effect of food levels on growth. Kuenzler (1961) found that in *Modiolus demissus* shell growth occurred throughout the year, but was more rapid during the warmer months. Temperature does influence metabolic activity and hence growth rate, but it is the availablility of food that determines whether or not growth will occur. This study suggests that for *Hyridella* living in the Waikato River, there are not sufficient algae present during the winter months for a maintenance ration.

A yearly energy budget for a population of *Hyridella* in the Waikato River, based on the above results, is given, along with budgets for other species in Table 15. It is a provisional budget based on the following assumptions:

(a) 100% retention of river algae by the gills, so the filtration rate equals the pumping rate.

(b) The ingestion ratios and assimilation efficiencies determined in the laboratory are applicable to animals in the Waikato River.

(c) The ratio of body to total (body + shell) weight is 1 : 3 as established by Kuenzler (1961).

(d) Filtering occurs for 45% of the time and the oxygen uptake of non-filtering animals is 40% of active respiration (Nobes, unpub. data).

(e) The biomass, derived from transect data (p 4) is typical for the river community.

TABLE 15. Budget parameters in $kcal.m^{-2}.y^{-1}$ and energy flux ratios for various molluscs. C is consumption, A assimilation, R respiration and P production. The biomass B is in $kcal.m^{-2}$.

Species	C	A	R	P	B	P/B	R/B	A/B	C/B	Reference
Scrobicularia plana	554	336	265	71	109	0.7	2.4	3.1	5.1	Hughes 1970
Littorina irrorata	644	290	249	41	-	-	-	-	-	Odum & Smalley cited in Hughes 1970
Crassostrea virginica	-	9788	5656	4132	2051	2.0	2.8	4.8	-	Dame 1976
Modiolus demissus	-	56	39	17	20*	0.9	2.0	2.8	-	Kuenzler 1961
Potamopyrgus antipodarum	1645	1497	1159	338	117	3	10	13	14	West 1975
Hyridella menziesi	352	126	17	109	9	12	1.8	14	39	Present study

* estimated, using the value of $1.83\ kcal.g^{-1}$ for the energy content of mussel tissue.

The values of the budget parameters obtained for *Hyridella* are comparable to those of other molluscs, indicating that it has a significant role in the river community. The flux ratios (e.g. P/B) can be used in a similar way to compare the various species in Table 15. Clearly *Hyridella* has a higher energy turnover rate than other bivalves and has similar abilities to *Potamopyrgus antipodarum*, a common gastropod mollusc in the Waikato River.

The energy assimilated by *Hyridella* is a small proportion of that removed from suspension (Table 16). Food not used is rejected as pseudofaeces and deposited on the substrate in which the mussels are embedded, as would be the faeces containing unassimilated food. Thus one role of mussels in the ecosystem is the capture of particulate organic matter. They not only reduce turbidity by removing suspended solids, but also act as energy traps, making the collected material available for other benthic organisms. In so doing they play a further role by greatly enhancing the recycling of nutrients in their ecosystem (Kuenzler 1961).

TABLE 16. Energy utilization by *Hyridella* feeding on various concentrations of *Chlorella*.

Food Concentration x 10^4 cells.ml^{-1}	Energy Assimilated cal.hr^{-1}	Energy Removal from Suspension cal.hr^{-1}	% Utilization
0.5	2.39	16.5	14
1.0	3.83	33.0	12
2.5	7.12	82.5	9
5.0	11.3	165	7
10.0	18.2	330	6

This intermediary role of mussels has been noted by other workers. Hinz and Scheil (1972) commented on the ability of mussels to clear water of suspended material. Their interest was in water purification, but they noted that pseudofaeces and faeces remained in the community. Stanćzykowska *et al.* (1975) recognised the importance of *Dreissena* in the cycling of nutrients in lake ecosystems, citing the work of Isvekova and Lvova-Katchanova (1972) which showed that suspended material agglutinated by the mussel was the most nutritive food for larval chironomids.

The dominant benthic groups present in the weed beds of the Waikato River are Oligocheata, Nematoda, Turbellaria, Chironomidae and *Potamopyrgus antipodarum* (Boubée, pers. comm.). All feed on particulate organic matter, although some Turbellarians are considered to be carnivores and *Potamopyrgus* grazes predominantly on periphyton, so the material collected and rejected by *Hyridella* would be a potential food source for the majority of them. Also the proportion of production used for growth would become available to the benthic carnivores and scavengers on death of the mussel, as well as the energy in the organic matrix of the shells over a longer time period. Thus the role of *Hyridella* is in (a) reducing the particulate matter content of the surrounding water,
(b) providing detritus for the benthic community and
(c) speeding nutrient cycling.

FURTHER RESEARCH

To define *Hyridella's* role more precisely further work needs to be done on several facets of its biology. Activity patterns are of prime importance in establishing daily and longer term energy flows. The instantaneous energy budget of an animal is inflated since it does not account for periods of quiescence. Diurnal patterns of valve activity by some freshwater mussels have been shown to occur (Hiscock 1950, Imlay 1968, Salánki and Véro 1969). They can be regulated by oxygen tension (Salánki 1965) and also influenced by mechanical disturbances (Imlay 1968). Filtering usually occurs during the active period and oxygen uptake can be five to ten times higher than that during quiescence (Salánki and Lukacsovics 1967). *Hyridella* does exhibit periodic valve activity, but factors influencing and regulating it need to be clarified.

As in many other species (Davies 1966, Lomte and Nagabhushanam 1971; Ansell 1973) oxygen uptake, or metabolism of *Hyridella* varies with body weight and temperature. However, starvation may (Bayne *et al.* 1976) or may not (Ansell and Sivadas 1973) decrease respiration in mussels and its effect on *Hyridella* needs to be known for accurate calculation of the energy budget during the winter months when available food is often below the maintenance level.

The filtration rate of some bivalves is inversely related to food concentration, influenced by temperature (Morton 1971, Walne 1972, McLusky 1973, Winter 1973, Schulte 1975) and in *Dreissena polymorpha* is affected by the algal species present (Morton 1971). Such relationships must be examined for *Hyridella* as the filtration rate not only affects the amount of food available for ingestion but also the proportion not used and which goes to other members of the benthos.

Many species of algae are present in the Waikato River (Coffee *et al.* 1975) and seven species were identified in the gut contents of some mussels taken from the river. Ideally, the budget parameters of ingestion ratio and assimilation efficiency should be known for all possible food sources for a precise yearly budget since algal composition is variable throughout the year.

The parameter 'production' could be subdivided into growth and gametes, the gametes representing an energy loss to the community, while that of growth is added to the energy pool and released on death. It was noticed that both faeces and pseudofaeces of *Hyridella* were bound in mucus. This mucus production is an energy loss to the animal and needs to be quantitatively defined. In the above budget this loss was not considered and could at least partly account for the high production obtained. Losses from soluable metabolites and excretion of nitrogen metabolism end products also need to be determined.

Finally, it would be interesting to compare river populations with those found in lakes. Environmental factors such as current, oxygen tension and temperature are in sharp contrast to those in rivers. Mussels are found in high densities, up to 200 animals.m^{-2}, in lakes (Devcich and Boubée, pers. comm.) and their role as turbidity reducers and benthic food harvesters may have a correspondingly greater impact in such ecosystems.

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APPENDIX 1

Experimental Data

Page

TABLE 17. Respiration and specific respiration rates of various sized *Hyridella* at ambient temperatures (19 - 24°C).

Flesh Dry Weight g	Length mm	Respiration Rate $\mu gO_2.hr^{-1}$	Specific Respiration Rate $\mu gO_2.hr^{-1}g^{-1}$	Flesh Dry Weight g	Length mm	Respiration Rate $\mu gO_2.hr^{-1}$	Specific Respiration Rate $\mu gO_2.hr^{-1}g^{-1}$
0.03	30.8	119	3957	0.21	47.8	375	1787
0.03	32.0	57	1900	0.22	47.1	146	663
0.03	37.4	51	1712	0.23	60.4	139	604
0.04	33.8	142	3561	0.23	60.4	269	1170
0.05	33.7	178	3552	0.25	63.3	310	1240
0.05	37.6	141	2812	0.27	49.2	343	1270
0.06	30.8	117	1947	0.27	59.8	383	1419
0.07	40.3	95	1360	0.30	60.2	280	933
0.08	40.2	102	1268	0.41	63.4	347	758
0.10	43.6	100	1001	0.41	64.4	352	858
0.11	43.3	324	2949	0.49	67.2	314	641
0.12	42.2	299	2496	0.50	64.2	502	1003
0.13	43.4	154	1185	0.65	69.1	367	564
0.13	47.4	240	1844	1.01	47.7	293	290
0.14	48.3	240	1717	1.02	78.6	558	548
0.15	47.6	149	996	1.38	62.9	214	564
0.16	31.9	142	889	1.39	74.6	325	234
0.16	49.2	255	1593	1.47	77.3	335	228
0.18	60.8	233	1295	1.71	78.3	433	253
0.21	43.9	186	885	1.94	80.9	503	259

TABLE 18. Specific respiration rate ($\mu g O_2 . hr^{-1} . gdwt^{-1}$) of *Hyridella* at 6, 10, 15 and 20°C.

Flesh Dry Weight	Length	Temperature °C			
g	mm	6	10	15	20
0.37	52.3	-	311	255	358
0.28	54.9	303	404	519	-
0.32	53.5	-	439	349	-
0.34	55.9	462	432	681	-
0.40	59.7	-	-	424	748
0.59	59.7	143	152	394	505
	Mean	303	348	437	537
	Error	92	54	60	114

TABLE 19. Specific respiration rate ($\mu g O_2 . hr^{-1} . gdwt^{-1}$) of *Hyridella* at 10, 20, 25 and 30°C.

Flesh Dry Weight g	Length mm	Temperature °C			
		10	20	25	30
0.34	-	271	434	681	1341
0.28	49.9	313	652	896	-
0.21	52.0	267	483	699	-
0.30	51.4	313	387	736	1050
0.25	52.6	181	380	595	1107
0.36	55.8	309	505	505	1028
0.41	57.8	224	424	737	837
0.40	59.9	146	369	418	1080
0.24	58.8	328	479	1003	2368
0.35	58.7	206	269	559	1035
0.30	55.8	300	467	589	1026
0.31	58.3	373	510	632	1471
0.21	55.1	509	657	1659	1659
0.24	54.4	251	421	577	-
0.49	54.2	162	229	400	823
0.52	56.7	175	290	512	668
0.45	58.3	104	445	539	843
0.44	58.7	209	455	589	1638
	Mean	258	436	685	1198
	Error	23	26	67	113

Table 20. Assimilation efficiencies, filtration rates and ingestion ratios of *Hyridella* with size and food concentration.

Flesh Dry Weight g	Length mm	Assimilation Efficiency %	Filtration Rate ℓ.hr^{-1}	Ingestion Ratio	Food Concentration x 10^4 cells.ml^{-1}
0.18	41.5	43.0	-	-	0.5
0.28	46.2	52.6	0.202	0.601	0.5
0.35	56.7	56.1	2.08	0.128	0.5
0.49	48.0	45.9	0.202	0.178	0.5
0.57	47.0	1.0	-	-	0.5
0.61	51.9	66.0	0.202	0.626	0.5
0.81	55.5	35.4	2.08	0.028	0.5
0.17	37.8	20.9	-	-	1.0
0.21	43.6	29.7	0.352	0.538	1.0
0.25	46.6	54.6	0.798	0.100	1.0
0.30	47.8	-	0.684	0.111	1.0
0.32	50.0	61.2	0.798	0.142	1.0
0.32	51.5	42.2	0.684	0.250	1.0
0.35	55.3	43.1	0.554	0.260	1.0
0.36	49.8	24.1	-	-	1.0
0.38	45.9	22.3	0.352	0.280	1.0
0.38	52.1	8.5	-	-	1.0
0.41	51.6	33.4	0.684	0.384	1.0
0.41	60.7	46.9	0.554	0.335	1.0
0.45	47.0	11.9	0.352	0.536	1.0
0.45	53.1	82.1	0.798	0.060	1.0
0.46	52.3	35.3	0.798	0.284	1.0
0.75	57.7	35.9	0.554	0.570	1.0
0.88	73.8	50.0	0.276	0.381	1.0
0.93	58.2	8.0	-	-	1.0
0.97	73.7	43.0	2.138	0.092	1.0
1.42	67.3	20.9	0.276	0.931	1.0
0.11	40.6	81.2	1.498	0.055	2.5
0.21	42.5	7.8	0.122	0.409	2.5
0.22	38.0	79.6	1.498	0.013	2.5
0.26	44.6	84.7	1.498	0.119	2.5
0.28	47.3	67.6	1.498	0.065	2.5
0.28	47.4	37.7	0.122	0.791	2.5
0.36	44.9	68.1	1.498	0.055	2.5
0.10	46.2	49.3	0.646	0.374	5.0
0.12	45.9	33.5	0.494	0.174	5.0
0.21	49.3	27.7	0.646	0.131	5.0
0.23	47.4	45.2	0.494	0.097	5.0
0.30	48.4	63.8	0.646	0.162	5.0
0.37	52.9	3.1	0.738	0.098	5.0
0.45	52.5	54.7	0.494	0.366	5.0
0.55	63.0	61.9	2.138	0.239	5.0
0.59	55.1	-	0.738	0.021	5.0
0.59	60.6	-	2.138	0.110	5.0
0.60	57.0	-	0.738	0.079	5.0
0.71	57.2	25.5	0.738	0.254	5.0
0.18	42.3	14.7	1.407	0.083	10
0.22	52.2	32.9	1.407	0.170	10
0.40	58.5	3.0	1.310	0.027	10
0.46	55.3	-	0.599	0.171	10
0.53	51.6	5.8	0.599	0.245	10
0.53	61.4	13.3	0.599	0.305	10
0.57	69.4	48.2	4.532	0.143	10
0.72	67.3	47.3	1.310	0.485	10
1.18	63.9	33.0	4.532	0.037	10

Formulae used for calculating filtering and feeding rates.

(i) The concentration of particles in suspension at any given time is

$$C_t = C_o e^{-\left(\frac{mn}{M} + a\right) t}$$ (Coughlan 1969)

where

C_o initial cell concentration
C_t cell concentration after time t
m - filtration rate of each animal
n - number of animals
M volume of suspension
a rate at which particles settle out of suspension.

By taking the natural logarithm of each size and rearranging, the filtration rate is given by

$$m \quad \frac{M}{n} \left(\frac{\log_c C_o - \log_c C_t - at}{t} \right)$$

(ii) The concentration of spheres in each size class was calculated by:

$$= \frac{A \times D^2}{d^2 \times V} \quad \text{no.ml}^{-1}$$

where
A - average number of spheres per field of view
D - diameter of filtering area of membrane filter (mm)
d - field of view of microscope (mm)
V - volume of sample taken (ml)

(iii) The cell concentration in the feeding chamber was determined by:

$$C_f \quad \frac{C_c \times v \times A_s}{A_c \times V} \quad \text{c.ml}^{-1}$$

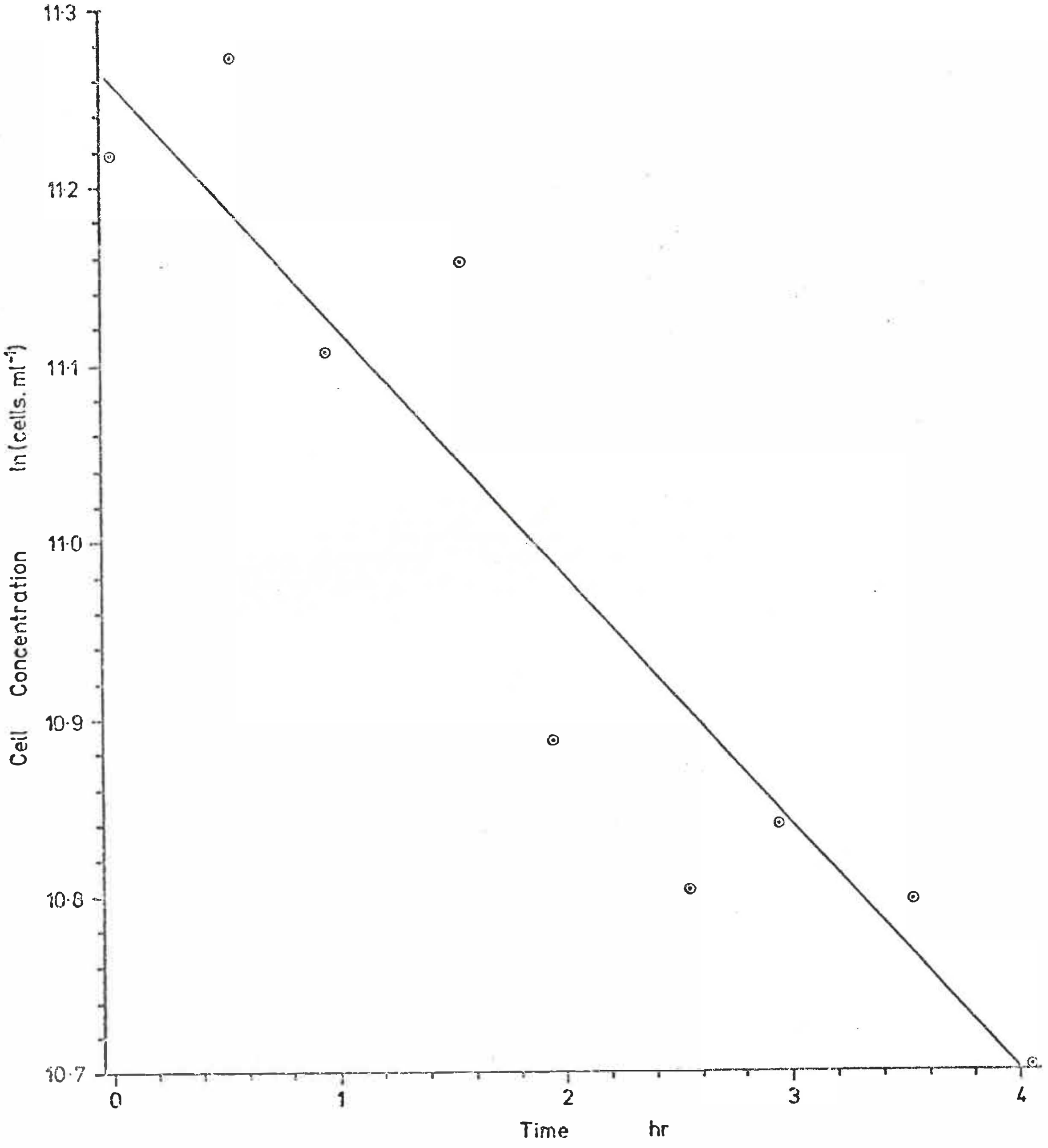


Fig. 22. The relationship between cell concentration (C_f cells.ml^{-1}) and time (t hr) in the feeding chamber containing no mussels. The equation for the regression line is:

$$\ln C_f = 11.26 - 0.143t \quad (p\ ***) \qquad (XVII)$$

where C_c - cell concentration of stock suspension $(c.ml^{-1})$

A_c - activity (cpm) of volume v (ml) of stock suspension

A_s - activity (cpm) of sample, volume V (ml) from feeding chamber.

(iv) The sedimentation constant a was found from a control experiment where

$$C'_t = C'_o e^{-at}$$

or $\log_e C'_t = \log_e C'_o - at$

C'_o initial cell concentration

C'_t cell concentration at time t

The relationship is shown in Fig. 22.

$a = 0.143 \pm 0.020\ hr^{-1}$

(v) The change in cell concentration in the feeding chamber is due to the sum of two processes, filtration by the animals and sedimentation. The number of cells removed by the animal is not the difference in the concentrations but a summation with time of the product of filtration rate and instantaneous cell concentration, assuming the filtration rate to be constant.

$$CR = \Sigma_o^t C_t . FR . dt$$

and from (i)

$$CR = \Sigma_o^t FR . C_o e^{-(\frac{mn}{M} + a)t} dt$$

Integrating

$$\therefore CR = FR.C_o \left[- \frac{e^{-(\frac{mn}{M} + a)t}}{(\frac{mn}{M} + a)} \right]_o^t$$

$$= FR.C_o \left(-e^{-(\frac{mn}{M} + a)t} + e^{-(\frac{mn}{M} + a)o}\right) / \left(\frac{mn}{M} + a\right)$$

Since FR is in $\ell.hr^{-1}$, C_o in cells.ml^{-1}, t is in hrs and $e^o = 1$

$$CR = FR \times C_o \times 10^3 \left(1 - e^{-(\frac{mn}{M} + a)t}\right) / \left(\frac{mn}{M} + a\right) \quad \text{cells.}$$

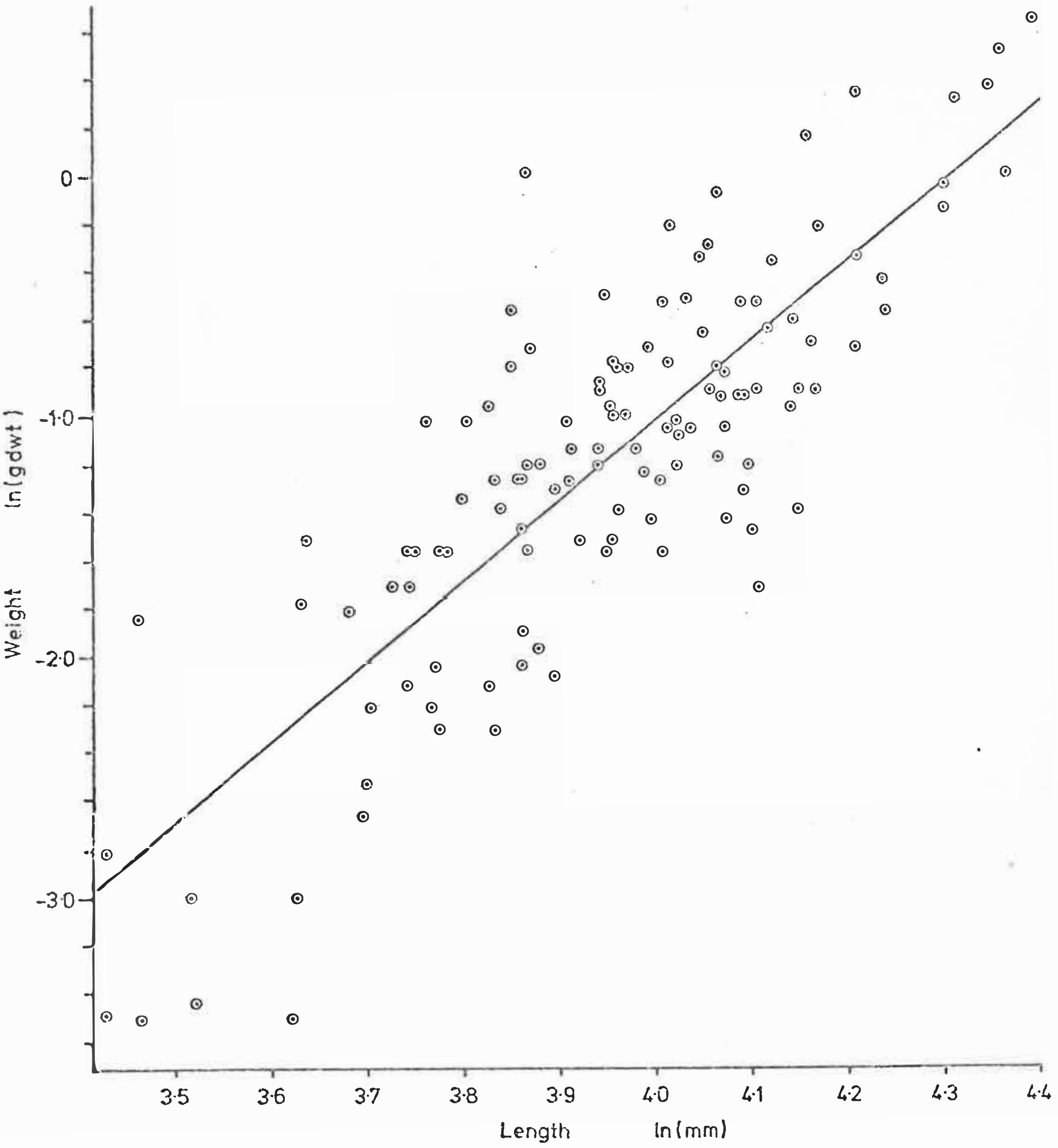


Fig. 23. Weight - length relationship of all *Hyridella menziesi* used in respiration and assimilation experiments. The equation for the regression line is:

$$W = 5.52 \times 10^{-7} L^{3.35} \quad (p\ ***) \qquad (XVIII)$$

where W is g. dry weight

L is mm

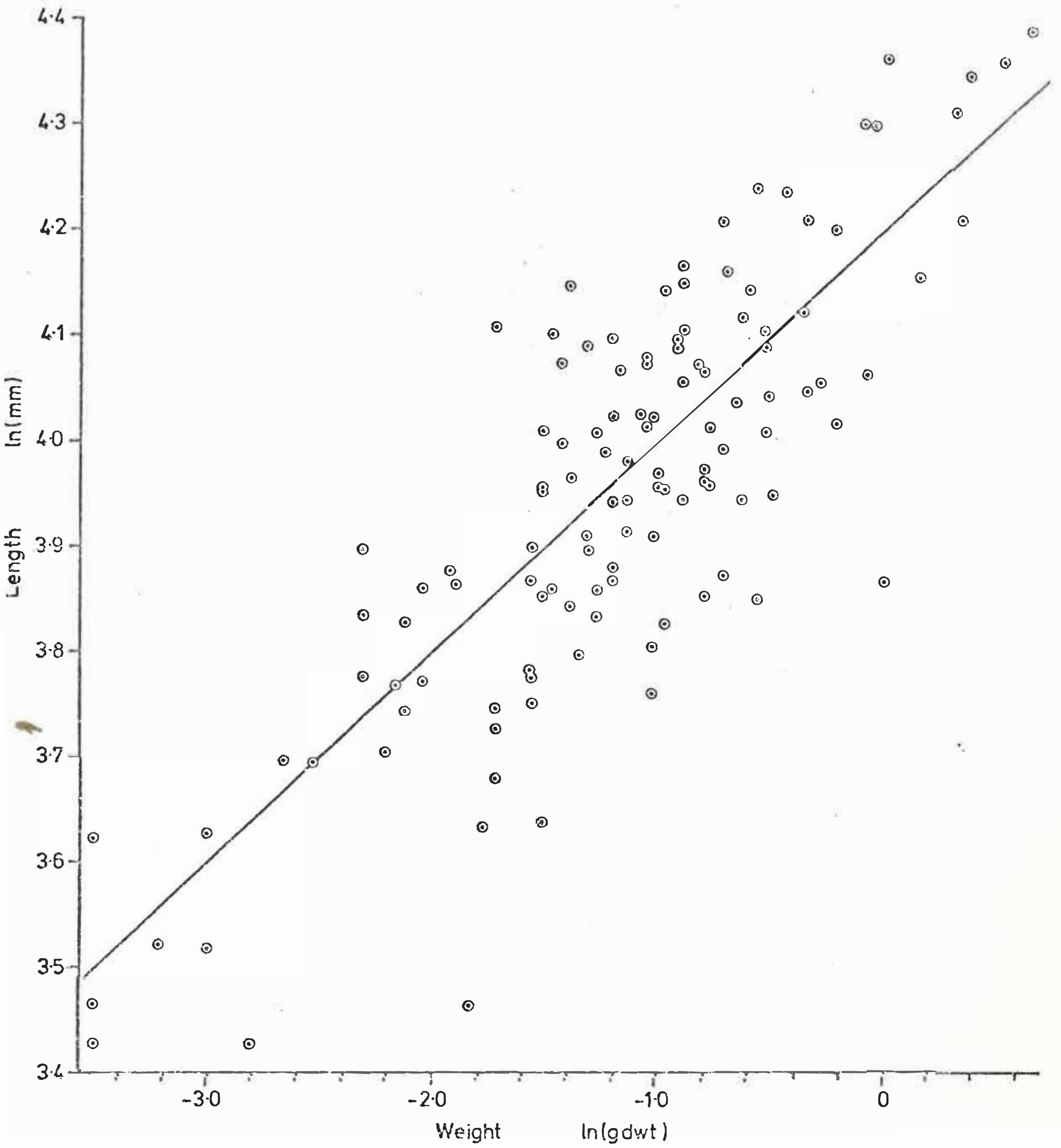


Fig. 24. Length-weight relationship of all *Hyridella menziesi* used in respiration and assimilation experiments. The equation of the regression line is:

$$L = 66.2\ W^{0.201} \quad (p\ ***) \qquad (XIX)$$

W and L as for Fig. 23.

APPENDIX 2

Corrections for Liquid Scintillation counting

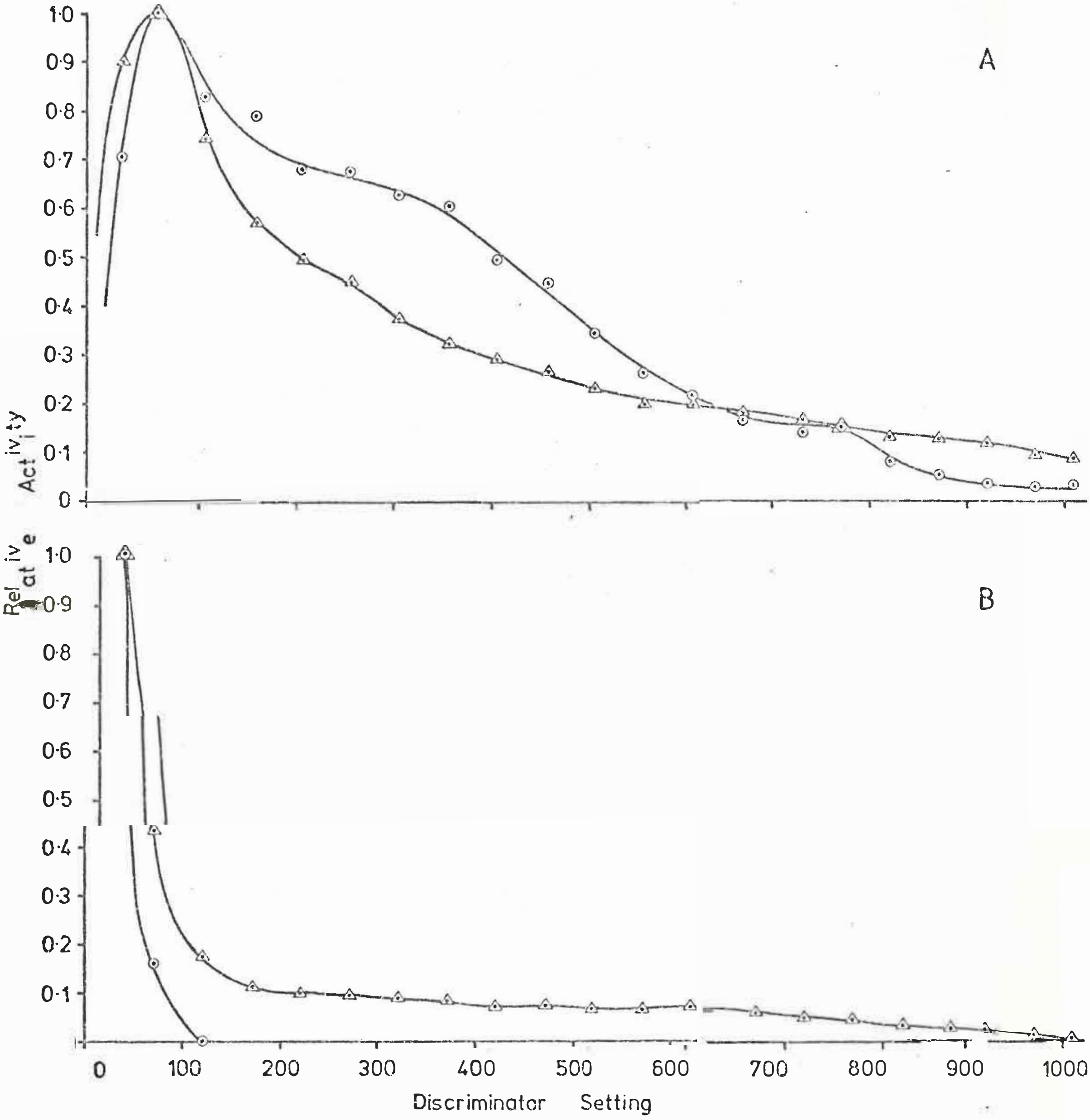


Fig. 25. Energy spectra of ^{14}C (⊙) and ^{144}Ce (△) at gain settings of 20% (A) and 1.72% (B). Window width is 40 divisions.

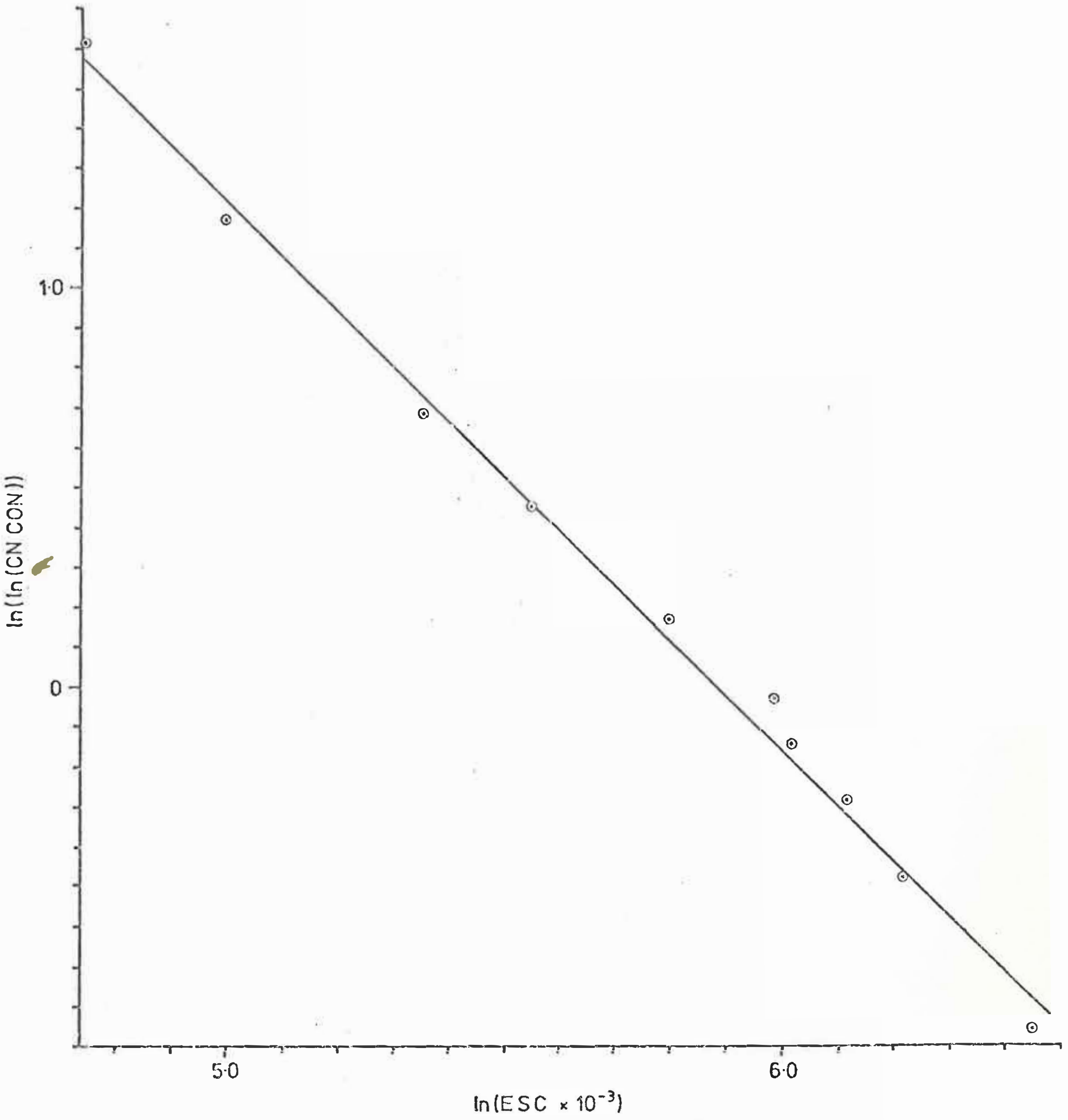


Fig. 26. The relationship between channel contribution ((counts, $\min^{-1}$ in ^{14}C counting channel) / (counts $\min^{-1}$ in ^{144}Ce counting channel)) by ^{144}Ce with increasing quenching, as indicated by the external standard counts (ESC). The equation of the regression line is:

$$D = 8.12 - 1.38H \quad (p\ ***) \qquad (XX)$$

where D = ln (ln channel contribution)

H = ln (ESC x 10^{-3})

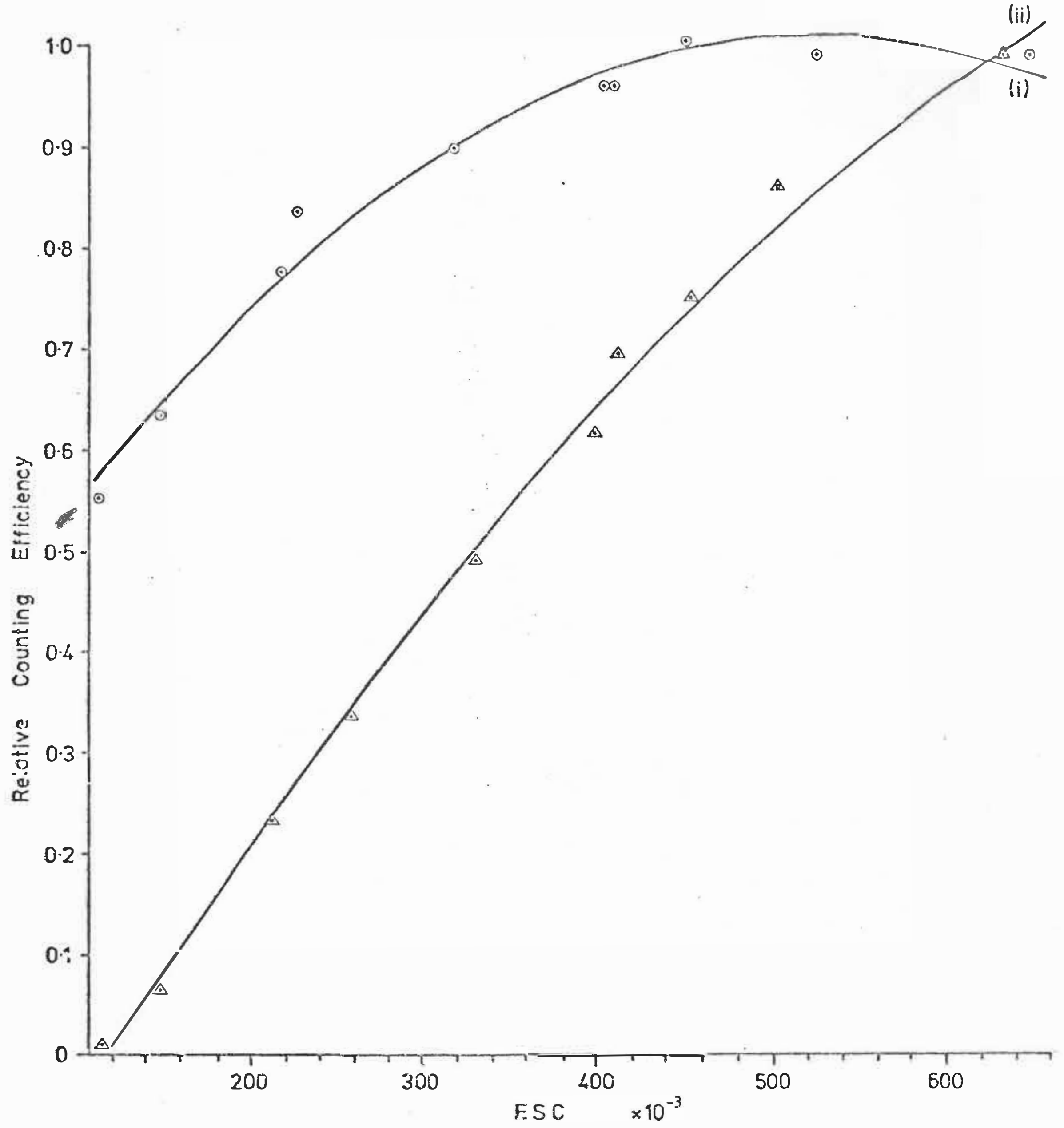


Fig. 27. The relative counting efficiencies (RCE) ((activity (cpm) of quenched standard)/(activity (cps) of unquenched standard)) of ^{14}C (⊙) and ^{144}Ce (△) standards with increasing quenching, as indicated by the external standard counts (ESC). The equations of the regression lines are:

(i) $\text{RCE } (^{14}C) = 0.31 + 0.0026 \text{ (ESC x } 10^{-3}) - 0.0000025 \text{ (ESC x } 10^{-3})^2$

$(p\ ***)$ (XXI)

(II) $\text{RCE } (^{144}Ce) = -0.34 + 0.0030 \text{ (ESC x } 10^{-3}) - 0.0000015 \text{ (ESC x } 10^{-3})^2$

$(p\ ***)$ (XXII)

Sample Calculation

	Raw Counts (cpm)		
	^{14}C Channel	^{144}Ce Channel	ESC Channel
Sample	3134.8	500.2	970.7
Sample and External Standard	163511	84165	430319
Mean Background (Bg)	49.7	8.1	22.9

External Standard Count = 430319 - 970.7 - 22.9 cpm

= 429325 cpm

ln (ln Channel Contribution) = 8.12 - 1.38 ln (ESC x 10^{-3}) (equation XX)

Channel Contribution = 2.19

RCE (^{14}C) = 0.312 + 0.00264 x (429.3) -0.00000247 x $(429.3)^2$ (equation XXI)

= 0.990

RCE (^{144}Ce) = -0.339 + 0.00304 x (429.3) -0.00000145 x $(429.3)^2$ (equation XXIII)

= 0.699

$$\text{Corrected Counts } ^{144}\text{Ce} = \frac{\text{Counts } ^{144}\text{Ce Channel} - \text{Bg}}{\text{RCE } (^{144}\text{Ce})} \text{ cpm}$$

$$= \frac{500.2 - 8.1}{0.699} \text{ cpm}$$

$$= 704 \text{ cpm}$$

$$\text{Corrected Counts } ^{14}\text{C} = \frac{\text{Counts } ^{14}\text{C Channel} - \text{Bg} - (\text{Chan. Cont. } (\text{Counts } ^{144}\text{Ce Channel} - \text{Bg}))}{\text{RCE } (^{14}\text{C})} \text{ cpm}$$

$$= \frac{3134.8 - 49.7 - (2.19 \times (500.2 - 8.1))}{0.990} \text{ cpm}$$

$$= 2028 \text{ cpm}$$

The calculations were done on a Hewlett-Packard Model 9100A programmable calculator.

APPENDIX 3

Regression equations with statistical data

Regression equations were obtained from the data by the statistical program Teddybear (J.B. Wilson, Otago) run on the Burroughs 6000 computer at the University of Auckland.

The equations in the text, identified by Roman numerals, are given with degrees of freedom (df), F value and probability.

	Regression	df	F	P
I	$\ln U = 1.197 + 0.0682T$	1/39	50.84	0.000
II	$\% C = 1.19 + 0.012t$	1/7	8.732	0.022
III	$\% Ce = 3.44 + 0.0046t$	1/7	0.1689	0.693
IV	$\% C = 0.094 + 0.042t$	1/7	16.06	0.005
V	$\% Ce = 1.18 + 0.053t$	1/7	13.36	0.008
VI	$\phi = 8.63 - 0.209t$	1/19	6261	0.000
VII	$\ln R = 6.03 + 0.410 \ln W$	1/38	67.31	0.000
VIII	$\ln RR = 6.03 - 0.592 \ln W$	1/38	141.2	0.000
IX	$\ln RR = 4.89 + 0.0662T$	1/85	160.1	0.000
X	$Q_{10} = 0.439 + 0.079T$	1/13	12.56	0.004
XI	$\ln D = -0.668 + 0.0617 L$	1/3	10.84	0.046
XII	$\ln P = 1.33 + 0.269 \ln W$	1/10	12.52	0.005
XIII	$R = 9.38 + 97.0 P$	1/10	6.865	0.026
XIV	$B = 0.0131 - 0.0112 W$	1/2	55.91	0.017
XV	$\ln A = 5.351 + 0.601 \ln W$	1/20	195.0	0.000
XVI	$\ln IR = 0.787 - 0.223 \ln FC$	1/3	17.22	0.025
XVII	$\ln AE = 5.608 - 0.128 \ln FR$	1/37	6.112	0.018
XVIII	$\ln C_i = 11.26 - 0.1429t$	1/7	48.96	0.000

XIX	$\ln W = -14.41 + 3.346 \ln L$	1/121	247.7	0.000
XX	$\ln L = 4.190 + 0.2008 \ln W$	1/121	247.7	0.000
XXI	$D \quad - 8.115 - 1.378\ H$	1/8	1334	0.000
XXII	$RCE\ (^{14}C) = 0.313 + 2.64 \times 10^{-3}$ $(ESC \times 10^{-3}) - 2.47 \times 10^{-6}$ $(ESC \times 10^{-3})^2$	2/7	168.0	0.000
XXIII	$RCE\ (^{144}Ce) \quad -0.339 + 3.04 \times 10^{-3}$ $(ESC \times 10^{-3}) - 1.45 \times 10^{-6}$ $(ESC \times 10^{-3})^2$	2/7	1488	0.000

APPENDIX 4

The inorganic nutrient solution (as used by the Plant Disease Division, D.S.I.R., Auckland) used for culturing *Chlorella vulgaris* was made from the stock solutions in the following Table.

Stock Solution		Composition		Amount Used
1 M	KNO_3	KNO_3	101.11 g. ℓ^{-1}	4 ml
1 M	$Mg(NO_3)_2$	$Mg(NO_3)_2 . 6H_2O$	256.43 g. ℓ^{-1}	2 ml
1 M	$Ca(NO_3)_2$	$Ca(NO_3)_2 . 4H_2O$	236.16 g. ℓ^{-1}	2 ml
0.2M	$KH_2 PO_4$	$KH_2 PO_4$	27.22 g. ℓ^{-1}	5 ml
FeNa	EDTA	Na_2EDTA	30 g. ℓ^{-1}	0.6 ml
		$FeSO_4 . 7H_2O$	25 g. ℓ^{-1}	
Trace Elements		H_3BO_3	2.86 g. ℓ^{-1}	1 ml
		$MnCl_2 . 4H_2O$	1.79 g. ℓ^{-1}	
		$ZnCl_2$	0.10 g. ℓ^{-1}	
		$CuSO_4 . 5H_2O$	0.08 g. ℓ^{-1}	
		$(NH_4)_6 Mo, O_{24} . 4H_2O$	0.04 g. ℓ^{-1}	

Table 21. Amount used and composition of stock solutions for an inorganic nutrient solution for culturing *Chlorella*.

To make up the culture medium, the quantities listed of stock solution were mixed with de-ionized water to make one litre, and spiked with 0.5% glucose.

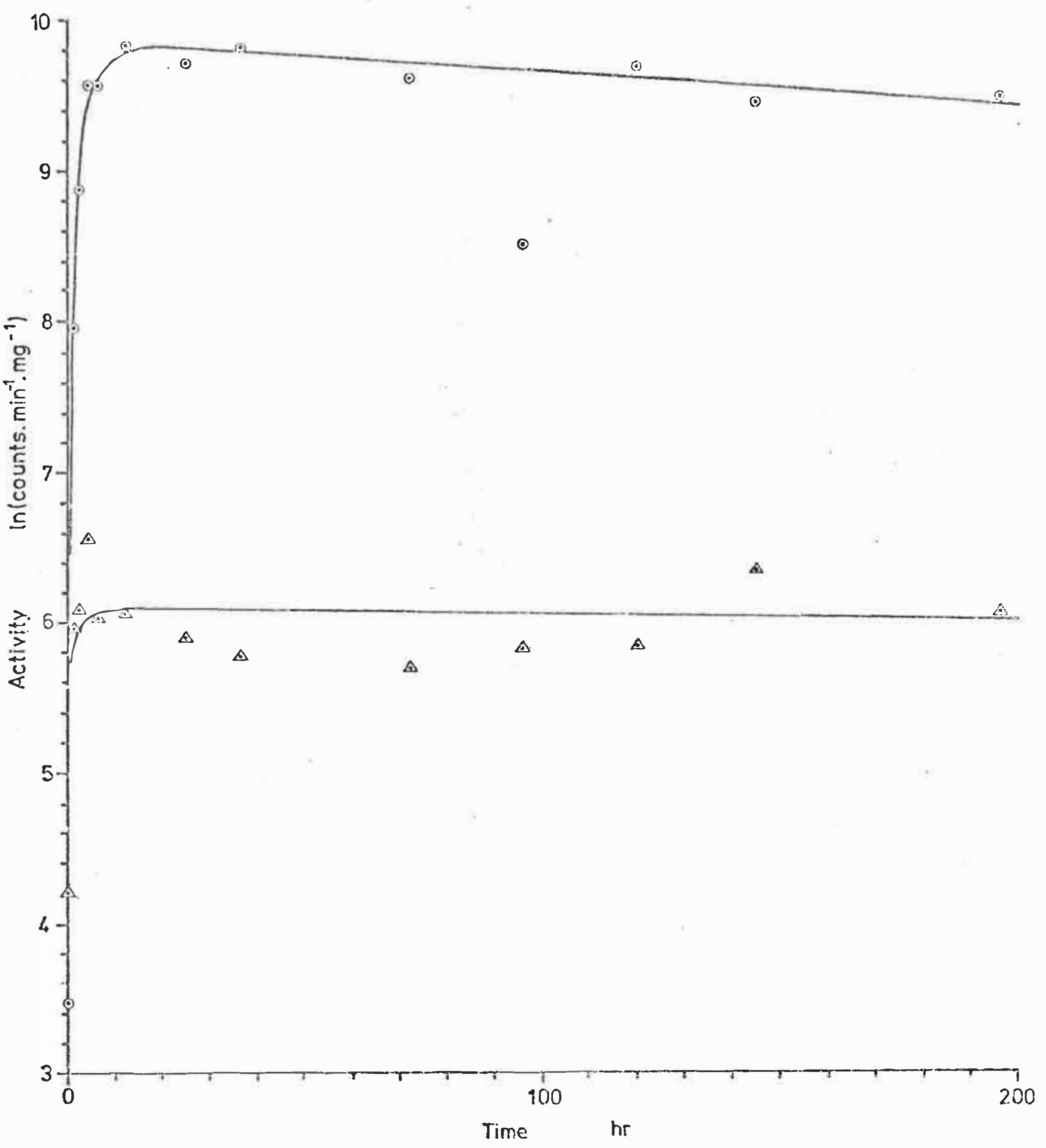


Fig. 28. Uptake of ^{14}C (⊙) and ^{144}Ce (⊡) from nutrient solution by *Chlorella*. Curves fitted by eye.

APPENDIX 5

THE GLOCHIDIUM OF *HYRIDELLA MENZIESI*

Freshwater mussels are characterized by a special juvenile stage in their life cycle, the glochidium, which temporarily parasitizes fish, attaching to the gill filaments, fins and lips, before developing into a free living organism. It is during this stage that degeneration of some larval structures and development of adult organs occurs (Pelseneer 1906). This juvenile stage is also a dispersal mechanism for the colonization of new areas in lakes. Restocking of upstream populations in streams and rivers is also effected and is important when numbers are reduced by events such as floods.

Glochidial release by *Hyridella* has been observed in the laboratory from adults ranging in size from 47.0 mm to 68.7 mm in length. From one of them, 900 juveniles were released over a 20 minute period. A byssus thread about 10 times longer than the body and paired sensory projections were seen on living specimens.

The glochidium has a shell that is assymetrical in lateral view (P 1. 2(a), (b)), the apex, on the ventral margin of each valve where the inward pointing hook is located, being anteriorly placed. With the hinge as base line, the angle included by it and the line from the anterior end of the apex is 77°, while the posterior angle is 53°. The length of the valves is 310 µm and the depth from the hinge to apex is 245 µm. The corresponding measurements made by Percival (1931) on *Diplodon lutulentus* glochidia (*Hyridella menziesi*, McMicheal and Hiscock, 1958) were: anterior angle, about 80°, posterior angle about 55°, length 360 µm and depth 280 µm.

Plate 2. Scanning electron photomicrographs of the glochodium of *Hyridella menziesi*.

a, fronto-lateral view of left valve.

b, ventral view of shell with valves open showing hinge line (L) and position of hooks (H) on ventral margin of valves.

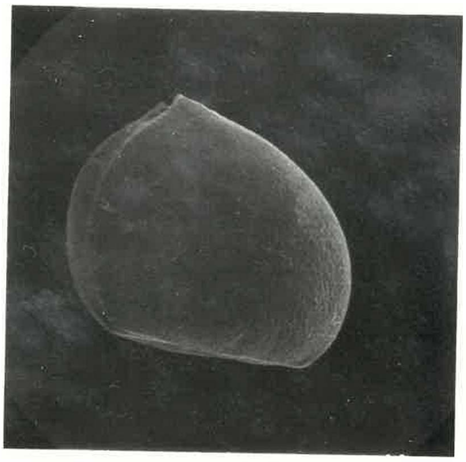
c, latero-anterior view of left valve showing hook.

d, inner surface of valve showing pores.

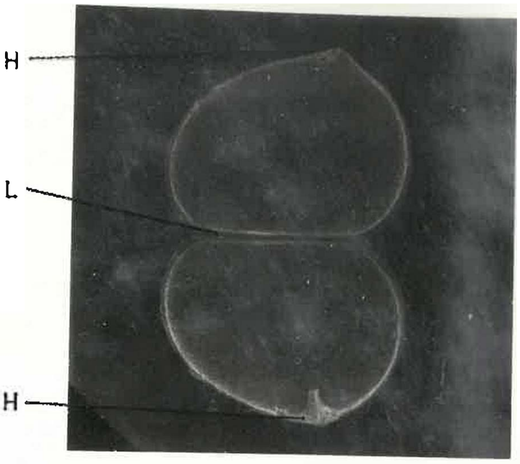
e, ventral view of larva showing lateral pits (P), sensory cells (S) and place of byssus thread attachment (B).

f, sensory cell with hairs.

Scale in µm.



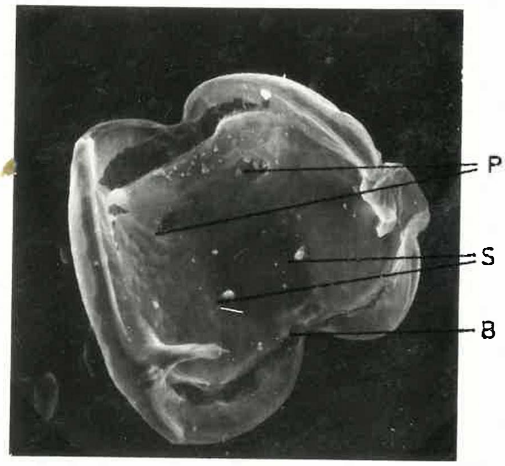
a



b

c

d



e

f

The shell has an irregular surface and is about 4 μm thick with pores 0.5 μm to 3.5 μm in diameter (Pl 2 (b), (d)). The hooks are without spines, pointed at their tips and strengthened by a flange on the inner margin of each valve (Pl 2(c)).

Paired lateral pits are present in the mantle tissue (Pl 2(e)) but they are not ciliated as in *Anodonta cygnea* (Wood 1974).

Only one pair of hair cells, not seen by Percival (1931), serve as sensory structures, with the hairs (Pl 2(f)) being erect in living larvae. Wood (1974) found their chemical sensitivity to be pronounced in *Anodonta*, being activated by substances which occur in the mucus or epidermal layers of certain freshwater fishes, although strong mechanical stimulation can also cause valve closure. Percival (1931) found infections of *Hyridella* glochidia on small fish present in the stream at his collection site, and it is likely that the hair cells of them are also chemosensory.

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