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A REVIEW ON THE KNOWLEDGE OF SUSPENSION-FEEDING IN LAMELLIBRANCHIATE BIVALVES, WITH SPECIAL REFERENCE TO ARTIFICIAL AQUACULTURE SYSTEMS

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ABSTRACT

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The principles of the mechanism of filter-feeding in suspension-feeding bivalves are described, with particular reference to food selection, particle retention efficiency, formation of pseudofaeces, and food concentration.

Laboratory experiments on the filter-feeding activity carried out in relation to body size, temperature, and food concentration are summarized. Relations existing between body size and filtration rate, pumping rate, oxygen consumption and gill area are expressed as functions of dry-tissue weight (W) by the general allometric equation $R = aW^b$, where R is the rate or ration under consideration, and a and b are constants at specific experimental conditions. Emphasis is laid on the relationships between food concentration and the amount of food ingested, with special reference to aquaculture systems. The daily amount of food ingested, expressed as percentage of dry-tissue weight, is used as an ecologically relevant index of feeding activity.

Data on assimilation and gross growth efficiency under different experimental conditions are presented. A new schematic presentation of the interrelationships between temperature, food concentration and the amount of food assimilated is given. Maintenance ration is described as a function of body size. Thus, by feeding above the calculated maintenance ration, growth will be achieved. Growth under different feeding regimes is discussed, with special reference to aquaculture application. For maximal growth, mussels should be maintained at a constant optimum food level by replacement of food removed per unit time.

The influence of low loads of suspended silt on the filter-feeding activity is quantified. The acceleration of growth obtained by low quantities of suspended silt in addition to algal suspensions is discussed, and its importance for culturing mussels, especially in colder regions where overwintering is necessary and costly, is emphasized.

INTRODUCTION

Farming of mussels, oysters and clams has been developed along empirical lines, very often based exclusively on practical experience. A better understanding, however, of the complex interactions of the biotic and abiotic en-

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vironmental parameters on growth of these molluscs and a more specific interpretation of the results obtained in the field, can be achieved only by laboratory experiments where all the experimental conditions are precisely defined and kept constant as much as possible. By a precisely defined change of one of these experimental conditions, it is possible to find out how an animal is affected by this specific change of its environment. For successful aquaculture efforts it is of great importance to know the optimal conditions for growth, as are the quality (Davis and Guillard, 1958; Walne, 1970; Owen, 1974a, b) and quantity of food, salinity, pH, temperature (Theisen, 1973; de Wilde, 1975), light intensity (Bayne, 1964; Medcof and Kerswill, 1965; Seed, 1969; Strömgren, 1976a, b), and current speed. Current speed with respect to a sufficient food supply may play an important role, especially in well protected and restricted coastal areas. Having determined all these optimum conditions, the selection of well-suited sites for aquaculture efforts will be highly facilitated.

This review is concerned with the filter-feeding activity, particle retention efficiency, ration of food ingested, assimilation efficiency, maintenance ration and growth in lamellibranchiate bivalves. The discussion on growth, however, is restricted to feeding experiments which are suitable to elucidate the complex integrations at least of some of the activities mentioned above. Furthermore, this review is mainly restricted to a representation of the activities of sublittoral bivalves. The activities of intertidal bivalves, on which a rhythmic pattern of feeding is imposed, should be discussed separately. It is quite clear that intertidal bivalves have to compensate, at least to a certain degree, for non-feeding periods by periods of increased activity; a feeding pattern which is completely different from continuously feeding sublittoral bivalves.

FILTER-FEEDING MECHANISM

Ciliary tracts and water current

In the lamellibranchiate bivalves, the gills represent the main food collecting organs. They are well equipped to create a current of water (lateral cilia) and to collect (eu-latero-frontal cirri) and to transport (frontal cilia) particulate material. The frontal cilia transport the collected particles, bound in mucus strings (Bernard, 1972), to the marginal grooves, the ciliary tracts of which in turn carry the retained particles via the palps to the mouth.

The different ciliary tracts have been investigated in considerable detail for many bivalves (for a summary of literature see Atkins, 1937; Winter, 1969; Owen, 1974 a, b; Jørgensen, 1975 b; Bayne et al., 1976 c, d), and from these investigations it is obvious that many bivalves, with respect to their ciliary equipment, are well adapted to the conditions of their specific natural environment.

More recently, Moore (1971), then Owen (1974 b) and Jørgensen (1975 b) have examined the micro-structure of the eu-latero-frontal cirri and have shown that these cirri form a mesh which has the dimensions of 0.6 μm by either 2.4 μm or 4.8 μm.

Control of pumping rate and particle retention efficiency

Fox et al. (1937), Fox and Coe (1943), Tammes and Dral (1955) and Jørgensen (1955) pointed out that small particles, down to colloids, are retained by *Mytilus edulis* and *M. californianus*. More recently, comprehensive studies on the efficiency of particle retention have been carried out by Haven and Morales-Alamo (1970), Vahl (1972 a, b, 1973 a, b) and Jørgensen (1975 b). In all the species investigated, particles were effectively retained down to about 7 μm in diameter (Fig. 1). Most of the species, however, were less effective than *M. edulis* which was able to effectively retain particles down to 2 μm in diameter. Particles below 1 μm were retained by all species, but only to a very limited degree.

Various mechanisms have been developed in suspension-feeding bivalves to regulate the efficiency of particle retention (Dral, 1967, 1968) and pumping rate. More recently, at least seven different mechanisms have been reviewed by Winter (1977), and from this review it is quite obvious that various bivalves, at least *Mytilus edulis*, have the ability for local and independent control of both pumping and particle retention efficiency. One of these mechanisms was reinvestigated by Wilson and Seed (1974; see also Dral, 1968), who were able to demonstrate for *Mytilus edulis* an inverse relationship between pumping activity and retention efficiency. With an increase in pumping activity (Fig. 2) there was a decrease in retention efficiency, and vice versa.

Selection of particles

It has been generally supposed that bivalves have the ability to select particles for ingestion by the activity of the gills and palps. The studies carried out by Bernard (1972, 1974), Winter (1972), and Foster-Smith (1975 b, c) revealed that in the species investigated no selection of particles occurred.

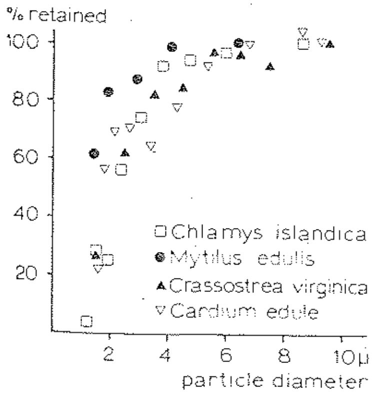

Fig. 1. Particle retention efficiency of various bivalves. Maximum efficiency for each species = 100% (redrawn from Vahl, 1973 b).

Winter (1972), feeding *M. edulis* with suspensions of unicellular algal cells and ferric hydroxide, pointed out that at low concentrations no pseudofaeces were formed and that, consequently, no selection occurred between these two different kinds of suspensions. Foster-Smith (1975 b), using a mixed suspension of *Phaeodactylum tricornutum* and alumina, showed that neither of the particles was selected in preference to the other, at any of the concentrations used. The ingested material always contained the same proportion of particles as the suspension filtered by the gills.

DETERMINATION OF FILTRATION RATES

The filtration rate of an animal is a parameter of great ecological importance. Having determined the filtration rate and knowing the concentration of suspended particles in the water, it is possible to calculate the amount of food retained by the gills and ingested by the animal, as long as no pseudofaeces are produced.

Filtration rate, which is defined as the volume of water filtered completely free of particles per unit of time, is frequently confused with pumping or ventilation rate, which is defined as the volume of water flowing through the gills per unit of time. Filtration rate and pumping rate only have the same numerical value if all particles entering the mantle cavity are completely (100%) retained by the gills. The pumping rate has been determined by so-called 'direct methods' which attempt to separate and measure the exhalant flow, while filtration rates have been determined by so-called 'indirect methods' measuring the removal of suspended particles from a known volume of water per unit of time.

The advantages and disadvantages of these two methods have been discussed in detail by Winter (1969, 1977), Owen (1974 a), Bayne et al. (1976 c), and Hildreth (1976). One of the main disadvantages of the indirect method which should be repeated here, is the continuously changing food concentration in the experimental medium. Consequently, by using the indirect method it is not surprising that it was not possible to detect any significant correlation between filtration rate and food concentration. Furthermore, the theoretical basis of the equation for the calculation of filtration rates using an indirect method is based on the assumptions that (a) the animal's pumping rate is constant and that (b) a constant percentage of particles (which may differ from 100% retention efficiency) is retained throughout the experiment (Coughlan, 1969). Since these assumptions are not necessarily true, the equation itself is one of the main disadvantages of the indirect method.

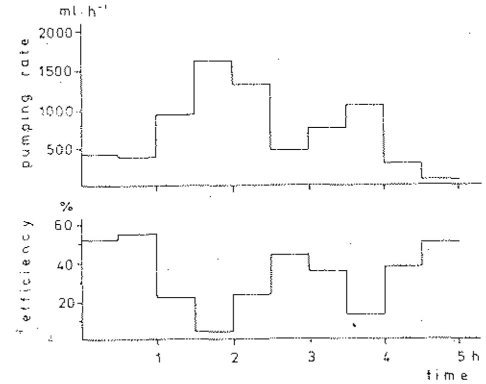

Fig. 2. Pumping rate and filtration efficiency of a single mussel, *Mytilus edulis*, recorded over 30-minute intervals in 5 mg/l of colloidal graphite (from Wilson and Seed, 1974).

Even when measurements of filtration rates in flow-through systems (comp. Bayne, 1971; Thompson and Bayne, 1972, 1974; Tenore and Dunstan, 1973) are performed in which the concentration of particles in the inflowing water is kept constant and the particle concentration in the outflowing water is determined, it is difficult in practice to maintain a constant food concentration in the experimental chamber, because the pumping rate (Dral, 1967; Wilson and Seed, 1974; Hildreth, 1976), the retention efficiency (Dral, 1967, 1968; Wilson and Seed, 1974) and, consequently, the filtration rate (Theede, 1963; Winter, 1969, 1970, 1973; Wilson and Seed, 1974) vary unpredictably, even under constant conditions. For critical reviews see Hildreth and Crisp (1976), Riisgard (1977) and Winter (1977).

To avoid at least some of these problems, Winter (1969, 1970, 1973) developed a new method for the determination of filtration rates (Fig. 3) which combines the advantages of the classical indirect method with those of a flow-through system. On the one hand, Winter ensured a homogeneous suspension by using a recirculating system by which about 3 l/min of the experimental medium are recirculated. This recirculating system has been constructed in such a way that no disturbance of the experimental animals could be observed. On the other hand, the particle concentration is kept constant at a definite predetermined food level by additions of fresh algal cells to replace those removed by the animals. The additions of fresh algal cells are automatically regulated by a photometer, thus ensuring that the particle concentration immediately around the animals is constantly monitored and kept constant within ± 1%. As fresh algal suspension is added, there is a corresponding outflow of water so that the experimental medium is continuously replaced. The flow rate of this part of the system depends on the concentration of the fresh algal suspension and the food consumption of the animals. Thus, the flow rate is partly regulated by the activity of the experimental animals, a principle which is well suited to avoid accumulation of excreted metabolites. This method is characterized by a high flexibility and makes possible reliable tests on the effects of food concentration and water current on filtration activity.

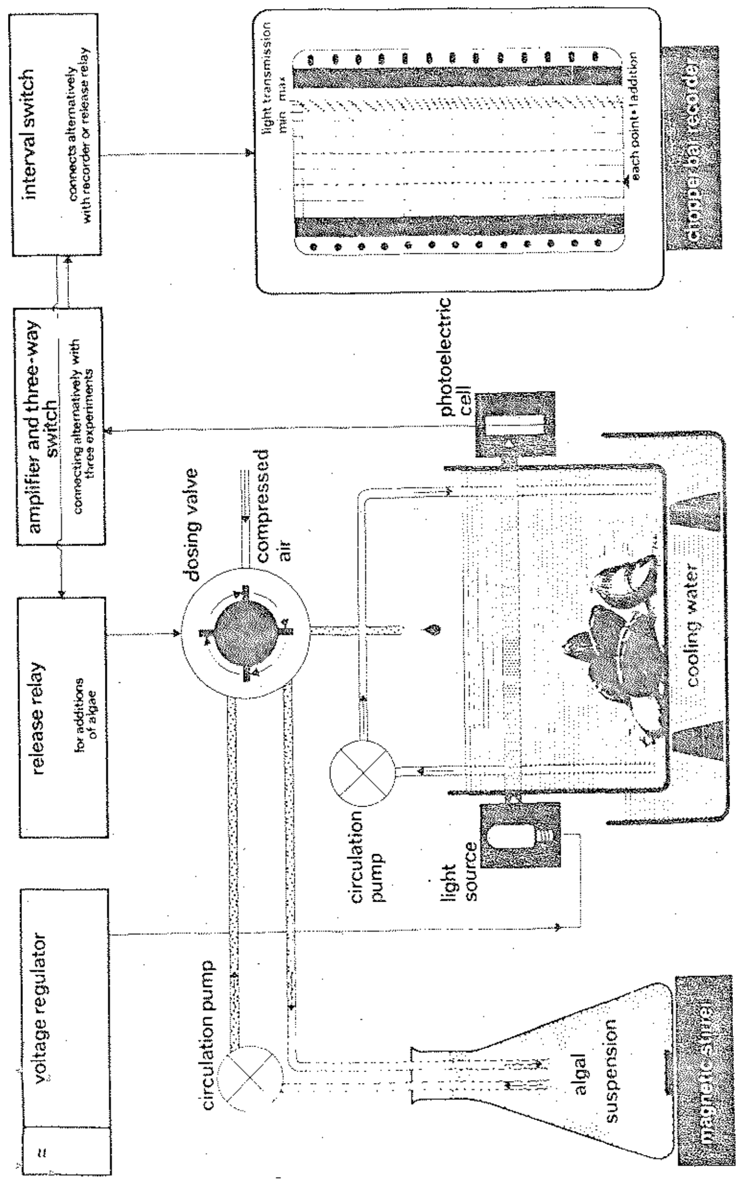

Fig. 3. Schematic diagram of the apparatus used by Winter (1973) for measuring filtration rates (from Winter, 1973).

FILTRATION RATE

Filtration rate in relation to body size

During the last 35 years, many data concerning filtration rates of filter-feeding bivalves have been recorded (for literature see Winter, 1969, 1973, 1976, 1977; Winter and Langton, 1976). It is well documented in the literature that filtration rate (F) increases with increasing body size (W; dry-tissue weight in g), following the general allometric equation $F = aW^b$. All weight specific filtration rates (F/W) in relation to body size so far recorded for *Mytilus edulis* and *M. californianus*, are summarized in Fig. 4. Weight specific filtration rates of ten further species of lamellibranchiate bivalves are represented in Fig. 5.

The values for a and b are summarized in Table I. From this Table it is obvious that many of the b-values are between 0.66 and 0.82 indicating a proportionality situated between surface area (0.67) and body weight (1.0). Low b-values such as 0.39 obtained by Thompson and Bayne (1974) in *Mytilus edulis,* clearly demonstrate a considerable underestimation of the filtration activity, especially in large individuals.

The b-values of 0.73 to 0.74 reported by Winter (1973) for *Mytilus edulis* are in accordance with those obtained by Krüger (1960) and Thompson and Bayne (1972) for oxygen consumption in *M. edulis.* These values are intermediary between 'standard' (0.616) and 'active' (0.797) metabolism; they seem to represent 'routine' metabolism, defined as the "metabolism associated with long-term feeding" (Thompson and Bayne, 1972, p. 1117). More recently, a b-value of about 0.75 has been postulated by Jørgensen (1976) on the basis

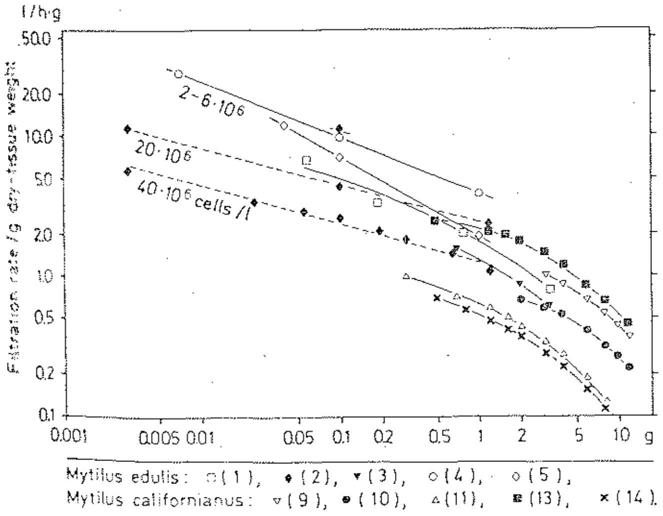

Fig. 4. Weight-specific filtration rates of *Mytilus edulis* and *Mytilus californianus* relative to body size. Detailed information, see Table I. Numbers in parentheses at bottom of figure correspond to numbers in the last column of Table I.

TABLE I

Relationship between filtration rate (F) and body size (W; dry-tissue weight) of different suspension-feeding bivalves, characterized by a and b, calculated according to the general allometric equation $F = a\,W^b$

Species/Authors	Suspension (10^6 cells/l)	Temp. (°C)	W (g)	a	b	Ref. nos.
Mytilus edulis						
Theede, 1963	Graph	15	0.058— 3.280	1.656	0.49	(1)
Winter, 1973	Duna, 20	12	0.003— 1.186	2.410	0.74	(2)
Winter, 1973	Duna, 40	12	0.003— 1.186	1.313	0.73	(2)
Willemsen, 1952	Silt	12—15	0.700— 3.100	1.273	0.38	(3)
Vahl, 1973 c	Iso + Mono, 2-6	10	0.007— 1.000	3.900	0.60	(4)
Thompson and Bayne, 1974	Tetra	15	0.050— 1.000	1.944	0.39	(5)
Jørgensen, 1949	Flag + Diat	16—19	0.147— 0.195	—	—	(6)
Jørgensen, 1960	Graph	13—14	0.195— 0.305	—	—	(7)
Jorgensen, 1975 a, b	Yeast	14	0.160— 0.170	—	—	(8)
Mytilus californianus						
Rao, 1953, Los Angeles	Graph	20	3.000—12.000	2.270	0.29	(9)
Rao, 1953, Los Angeles	Graph	16	2.000—12.000	1.162	0.37	(10)
Rao, 1953, Los Angeles	Graph	10	0.300— 2.000	0.604	0.56	(11)
Rao, 1953, Friday Harbor	Graph	16	2.000—12.000	2.069	0.27	(12)
Segal et al., 1953, Friday Harbor	Graph	21	0.500— 2.000	2.156	0.80	(13)
Segal et al., 1953, Friday Harbor	Graph	8	0.500— 2.000	0.511	0.53	(14)
Bayne et al., 1976 a	Algae, high ration	15	0.300— 5.000	1.610	0.46	(15)
Bayne et al., 1976 a	Algae, low ration	15	0.300— 5.000	1.018	0.42	(16)
Pecten irradians						
Chipman and Hopkins, 1954	Nitz + Chlam	24	0.660— 4.120	4.742	0.82	(17)
Arctica islandica						
Winter, 1969	Chlam, 20	12	0.280—10.000	1.602	0.66	(18)
Modiolus modiolus						
Winter, 1969	Chlam, 20	12	0.430— 3.950	0.929	0.74	(19)
Cerastoderma edule						
Vahl, 1973 a	Iso + Dun	10	0.024— 0.430	2.000	0.58	(20)
Chlamys opercularis						
Vahl, 1972 b	Iso + Mono	12	ca. 0.6	—	—	(21)
Mercenaria mercenaria						
Coughlan and Ansell, 1964	Dyes	18—20	0.360— 4.810	2.595	0.73	(22)
Modiolus demissus						
Kuenzler, 1961	Nitz	10	0.010—0.810	3.444	0.76	(23)
Cerastoderma lamarcki						
Sanina, 1976	Chlam + Car, 17.9	18—21	0.001— 0.031	2.722	0.74	(24—1)
Sanina, 1976	Chlam + Car, 200.5	18—21	0.002— 0.033	0.794	0.58	(24—2)
Sanina, 1976	Chlam + Car, 270	18—21	0.002— 0.033	0.308	0.57	(24—3)
Didacna longipes						
Sanina, 1976	Chlam + Car, 60.3	18—21	0.002— 0.126	0.613	0.52	(25)
Didacna trigonoides						
Sanina, 1976	Scen, 39.8	18—21	0.002— 0.157	1.324	0.75	(26)

Abbreviations: Car = *Carteria* sp.; Chlam = *Chlamydomonas* sp.; Diat = diatoms; Dun = *Dunaliella euchlora*; Duna = *Dunaliella marina*; Flag = flagellates; Graph = colloidal graphite; Iso = *Isochrysis galbana*; Mono = *Monochrysis lutheri*; Nitz = *Nitzschia closterium*; Scen = *Scenedesmus quadricauda*; Tetra = *Tetraselmis suecica*.

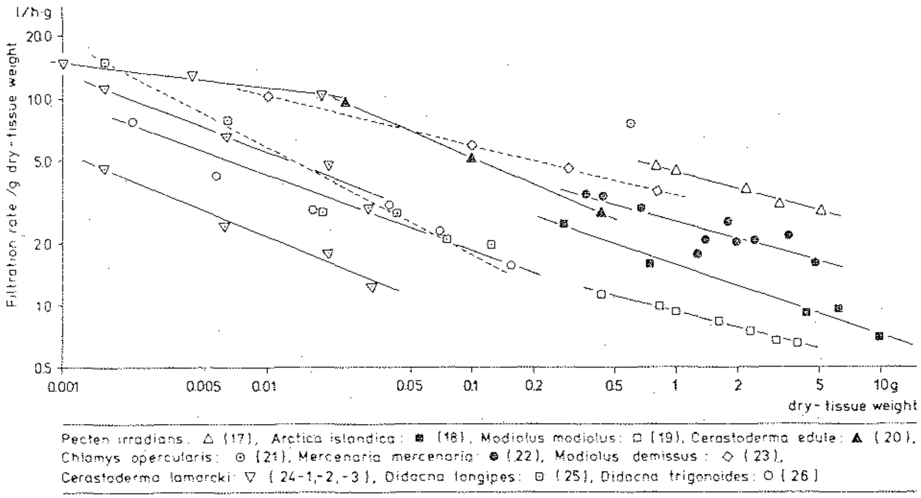

Fig. 5. Weight-specific filtration rates of various eulamellibranchiate bivalves relative to body size. Numbers in parentheses at bottom of figure correspond to numbers in the last column of Table I.

of theoretical considerations to represent the typical relationship in suspension feeding bivalves.

Filtration rate in relation to temperature

It is well known from literature that filtration rate is greatly influenced by temperature (for literature see Theede, 1963; Winter, 1969; Dame, 1972; Widdows, 1973; Wilson and Seed, 1974; Schulte, 1975; Bayne et al., 1976 c). Two of the typical curves are shown in Fig. 6, representing data obtained by Theede (1963) and Schulte (1975) for two different populations of *Mytilus edulis.* From these curves it is obvious that filtration rate increases with increasing temperatures up to an optimum temperature. With any further increase in temperature above this optimum, the filtration rate

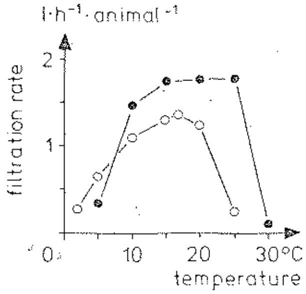

Fig. 6. Influence of different temperatures on filtration rates of *Mytilus edulis* at an algal concentration of 5 × 10^6 *Platymonas suecica* cells/l. Circles: Schulte (1975; 4 cm mussels); squares: Theede (1963; 4.5 cm mussels) (from Schulte, 1975).

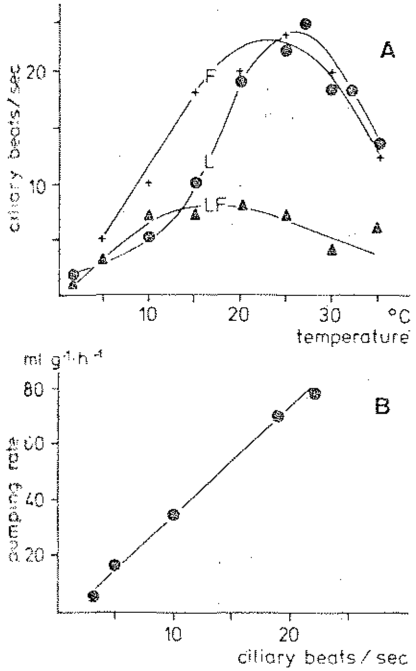

Fig. 7. (A) Beat frequency of the various gill cilia of *Crassostrea gigas* relative to temperature. L = lateral cilia; LF = eu-latero-frontal cirri; F = frontal cilia. (B) Relation between beat frequency and pumping rate of *Crassostrea gigas* (redrawn from Bernard, 1972).

decreases drastically. Almost the same temperature-related pattern (Fig. 7 A) is reflected by the beat frequency of the various types of gill cilia, and, therefore, it is not surprising that there exists a linear relationship (Fig. 7 B) between the lateral ciliary beat frequency and the rate of water transport (Bernard, 1972).

Various temperature coefficients, Q_{10}, concerning the relationships between filtration rate and temperature are summarized in Table II. From this Table it is clear that there is a great deal of variation depending on the species and the temperature range under consideration. In general, the values for Q_{10} are much higher at a lower temperature range indicating a more rapid increase in filtration activity at low temperatures.

Filtration rate in relation to food concentration

Filter-feeding activity is a function of cell concentration which has been well documented by several authors for different species of lamellibranchiate bivalves (Loosanoff and Engle, 1942, 1947; Loosanoff, 1962; Flügel and Schlieper, 1962; Schlieper, 1963; Dral, 1967, 1968; Winter, 1969, 1970, 1973, 1976, 1977; Walne, 1972, his fig. 2; Wilson and Seed, 1974; Schulte, 1975; Sanina, 1976; Epifanio and Ewart, 1977). In general, the filtration rate

TABLE II

Temperature coefficients (Q_{10}) for increase in filtration rates (l/h) by lamellibranchs (from Schulte, 1975)

Species and source	l/h	Temperature (°C)	Q_{10}	Temperature range (°C)
Arctica islandica (Winter, 1969)	2.0 4.1	4 14	2.05	4—14
Mytilus edulis (Theede, 1963)	0.620 1.330	4 14	2.15	4—14
Hiatella arctica (Ali, 1970)	0.0055 0.0341	5 15	6.2	5—15
M. edulis (Schulte, 1975)	0.353 1.751	5 15	4.96	5—15
M. edulis (Theede, 1963)	1.100 1.240	10 20	1.13	10—20
A. islandica (Winter, 1969)	3.50 4.30	10 20	1.23	10—20
H. arctica (Ali, 1970)	0.0165 0.0121	10 20	0.75	10—20
M. edulis (Schulte, 1975)	1.468 1.796	10 20	1.22	10—20
M. edulis (Schulte, 1975)	1.751 1.798	15 25	1.001	15—25
M. edulis (Schulte, 1975)	1.796 0.106	20 30	0.059	20—30

decreases with increasing cell concentrations. This indicates that bivalves regulate the amount of water filtered clear of particles in relation to food concentration. Bearing in mind the various mechanisms, which have been described with respect to a regulation of retention efficiency and pumping rate, such a regulating ability is not surprising and has to be considered as the main function of these mechanisms.

Winter (1973) showed that *Mytilus edulis* regulates the filtration rate (Fig. 8 within the range 10 × 10^6 to 40 × 10^6 *Dunaliella marina* cells/l, in such a way that the amount of algae filtered-out is more or less constant (as an average ov a period of 5 days). More recently, Sanina (1976) investigated the relationship between filtration rate and food concentration in *Cerastoderma lamarcki*, *Didacna longipes*, *Didacna trigonoides*, *Hypanis angusticostata*, and *Mytilaster lineatus*. Depending on the range of food concentrations used in the different experiments, Sanina demonstrated (Fig. 5), in accordance with the results found by Winter (1973), a very similar filter-feeding behaviour for all the species investigated. Further examples concerning these relationships have been recently summarized and discussed by Winter (1977). This summary includes the investigations carried out by Davids (1964), Ali (1970), Walne (1972), Thompson and Bayne (1972, 1974), and Foster-Smith (1975 a).

A very schematic representation of relationships between food concentration and filtration rate is given by Fig. 9. From a low threshold concentration (*A*) onwards, filtration rate increases rapidly and is then kept constant up to a food concentration (*B*) at which a maximum amount of food is ingested. As soon as this maximum ingestion rate is reached, the filtration rate decreases continuously in such a way that the amount of food ingested is kept constant (compare Lehman, 1976, his fig. 3, dashed lines; Lam and Frost, 1976, their fig. 9). This pattern remains unchanged until the food concentration (*C*) is reached at which the production of pseudofaeces begins. At still higher food concentrations (higher than *C*) however, filtration and ingestion rate are drastically reduced (see Winter, 1969, 1970, 1976).

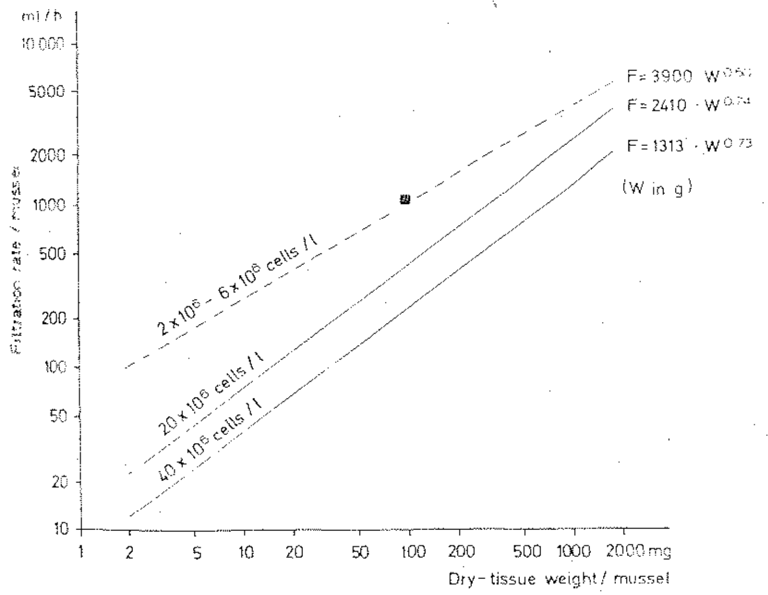

Fig. 8. *Mytilus edulis*. Filtration rate in relation to body size and food concentration. Broken line represents filtration rates determined by Vahl (1973 c) at 10°C and food concentrations within the range 2 × 10^6 to 6 × 10^6 algal cells/l, feeding a 1:1 mixture of *Isochrysis galbana* and *Monochrysis lutheri*. Solid lines represent filtration rates determined by Winter (1973) at 12°C and constant concentrations of 20 × 10^6 and 40 × 10^6 *Dunaliella marina* cells/l. The square represents the filtration rate determined by Winter (1973) at the constant concentration of 10 × 10^6 *Dunaliella* cells/l (12°C).

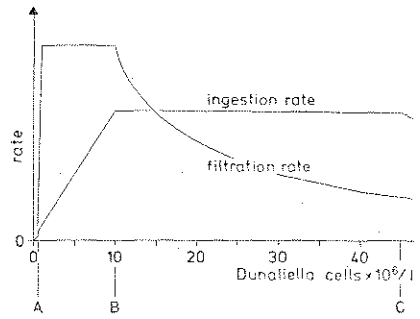

Fig. 9. Concept of the interrelationships existing between filtration rate, ingestion rate, and food concentration (12°C). For further explanations, see text.

This very clear relationship between food concentration and filter-feeding behaviour has to be taken into consideration in calculations concerning the food requirements of bivalves. Furthermore, there cannot be any question that it must be important for filter-feeders, when feeding in high concentrations of suspension, to maintain an optimum rate of ingestion.

It has already been discussed that filtration rate is an increasing function with body size. In connection with food concentration, however, it should be pointed out that small as well as large individuals of a species, at least for *Mytilus edulis*, react in the same manner to different algal concentrations (comp. Fig. 8).

The regulation of the filtration rate is not only influenced by cell concentration, expressed as the number of algal cells suspended/l, but is also a function of algal size (comp. Epifanio and Ewart, 1977). The manner in which algal size (shape) and algal concentration together influence the filter-feeding activity (Table III) is indicated by the 'pseudofaeces-free cell density', being defined as the concentration which is just below the threshold of pseudofaeces production (Loosanoff and Engle, 1947; Winter, 1969; Schulte, 1975). From Table III it is obvious that the concentration level under consideration increases with a decrease in particle size. The pseudofaeces-free cell density seems to be very close or equal to the optimum food concentration, since filtration activity is reduced to low-energy-consuming filtration rates and all algal cells filtered-out are ingested. This conclusion is of fundamental importance, especially for artificial aquaculture systems.

Filtration rate in relation to tidal rhythmicity

Fluctuations in filtration rate of sublittoral bivalves (comp. Winter, 1973) may be considerable but not related to the tidal cycle nor to any other environmental variable (see Jørgensen, 1960; Theede, 1963; Davids, 1964; Widdows and Bayne, 1971). Wilson and Seed (1974) pointed out, which is in agreement with my own observations (unpublished data), that there was no

TABLE III

Effect of algal concentration and algal size on the filtration mechanism. The data on food concentration should be regarded as indicating continuous loads. The experimental temperature was around 20°C (modified from Winter, 1969)

Authors	Species	Food	Size (μm)	Pseudofaeces-free cell density × 10^6 cells/l
Loosanoff and Engle (1947)	*Crassostrea virginica*	*Chlorella* sp.	5	450
Dean (1957)	*Crassostrea virginica*	*Chlorella* sp.	5	450
Winter (1969)	*Modiolus modiolus*	*Dunaliella* sp.	7.5 × 5	60
Winter (1969)	*Arctica islandica*	*Dunaliella* sp.	7.5 × 5	60
Schulte (1975)	*Mytilus edulis*	*Platymonas suecica*	7.2 × 9.4	35—40
Winter (1969)	*Modiolus modiolus*	*Chlamydomonas* sp.	10 × 7.5	50
Stickney (1964)	*Mya arenaria*	*Dicrateria* sp.	?	50
Davis (1964)	*Mytilus edulis*	*Phaeodactylum tricornutum*	3.2—4.2 × 19.2—27.2	30—40
Loosanoff and Engle (1947)	*Crassostrea virginica*	*Nitzschia closterium*	? (40—50)	20—30
Loosanoff and Engle (1947)	*Crassostrea virginica*	*Euglena viridis*	60	2

evidence for any intrinsic tidal rhythm in feeding. Thompson and Bayne (1972) recorded continuous feeding by *Mytilus edulis* whenever food cells above a certain threshold (food concentration above '*A*', comp. Fig. 9) were presented.

It is clear, however, that a rhythmic pattern of feeding is imposed on intertidal bivalves (Verwey, 1952; Langton and Gabbott, 1974; Langton, 1975, 1977; Mathers, 1976), but this is not to be discussed here. Intertidal mussels have to compensate, for example, for non-feeding periods by periods of increased activity. Such a compensation, however, is achieved only to a certain degree and consequently, the growth rate of mussels varies with the length of tidal exposure to air (Newcombe, 1935; Baird, 1966; Reynolds, 196 Seed, 1969).

INGESTION RATE

The amount of food ingested (per unit of time) is a function of body size, temperature, and food concentration. As long as no pseudofaeces are produce the amount of food ingested is equal to the amount of food filtered. A concep of the interrelationship between body size, food concentration, and the amount of food ingested is represented in Fig. 10. The concept is based on th data obtained by Winter (1973), feeding *Mytilus edulis* of different body sizes at various constant concentrations of *Dunaliella marina* at 12°C. The influence of temperature on the amount of food ingested can be seen from Table V.

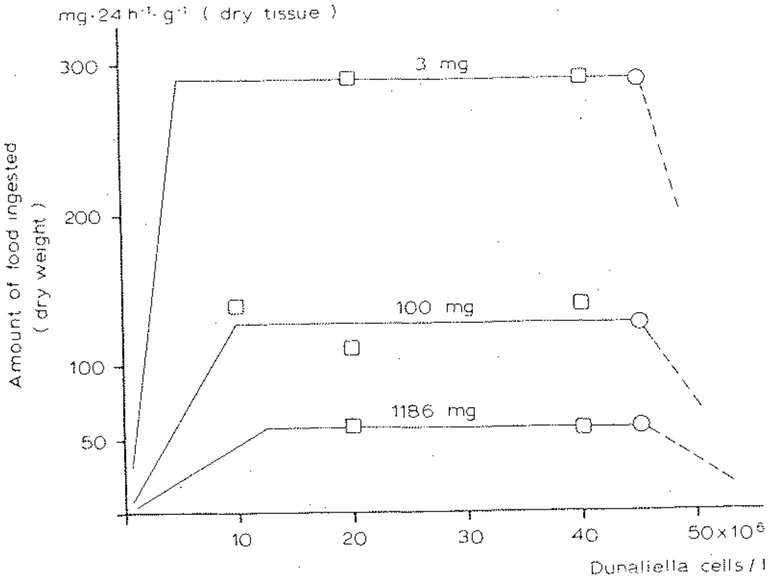

Fig. 10. *Mytilus edulis*. Concept of the interrelationships between food concentration, body size, and the amount of food ingested (as an average for 5 days, at 12°C). The representation is based on data obtained by Winter (1973), feeding *Mytilus edulis* of different body size at various constant concentrations of *Dunaliella marina*. Squares represent measured values. Circles represent the pseudofaeces-free cell density. From Vahl's data (1973 c) it appears that very small mussels are able to sustain very high filtration rates at very low food concentrations.

The daily amount of food ingested, expressed as percentage of dry-tissue weight, may be used as an ecologically relevant index of feeding activity. In Fig. 11 (solid symbols), this index of feeding activity has been plotted against body size (dry-tissue weight), and it is quite obvious from this graph that the daily amount of food ingested, expressed as percentage of body weight, increases very rapidly with a decrease in body size. This means that the relative amount of food ingested is much higher in smaller than in larger individuals. Again, this relation follows the general allometric equation (see Table VII).

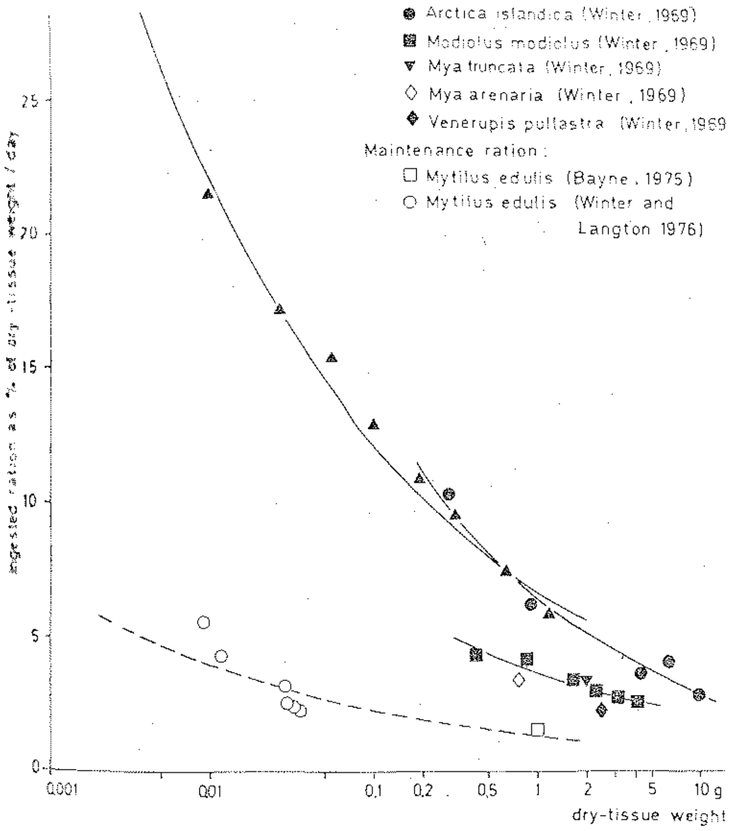

Fig. 11. Relationship between ingested ration (expressed as percentage of dry-tissue weight/day) and body size (dry-tissue weight). Experiments were carried out at 12°C and various food concentrations, over periods of up to 5 days. Maintenance ration, expressed as percentage of dry-tissue weight/day, in relation to body size (dry-tissue weight) is presented by the dashed line. The data are based on a feeding period of one month. For further details, see Winter and Langton (1976).

OXYGEN CONSUMPTION

Oxygen consumption is a good measure of metabolic activity related to various biotic and abiotic parameters, including the physiological condition of the animal under consideration.

The rate of oxygen uptake (Fig. 12) increases with increasing body size (see Jørgensen, 1976), a function that may also be described by the general allometric equation (Table VII). Furthermore, oxygen consumption increases with increasing temperature (Fig. 12) up to an optimum temperature, generally reflecting the situation which has already been described for filter-feeding activity (Fig. 6). Further details on oxygen consumption in bivalve molluscs are summarized in a comprehensive review by Bayne et al. (1976 c).

ASSIMILATION EFFICIENCY

The amount of food assimilated expressed as percentage of the amount of food ingested, is defined as assimilation efficiency. Assimilation efficiency depends, above all, on the quality and quantity of the food ingested. The following statements are based on a constant food quality with regard to the digestibility of the food.

Assimilation efficiency in relation to body size

From Table IV it is obvious that for *Modiolus modiolus* (Winter, 1969) and *Mytilus edulis* (Vahl, 1973 c) the assimilation efficiency remains more or less constant within the range of body size investigated. This means that in *Modiolus* and *Mytilus* the filtration rate and/or the amount of food ingested are regulated in such a way that the assimilation efficiency is independent of body size. The same holds true for *Arctica islandica* (Winter, 1969) up to a body size of about 4.4 g dry-tissue weight; the average assimilation efficiency up to this size is about 70%. Larger individuals show a considerable reduced assimilation efficiency averaging about 46%. Also for *Modiolus modiolus* a slight effect of body size on assimilation efficiency seems to exist, but it should really be investigated further. Further data on assimilation efficiency are summarized in Table IV. Compare also *b*-values in Table VII.

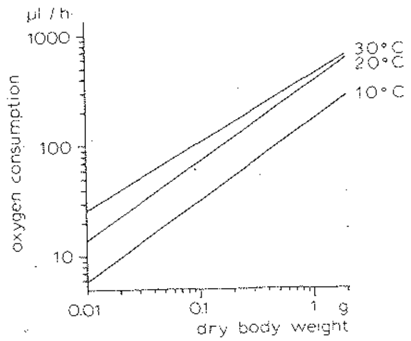

Fig. 12. *Crassostrea virginica.* Oxygen consumption in relation to body size (dry-tissue weight) and temperature (from Dame, 1972).

Assimilation efficiency in relation to temperature

Assimilation efficiencies for *Modiolus modiolus* and *Arctica islandica* in relation to temperature are shown in Table V. In general, from this Table it is clear that there is no significant increase in assimilation efficiency within the temperature range 4 to 12°C. Thus, the filtration rate and/or the amount of food ingested are regulated in such a way that assimilation efficiency is not only more or less independent of body size, but also independent of temperature. However, at the high temperature of 20°C, which is not experienced by these species in their natural environment (German Bight), the assimilation efficiency is significantly higher than at the lower temperatures.

Assimilation efficiency in relation to food concentration

There is a considerable degree of confusion when considering assimilation efficiency in relation to food concentration. There should not be any question that assimilation efficiency is primarily correlated with the amount of food ingested. When, however, the filtration rate and ingestion rate are related to food concentration in such a manner that at different food concentrations (within the range from '*B*' to '*C*', comp. Fig. 9) constant amounts of food are ingested, then it is not surprising that these equal amounts of food are assimilated with the same efficiency. When this situation is found, for example in the experiments carried out by Winter (1973) with *Mytilus edulis*, then assimilation efficiency is independent of food concentration. For further information see Winter (1977).

Moreover, from Fig. 13 it may be seen that with an increase in temperature there is a shift towards higher food concentrations at which maximum amounts of food are assimilated, and an increase in the range of concentration within which maximum amounts of food are assimilated.

GROWTH

It is not the aim of this section to present a comprehensive summary of all the growth data so far obtained, but to describe at least some of the relationships existing between food concentration, ration of food ingested and growth.

Growth as a function of ingested food ration

One of the main factors influencing growth is the amount of food ingested. From feeding experiments carried out by Winter and Langton (1976) with

TABLE IV

Assimilation efficiency in different suspension-feeding bivalves, at different food concentrations of various unicellular algal cultures and at different temperatures (Amount of food ingested = 100%)

Species/Authors	Dry-tissue weight (g)	Food	Algal concentration (10^6 cells/l)	Temp. (°C)	Method	Assimilation efficiency (%)
Modiolus modiolus						
Winter, 1969	2.31	Chlam	10	20	Biuret	90.4
	2.31	Chlam	20	20	Biuret	92.9
	2.31	Chlam	40	20	Biuret	94.2
	0.43	Chlam	20	12	Biuret	90.2
	0.84	Chlam	20	12	Biuret	90.0
	1.63	Chlam	20	12	Biuret	83.9
	2.31	Chlam	20	12	Biuret	82.5
	3.10	Chlam	20	12	Biuret	84.7
	3.95	Chlam	20	12	Biuret	85.2
Arctica islandica						
Winter, 1969	4.40	Chlam	10	12	Biuret	88.1
	4.40	Chlam	20	12	Biuret	67.2
	4.40	Chlam	40	12	Biuret	61.9*
	0.28	Chlam	20	12	Biuret	74.6
	0.92	Chlam	20	12	Biuret	68.8
	4.40	Chlam	20	12	Biuret	67.2
	6.28	Chlam	20	12	Biuret	47.8
	10.00	Chlam	20	12	Biuret	43.3
Mya truncata						
Winter, 1969	2.02	Chlam	20	12	Biuret	72.9
Mya arenaria						
Allen, 1962	76**	Phaeo	30—60	17—18	^{32}P	80.0*
Winter, 1969	0.74	Chlam	40	12	Biuret	82.0
Cerastoderma edule						
Winter, 1969	0.95	Chlam	20	12	Biuret	83.2
Venus striatula						
Allen, 1962	21**	Phaeo	30—60	17—18	^{32}P	90.0*
Dreissena polymorpha						
Mikheyev and Sorokin, 1966	8—28**	Chlo	?	?	^{14}C	30.0*
	8—28**	Bac	?	?	^{14}C	49.0*
Mytilus edulis						
Winter, 1969	0.88	Duna	20	12	Biuret	71.9
Widdows and Bayne, 1971	?	Tetra	1.5	5—15	Conover's ratio, 1966	84 ± 4
	?	Tetra	5.5	5—15		69 ± 5
Vahl, 1973	0.007 —1.0	Iso + Mono	2—6	10	Conover's ratio	78.2
Tenore and Dunstan, 1973 a	0.47	Phyto	?	19—21	Carbon	73.4
Mercenaria mercenaria						
Tenore and Dunstan, 1973 a	0.84	Phyto	?	19—21	Carbon	74.7
Crassostrea virginica						
Tenore and Dunstan, 1973 a	0.59	Phyto	?	19—21	Carbon	83.7

Abbreviations: Bac = various Bacteria; Chlam = *Chlamydomonas* sp.; Chlo = *Chlorella* sp.; Duna = *Dunaliella marina*; Iso = *Isochrysis galbana*; Mono = *Monochrysis lutheri*; Phaeo = *Phaeodactylum* sp.; Phyto = Phytoplankton; Tetra = *Tetraselmis suecica*.

* Amount of food filtered = 100%

**Shell length in mm.

TABLE V

Assimilation efficiency in relation to the amount of food ingested and temperature (data from Winter, 1969)

Species	Temperature (°C)	Amount of food ingested (mg/day)	Assimilation efficiency (%)
Modiolus modiolus	4	33.5	77.5
(2.31 g dry-tissue	12	70.4	82.5
weight)	20	101.5	92.9
Arctica islandica	4	80.4	67.3
(4.40 g dry-tissue	12	161.3	67.2
weight)	20	172.7	83.6

Mytilus edulis over periods of 3 months (Fig. 14), it is quite obvious that with increasing amounts of food available (= ingested), there is an increase in growth rate (see also Winter, 1974; Langton et al., 1977).

Since all the feeding levels in Fig. 14 were below the level necessary to cause the production of pseudofaeces, the gross growth efficiency (Fig. 15) also reflects the increase in dry-tissue weight with increasing ration. The gross growth efficiency is defined as the increase or decrease in body weight, expressed in percentage of the amount of food ingested. The gross growth efficiency (Fig. 15) increased from a negative value of −2.8 at a ration of 0.78 mg dry weight of algal cells/mussel/day to a maximum of 28.0 at a ration of 3.00 mg dry weight of algal cells/mussel/day.

Data on gross growth efficiency (K_1), however, vary between and within species depending on animal size (Jørgensen, 1976) and on the quantity and quality of food ingested, as well as on the different methods used for measuring it. For small oyster spat of 0.12 to 0.45 mg dry-meat weight, Walne and Spencer (1974; on the basis of dry weight measurements) calculated the gross growth efficiency to lie between 10 and 20%. Thompson and Bayne (1974; on the basis of calories) calculated values of K_1 varying from −3.0 to 42.0% for mussels (*Mytilus edulis*) ranging from 100 to 2000 mg when maintained at an intermediate food level. Tenore et al. (1973; on the basis of organic carbon) compared gross growth efficiencies for different sized bivalves and found it to vary from 10.0% for *Mytilus edulis* (258 mg dry-meat weight) to 26.7% for *Mercenaria mercenaria* (737 mg). More recently, Langton et al. (1977; on a protein-N basis) calculated values of K_1 from 33.3 to 49.6% for small individuals of *Tapes japonica* (initial dry-meat weight, 32.4 mg). These relatively high values, for example, are not surprising because high values are to be expected when calculating gross growth efficiency on a protein-N basi

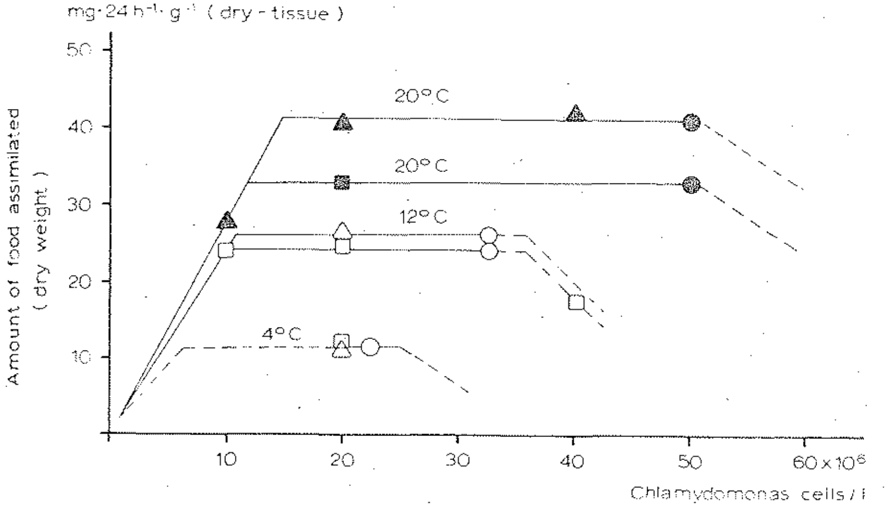

Fig. 13. Concept of the interrelationships between temperature, food concentration and the amount of food (protein) assimilated. The representation is based on data obtained by Winter (1969), feeding *Arctica islandica* (squares) and *Modiolus modiolus* (triangles) at different constant food concentrations (*Chlamydomonas* sp.) and different temperatures. Circles represent the pseudofaeces-free cell density. A direct comparison of the amounts of food assimilated is not possible because animals of different body size were used in these experiments (*A. islandica*, 4.40 g dry-tissue weight; *M. modiolus*, 2.31 g).

Maintenance ration as a function of body size

The maintenance ration, which is equivalent to a gross growth efficiency of zero, is a function of body size. From Fig. 11 it is obvious that maintenance ration, expressed as percentage of dry-tissue weight, amounts to about 5% for very small mussels (at 12°C) with an average dry-tissue weight of 3 mg, while a 1 g mussel only needs 1.5% of its dry-tissue weight (Bayne, 1975) to maintain body weight. The higher percentage for small individuals indicates their relatively high metabolic rate. The knowledge of maintenance ration (as a function of body size and temperature) is of great importance with respect to aquaculture efforts. As long as the amount of food which is given to the mussels is above the level of maintenance ration, growth will be achieved.

Growth under different feeding regimes

From growth experiments carried out with *Mytilus edulis* over the period of one month, Winter and Langton (1976; see also Langton and McKay, 1976) found that growth is not only influenced by the total amount of food presented. Line ‘A’ in Fig. 16 represents the growth rate obtained at constant food concentrations (food supply according to the filter-feeding activity). In ‘B’ the same amounts of food/day were given to the animals at 1-h intervals (by

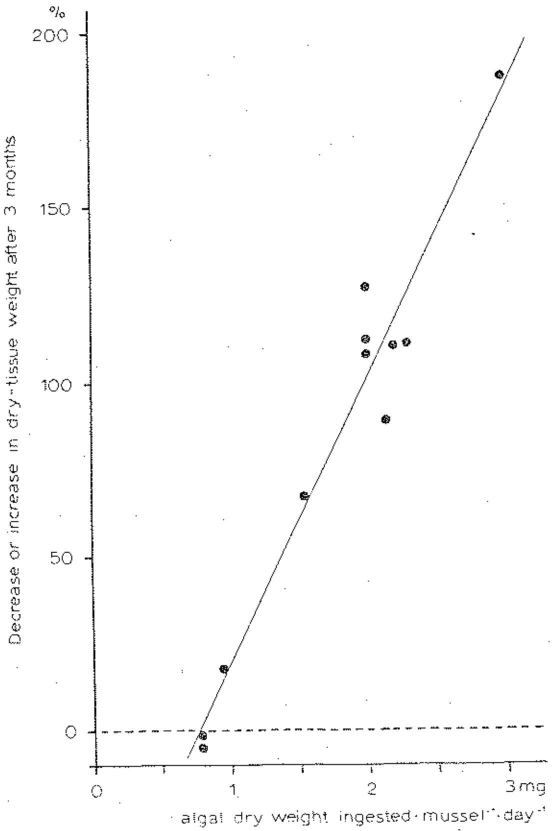

Fig. 14. Decrease or increase in dry-tissue weight for *Mytilus edulis* relative to the amount of food ingested over 3-month periods. For further details, see Winter and Langton (1976).

24 equal food additions/day), while in 'C' the same amounts of food were given by 6 food additions/day, that is at 4-h intervals. The results of these feeding experiments are calculated and summarized in Table VI. From this Table it can be seen that at constant food concentrations the increase in dry-tissue weight after one month is more or less twice as high as the growth obtained at either of the other two feeding regimes. These results point out the great importance of a continuous food supply, a fact that should be taken into consideration whenever artificial aquaculture systems will be established (comp. also Kirby-Smith and Barber, 1974).

The differences in growth, obtained by the different feeding regimes, are primarily the result of the filter-feeding behaviour of the mussels at different food concentrations. In the feeding experiments at constant food concentratio it is always guaranteed,

(a) that the cell concentration is high enough, at least above food concentration '*B*' in Fig. 9,

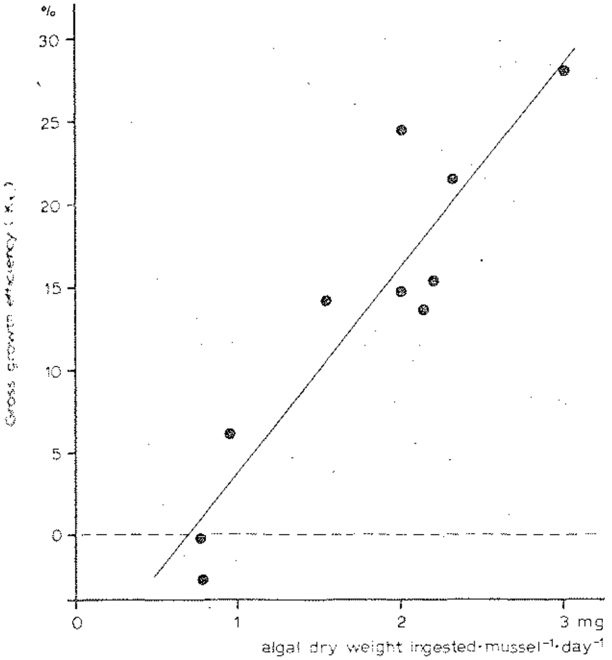

Fig. 15. Gross growth efficiency (K_1) of *Mytilus edulis* as a function of the ingested ration over a 3-month period (from Winter and Langton, 1976).

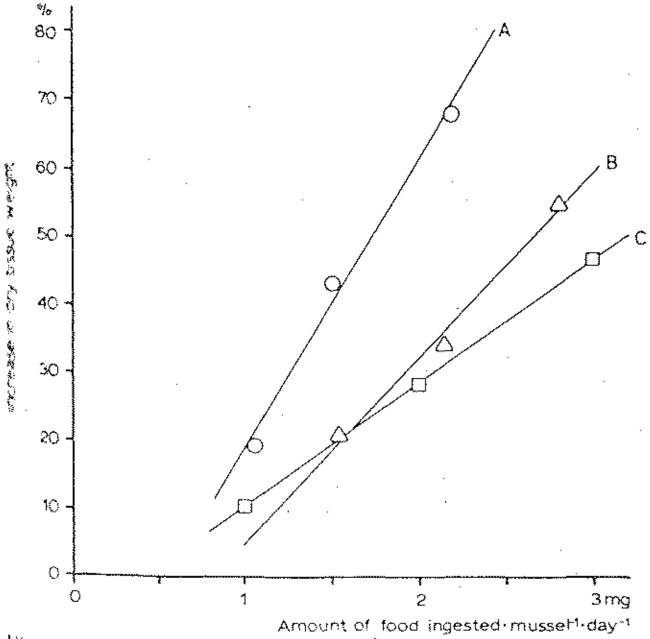

Fig. 16. Growth of *Mytilus edulis* under different feeding regimes. Feeding at constant cell concentrations (A), or at 1-h (B) and 4-h (C) intervals, respectively. For further details, see Winter and Langton (1976).

(b) that there are no periods of rest in filter-feeding (food concentration not below '*A*' in Fig. 9),

(c) that no formation of pseudofaeces (loss of food and organic material in the form of mucus) takes place (food concentration below 'C' in Fig. 9), and

(d) that a more or less steady food intake and, consequently, food digestion is possible.

The relatively low growth rate at the highest food level, when feeding at 4-h intervals, is caused by an accumulation of food within the tanks from feeding period to feeding period (concentration finally above 'C'). At the lowest food level, feeding at 4-h intervals seems to be more economical than feeding at 1-h intervals because the concentration is not so greatly reduced that a sufficient amount of food can be obtained only at maximum filtration activity.

Influence of suspended silt on growth

From Fig. 17 A it is obvious that the filter-feeding activity of *Mytilus edulis* fed with unicellular algal cells within the range of optimal food concentration (from 20 × 10^6 to 40 × 10^6 *Dunaliella marina* cells/l; at 12°C), is highly stimulated by low quantities of suspended silt (12.5 mg dry-weight/l) over long periods of time (Winter, 1976). As a consequence of this, more food is ingested and better growth is obtained per unit of time (Fig. 17 B and C). The highest increase in dry-tissue weight (88.8% after 26 days) was obtained at suspended silt and the medium cell concentration of 40 × 10^6 *Dunaliella marina* cells/l. This increase in dry-tissue weight was increased by 32%, compared with the corresponding increase obtained at the same food concentration, but without suspended silt (for further details and discussion see Winter, 1976; comp. also Loosanoff, 1962; Murken, 1976). Such an acceleration of growth is of fundamental importance for culturing mussels, especially in colder regions, where overwintering is necessary and costly.

TABLE VI

Comparison of three feeding regimes administered to *Mytilus edulis* on the basis of the calculated regression lines (see Fig. 16). Feeding at constant cell concentrations (A) or at 1-h (B) and 4-h (C) intervals, respectively (data from Winter and Langton, 1976)

Amount of food ingested/ mussel/day (dry weight) (mg)	Increase in dry-tissue weight (in % of the initial dry-tissue weight)		
	Experiment		
	A	B	C
1	18.8	4.9	10.4
2	61.0	31.9	28.4
3	101.1	59.0	46.4

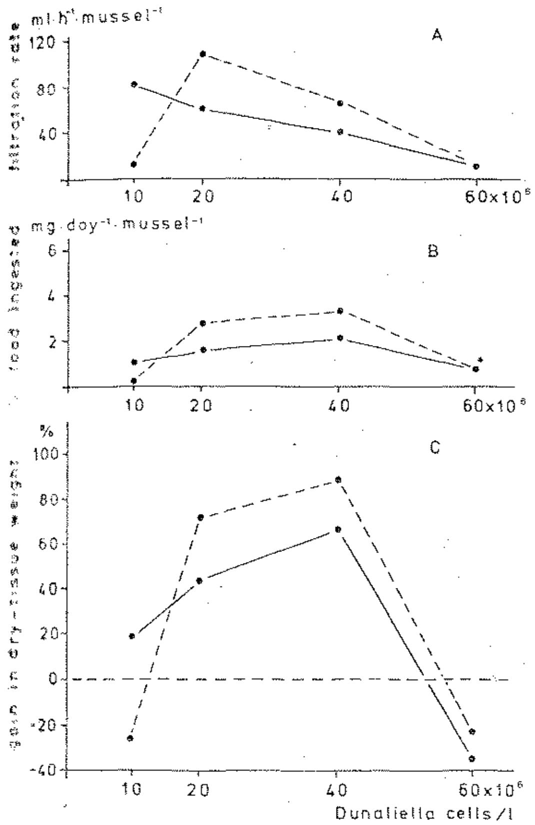

Fig. 17. Feeding experiments with *Mytilus edulis* at constant concentrations of *Dunaliella marina* and suspended silt (12.5 mg dry weight/l) over 26-day periods, at 12°C and a salinity of 25‰. The filtration rate (A), the amount of food ingested (B), and the decrease or increase in dry-tissue weight (C) are presented as a function of food concentration. Solid lines represent experiments with *Dunaliella*, broken lines with *Dunaliella* and silt as food suspension. For further details, see Winter, 1976. (*Pseudo-faeces included).

CONCLUSIONS

The relationships between body size and filtration rate, ration ingested, oxygen consumption, ration assimilated, rate of excretion, and maintenance ration follow the general allometric equation (Table VII). Quantifications of this kind make possible useful predictions for the culture of economically important species. The knowledge of maintenance ration in relation to body size and temperature may be used as a deciding factor for calculating the amount of food necessary for growth in artificial mussel culture systems or for the selection of suitable sites with respect to aquaculture efforts in the field. On the other hand, high food concentrations result in the production of pseudo-faeces, represent a loss of potentially utilizable algal cells and organic matter in the form of mucus, and increase the risk of fouling. For maximal

TABLE VII

Relationships between metabolism and body size, following the general allometric equation $R = aW^b$, where R = rate or ration under consideration; W = body size (dry-tissue weight in g); a and b are constants. Indices attached to R indicate food concentration (× 10^6 cells/l), to a indicate temperature (in °C)

A. Rate of filtration (l/h)

Mytilus edulis	(1)	FR_{2-6}	$= 3.900_{10}\ W^{0.60}$
	(2)	FR_{20}	$= 2.410_{12}\ W^{0.74}$
	(3)	FR_{40}	$= 1.313_{12}\ W^{0.73}$
Modiolus modiolus	(4)	FR_{20}	$= 0.929_{12}\ W^{0.74}$
Cerastoderma edule	(5)	FR	$= 2.000_{10}\ W^{0.58}$
Arctica islandica	(6)	FR_{20}	$= 1.602_{12}\ W^{0.66}$
Pecten irradians	(7)	FR	$= 4.742_{24}\ W^{0.82}$
Didacna trigonoides	(8)	FR_{40}	$= 1.324_{20}\ W^{0.75}$
Mytilus californianus	(9)	FR	$= 1.610_{15}\ W^{0.46}$

B. Gill area (cm²)

Mytilus edulis	(1)	GA	$= 34.34\ W^{0.65}$

C. Ration ingested per day as % of W (%)

Mytilus edulis	(1)	IR_{20-40}	$= 6.680_{12}\ W^{-0.26}$
Modiolus modiolus	(2)	IR_{20}	$= 3.710_{12}\ W^{-0.26}$
Arctica islandica	(3)	IR_{20}	$= 6.450_{12}\ W^{-0.34}$

D. Rate of oxygen consumption (ml O_2/h)

Mytilus edulis	(1)	OR	$= 0.370_{10}\ W^{0.75}$
	(2)	OR	$= 0.320_{15}\ W^{0.70}$
	(3)	OR	$= 0.550_{15}\ W^{0.77}$
Mytilus californianus	(4)	OR	$= 0.630_{19}\ W^{0.84}$
	(5)	OR	$= 0.540_{13}\ W^{0.65}$
Cerastoderma edule	(6)	OR	$= 0.370_{10}\ W^{0.77}$

E. Ration assimilated as % of food ingested (%)

Mytilus edulis	(1)	AR_{2-6}	$= 78.16_{10}\ W^{-0.02}$
Modiolus modiolus	(2)	AR_{20}	$= 87.49_{12}\ W^{-0.04}$
Arctica islandica	(3)	AR_{20}	$= 66.31_{12}\ W^{-0.14}$

F. Rate of excretion of ammonia-nitrogen (μg/h)

Mytilus californianus	(1)	ER_{NH_4}	$= 23.88_{13}\ W^{0.82}$

G. Ration of maintenance per day as % of W (%)

Mytilus edulis	(1)	MR	$= 1.280_{12}\ W^{-0.25}$

References: A/1, Vahl, 1973 c; A/2, A/3, Winter, 1973; A/4, Winter, 1969; A/5, Vahl, 1973 a; A/6, Winter, 1969; A/7, Chipman and Hopkins, 1954; A/8, Sanina, 1976; A/9, Bayne et al., 1976 a; B/1, Vahl, 1973 c; C/1, Winter, 1973; C/2, C/3, Winter, 1969; D/1, Vahl, 1973 c; D/2, Krüger, 1960; D/3, Bayne et al., 1973; D/4, Wheden and Sommer, 1937; D/5, Bayne et al., 1976 a; D/6, Vahl, 1973 a; E/1, Vahl, 1973 c; E/2, E/3, Winter, 1969; F/1, Bayne et al., 1976 b; G/1, Winter, 1977.

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growth, mussels should be maintained at a constant optimum food level, by replacement of food removed in unit time. The filter-feeding activity is highly stimulated by low quantities of suspended silt resulting in better growth per unit time. Such an acceleration of growth is of fundamental importance for culturing mussels, especially in colder regions where overwintering is necessary. With respect to aquaculture the application of these principles would result in increased efficiency and reduced costs of plant production.

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