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Physiological energetics of mussel larvae *(Mytilus edulis)*. II. Food uptake

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ABSTRACT: Food uptake of marine mussel larvae (*Mytilus edulis* L.) was estimated in relation to larval size, temperature (6, 12, 18 °C) and food concentration (1, 2, 5, 10, 20 and 40 *Isochrysis galbana* cells μl^{-1}). Filtration rates were maximal at low food concentrations (between 1 and 5 cells μl^{-1}). This was called 'filtration capacity' and expressed as a function of larval size. Ingestion rates reached a plateau with increasing food concentration above 10 cells μl^{-1}. Maximum rates were called 'ingestion capacity' and expressed as weight and volume of particles passed through the gut. When previously starved larvae enter a food suspension of more than 10 cells μl^{-1}, ingestion rate overshoots the ingestion capacity level for up to 1.5 h at 12 °C. This is caused by filling of the gut, because it was not paralleled by an overshoot of the filtration rate above the filtration capacity level. Particles between 1 and 9 µm diameter were taken up, with maximum retention efficiency at about 3.5 µm particle diameter.

INTRODUCTION

Food uptake of filter feeders can be characterized by their filtration and ingestion rate. These vary with many environmental factors. Among them, food concentration is of outstanding importance. With food concentration as a variable, filtration and ingestion rates interact in a particular way. Basic features have been outlined, e.g. by Winter (1978) for adult bivalves.

Planktonic larvae of the marine mussel *Mytilus edulis* must take up food in order to complete their development. They are referred to as planktotrophic according to the classifications of Thorson (1946, 1950), Ockelmann (1965) and Mileikovsky (1971). They are filter feeders and catch their food by means of the velum which at the same time effects swimming. Strathmann et al. (1972) described the feeding apparatus as 'opposed band system'; by means of 2 ciliary bands the food particles are brought into a food groove which lies between them. There the food is ensnared and transported to the mouth.

Feeding of bivalve larvae (especially oyster larvae) has been frequently estimated in aquaculture systems. Experiments were thus conducted at rather high food concentrations and ecologically unrealistic high temperatures with regard to temperate zones (e.g. Jørgensen, 1943; Walne, 1956, 1965, 1966; Wilson, 1980 and Gerdes, 1983).

The first to report feeding rates of *Mytilus* larvae was Bayne (1965). However, interpretation of his data suffers from the high food densities at which he worked (Riisgård et al., 1980). More recent estimates have been aware of this problem (Riisgård et al., 1981; Jespersen and Olsen, 1982).

Here, ingestion and filtration rates have been examined at various food concentrations and larval sizes at three ecologically realistic temperatures. This is the second paper in a series of 4 whose aim is to examine important components of the energy budget of mussel larvae.

MATERIALS AND METHODS

Food uptake

Food uptake was estimated with laboratory-reared larvae. Rearing procedure is described by Sprung (1984a). In order to relate data of food uptake to those of growth and respiration described by Sprung (1984a, b), conditions were standardized with respect to temp-

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erature (6, 12 and 18 °C) and food concentration (1, 2, 5, 10, 20 and 40 *Isochrysis* cells μl^{-1}).

The basic experimental procedure has been adopted from Riisgård et al. (1980). Experiments were conducted in temperature-constant rooms at artificial light. If the experimental temperature deviated from that of rearing, the larvae were adapted to it over 3 to 6 d. The larvae were starved 2 d before the experiment in order to provide uniform conditions.

Feeding rates were estimated in beakers with about 800 ml 0.45 µm filtered seawater (salinity: 29 to 33 ‰). They were aerated in order to provide mixing. Algal concentrations were checked by means of 20 ml samples. They were removed from the well-mixed culture vessel by means of a pipette and counted 5 times in a Coulter Counter (Model TA_{II}, 100 µm tube). Besides the experimental beaker a blank of similar algal concentration without larvae was examined.

Data were evaluated by a regression line described by the formula:

$$\text{Ingestion rate} = -\frac{\bar{c}}{L} \times \left(\frac{d \ln c_i}{d t} - \frac{d \ln c_b}{d t}\right) \quad (1)$$

where c = Algal concentrations in experiment (c_i) and blank test (c_b); at least 6 data points were evaluated after an appropriate adaptation period to the food concentration right at the beginning. In some cases algae had to be added anew during the experiment, if the actual concentration drifted too far away from the desired standard concentration. t = Time; algal concentration was estimated in intervals of half to several hours. L = Larval density; it lay between 1 (large mussels) and about 20 (small mussels) ml^{-1}; large mussels were counted individually; larval densities of the smaller ones were estimated by sampling 16 times 1 ml from the experimental beaker. $\bar{c}$ = Arithmetic mean of all cell concentrations estimated for a regression line; the otherwise logical geometric mean would have stressed the underestimation of the algal concentration which influences food uptake. Due to digestive processes it is the food condition some time before which influences the feeding behaviour rather than the actually registered.

Retention efficiency

Filtration rate was estimated simultaneously for different size fractions by means of a Coulter Counter. The experimental setup was basically the same as for the food uptake. At the beginning of the experiment a suspension with about the same volume (product of particle number and particle volume) for each size fraction was mixed. For this the following particles were used: a coccolithophoride (Ø 9 to 14 µm) *Isochrysis* (Ø 3 to 7 µm), Chlorella (Ø 2.8 to 5.7 µm) and unspecific particles in the seawater (< 3 µm). Filtration rates were compared with a blank test. The channel of the Coulter Counter with the highest rate was defined as 100 %

Two spectra of this kind have been recorded: one at 12 °C (2 data points evaluated for each channel), the other at 18 °C (3 data points evaluated for each channel). The data were fitted by the least square method to a second order polynomial equation. Subsequently the maximum was corrected to 100 %. As no differences were to be expected, both graphs have been included in one.

RESULTS

Retention efficiency

Retention efficiency was maximal at a particle diameter of 3.5 µm (Fig. 1). Particles down to 1 µm diameter were retained with declining efficiency. The maximum ingestable particle size lay at about 9 µm diameter. In an additional experiment it could be demonstrated that the alga *Scripsiella faeröense* (diameter: about 20 to 25 µm) could not be ingested. The larvae had permanently empty guts.

Food uptake

For comparison with data of growth and respiration, the data on food uptake had to be transformed twice: (1) To bring them exactly to the standard food concentration (see 'Materials and Methods'), the data were interpolated in a plot of ingestion rate versus food concentration for each larval size tested (Fig. 2). The graphs have been fitted by eye, because all mathematical descriptions tested implied artificial trends. (2) Data from this plot (Table 2) were related to shell length for each standardized food concentrations and fitted with an allometric equation. The constants are given in Table 3. Calculations in subsequent papers are based on these equations.

Filtration

Filtration rates were calculated from the ingestion rates in Fig. 2 for the standard food concentrations:

$$\text{Filtration rate} = \frac{\text{Ingestion rate}}{\text{Particle concentration}} \quad (2)$$

The typical interrelation between filtration and ingestion has been described in Fig. 3: the ingestion

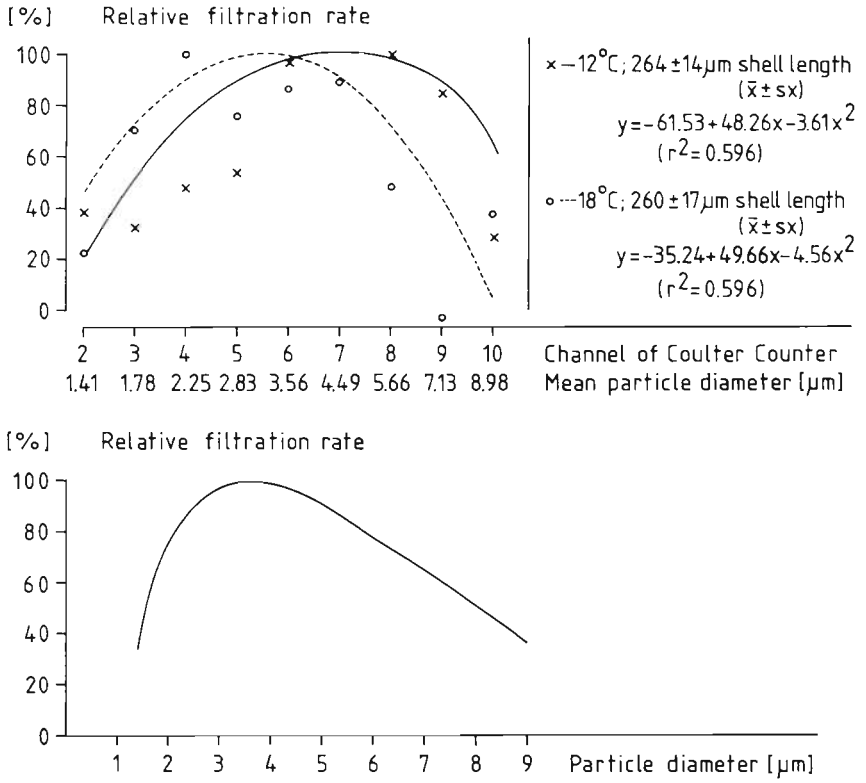

Fig. 1. *Mytilus edulis*, larvae. Size spectrum of particle retention; upper diagram: 2 spectra and their original data; lower diagram: mean of both spectra corrected to a maximum of 100 %: $y = -49.31 + 49.89x - 4.17x^2$. x: channel of Coulter Counter; y: retention efficiency (% of the maximum); r^2: correlation coefficient

rate increases until attaining a plateau at 10 *Isochrysis* cells μl^{-1}. The filtration rate decreases with the particle concentration at higher *Isochrysis* densities. At low particle concentrations, the trend is reversed. The latter phenomenon has been interpreted as an experimental artifact (see 'Discussion').

Maximum filtration rates are considered an estimate of the filtration capacity (marked in Table 1). For 2 reasons this assumption must be valid: first of all the amount of food ingested is probably not yet limiting for the food uptake, because a plateau in the ingestion rate has not yet been attained (Fig. 2). Secondly, the cell size of *Isochrysis* (mean diameter estimated as 4.6 µm with a Coulter Counter) is retained with nearly maximum efficiency. Estimates of the filtration capacity at different temperatures and larval sizes have been graphically displayed in Fig. 4.

Table 1. *Mytilus edulis*, larvae. Filtration rates at various shell lengths, food concentrations (*Isochrysis* cells μl^{-1}) and temperatures; data from Fig. 2; maximum values are marked

Temperature	Shell length (µm)	Filtration rate ($\mu l\ h^{-1}$) 1 c. μl^{-1}	2 c. μl^{-1}	5 c. μl^{-1}	10 c. μl^{-1}	20 c. μl^{-1}	40 c. μl^{-1}
6 °C	139	5.0	*5.5*	3.6	2.3	1.6	0.8
	196	6.0	*15.5*	8.4	3.7	1.7	0.8
	261	7.0	*24.0*	12.6	8.3	5.1	3.4
12 °C	141	15.0	*19.0*	13.8	6.6	2.9	1.2
	187	10.0	18.0	*19.4*	13.0	8.5	3.8
	219	17.0	*37.5*	19.8	11.3	6.1	3.2
	229	40.0	45.0	*69.8*	36.6	17.0	6.3
	251	25.0	43.5	*73.0*	42.2	19.9	6.9
	286	37.0	*85.0*	72.6	35.7	15.8	6.3
18 °C	156	*19.0*	15.5	12.4	8.2	4.4	2.1
	186	–	–	*50.0*	25.0	12.5	6.3
	195	*37.0*	*28.6*	19.4	11.1	6.1	3.2
	245	5.0	35.0	*42.0*	34.0	21.5	11.0

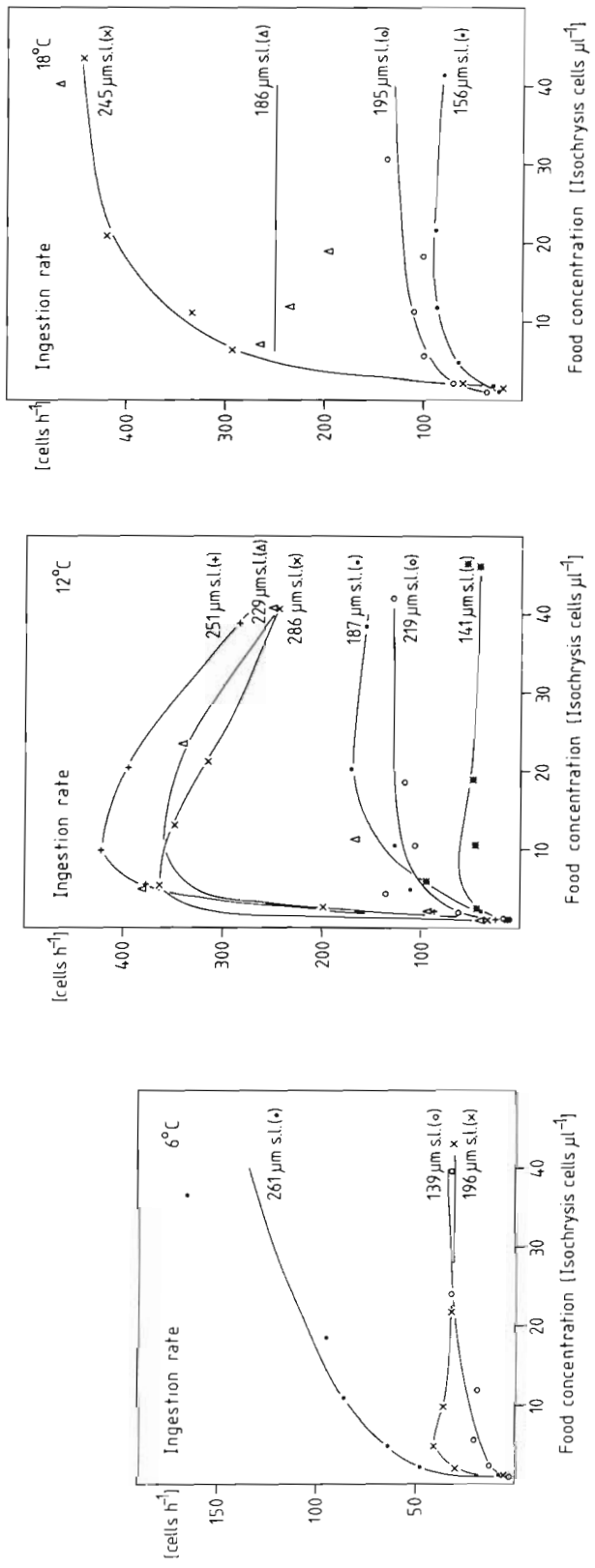

Fig. 2. *Mytilus edulis*, larvae. Estimates of the ingestion rate at various food concentrations, temperatures and larval sizes (s.l.: shell length); curves fitted by eye

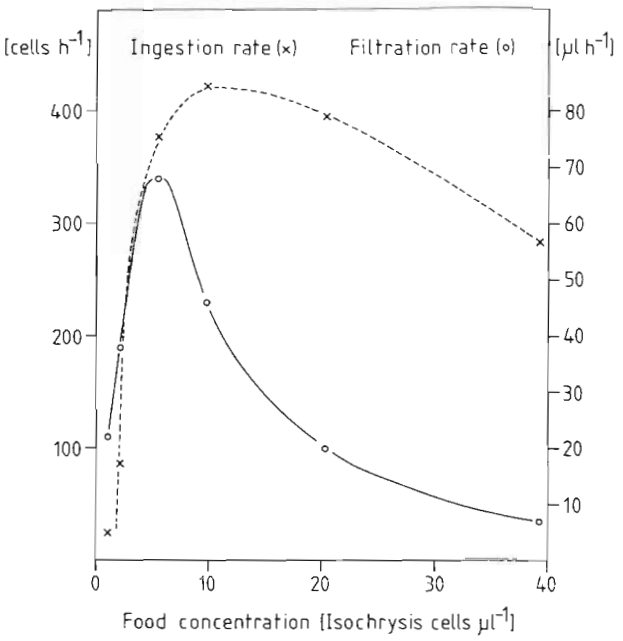

Fig. 3. *Mytilus edulis*, larvae of 251 µm shell length. Interrelation between ingestion and filtration rate at 12 °C

Ingestion

Ingestion rates at standard food concentrations have been compiled in Table 2. Data in brackets have been corrected assuming that the filtration rate is maintained on the filtration capacity level.

Maximum ingestion rates are marked. In this context they are called 'ingestion capacity'. It denotes the maximum amount of food the larva can ingest under the conditions given. Fig. 5 depicts ingestion capacity as a function of shell length at the 3 standard temperatures. Ingestion capacity has been expressed in 3 ways: as *Isochrysis* cells ingested per time unit, as volume ingested per time unit (1 *Isochrysis* cell was estimated as 50 µm^3 with the Coulter Counter), and as percentage of body weight per time unit.

Temperature influences ingestion capacity strongly between 6 and 12 °C, only to a minor extent between 12 and 18 °C. The same is true for the filtration capacity and is also reflected by growth rates previously reported (Sprung, 1984a).

Food uptake after a starvation period

All estimates referred to up to now, have been long-term rates. In the 12 °C-experiments the feeding rates directly after entering the food suspension after 2 d of starvation have also been recorded. Ingestion rates have been related to long-term rates, filtration rates to

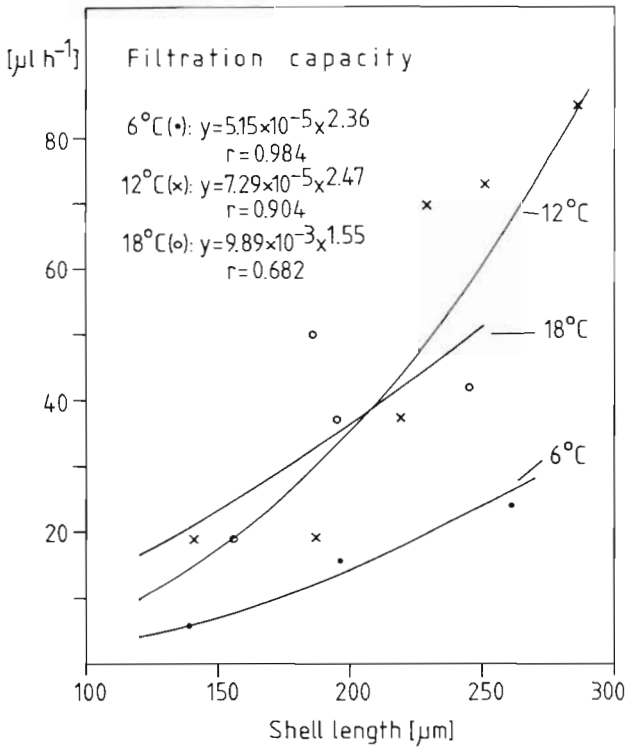

Fig. 4. *Mytilus edulis*, larvae. Filtration capacity of larvae of various sizes at the experimental temperatures (data points see Table 1); x: shell length (µm); y: filtration capacity (µl h^{-1}); r: correlation coefficient

the filtration capacity calculated for the particular larval size (from Table 1). The rates have been artificially subdivided in intervals of half hours, because the samples had often not been taken exactly at these points of the time scale.

The arithmetic mean of each time interval of 5 larval sizes examined are presented in Fig. 6. It demonstrates that after entering a particle concentration of more than 10 *Isochrysis* cells μl^{-1}, the ingestion rate is abnormally high for up to 1.5 h. This is more pronounced at higher food concentrations. The overshoot in ingestion is not caused by an overshoot of the filtration rate above the filtration capacity.

DISCUSSION

Food uptake as a function of food concentration estimated here resembles greatly the results found by other authors for many filter feeding animals: e.g. ciliate *Stentor coerulus* (Wenzel and Liebisch, 1975), bryozoan *Zoobotryon verticillatum* (Bullivant, 1968), rotifer *Brachionus plicatilis* (Chotiyaputta and Hirayama, 1978), adult freshwater and marine mussels, *Dreissena polymorpha* (Walz, 1978) and *Mytilus edulis* (Winter, 1973), brine shrimp *Artemia salina* (Reeve, 1963), copepod *Calanus pacificus* (Frost, 1972) and the cladocerans *Daphnia pulex* (Geller, 1975) and *Daphnia magna* (Rigler, 1961; Kersting and v. d. Leeuw, 1976; Porter et al., 1982). Roughly, their behaviour can be separated in 2 distinct patterns: food uptake in dilute food concentrations and food uptake in dense food concentrations.

Food uptake in dense food concentrations

This is characterized by a constant ingestion rate over a wide range of food concentrations and a declin-

Table 2. *Mytilus edulis*, larvae. Ingestion rates at various shell lengths, food concentrations (*Isochrysis* cells μl^{-1}) and temperatures; data from Fig. 2; values in brackets have been calculated for no reduction in filtration rate at low food concentrations (see also text); marked are the maximum estimates

Temperature	Shell length (µm)	Ingestion rate (*Isochrysis* cells h^{-1}) 1 c. μl^{-1}	2 c. μl^{-1}	5 c. μl^{-1}	10 c. μl^{-1}	20 c. μl^{-1}	40 c. μl^{-1}
6 °C	139	5 (6)	11	18	*23*	*31*	*32*
	196	6 (16)	31	*42*	*37*	*33*	32
	261	7 (24)	48	63	*83*	*101*	*135*
12 °C	141	15 (19)	38	*69*	*66*	*57*	47
	187	10 (19)	36 (39)	97	*130*	*170*	*153*
	219	17 (38)	75	99	*113*	*122*	*129*
	229	40 (70)	90 (140)	*349*	*366*	*340*	252
	251	25 (73)	87 (146)	*365*	*422*	*397*	277
	286	37 (85)	170	*363*	*357*	*316*	250
18 °C	156	19 (19)	31	73	*86*	*88*	*84*
	186	–	–	*250*	*250*	*250*	250
	195	37 (37)	70	102	*110*	*120*	*124*
	245	5 (42)	70 (84)	240	*320*	*414*	*442*

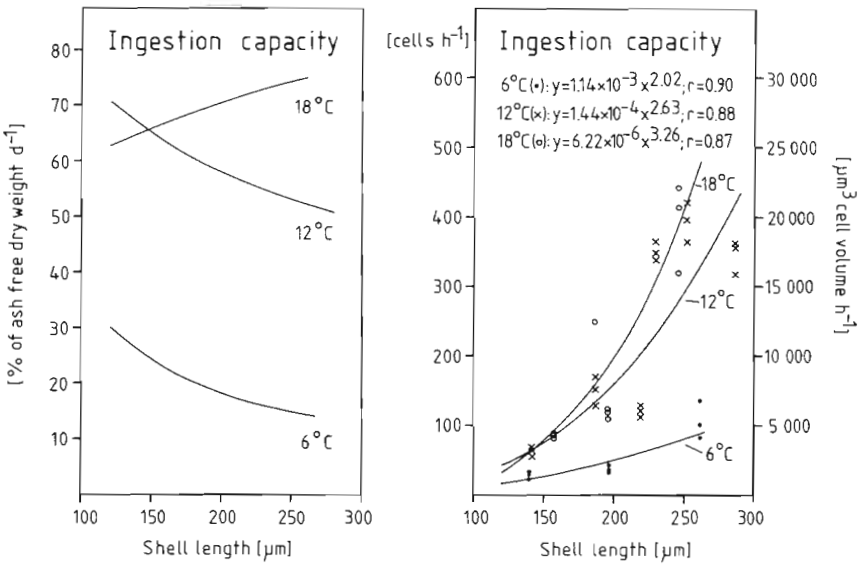

Fig. 5. *Mytilus edulis*, larvae. Ingestion capacity of larvae of different sizes at the experimental temperatures; data points see Table 2; y: ingestion capacity (cells h^{-1}); x: shell length (µm); r: correlation coefficient; see also text

ing filtration rate with increasing food concentration. I have called this particular constant ingestion rate the ingestion capacity in this context. It is limited by the passage of the food through the gut. That is why the volume of food ingested describes it better rather than its weight or energy content. However, next to other variables (e.g. temperature) the ingestion capacity depends also on the digestibility of the food, as pointed out by McMahon and Rigler (1965) for daphnids.

As not all the food filtered out can be ingested, a certain part must be rejected. This can be effected either by the cilia (Strathmann et al., 1972) or in form of pseudofaeces (Yonge, 1926). In the experiments described here, ingestion was only estimated indirectly by recording a particle decrease. Pseudofaeces would have probably also contributed to that particle loss. In the range of food concentrations investigated here, it seems thus more likely that particles have been rejected by the cilia. Otherwise this plateau in ingestion would not have been detected.

In very dense food concentrations, however, the ingestion rate can decrease. This phenomenon could

Table 3. *Mytilus edulis*, larvae. Constants of the fitted curves: ingestion rate (*Isochrysis* cells h^{-1}) *versus* shell length (µm) at standard food concentrations; based on corrected data from Table 2; r: correlation coefficient; n: number of data points evaluated

Temperature	Food concentration (*Isochrysis* cells μl^{-1})	Ingestion rate = b × shell length^m b	m	r	n
6 °C	1	1.11×10^{-4}	2.22	0.983	3
	2	1.03×10^{-4}	2.36	0.984	3
	5	9.59×10^{-4}	2.00	0.989	3
	10	1.03×10^{-3}	2.02	0.871	3
	20	3.29×10^{-3}	1.82	0.863	3
	40	4.65×10^{-4}	2.21	0.839	3
12 °C	1	6.88×10^{-5}	2.49	0.902	6
	2	1.47×10^{-4}	2.47	0.905	6
	5	8.79×10^{-5}	2.71	0.853	6
	10	8.88×10^{-5}	2.72	0.871	6
	20	1.33×10^{-4}	2.64	0.876	6
	40	2.72×10^{-4}	2.48	0.913	6
18 °C	1	2.99×10^{-3}	1.75	0.928	3
	2	5.10×10^{-4}	2.20	0.937	3
	5	6.55×10^{-4}	2.34	0.704	4
	10	1.29×10^{-4}	2.67	0.786	4
	20	7.62×10^{-6}	3.56	0.925	4
	40	1.29×10^{-6}	3.56	0.925	4

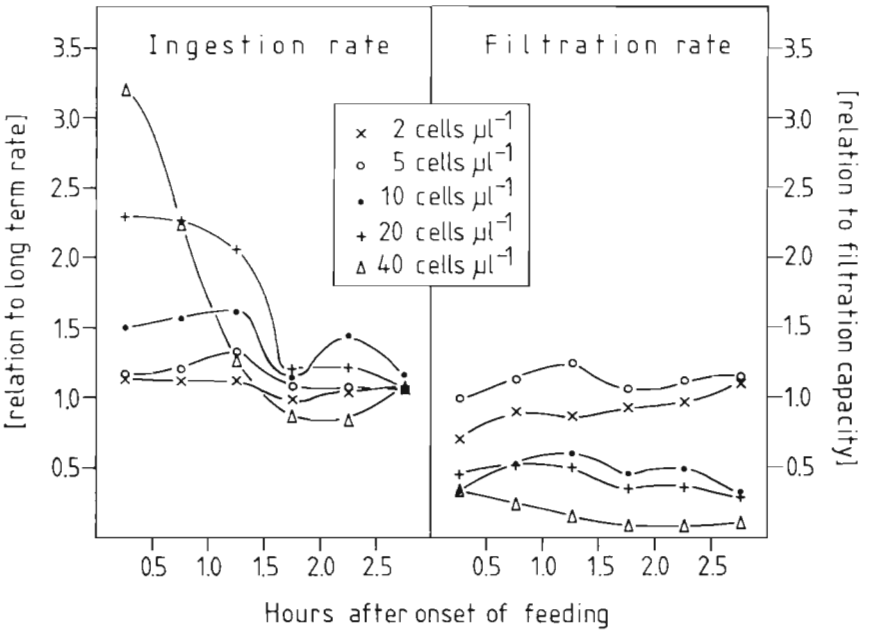

Fig. 6. *Mytilus edulis*, larvae. Ingestion and filtration rate in different food densities (*Isochrysis* cells h^{-1}) after a starvation period of 2 days; mean of 5 series at 12 °C with larvae of different sizes

also be noted with data of the 12 °C-experiments. It parallels a decline in growth at that temperature (Sprung, 1984a).

Yonge (1926) has observed that bivalve larvae can entangle themselves in a net of pseudofaeces in dense food suspensions. This restricts motility. This, however, cannot have caused the decrease, because in the 6 and 18 °C-experiments the ingestion rate remained fairly constant in this particular range. The reason may be looked for in dissolved substances produced by the *Isochrysis* culture; they are known to be toxic for bivalve larvae under special conditions (Guillard, 1958). Production may have been reduced in the 6 and 18 °C-experiments because of the temperature change (cultivation at 10 °C).

Ingestion capacity levels can only be estimated in long-term experiments. When entering a dense food suspension after a starvation period, the ingestion rate can show an overshoot with abnormally high short term values (Fig. 6). This phenomenon has frequently been observed with planktonic organisms, e.g. copepods (Mullin, 1963; McAllister, 1970, 1971; Frost, 1972), cladocerans (McMahon and Rigler, 1965; Geller, 1975), and rotifers (Schlosser and Anger, 1982). It is just the filling of the empty gut which causes this experimental feature. By means of this behavioural mode planktonic animals can optimize uptake of patchy distributed food.

Food uptake in dilute food concentrations

This is characterized by a constant filtration rate and an increase of ingestion rate with increasing food concentration. I have called this particular filtration rate 'filtration capacity' in this context: it is the filtration rate which is not restricted by the process of food ingestion. For mussel larvae the transition from 'dilute' to 'dense' food concentrations (the incipient limiting level) lies between 5 and 10 *Isochrysis* cells μl^{-1}. In most cases filtration rates of bivalve larvae have been previously estimated in higher particle densities. Although this provides a reasonable estimate of the ingestion capacity, filtration capacity has been frequently underestimated (Table 4).

A decrease of the filtration rate at very low particle concentrations has been discussed controversely in the literature, since it had been first described by Adams and Steele (1966) and Parsons et al. (1967) for copepods. Computer models have demonstrated that this behaviour makes sense. Filtration is an energy consuming process. If filtration activity is only enhanced when a certain amount of food particles is present in the water, this serves in economizing the behaviour (Lam and Frost, 1976; Lehman, 1976).

It seems doubtful that this argument is also valid for mussel larvae. Although feeding of bivalve larvae can probably be stopped whilst continuing to swim (Strathmann et al., 1972), this cannot mark a significant saving of energy, because the cilia have to move anyhow. If this is so, why should the larva not make use of those few food particles which it needs so urgently in a nutritionally dilute environment?

The apparent reduction in filtration activity is probably caused by a process which one tends to ignore when estimating food uptake with a particle counter. Next to the divisoin of the food alga, particles can enter into the experimental system by many sources, e.g. by

Table 4a. Bivalve larvae. Filtration rates reported in literature

Species	Shell length (µm)	Temperature (°C)	Food concentration (cells µl^{-1})	Food alga	Filtration rate (µl h^{-1})	Source
Ostrea edulis	200	20–22	15–26	'flagellates'	27.1	Jørgensen (1943) with data from Bruce et al. (1940)
Ostrea edulis	218–280	19–25	31–54	*Isochrysis*	18–20	Walne (1956)
Ostrea edulis	219	23–24	8–123	*Isochrysis*	15–42	Walne (1965)
Ostrea edulis	178–184	24	8–230	*Isochrysis*	0.8–10	Walne (1965)
Ostrea edulis	231	21–22	0–123	*Isochrysis*	13.8–27.5	Walne (1965)
Ostrea edulis	180–260	21	20–50	*Isochrysis*	12.5–25.0	Walne (1966)
Ostrea edulis	228	?	50–400	*Isochrysis*	0.3–9	Wilson (1980)
Ostrea edulis	250	?	40–220	*Dunaliella*	1.8–5.4	Wilson (1980)
Crassostrea gigas	87–151	25	100	*Isochrysis*	2.8–7.0	Gerdes (1983)
Crassostrea gigas	89–294	25	50+50	*Isochrysis* + *Chaetoceros*	2.3–93.5	Gerdes (1983)
Mytilus edulis	170–260	18	25–380	*Isochrysis*	4–25	Bayne (1965)
Mytilus edulis	260	16	64	*Isochrysis*	12.5	Bayne (1965)
Mytilus edulis	260	11	60	*Isochrysis*	2	Bayne (1965)
Mytilus edulis	150	12	1.5–5.5	*Isochrysis*	11.4	Riisgård et al. (1980)
Mytilus edulis	120–250	15	3–6	*Isochrysis* + *Monochrysis*	16.2–141	Riisgård et al. (1981)
Mytilus edulis	120–250	17–19	3–12	*Isochrysis* + *Monochrysis*	10.6–85.3	Jespersen and Olsen (1982)
Mytilus edulis	120–250	6	1–5	*Isochrysis*	4–21	This paper
Mytilus edulis	120–250	12	1–5	*Isochrysis*	10–61	This paper
Mytilus edulis	120–250	18	1–5	*Isochrysis*	17–52	This paper

Table 4b. Bivalve larvae. Ingestion rates reported in literature

Species	Shell length (µm)	Temperature (°C)	Food alga	Ingestion rate (cells h^{-1})	Source
Ostrea edulis	180–195	20–22	'Flagellate I'	1000	Bruce et al. (1940)
Ostrea edulis	218–280	19–25	*Isochrysis*	1040	Walne (1956, 1959)
Ostrea edulis	178–184	24	*Isochrysis*	133–600	Walne (1965)
Ostrea edulis	219	23–24	*Isochrysis*	591–1517	Walne (1965)
Ostrea edulis	231	21–22	*Isochrysis*	456–2333	Walne (1965)
Ostrea edulis	180–260	21	*Isochrysis*	830–2500	Walne (1966)
Ostrea edulis	228	?	*Isochrysis*	90–900	Wilson (1980)
Crassostrea gigas	> 200	20	*Isochrysis*	2600	Malouf and Breese (1977)
Mytilus edulis	150	12	*Isochrysis*	81–89	Riisgård et al. (1980)
Mytilus edulis	Whole size spectrum	15	*Isochrysis* + *Monochrysis*	150–800	Jespersen and Olsen (1982)
Mytilus edulis	120–250	6	*Isochrysis*	18–80	This paper
Mytilus edulis	120–250	12	*Isochrysis*	41–292	This paper
Mytilus edulis	120–250	18	*Isochrysis*	38–408	This paper

little air bubbles formed by stirring, by faeces or mucus produced by the larvae, by dust particles absorbed onto the water surface and so on. Ingestion rates are only estimated correctly, if these processes have only minor effects in the size spectrum recorded. If the particle peak followed is too small, this assumption is no longer valid. This seems to have been the case at the lowest particle concentration examined.

Size spectrum of food uptake

Size spectra of food uptake described by means of a Coulter Counter can be biased by the same phenomenon. Utmost care had to be taken for homogeneous particle distribution in these experiments. Non-homogeneous particle distribution will normally show the highest filtration rate at a particle peak, because

here particle production is lowest relative to the particle number filtered out. Thus, apparently the mussel selects this particle peak. However, this is an artifact. Any selective modes demonstrated by this experimental setup should be critically regarded (e.g. Wilson, 1980).

The size spectrum of particles retained recorded here agrees with that published by Riisgård et al. (1980) for mussel larvae and Walne (1965) for oyster larvae. Of what particles does the size spectrum between 1 and 10 µm diameter consist in the seawater? What is the nutritional value of the food particles?

Small phytoplanktonic organisms

A great deal of them may be made up of naked flagellates. The high nutritional value of many species of flagellates for bivalve larvae has been documented (e.g. *Chromulina pleiaides, Isochrysis galbana, Monochrysis lutheri;* see Loosanoff and Davis, 1950; Davis and Guillard, 1958; Guillard, 1958; Stickney, 1964; Walne, 1956, 1963, 1964, 1970).

However, according to many literature data on flagellates in near shore seawater, their concentration is far too low to provide a realistic substratum for bivalve larvae to live on (Cole, 1939; Knight-Jones, 1952; Drinkwaard, 1961; Millar, 1961; Durbin et al., 1975; Boalch et al., 1978). Other authors, in contrast, give quite reasonable figures (Throndsen, 1978; Riisgård and Poulsen, 1981; Pedersen [in Jespersen and Olsen, 1982]).

Probably diatoms form only a small part of the larval diet in nature due to their size and morphology (spines, chains, etc.). Exceptions are e.g. *Phaeodactylum tricornutum, Chaetoceros calcitrans* or *Cyclotella nana* (Davis and Guillard, 1958; Loosanoff and Davis, 1963; Walne, 1979).

Bacteria

It dates back to the experiments of Davis (1953) that bacteria are looked upon as inadequate food for bivalve larvae. Besides this, many strains have harmful effects (e.g. Walne, 1958; Guillard, 1959; Loosanoff and Davis, 1963; Tubiash et al., 1965; Tubiash, 1972; Brown, 1973; Garland et al., 1983). And, indeed when occurring individually, most bacteria (diameter 0.3 to 0.8 µm) are too small to be ingested by bivalve larvae. Only a few authors have pointed out that bacteria also have nutritional value for them (Imai and Hatanaka, 1949; Hidu and Tubiash, 1963; Martin and Mengus, 1977).

Detritus

Information on this group is rather conflicting because of its heterogeneous composition. Basically larvae can make use of it as food source, as demonstrated e.g. by Carriker (1956) and Masson (1977). Rearing larvae with artificial detritus in form of dried and pulverized algae has also been successful (Hidu and Ukeles, 1964; Chanley and Normandin, 1967). Other experiments to demonstrate the nutritional value of detritus have failed (Loosanoff et al., 1951; Davis, 1953; Loosanoff, 1954; Loosanoff and Davis, 1963).

Next to particulate food, bivalve larvae can also take up dissolved organic substances, especially dissolved free amino acids (Davis and Chanley, 1956; Ukeles, 1975; Rice et al., 1980; Manahan, 1983). Although having some significance especially during the absence of particulate food in terms of longer survival periods (Gustafson, 1980; Sprung, 1984c), its total contribution to the diet is obviously rather low (Rice et al., 1980).

Thus, although many quantitative aspects of bivalve larval feeding are well documented, at least for defined laboratory conditions, knowledge of its natural diets remains rather speculative.

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