Physiological energetics of mussel larvae *(Mytilus edulis).* III. Respiration

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ABSTRACT: Respiration rates of *Mytilus edulis* L. eggs, trochophore and veliconcha larvae of different sizes have been estimated at 6, 12 and 18 °C. They were related to data of body weight and filtration capacity. Maximum swimming speeds observed corresponded to the velocity with which the larva sinks. The significance of activity could thus be discussed regarding the sinking rates of the larva; expressed as percentage of the respiration rate it was highest at low temperatures and increased with larval size.

INTRODUCTION

Measurement of oxygen consumption is assumed to provide a reasonable estimate of metabolic heat loss of mussel larvae. These small organisms, however, require a special measuring procedure. Polarographic and volumetric methods fitted for this purpose (e.g. Cartesian and gradient diver) have been tested successfully (Zeuthen, 1947; Davenport, 1976; Riisgård et al., 1981).

Like most bivalve larvae, mussel veliconcha are capable of actively regulating their position in the water column. They do this by means of cilia, which are situated on a velum, and which effect feeding at the same time (Strathmann et al., 1972). The speed of vertical migration of various species has been reported as being about 0.5 to 7 mm s^{-1} (Isham and Tierney, 1953; Turner and George, 1955; Konstantinova, 1966; Wood and Hargis, 1971; Cragg and Gruffydd, 1975; Hidu and Haskin, 1978; Cragg, 1980; Mann and Wolf, 1983).

Trochophores and early veligers generally swim continuously and tend to accumulate at the water surface. After some days, together with the formation of a shell, pauses in ciliary beating occur: they alternately sink and swim up in a vertically orientated spiral. This swimming pattern has been described for various species of bivalve larvae: e.g. *Mytilus edulis* (Bayne, 1964), *Ostrea edulis* (Cragg and Gruffydd, 1975), *Pecten maximus* (Cragg, 1980) and *Arctica islandica* (Mann and Wolf, 1983).

It must be assumed that a great part of the metabolic energy is lost by activity; Zeuthen (1947) has calculated that it may contribute to 8 to 50 % of the respiration of a mussel larva.

Here, next to respiration rates, estimates on the energy inherent in larval movement are presented. This is the third paper in a series of 4 in which important components of the energy budget of mussel larvae are described.

MATERIALS AND METHODS

Measurement of respiration rates

Respiration rates have been estimated in a gradient diver with laboratory-reared larvae. The rearing procedure has been described by Sprung (1984a).

The experimental setup of the gradient diver was only slightly different from that of Nexø et al. (1972). The salt gradient was built up in a 500 ml graduated cylinder with Na_2SO_4 (density: 1.00 to 1.06 mg mm^{-3}). Usually the divers had a gas volume of 3 to 6 µl (span: 2 to 12 µl). They were charged with 2 (large mussels) to 100 (small) larvae in order to effect a distinct migration within 1 d. After an adaptation of at least 30 min, its position in the gradient was recorded by eye every few

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hours. For one diver one data point has been estimated from a linear regression of its position (corrected by a control diver) versus time.

Measurements were conducted in temperature-constant rooms. Normally experimental and rearing temperature were identical. In case it differed, the larvae were adapted to the experimental temperature for 5 d. A special situation was given for the eggs and trochophores. The adults had been kept at about 8 °C. In order to effect spawning, they were transferred individually into Erlenmeyer flasks. The flasks were filled with water of 18 °C and brought into a 12 °C room. At 6 °C the measuring procedure started 5 h after release, the trochophores were 2 d old. At 12 and 18 °C measuring procedure started directly after release of the eggs, the trochophores were 1 d old.

The larvae were fed with an *Isochrysis* culture directly before they were brought into the diver or they had starved for 1 d. Within the process of evaluation, the volume of oxygen consumed was corrected to standard conditions. For transformation to energy units, 1 ml O_2 was taken as 20.1 Joule (Crisp, 1971).

Estimation of energy inherent in movement

The energy inherent in larval movement was estimated by the sinking rate. In this particular situation, the larva is drawn through the water by a defined force F. It is the difference between the gravity pull G and the buoyancy in seawater B:

$$F = G - B \qquad (1)$$

The force F is necessary to overcome the friction of the water.

Gravity pull G was estimated from larval wet weight WW_{larva} (Sprung, 1984b) and gravity g. Buoyancy B was estimated from larval volume, the density of seawater $\varrho_{seawater}$ and gravity g. Density of the seawater $\varrho_{seawater}$ was checked by an araeometer. Salinity ranged between 29.7 and 33.3‰. The volume of the larva was estimated separately for the shell and the soft part multiplying its wet weight (WW_{tissue} resp. W_{shell}) with an estimate of its density ϱ. For the tissue, the density was assumed as $\varrho_{tissue} = 1.3 \times 10^{-3}$ kg m^{-3}. It was calculated for an egg of 77.8 μm diameter with a wet weight of 323 ng (Sprung, 1984b). For the shell a density of $\varrho_{shell} = 2.5 \times 10^{-3}$ kg m^{-3} was assumed according to the density of shells of adult mussels (Sprung, 1980).

$$F = \left(WW_{larva} - \left(\frac{WW_{tissue}}{\varrho_{tissue}} + \frac{WW_{shell}}{\varrho_{shell}}\right) \times \varrho_{seawater}\right) \times g \qquad (2)$$

The sinking rate was followed in a glass tube of 1.3 cm diameter with a stopwatch over a distinct distance. For one point, the arithmetic mean of 5 to 17 measurements was formed. Experiments were conducted in temperature-constant rooms. The larvae were killed with formalin just before the measurements.

RESULTS

Respiration rates have been represented graphically in Fig. 1. Rates measured directly after feeding and after 1 d of starvation did not differ significantly. They
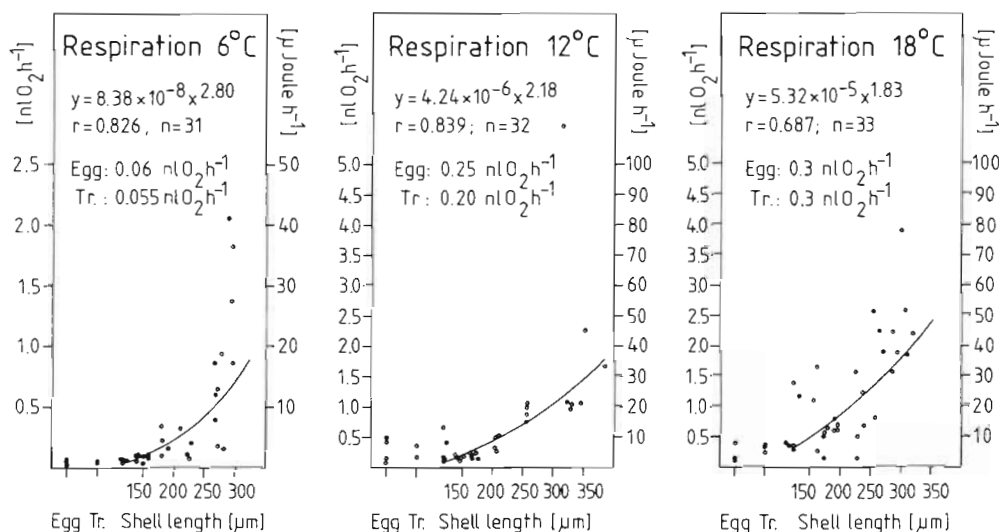

Fig. 1. *Mytilus edulis,* eggs and larvae. Respiration rates; y: respiration of a single individual (nl O_2 h^{-1}); x: shell length (μm); r: correlation coefficient; n: number of data points; mean respiration of an egg and a trochophore (tr.); conversion: 1 ml O_2 = 20.1 Joule

were thus pooled. Rates are plotted against the arithmetic mean of larval shell length in the diver. Fit and mean respiration of eggs and trochophores are also indicated.

Sinking rates recorded are presented in Fig. 2. Data points have been fitted as a function of shell length.
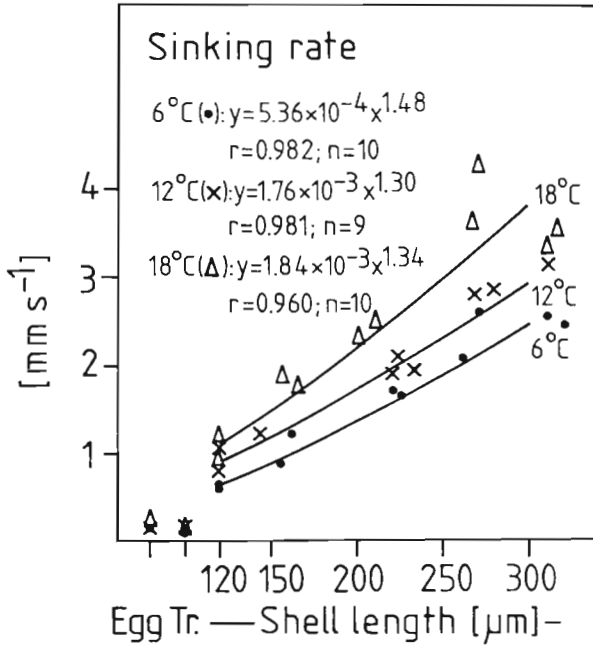
Sinking rate

$6\,°C\,(\bullet)\!: y = 5.36 \times 10^{-4} x^{1.48}$

$r = 0.982; \ n = 10$

$12\,°C\,(x)\!: y = 1.76 \times 10^{-3} x^{1.30}$

$r = 0.981; \ n = 9$

$18\,°C\,(\triangle)\!: y = 1.84 \times 10^{-3} x^{1.34}$

$r = 0.960; \ n = 10$

Fig. 2. *Mytilus edulis,* eggs and larvae. Sinking rates at 6, 12 and 18 °C; y: sinking rates (mm s^{-1}); x: shell length (µm); r: correlation coefficient; n: number of data points; one point represents the mean of 5–17 observations; tr.: trochophore

For calculation of the energy inherent in movement, it was assumed that the larva would swim in a horizontal direction with a velocity corresponding to the sinking rate. Table 1 demonstrates that this is a realistic assumption. These velocities have been recorded with a stopwatch under a dissecting microscope at the temperatures indicated. The capacity of the movement has been calculated from the product of sinking rate and force F described under 'Materials and Methods'. This value was doubled according to the assumption made above: one component serves to compensate sinking, the other to move the larva in the horizontal

Table 1. *Mytilus edulis,* larvae. Maximum recorded horizontal swimming velocities

Temperature (°C)	Shell length (µm) ($\bar{x} \pm sx$)	Swimming velocity (mm s^{-1})
6	261 ± 23	1.25
12	226 ± 27	2.00
18	245 ± 29	3.30

Efficiency of movement

$6\,°C\!: y = 1.22 \times 10^{-8} x^{4.15}$

Tr.: 0.086 nJ h^{-1}

$12\,°C\!: y = 3.84 \times 10^{-8} x^{3.94}$

Tr.: 0.101 nJ h^{-1}

$18\,°C\!: y = 4.19 \times 10^{-8} x^{4.01}$
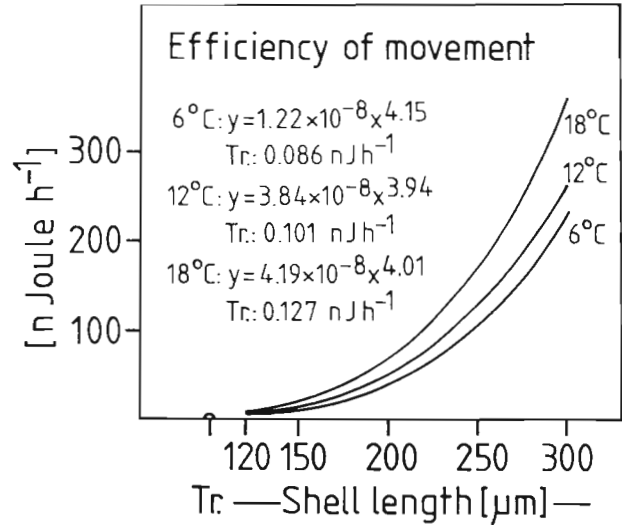
Tr.: 0.127 nJ h^{-1}

Fig. 3. *Mytilus edulis,* larvae. Efficiency of swimming in a horizontal direction with a speed corresponding to the sinking rate; calculated from the sinking rate (Fig. 2) and weight data (Sprung, 1984a); y: efficiency (nJoule h^{-1}); x: shell length (µm)

direction. This efficiency has been graphically represented in Fig. 3. It is markedly higher with the veliconcha than with the trochophore. Due to the higher sinking rate, the efficiency increases with larval size and temperature.

With respect to the temperature, this trend is just reversed when referring the efficiency to the respiration rates of the veliconcha (Fig. 1). However, it still increases with larval size (Fig. 4).
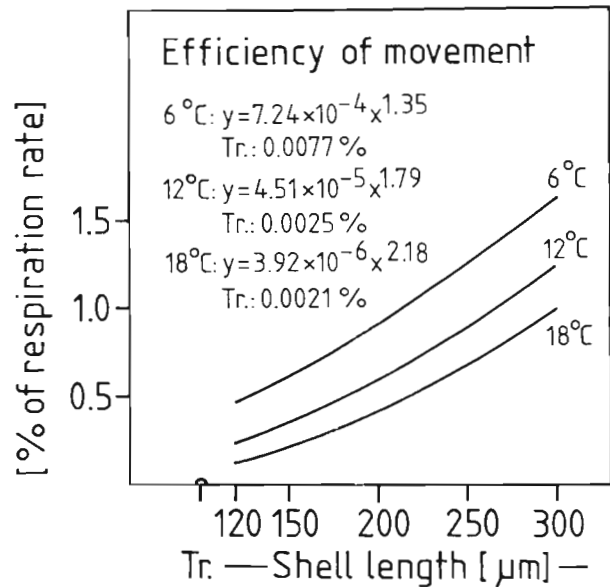
Efficiency of movement

$6\,°C\!: y = 7.24 \times 10^{-4} x^{1.35}$

Tr.: 0.0077 %

$12\,°C\!: y = 4.51 \times 10^{-5} x^{1.79}$

Tr.: 0.0025 %

$18\,°C\!: y = 3.92 \times 10^{-6} x^{2.18}$

Tr.: 0.0021 %

Fig. 4. *Mytilus edulis,* larvae. Efficiency of swimming as percentage of the respiration (calculated from Fig. 1 and 3); y: efficiency of swimming (% of the respiration); x: shell length (µm)

DISCUSSION

Like the other variables of the energy budget investigated before, respiration is dependent (directly or indirectly) on many factors. They have been compiled and discussed by Zeuthen (1947) in general. Here only the important ones in this context will be considered.

Respiration and temperature

Table 2 lists the Q_{10} values. Especially for eggs and trochophores they are difficult to interpret. This is due a great deal to the imperfect temperature adaptation caused by the thermal spawning stimulus. For the shelled larvae, the Q_{10}-values between 6 and 12 °C and between 12 and 18 °C are very similar. This is in contrast to the temperature influence on growth and food uptake which levels off between 12 and 18 °C (Sprung, 1984 a,b). This indicates that *Mytilus edulis* larvae approach their maximum tolerable temperature limit. It lies at about 25 °C (Hrs-Brenko and Calabrese, 1969; Lough, 1974).

Respiration and activity

Applying a quite different method, Vlymen (1970) obtained similar results as calculated here for copepods: he estimated the energy inherent in motion as 0.1 to 0.3 % of the registered respiration. However, Klyashtorin and Yarzhombek (1973) argued that it is wrong to conclude that activity has consequently hardly any effect on respiration. Metabolic effort is only converted to the energy of the moving body with a certain efficiency. This concerns the transformation of chemical energy (as ATP) to the beats of the appendages (or cilia) and the transformation of this energy to the surrounding water. For the metabolic effort one must assume a value which can be 20 times higher than the energy inherent in motion. Consequently, the estimations presented here, do not contradict Zeuthen's (1947) calculation. Attention should be thus drawn to the trends rather than to the absolute values.

If swimming speed and sinking rate are also correlated in early larval stages, activity is more expensive for the veliconcha than for the trochophore (Fig. 3). This would make sense, because for the trochophore activity serves only in regulating the position of the larva. For the veliconcha, in contrast, swimming runs parallel with the process of food uptake.

Assuming that the graphs calculated in Fig. 1 are valid for a similar state of activity, it turns out that the larva has to spend a greater part of its metabolic activity for swimming with increasing size, especially at low temperatures (Fig. 4). This may have consequences for growth. Possibly the sigmoidal growth curves at 6 °C (Sprung, 1984a) can be attributed to this finding.

Activity is one sore point in nearly all estimations of the respiration rate of bivalve larvae. In order to effect a measurable rate within a reasonable time, the larvae have to be highly concentrated.

This influences motility and may explain a good deal of the variability of these estimations. Walne (1966) and Millar and Scott (1967) observed reduced respiration rates with increasing concentration of oyster larvae. In contrast, Zeiss (1963) found an elevated oxygen consumption with daphnids at high concentrations. Despite this fact and different methods employed, respiration rates reported in the literature generally agree (Table 3).

Respiration and nutrition

Digestive processes cause an elevated metabolism in many organisms. This phenomenon is called specific dynamic action. It has been documented also for adult mussels (Bayne and Scullard, 1977). It was originally intended to have it included in the respiration rate when measuring directly after feeding and to exclude it when the larva had starved for one day. Obviously either the specific dynamic action lay below the accuracy of the method or it took only some 1 to 2 h and was thus much shorter than the whole measuring procedure. The latter hypothesis would be supported by data on the digestion of gastropod larvae (Pechenik and Fisher, 1979).

Table 2. *Mytilus edulis.* Temperature dependence of the respiration of eggs, trochophores and larvae of different shell lengths (calculated from Fig. 1)

Temperature range	Q_{10} – values						
	Egg	Trochophore	120 μm	150 μm	200 μm	250 μm	300 μm
6–12 °C	10.8	8.6	5.3	3.7	2.9	2.4	1.6
12–18 °C	1.4	2.0	3.9	3.8	3.1	2.3	2.5

Table 3. Bivalves, larvae. Literature data on respiration rates; *calculated from the ash free dry weight assuming that 15 % of it belongs to the shell

Species	Shell length (μm) resp. age	Temperature (°C)	Respiration rate (nl O₂ h⁻¹)	Respiration rate (ml O₂ [g dw]⁻¹)	Method	Source
Ostrea edulis	170–190 after 7 d without food	20 20	0.4–1.2 0.2–0.8	1.6–4.8 2.0–8.0	Winkler titration Winkler titration	Millar and Scott (1967) from Crisp (1974)
Ostrea edulis	180	22	1.6	6.4	Winkler titration	Walne (1966) quoted by Crisp (1975)
Ostrea edulis	170	18–20	?	5–6	Biochem. analysis	Holland and Spencer (1973) quoted by Crisp (1975)
Ostrea edulis	179 222 266	20–22 20–22 20–22	0.6 2.5 5	? ? ?	Biochem. analysis	Gabbott and Holland (1973)
Ostrea edulis	171–279	22–24	2.7–24	8.2–8.7*	Winkler titration	Helm (in Bayne, 1983)
Crassostrea gigas	Whole size spectrum	25	0.4–6.1	2.4–5.8	O₂-electrode	Gerdes (1983)
Crassostrea virginica	60–200	26	0.2–20	?	All-glass differential micro respirometer	McInnes and Thurberg (1973)
Adula californiensis	3 d	7–21	0.1–0.25	?	Gilan differential respirometer	Lough and Gonor (1973)
Mytilus edulis	?	?	0.5–1.8	2.8–10	Cartesian diver	Zeuthen (1947) from Crisp (1974)
Mytilus edulis	?	18	0.18	?	Biochem. analysis	Bayne et al. (1975) from Bayne (1976)
Mytilus edulis	169	15	0.75	?	O₂-electrode	Davenport (1976)
Mytilus edulis	120–300	15	0.19–3.4	3.1–4.2	Gradient diver	Riisgård et al. (1981)
Mytilus edulis	120–300 120–300 120–300	6 12 18	0.055–0.7 0.14–1.06 0.34–1.81	1.2–1.5 1.8–3.8 3.1–9.4	Gradient diver	This paper

With adult mussels, Thompson and Bayne (1972) have observed a reduced metabolic activity below the normally maintained level during the process of starvation. This phenomenon must also be postulated for its larvae. As reported elsewhere (Sprung, 1984c) mussel larvae can survive under laboratory conditions without food for weeks or even months. In case they maintain their respiration level, it can be calculated that for most larval sizes tested its body mass must be respired down to less than 1 %. This is contrary to the visual impression the larvae give prior to death. Probably metabolism can be reduced drastically by ceasing to swim.

This calculation, however, ignores the fact that the substrate respired changes during the process of starvation. With planktonic organisms, mainly lipids are respired in short starvation periods of few days; in longer starvation periods proteins are used up, which form predominantly structural components (Holland, 1978). Starving bivalve larvae also show this mode as could be demonstrated by biochemical analysis (Millar and Scott, 1967; Holland and Spencer, 1973; Bayne et al., 1975).

Jørgensen (1960, 1962, 1976) has pointed out that with suspension feeders, filtration and respiration rate are closely correlated. This must be so, because the respiration rate is an estimate of the energy loss of the animal and the filtration rate an important factor limiting energy uptake. Data for this relationship have been graphically represented in Fig. 5. Literature data for bivalve larvae reported previously are lower: 15 and 40 l water filtered per ml oxygen consumed (oyster larvae; Jørgensen, 1962) and 16 to 26 l water filtered per ml oxygen consumed (*Mytilus* larvae; Riisgård et al., 1980).

Respiration and body size

In Fig. 6 data from Fig. 1 have been transformed to weight-specific respiration rates with data from Sprung (1984a). They confirm the general phenomenon that weight-specific respiration decreases with body size. For planktonic larvae, the value generally range between 1.6 and 10 ml O_2 h^{-1} and g dry weight (Crisp, 1975; Holland, 1978). This is also confirmed here.

Consequently respiration can be related to body size by the allometric equation:

$$\text{Respiration rate} = b \times \text{body size}^m \qquad (3)$$

With weight data from Sprung (1984a) the exponents given in Table 4 can be calculated. For mussel larvae, Zeuthen (1947, 1953) quotes an exponent of 0.8 and Riisgård et al. (1981) of 0.90. Conover (1968, 1978) calculated for planktonic organisms a mean of 0.81
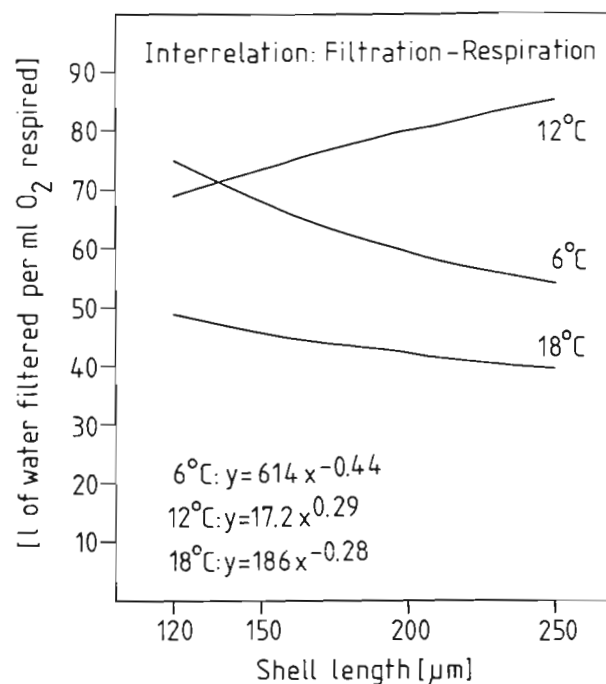

Fig. 5. *Mytilus edulis,* larvae. Interrelation between filtration and respiration rate; calculated with regression lines from Fig. 1 and Sprung (1984b); y: liter of water filtered per ml O_2 respired; x: shell length (μm)
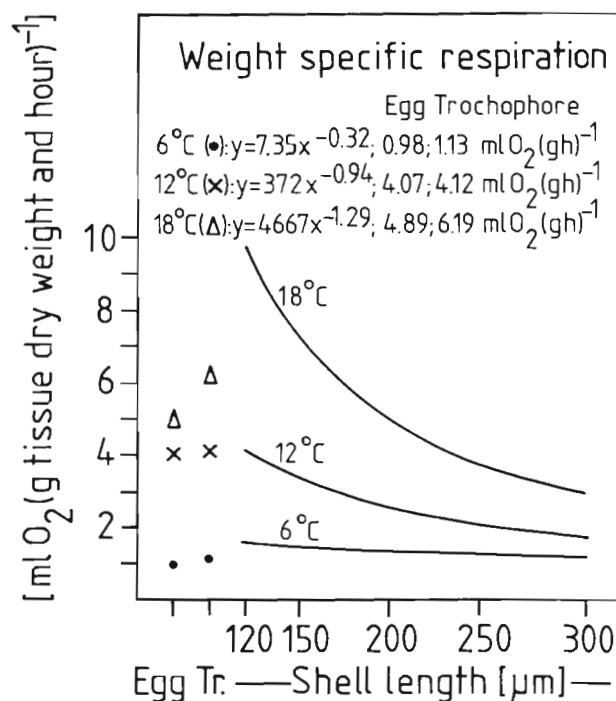

Fig. 6. *Mytilus edulis,* eggs and larvae. Weight specific respiration; calculated with data from Fig. 1 and Sprung (1984a); y: weight specific respiration (ml O_2 [g tissue dry weight and hour]$^{-1}$); x: shell length (μm)

Table 4. *Mytilus edulis*, larvae. Weight exponents (tissue dry weight) of the ingestion capacity, the filtration capacity and respiration rate; calculated with data from Fig. 1 and Sprung (1984a, b)

Temperature:	6 °C	12 °C	18 °C
Filtration capacity:	0.75	0.79	0.50
Ingestion capacity:	0.65	0.84	1.04
Respiration rate:	0.90	0.70	0.59

according to data of various authors. He believes that the exponent is independent of temperature. Although different exponents have been calculated for each temperature tested (Table 4), the results do not necessarily contradict this statement. The differences between 6 and 12 °C as well as between 12 and 18 °C are not significant. Probability that the exponents of the 6 and 18 °C data are identical, however, is only 2.5 % (calculated according to Sachs, 1978, p. 348).

During the whole process of growth, exponents m of the respiration rate are expected to be higher than those of food uptake (Vahl, 1973; Winter, 1978). This can only be found with the 6 °C values (Table 4). That this is not the case with the 12 and 18 °C data may be attributed to the fact that the whole digestive system is still developing in small larvae. Although definite conclusions are very uncertain with this set of data, this would argue for a separate discussion of growth phenomena with the larvae apart from the adult mussels.

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