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Physiological energetics of mussel larvae *(Mytilus edulis)*. I. Shell growth and biomass

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ABSTRACT: Development and shell growth of the larvae of the marine mussel *Mytilus edulis* L. were recorded in laboratory cultures. Experiments were conducted at 6, 12 and 18 °C and food concentrations of 1, 2, 5, 10, 20, and 40 *Isochrysis galbana* cells μl^{-1}. After fertilization, the eggs developed to the D-shaped stage within 104 h at 6 °C, 42 h at 12 °C, and 32 h at 18 °C. Rearing was not successful with 1 *I. galbana* cell μl^{-1}. At other food conditions, growth rate increased with concentration of *I. galbana* up to a plateau at about 10 cells μl^{-1}. Growth curves (shell length *vs.* time) were sigmoidal at the lowest food concentrations at 6 °C; in all other cases they were linear with a maximum rate of 3.4 $\mu m\ d^{-1}$ at 6 °C, 8.1 $\mu m\ d^{-1}$ at 12 °C, and 11.8 $\mu m\ d^{-1}$ at 18 °C. Total dry weight and ash weight were estimated for various larval stages. Based on these data, tissue dry weight, tissue wet weight, total wet weight and shell weight were calculated. Eggs, trochophores and the food organism *I. galbana* were analysed for their elemental composition (CHN). Body growth was estimated by data on shell growth and body weight.

INTRODUCTION

The bivalve *Mytilus edulis* L. is a typical benthic invertebrate of many temperate marine coasts. It reproduces by means of a planktonic larva. Characteristics of this reproductive strategy are: (1) High fecundity (Thompson, 1979; Bayne et al., 1983; Sprung, 1983); (2) high larval mortality – up to more than 99 % has been estimated for various bivalves (Thorson, 1946; Yap, 1977; Gledhill, 1980; Brousseau et al., 1982); (3) high dispersal – in contrast to the adult phase (Crisp, 1974, 1975).

Mytilus edulis is of separate sex. The eggs are fertilized after being released into the water. Its subsequent development has been described e.g. by Field (1922) and Bayne (1976). It can be divided into 3 distinct phases:

Lecithotrophic phase: it takes a few days and comprises cleavage, formation of cilia (trochophore stage), a velum and a shell gland. This phase ends with the secretion of a D-shaped shell of 100 to 120 µm length.

Growth phase: the larva starts feeding and increases in weight. Growth rings are secreted by the mantle edges, and the shell loses its D-shape. This stage is called 'veliconcha' (Werner, 1940). It persists for some weeks.

Settling phase: at about 270 µm shell length a foot has developed next to the velum, with which the larva tests the substrate for settling. This pediveliger stage (Carriker, 1956, 1961) can, however, stay in the plankton up to a shell length of 360 µm (own obs.). It has been excluded to a great extent from these experiments, because Bayne (1965, 1971) has examined it for *Mytilus edulis*.

Although the morphology of *Mytilus* larvae has been frequently described in the literature (e.g. Le Pennec and Masson, 1976; Booth, 1977; Lutz and Hidu, 1979; Le Pennec, 1980; older literature reviewed by Bayne, 1976), data on its physiology have been rare up to recent years.

This is due to practical reasons. Although the first successful rearing of *Mytilus* larvae dates back to Matthews (1913), many difficulties had to be overcome in developing rearing techniques, especially in testing adequate food. Experiments focussed mainly on commercially important species. Much work done during the past 4 decades has been devoted to this aspect (reviewed by Loosanoff and Davis, 1963 and Walne, 1979).

Progress in ecosystem research has prompted the

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need for data on energy budgets of important species (Jørgensen, 1983). Thus, during the past years research in this field has been enhanced. For bivalve larvae, in addition to older publications (Jørgensen, 1952; Walne, 1965; Gabbott and Holland, 1973), the papers of Riisgård et al. (1980, 1981), Jespersen and Olsen (1982) and Gerdes (1983 a, b) must be mentioned in this context.

In a series of 4 papers the attempt is made to estimate important budget data of *Mytilus edulis* larvae at 3 temperatures with respect to larval size and to food concentration. Here the results of experiments on development and shell growth as well as weight data are presented. Subsequent papers will deal with food uptake, respiration and ecologically relevant efficiencies.

MATERIALS AND METHODS

General conditions

Mussels with ripe gametes were brought from the rocky shore of Helgoland into the laboratory during spring. They were kept at 7 to 9 °C and fed with *Dunaliella tertiolecta* and *Isochrysis galbana* for several weeks or months until the beginning of experiments.

For stimulating them to spawn, the mussels were cleaned with tap water and transferred separately into 250 ml Erlenmeyer flasks. The flasks were filled with water of 18 °C and placed in a 12 °C temperature-constant room. The water was vigorously aerated. After spawning, the eggs were filtered through a sieve of 112 µm mesh size and the sperm through a sieve of 40 µm mesh size in order to remove faeces and other particles.

Larvae were reared in 5 l bottles filled with 0.45 µm membrane filtered seawater of 28 to 33 ‰ salinity The bottles were placed in temperature-constant rooms of 6, 12 and 18 °C under artificial light with a diurnal rhythm. They were slightly aerated.

The cultures were started with a density of about 10 to 30 eggs ml^{-1}. Eggs were inseminated by a droplet of sperm. Water was changed for the first time, when most larvae had formed a D-shell, i.e. after 2 d at 18 °C, after 3 d at 12 °C and after 5 d at 6 °C, and later on every tenth day. Larvae were then sieved off on a screen of 40 µm mesh size (larger mussels on 112 and 150 µm mesh size); dead larvae or unfertilized eggs were left on the bottom of the experimental vessel and discarded.

Larvae were fed exclusively with the flagellate *Isochrysis galbana* from the first water change on. The alga was cultivated at 10 °C in f/2 medium (Guillard and Ryther, 1962). By means of this low and suboptimal temperature (Kain and Fogg, 1958) algae were prevented from sticking together and sinking to the bottom especially in the 6 °C cultures. The algae were spun off before use.

Development to the D-larva

Immediately after spawning, eggs and sperm were brought into temperature-constant rooms of 6, 12 and 18 °C. Gametes were adapted to the temperature for 1 h. Eggs were inseminated by a droplet of sperm. Every 20 min (later, at longer intervals) a sample was classified under a microscope according to the drawings of Field (1922). The group with the most advanced stage was taken as reference.

Shell growth

Deviating from the rearing conditions described above, cultures were started with a concentration of about 1 egg ml^{-1}. Water was changed every fifth day at 12 and 18 °C and every tenth day at 6 °C with a 40 µm sieve irrespectively of larval size. Food concentration was standardized to 1, 2, 5, 10, 20 and 40 *Isochrysis* cells μl^{-1}; it was kept fairly constant by maintaining an equilibrium of feeding mussels and growing algae. Algal concentration was checked daily by means of a Coulter Counter and corrected if necessary.

At every water change the shell length of 20 and later in the experiment of 30 larvae taken at random was measured by means of a micrometer with an accuracy of ± 6 µm. The largest 10 or 15, respectively were selected and the arithmetic mean and the standard deviation determined. By means of this procedure a bias caused by crippled animals was avoided. These data are thus compatible with estimates of weight, feeding and respiration, where crippled mussels were discarded by coarser mesh sizes at the water changes.

The cultures were terminated when either the first animals had settled on the bottom of the vessel or when no survivours were left.

Weight data

Specimens were sampled by means of a sieve (40, 112, or 150 µm mesh size according to the larval size) from the surface water of the cultures. They were resuspended in a small volume (ca. 10 to 50 ml) of 0.45 µm filtered seawater. The larval density in this volume was estimated by subsampling: eggs and trochophores were counted with a Coulter Counter;

with the veliconcha 16 times 1 ml was checked under a dissecting microscope after an appropriate dilution of the subsample. Defined quantities of this small volume (in most cases 1 ml) were filtered off on pre-ashed and pre-weighed glass fibre filters, which had been punched to a diameter of 8 mm. Only the pediveligers were counted individually.

The larvae were washed twice with double distilled water and subsequently freeze-dried for at least 6 h. Often they were stored at −18 °C until analysis. Before determining the dry weight on an electronic autobalance (Perkin-Elmer AD-2) they were freeze-dried again. For removing the organic substance, the filters were ashed for 3 h at 500 °C and reweighed. The data were corrected by means of blank tests.

The larvae examined had been cultivated at 12 °C except the pediveligers which had been cultivated at 6 °C. They had been starved for several hours to one day prior to filtration.

Following parameters were calculated from the dry and the ash weight: Ash free dry weight: difference between total dry weight and ash weight. Shell weight: from the ash weight assuming that 5.8 % of the shell is ash and that the ash content of the soft body is negligible (according to data of adult mussels from Sprung, 1980; see also Jespersen and Olsen, 1982). Tissue dry weight: difference between total dry weight and shell weight. Tissue wet weight: from the tissue dry weight assuming that 81 % of the soft body consists of water (according to data of adult mussels from Sprung, 1980). Total wet weight: sum of shell weight and tissue wet weight.

Elemental composition of eggs, trochophores and the food organism *Isochrysis galbana* was determined in a CHN-analyser (Carlo Erba, Mod. 1106). The analyser was calibrated after every tenth sample with acetanilid (2–3 calibrations). The *I. galbana* concentration was estimated by means of a Coulter Counter. As preliminary experiments showed, washing with distilled water caused a loss of organic substance of the alga. This step was thus left out in the analytical procedure. Samples were evaluated with respect to the elemental composition of the ashed filters.

RESULTS

The sequence of developmental stages is described in Fig. 1. At 18 °C the first group of larvae developed to the D-shaped stage within 32 h after fertilization, at 12 °C within 42 h and at 6 °C within 104 h.

Fig. 2 gives growth data and fitted growth curves. In most cases a linear fit showed the highest correlation coefficient; therefore it was applied here. Only at the 3 lowest food concentrations tested at 6 °C was a sigmoidal growth curve evident. These curves have been fitted by eye, because all curve fittings tested gave too high growth rates at the point of inflexion compared with those of the other food concentrations. At a food concentration of 1 *Isochrysis* cell μl^{-1} many larvae started growing However, none reached the pediveliger stage. All other food concentrations were high enough to rear larvae successfully.

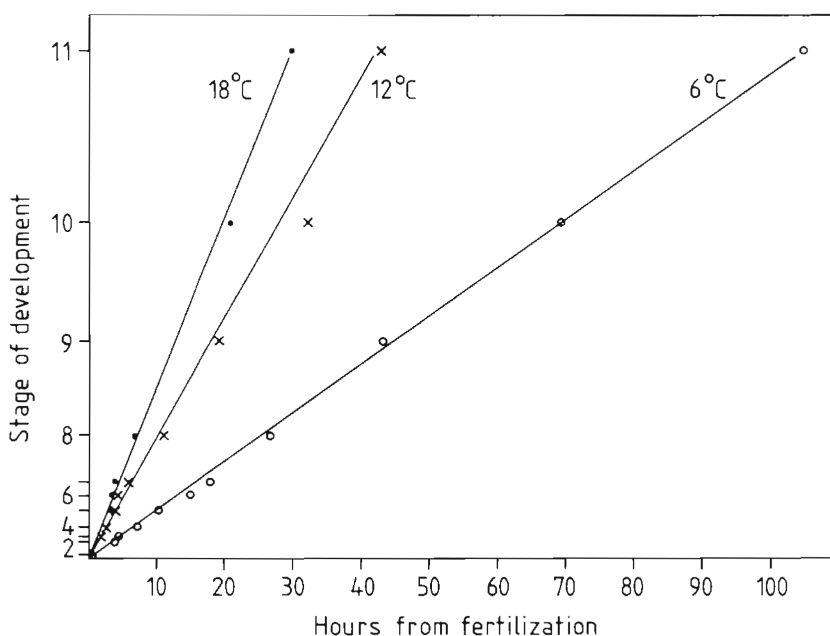

Fig. 1. *Mytilus edulis,* larvae. Time sequence of some steps in the development of the fertilized egg at experimental temperatures; lines fitted by eye;1: first polar body; 2: second polar body; 3: first cleavage (unequal); 4: second cleavage (equal); 5: first cleavage of the micromeres; 6: micromeres start growing around macromeres; 7: micromeres surround macromeres completely; 8: larva starts swimming; 9: flagellum is formed; 10: velum is formed; 11: formation of a D-shaped shell completed

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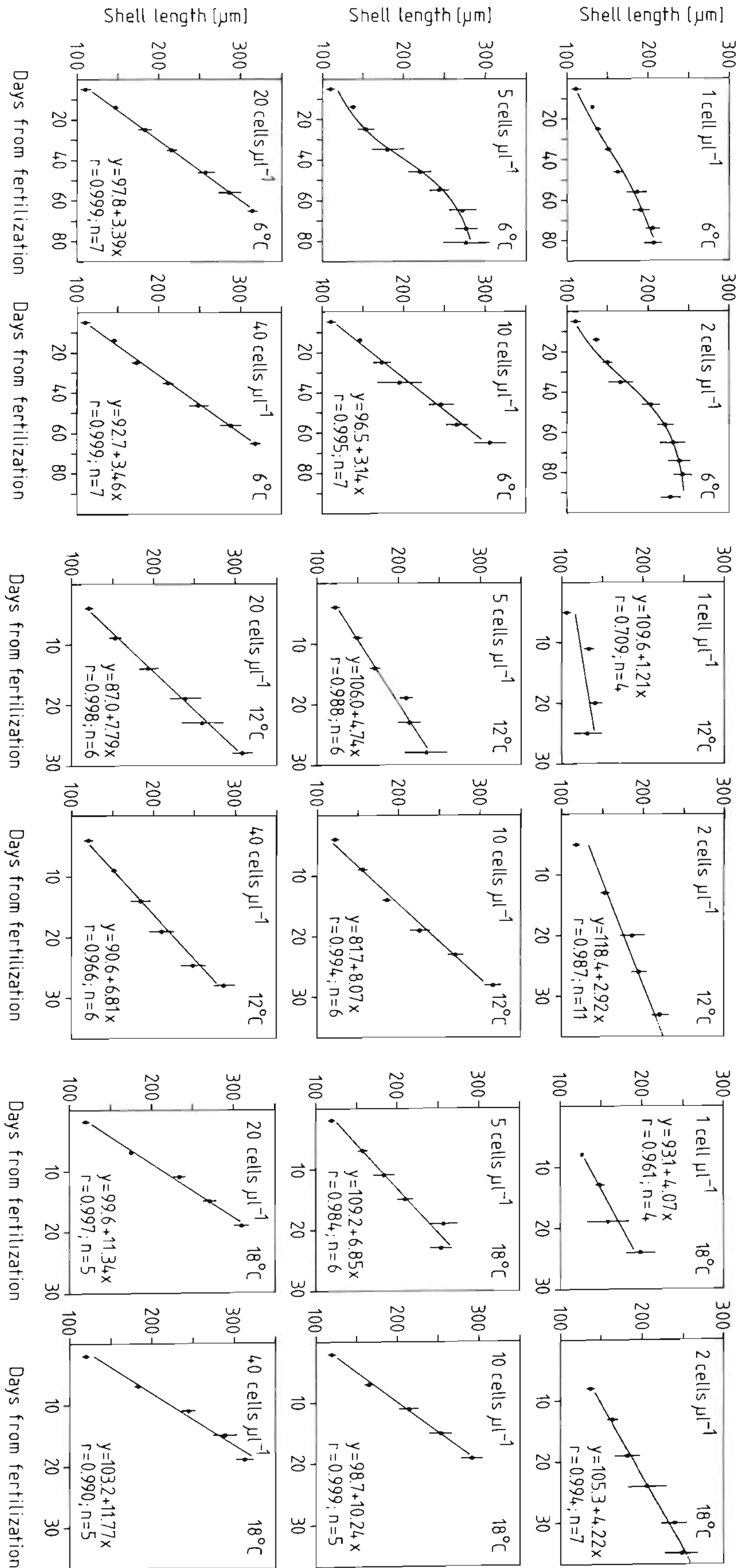

Fig. 2. *Mytilus edulis*, larvae. Shell growth at various food concentrations (*Isochrysis* cells µl^{-1}) and experimental temperatures; for fit and manipulation of data points see text; y: shell length (µm); x: days from fertilization; r: correlation coefficient; n: number of data points

Table 1 *Mytilus edulis,* larvae. Weight data; $\bar{x}$: arithmetic mean; ± standard deviation; n: number of estimates; b: blank tests; see text for further explanations

Stage	Egg diameter or shell length (µm)			Total dry weight (ng)			Ash weight (ng)			Ash free dry weight	Shell weight	Tissue dry weight	Tissue wet weight	Total wet weight
	$\bar{x}$	±	n	$\bar{x}$	±	n+b	$\bar{x}$	±	n+b	(ng)	(ng)	(ng)	(ng)	(ng)
Egg	∅ 77.8	1.4	10	67.4	6.1	9+6	6.0	1.4	4+3	61.4	–	61.4	323	323
Trochophore	–	–	–	51.5	4.4	11+5	3.0	2.9	4+2	48.5	–	48.5	255	255
D-Larva	120	4	10	134.2	17.4	11+5	84.2	6.3	6+3	50.0	89.3	44.9	236	326
Veliconcha	140	9	20	245.9	10.3	10+6	170.3	7.6	5+3	75.6	180.8	65.1	343	523
Veliconcha	140	9	20	231.2	19.9	10+6	188.8	25.3	4+3	42.4	200.4	30.8	162	363
Veliconcha	173	7	20	541.6	25.3	10+6	388.1	13.1	5+3	153.5	412.0	129.6	682	1094
Veliconcha	173	7	20	491.5	27.5	10+6	332.3	26.6	5+3	159.2	352.8	138.7	730	1083
Veliconcha	252	13	20	952	82	10+6	626	91	5+3	326	664.5	287.8	1515	2179
Veliconcha	252	13	20	982	44	8+6	671	22	4+3	311	712.3	270.2	1422	2134
Pediveliger	298	23	20	1829	447	8+8	947	217	4+4	882	1005.3	824.0	4337	5342

Weight data have been compiled in Table 1, and the graphs describing weight as a function of shell length are given in Fig. 3. Elemental analysis of the eggs, trochophores and *Isochrysis* provided the results presented in Table 2.

The energy content of the larvae was calculated from its ash free dry weight, that of *Isochrysis* from its carbon content despite of its unusual C/N ratio. It was assumed that 1 ng carbon corresponded to 0.04 mJoule or 0.5 ng ash free dry weight, respectively (Finlay and Uhlig, 1981). One *Isochrysis* cell must thus contain 0.608 µJoule.

The histograms in Fig. 4 have been constructed from regression lines in Fig. 3 and the data in Table 2. Relative shell weight declines with larval size. Note also that ash forms only a small part of the tissue dry substance of trochophores.

From shell growth, tissue growth was estimated (Table 3). It has been expressed in terms of absolute and relative increase in ash free dry weight. The results are illustrated in Fig. 5 and 6. At 6 and 18 °C growth rate increased with algal concentration. A plateau was attained at 10 cells μl^{-1}. At 12 °C growth rates even declined at food concentrations above 10 cells μl^{-1}.

Relative growth rates declined constantly with larval size at the 3 temperatures and all food concentrations tested.

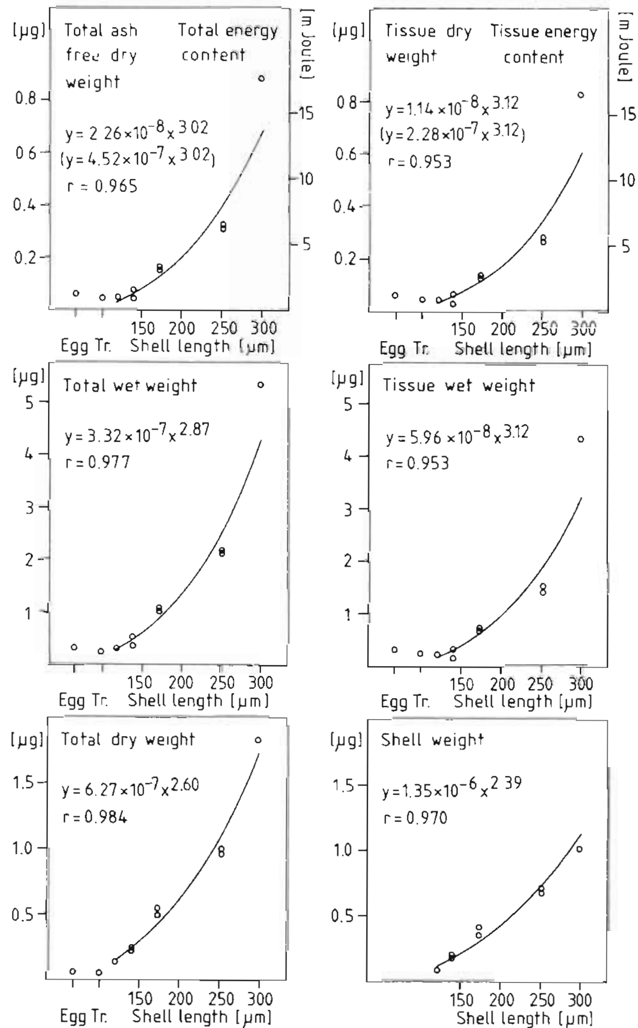

Fig. 3. *Mytilus edulis,* larvae. Fitted graphs and weight data (from Table 1); y: weight (µg); x: shell length (µm); r: correlation coefficient; equation in brackets for energy content (mJoule)

DISCUSSION

The lecithotrophic phase of *Mytilus edulis* larvae was examined by Field (1922), Rattenbury and Berg (1954) and Bayne (1965). Data of its total duration are compiled in Fig. 7.

Table 2. Elemental composition (carbon, hydrogen, nitrogen) of eggs and trochophore larvae (1 d old at 12 °C) of *Mytilus edulis* and of its food organism *Isochrysis galbana*; $\bar{x}$ arithmetic mean; ± standard deviation; n + b number of samples and blank tests

Sample	C		H		N		Unit	C/N		
	$\bar{x}$	±	$\bar{x}$	±	$\bar{x}$	±		$\bar{x}$	±	n + b
Egg (∅ 78 µm)	32.8	0.8	5.7	0.2	6.2	0.2	ng	5.3	0.1	5 + 3
Trochophore	26.5	1.0	5.4	0.2	4.3	0.2	ng	6.1	0.3	6 + 3
Isochrysis galbana	15.2	1.1	2.7	1.1	0.7	0.1	pg	21.2	3.0	5 + 3

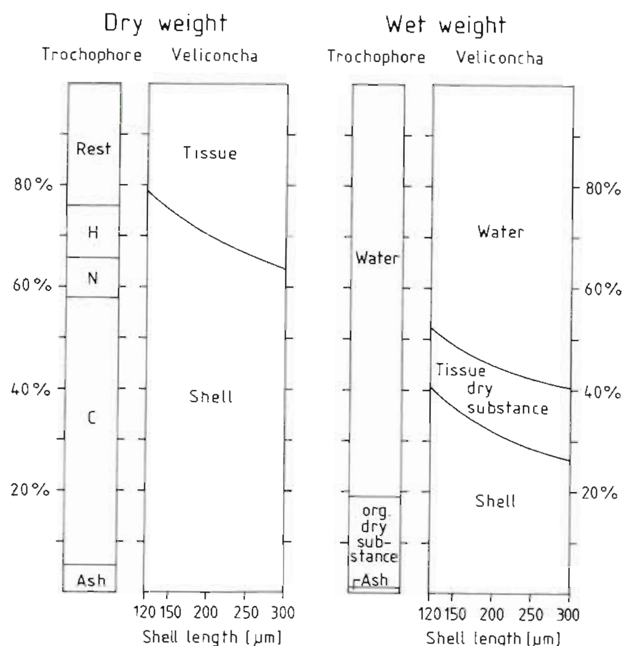

Fig. 4. *Mytilus edulis*, larvae. Composition of dry and wet substance (data from Table 1, 2 and Fig. 3)

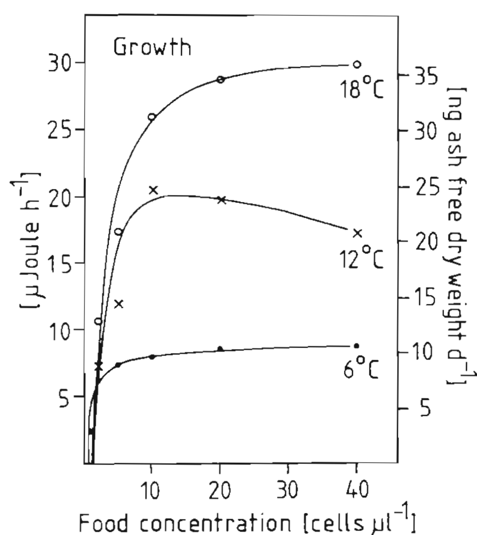

Fig. 5. *Mytilus edulis*, larvae (200 µm shell length). Growth at various temperatures and food concentrations (*Isochrysis* cells μl^{-1}); graphs fitted by eye according to data from Table 3 and Sprung (1984)

Development at 12 and 18 °C recorded here is faster than that reported elsewhere. Next to natural variation and differences caused by pretreatment of the adults, at least 2 reasons account for this. My own experiments refer to the fastest group of larvae, whereas the other authors may have chosen the mean of all stages observed.

Secondly, according to my own experience, development is depressed in dense larval cultures. Obviously, Field's (1922) data are greatly influenced by it. This is supported by his drawings which show forms with incomplete or crippled D-shells as often encountered in overcrowded cultures.

Growth is the most frequently controlled physiological parameter in experiments with bivalve larvae. For practical reasons shell length is normally taken as reference. Here tissue growth has been calculated from shell growth. This step cannot be made without objections, because it can wipe out differences existing between the weight of larvae of the same shell length. Attention has been drawn to this fact by Lucas and Costlow (1979) working with larvae of the snail *Crepidula fornicata* and by Gustafson (1980) experimenting with *Mya arenaria* larvae.

However, Fig. 8 demonstrates that actively swimming larvae – as referred to here – show a rather distinct relation between mean body weight and shell length. The weight of larvae from the same culture after 10 d of starvation has been compared with the graph from Fig. 3. At 122 µm shell length, 10 estimations of the dry weight and 5 estimations of the ash weight have been made; at 146 µm shell length, 9 and 3 estimations; at 178 µm shell length, 8 and 4. The weight of starved and non-starved larvae was almost identical. For certain, the larvae must have lost weight during the 10 d due to respiratory processes. Apparently, when estimating these data, only the strongest – probably the heaviest – larvae could still swim up. Their weight just corresponded to the mean 10 d before with the lighter larvae included. That is why extrapolation from shell length to shell weight must be valid for actively swimming larvae.

Dry weight of bivalve larvae has been estimated by Walne (1965), Holland and Spencer (1973), Gerdes

Table 3. *Mytilus edulis*, larvae. Growth data; increase in shell length (μm d^{-1}); increase in ash free dry weight, absolute (ng d^{-1}) and relative (% afdw d^{-1}); calculated from data given in Fig. 2 and 3

Temperature	Food concentration (*Isochrysis* cells μl^{-1})	120 μm shell length			150 μm shell length			200 μm shell length			250 μm shell length		
		μm d^{-1}	ng d^{-1}	% afdw d^{-1}	μm d^{-1}	ng d^{-1}	% afdw d^{-1}	μm d^{-1}	ng d^{-1}	% afdw d^{-1}	μm d^{-1}	ng d^{-1}	% afdw d^{-1}
6 °C	1	1.3	1.4	3.4	1.3	2.2	2.6	1.0	3.0	1.5	–	–	–
	2	2.1	2.3	5.3	2.3	3.9	4.7	2.5	7.6	3.8	–	–	–
	5	2.1	2.3	5.3	2.3	3.9	4.7	2.9	8.8	4.4	2.9	13.8	3.5
	10	3.1	3.4	7.8	3.1	5.3	6.4	3.1	9.4	4.8	3.1	14.8	3.8
	20	3.4	3.7	8.7	3.4	5.8	6.8	3.4	10.3	5.1	3.4	16.2	4.1
	40	3.5	3.8	8.7	3.5	5.9	7.0	3.5	10.6	5.3	3.5	16.7	4.2
12 °C	1	1.2	1.3	3.1	–	–	–	–	–	–	–	–	–
	2	2.9	3.1	7.3	2.9	4.9	5.8	2.9	8.8	4.4	2.9	13.8	3.5
	5	4.7	5.1	12.0	4.7	8.0	9.5	4.7	14.3	7.2	4.7	22.4	5.8
	10	8.1	8.8	20.4	8.1	13.8	16.2	8.1	24.6	12.2	8.1	38.6	9.8
	20	7.8	8.4	19.5	7.8	13.2	15.8	7.8	23.7	11.8	7.8	37.2	9.4
	40	6.8	7.4	17.3	6.8	11.5	13.8	6.8	20.6	10.3	6.8	32.4	8.2
18 °C	1	4.1	4.4	10.3	4.1	7.0	8.3	–	–	–	–	–	–
	2	4.2	4.5	10.6	4.2	7.1	8.5	4.2	12.7	6.4	4.2	20.0	5.1
	5	6.9	7.5	17.3	6.9	11.7	13.8	6.9	20.9	10.4	6.9	32.9	8.3
	10	10.2	11.0	26.0	10.2	17.3	20.6	10.2	31.0	15.5	10.2	48.6	12.4
	20	11.3	12.2	28.8	11.3	19.2	22.9	11.3	34.3	17.2	11.3	53.8	13.8
	40	11.8	12.8	29.6	11.8	20.0	23.8	11.8	35.8	17.8	11.8	56.2	14.3

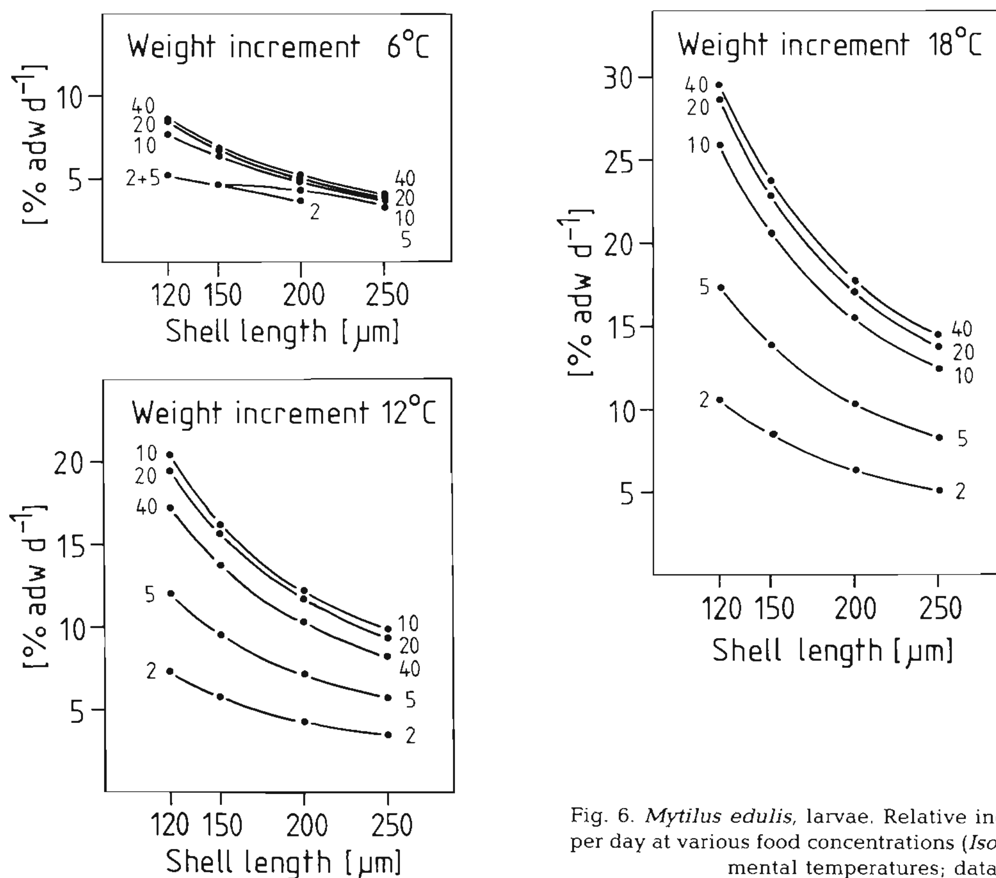

Fig. 6. *Mytilus edulis*, larvae. Relative increase in ash free dry weight per day at various food concentrations (*Isochrysis* cells μl^{-1}) and experimental temperatures; data from Table 3

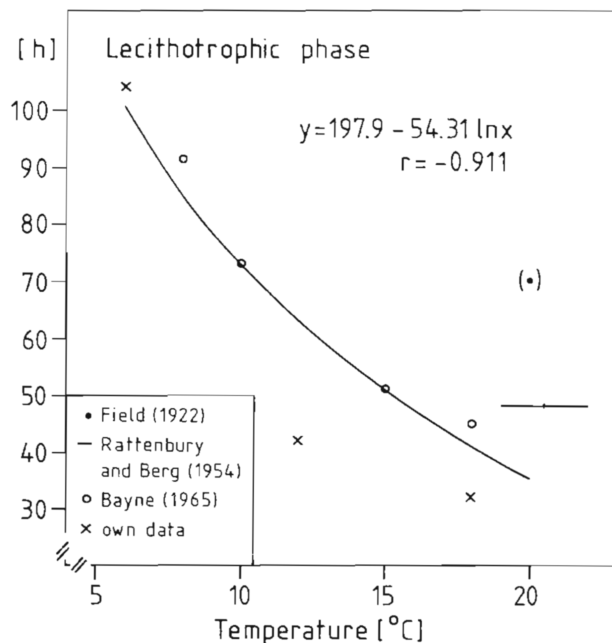

Fig. 7. *Mytilus edulis*, larvae. Duration of the lecithotrophic phase (y) as a function of temperature (x) (Field's data excluded); r: correlation coefficient

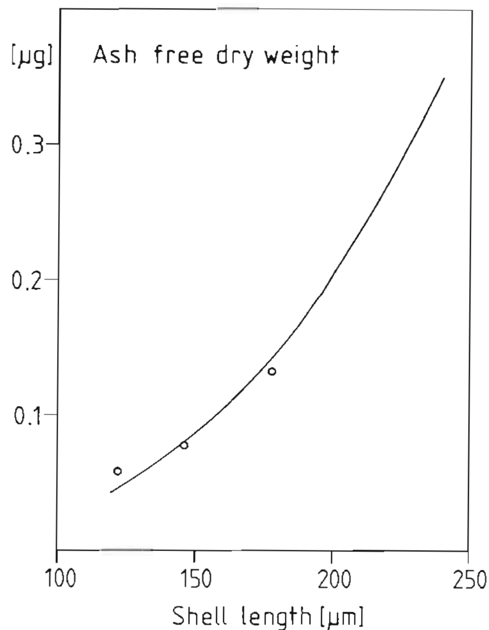

Fig. 8. *Mytilus edulis*, larvae. Three weight estimations of actively swimming larvae after a starvation period of 10 d and the graph from Fig. 3; see also text

(1980), Nascimento (1980), Jespersen and Olsen (1982) and Helm (cited by Bayne, 1983). In most cases data lay somewhat above the estimates reported here.

Holland and Spencer (1973) recorded a decrease of shell weight of *Ostrea edulis* larvae as a proportion of total weight with increasing larval size (from 83 to 73.5 % over the whole size spectrum). This corresponds to my own findings and is also implied by the data of Jespersen and Olsen (1982). For this reason extrapolation of tissue weight from total dry weight simply by a constant factor is biased when examining the whole size spectrum.

Growth is influenced by a number of factors; some of them are discussed below.

Food concentration

Algal concentrations at which other authors reported optimal growth are summarized in Table 4. In dense larval cultures, the optimum can shift to higher food concentrations as demonstrated by Malouf and Breese (1977). This is, however, not the only factor explaining deviating results. Next to this, interactions are to be expected with larval size (Rhodes and Landers, 1973), rearing temperature as well as other factors.

At algal concentrations above the optimum, growth rates often decline. Two reasons may account for this: (1) dense algal concentrations hamper the feeding apparatus of the larva (Yonge, 1926); (2) bivalve larvae are known to react sensitively to dissolved substances (Loosanoff and Davis, 1963; Le Pennec et al., 1973; Sastry, 1979). Such dissolved substances may be algal metabolites (Davis, 1953; Loosanoff and Davis, 1963). Especially *Isochrysis* is known to produce substances toxic for bivalve larvae under certain conditions (Guillard, 1958). Apparently this is the reason why at 12 °C a maximum has been attained so early. As *Isochrysis* had been cultivated at 10 °C, it may have ceased to produce metabolites in the 6 and 18 °C cultures due to the temperature change, whereas at 12 °C it might have continued.

Larval density

It is hardly feasible to conduct laboratory experiments with natural larval densities. Maximum values reported from natural assemblages range between 3 to 40 larvae l^{-1} (Fish and Johnson, 1937; Thorson, 1946; Rees, 1954; Schram, 1970; Hernroth and Ackefors, 1979). Larval growth rate is known to decline in laboratory cultures with increasing larval density (Davis, 1953; Loosanoff, 1954; Loosanoff and Davis, 1963). Possible reasons must be looked for in the number of collisions or the production of excretes. According to my own observations larval density has only minor effects on growth below 1 larva ml^{-1}.

Table 4. Literature data on optimum *Isochrysis* concentrations for bivalve larval rearing; Jespersen and Olsen's (1982) data for a mixture of *Isochrysis* and *Monochrysis*

Species	Larval density (ml^{-1})	Optimum growth condition (cells μl^{-1})	Source
Ostrea edulis	1	50–100	Walne (1956; 1959; 1963; 1966)
Ostrea edulis	2	300	Wilson (1979)
Ostrea edulis and *Mercenaria mercenaria*	10–15	50–400	Davis and Guillard (1958)
Crassostrea virginica	15	25–325	Rhodes and Landers (1973)
Mytilus edulis	3–10	100	Bayne (1965)
Mytilus edulis	0.1–0.2	40–50	Jespersen and Olsen (1982)

Temperature

For the development to the D-larva a Q_{10}-value of 4.6 between 6 and 12 °C and of 1.5 between 12 and 18 °C can be calculated; for the maximum growth rate it is 4.0 and 1.9, respectively. This may demonstrate that both processes are influenced by temperature in a similar way.

Larval size

With various bivalve species the following authors recorded different types of growth curves for larvae (shell length *vs.* time):

- exponential: e.g. Walne (1966), His and Robert (1982), Robert et al. (1982), Helm (quoted by Bayne, 1983);
- sigmoidal: e.g. Loosanoff et al. (1951), Walne (1956), Bayne (1965), Gerdes (1983a);
- linear: e.g. Ansell (1961), Carriker (1961), Walne (1965), Yoo (1969), Breese and Robinson (1981), Jespersen and Olsen (1982) and Lutz et al. (1982).

What the growth curve looks like and what kind of fit has to be applied, must be decided individually. The validity of a sigmoidal growth curve has been discussed by Bayne (1976). Gerdes (1983a) provides evidence that it is caused by a depressed feeding rate on the pediveliger stage when the larva starts reducing its velum.

In my own experiments at 6 °C, however, the growth curves leveled off far before reaching the pediveliger stage. Thus, sigmoidality must have different causes here. As will be demonstrated in a subsequent paper, the energy for swimming as a proportion of the measured respiration increases with larval size, especially at low temperatures. Possibly, in this case, the mussel has to spend so much energy to move that this affects growth.

According to the classification by Fry (1971; see also Brett, 1979), larval size is the limiting factor for larval growth. It is modified by the controlling effect of temperature and food concentration. This is manifested by the declining relative weight increase with larval size (Fig. 6).

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