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**Influence of food concentration on the physiological energetics and growth of Ostrea edulis larvae**

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**Abstract** Feeding, respiration and growth rates of oyster (Ostrea edulis L.) larvae reared at five food levels were measured throughout the entire larval period. Energy budgets were derived as a function of algal (Isochrysis galbana Parke) food concentration. Ingestion rate (IR, cells h\(^{-1}\)) and oxygen consumption rate (\(V_{O_2}\), nl h\(^{-1}\)) were almost isometric functions of larval size [ash-free dry weight, (AFDW, \(\mu\)g)], characterized by the equations: \(IR = 803.9\) AFDW\(^{1.13}\) \(\text{and } V_{O_2} = 4.85\) AFDW\(^{1.09}\). Ingested ration was directly correlated to cell concentration up to a maximum at 200 cells \(\mu\)l\(^{-1}\), with further increases failing to support higher ingestion rates. Likewise, growth rate linearly increased with food ration up to 100 cells \(\mu\)l\(^{-1}\) (max. growth efficiency, \(K_g = 25\%\)) and reached a maximum at 200 cells \(\mu\)l\(^{-1}\) (growth rate = 5.6 \(\mu\)m d\(^{-1}\)), with further increases in food not supporting significantly faster growth. Maintenance ration was 2 to 3\% daily dry weight (DW); optimum ration increased during larval development from 5 to 20\% DW; maximum ration was 20\% DW. During larval rearing, an increasing feeding schedule of 50, 100 and 200 cells \(\mu\)l\(^{-1}\) from Days 0, 5 and 10, respectively, is recommended.

**Introduction**

Physiological energetics provide an understanding of how energy from food in a developing animal is partitioned among the metabolic costs of digestion, maintenance, activity and growth, and how much remains available for net growth. This partition is reflected in the equation of the energy balance originally introduced by Ivlev (1945) and Winberg (1956), and which is now widely applied to the study of molluscan physiology (reviewed by Bayne and Newell 1983)

\[
G = I - F - N - R = A - R,
\]

where \(G = \text{growth, } I = \text{ingestion, } F = \text{faecal loss, } N = \text{nitr}
ogen excretion, \(R = \text{respiration and } A = \text{assimilation. Increased net energy gain in bivalve molluscs is limited by ingestive (I) and digestive (I-F) capacities rather than by metabolic costs (N+R) (Bayne et al. 1989).}

Far fewer data on bivalve larvae are available, although studies by Wilson (1980), Jespersen and Olsen (1982), Sprung (1984a, b, c, d), Crisp et al. (1985) and MacDonald (1988) contributed to the understanding of larval energetics. Since molluscan larvae are phytoplankton grazers, algal cell concentration is the main factor influencing their energy budget. Because of its economic importance, the European flat oyster Ostrea edulis has been the subject of pioneer studies by Walne (1965), who concluded that increased algal concentration increased the number of algal cells captured per larva, despite a reduced feeding activity in terms of volume of water cleared of particles. Using \(^{14}\)C-labeled algae, Walne demonstrated increased algal ingestion up to a maximum at 150 to 200 Isochrysis galbana cells \(\mu\)l\(^{-1}\). Subsequently, Wilson (1979) and Crisp et al. (1985) characterized the dependence of ingestion on particle concentration as a parabolic curve, with a maximum between 200 and 300 cells \(\mu\)l\(^{-1}\).

In general, mussel (Mytilus edulis) larvae showed higher feeding rates at lower algal concentrations; this was at least partially due to the use of different larval sizes and densities. Growth, as measured by shell length increase, peaked at 20 to 50 cells \(\mu\)l\(^{-1}\) (Jespersen and Olsen 1982; Sprung 1984d). However, when comparing oviparous species, differences in trophic behaviour must be taken into account, since mussel larvae undergo an initial stage of either complete or partial dependence on the stored energy reserves in the egg (Bayne 1976), whereas when Ostrea edulis larvae are released they are fully dependent on exogenous food sources.

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In addition to the limited amount of data available, some of the following points have not been examined in studies of the bioenergetics of oyster larvae: (i) Long-term growth experiments at sustained food level conditions are necessary to corroborate short-term feeding-rate responses; such trials are especially feasible when larval stages with high growth rates are used. (ii) Larval growth should be measured as weight increase, or the allometric length:weight relationship should be established under the particular experimental conditions, since shell growth has been demonstrated to occur even when tissues are being depleted. (iii) Ingestion rates are more comparable between experiments when they are expressed as algal weight consumed rather than number, since Isochrysis galbana weight per cell can vary by >100%, depending on batch and culture phase.

The object of this study was to investigate the growth performance of Ostrea edulis larvae at different food levels and to explain actual growth on the basis of the physiological parameters involved in the energy balance.

Materials and methods

General methods

Oyster (Ostrea edulis L.) larvae were obtained during early spring from our own stock of adults (Instituto Español de Oceanografía, A Coruña, Spain), conditioned according to Pérez Camacho et al. (1977). The newly released larvae were retained in 80 μm nylon sieves fitted to the conditioning-tank outlets. The total number and the initial (Day 0) mean length was determined for all larval batches used for experiments. At least three samples were taken of each larval stock for counting and measuring in 1 ml Sedgewick Rafter cell. Larval length (antero-posterior axis) was measured by a graduated eyepiece at 100× magnification (n = 50). All experiments were conducted in a constant-temperature room at 20°C, and larvae were fed with the unicellular alga Isochrysis galbana Parker collected in the initial stationary phase. The nominal food concentrations tested were 20, 50, 100, 200, and 300 cells μl-1. All cell counts were made with a TAI Coulter Counter fitted with a 100 μm aperture sampling tube. The seawater used for the larval cultures was filtered with a set of cartridge filters (100, 10 and 1 μm) and was irradiated with ultraviolet light. Chloramphenicol (8 mg l-1) was added to further retard bacterial growth. Gentle aeration was provided by glass rods fitted to a filtered air pump.

Food uptake

Food uptake rates were measured using larvae in four different developmental stages (mean length = 200, 260, 283 and 314 μm). Larvae were delivered into gently aerated 1-litre beakers at a density of 5 to 10 ml-1, depending on their size (lower densities for larger larvae). Experimental concentrations were duplicated and a control without larvae was established for each food level. The initial algal concentration was determined after 30 min, to allow larvae to recover full activity, and subsequently at 1 or 2 h intervals. All experiments were ended before algal concentration decreased below 60% of the initial concentration. Ingestion rate (IR, Isochrysis galbana cells h-1) and clearance rate (CR, μl h-1) were calculated according to the equations (modified from Quayle 1948):

\[ IR = V \times n \times (c_0 - c_f) / t \]
\[ CR = V \times n \times (c_0 - c_f) / (t \times F) \]

where V = water volume, n = number of larvae, t = time interval, \( c_0 \) = final cell concentration in controls and \( c_f \) = final concentration in experimental beaker. In general, \( c_0 \) was almost identical to the initial concentration in both experimental and control beakers. After the physiological measurements had been made, all larvae from each beaker were filtered, measured, and weighed as previously described. The food-uptake rates of larvae of different sizes were then compared, standardizing for a 1 μg AFDW larva as described by Bayne et al. (1987).

Respiration

The rates of oxygen consumption by larvae were measured in sealed 100 ml conical flasks using YSI (BOD 5720 A) oxygen probes. Four replicates and a blank were measured for each larval size. The oxygen consumption of one of the replicates in each treatment was monitored by an oxygen sensor to record the decline in oxygen. Only decreases in 10 and 30% were included in calculations, since decreases < 10% were considered as falling within the possible error of the apparatus, whereas decreases of >30% could deleteriously have affected normal respiration rates. The flasks were filled with algal-free aerated and stabilized seawater at 22°C ± 1°C, taking care to exclude air bubbles. We did not attempt to measure oxygen-consumption rates in the presence of algae.

The oxygen consumption rate (\( V_{O_2} \), ml h-1) was calculated using the following equation:

\[ V_{O_2} = (\text{Vol} \times n \times (c_0 - c_f)) \]

where \( V \) = the volume of water, \( n \) = the number of larvae, \( t \) = the time interval and \( c_0 \) and \( c_f \) are the final oxygen concentrations in the blank and the experimental flasks, respectively. Metabolic energy expenditure was calculated from the oxygen consumption using the equivalent of 450 kJ mol-1 O2 (Gnaiger 1983).

Growth

In growth experiments, larvae were reared at a density of 2 ml-1 in 6-litre plastic tanks with 5 litres of seawater. Food was added every 2 d, or every day if necessary, to avoid any substantial decrease in cell concentration. Experimental concentrations were triplicated and a control without larvae was established for each food level. The algal cell concentration was recorded before and after each water change and food addition.

Mortality, percentage of eyed larvae, mean length, dry weight (DW) and ash-free dry weight (AFDW) of larvae were recorded weekly. The percentages of dead and eyed larvae were calculated from observation of a sample of 150 larvae under a microscope: dead larvae are easily identified by their lack of tissue structure and later as empty shells. Samples of a known number of larvae were dried on washed, ashed, and tared Whatman GF/C filters at 90°C until constant weight to obtain DW. Organic matter content was estimated as weight lost after ashing in a furnace at 450°C overnight. Weights were determined using a Mettler balance with a precision of ±0.1 μg. Assimilation ration (A) was calculated from growth (G) and respiration (R) in accordance with the the energy-balance equation (Eq. 1) as:

\[ A = G - R \]

Gross growth efficiency (\( K_1 \)) and net growth efficiency (\( K_2 \)) were calculated from G, A and ingestion (I), following the equations (modified from Ives 1945):

\[ K_1 = G / I \]
\[ K_2 = G / A \]

Results

Allometric relationship of weight vs length

The relationship between weight (DW and AFDW) and shell length (L) in Ostrea edulis larvae is expressed by the
following allometric equations:

\[ DW = 1.22 \times 10^{-6} L^{2.64}, \quad r = 0.89; \quad n = 12, \quad (8) \]
\[ AFDW = 0.83 \times 10^{-6} L^{2.50}, \quad r = 0.88; \quad n = 10, \quad (9) \]

and is illustrated in Fig. 1.

Food uptake

Food-uptake rates increased exponentially with larval size up to 280–290 μm. However, longer larvae did not take up food at a faster rate. This saturation in uptake coincided with crawling behaviour and the withdrawal of the velum by the larvae as they approached metamorphosis. Therefore, the relationship between food uptake rates (IR as cells h\(^{-1}\) and CR as μl h\(^{-1}\)) and size (L in μm, DW and AFDW in μg) can be described by the following allometric equations: \( n = 6 \) (excluding premetamorphic larvae >290 μm in length):

\[ IR = 1.29 \times 10^{-6} L^{3.54}, \quad r = 0.93, \quad (10) \]
\[ IR = 192.5 DW^{1.24}, \quad r = 0.98, \quad (11) \]
\[ IR = 803.9 AFDW^{1.13}, \quad r = 0.98, \quad (12) \]
\[ CR = 5.34 \times 10^{-6} L^{2.55}, \quad r = 0.97, \quad (13) \]
\[ CR = 2.59 DW^{0.77}, \quad r = 0.97, \quad (14) \]
\[ CR = 8.93 AFDW^{0.98}, \quad r = 0.98, \quad (15) \]

Fig. 2 presents the regression line for IR plotted against larval length. Data from Beiras (1992) obtained under the same experimental conditions have been included, and do not cause any major change in the resulting regression model (compare equation in Fig. 2 to Eq. 10).

\[ CR \] was maximum at low cell concentrations, decreasing with increasing food concentration (Fig. 3). Conversely, \( IR \) was directly correlated to cell concentration up to a maximum at 200 μl\(^{-1}\), but further food increases failed to induce higher ingestion rates (Fig. 4).
Fig. 4  *Ostrea edulis.* Ingestion rate (IR) as a function of algal cell concentration for four larval sizes (shell length). Further details as in Fig. 3

Fig. 5  *Ostrea edulis.* Ingestion rate (IR, △) and clearance rate (CR, *) standardized to 1 mg AFDW larva using allometric weight exponent, as a function of algal cell concentration. A reciprocal model and a parabolic model were fitted to IR and CR data, respectively [see Eqs. (16) and (17)].

Fig. 5 shows a decrease in weight-specific clearance rate, CRs (standardized for a 1 µg AFDW larva using the regression weight exponent) with increasing algal cell concentration, C. This can be described by a reciprocal model:

\[
\frac{1}{CR_s} = 0.072 (\pm 0.0100) + 5.7 \times 10^{-4} (\pm 0.67 \times 10^{-4}) C; r = 0.84; n = 33.
\]  

(16)

The "best fit" model for the weight-specific ingestion rate, IRs (also standardized for a 1 µg AFDW larva) was achieved by using the logarithm of ingestion expressed as a parabolic function of particle concentration (Fig. 5). This explained 80% of the experimental variance \((r^2 = 79.9\%\)), and is characterized by the following equation:

\[
\ln IR_s = -1.76 (\pm 0.115) + 0.0215 (\pm 0.00223) C - 5.8 \times 10^{-5} (\pm 0.74 \times 10^{-5}) C^2;
\]

\[ r = 0.894; \quad p < 0.00001. \]

(17)

### Growth

Larvae displayed a linear increase in growth rate with increasing food ration up to 100 cells µl⁻¹, reaching a maximum at 200 cells µl⁻¹ (Table 1). Further increases in food availability did not support significantly faster growth. Larvae require increasing amounts of food to maintain their maximum growth potential (Fig. 6). Thus, 20 cells µl⁻¹ did not induce maximum growth rate from the start of development, 50 µl⁻¹ was sufficient up to lengths of 205 µm (6 d), but larger larvae required 100 µl⁻¹ and later 200 cells µl⁻¹ to sustain a maximum growth rate.

Gross growth efficiencies \((K_f)\) were between 10 and 25%, and were consistently maximum at 100 cells µl⁻¹, declining at higher food levels (Fig. 7). Throughout larval development, food was more efficiently converted to body

<table>
<thead>
<tr>
<th>Concentration</th>
<th>α</th>
<th>Growth rate, b</th>
<th>r</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>20 cells µl⁻¹</td>
<td>0.4</td>
<td>188.2 ± 1.09</td>
<td>0.95 ± 0.159</td>
<td>0.97</td>
</tr>
<tr>
<td>50 cells µl⁻¹</td>
<td>1</td>
<td>187 ± 3.6</td>
<td>1.8 ± 0.53</td>
<td>0.93</td>
</tr>
<tr>
<td>100 cells µl⁻¹</td>
<td>2</td>
<td>184 ± 3.3</td>
<td>3.9 ± 0.38</td>
<td>0.99</td>
</tr>
<tr>
<td>200 cells µl⁻¹</td>
<td>4</td>
<td>178 ± 5.7</td>
<td>5.6 ± 0.66</td>
<td>0.98</td>
</tr>
<tr>
<td>300 cells µl⁻¹</td>
<td>6</td>
<td>176 ± 7.6</td>
<td>5.7 ± 0.87</td>
<td>0.97</td>
</tr>
</tbody>
</table>

### Respiration

The oxygen consumption rate \((V_O; \text{ nl h}^{-1})\) per larva increased during development from 1 to 2 nl h⁻¹ at release to 10 nl h⁻¹ at the latest pediveliger stages. The relationship between \(V_O\) and larval size is described by the following allometric equations \((n = 12)\):

\[
V_O = 1.37 \times 10^{-2} L^{0.5}; \quad r = 0.912; \quad p < 0.00001.
\]  

(18)

\[
V_O = 1.48 DW^{0.19}; \quad r = 0.911; \quad p < 0.00001.
\]  

(19)

\[
V_O = 4.85 AFDW^{0.09}; \quad r = 0.912; \quad p < 0.00001.
\]  

(20)
biomass at moderate rations (20 to 100 cells µl⁻¹; K₁ 15 to 25%) than at higher rations (200 to 300 cells µl⁻¹; K₁ 10
to 15%). Net growth efficiencies (K₂, Fig. 7) varied
between 15 and 35% at low food rations (20 and 50 cells
µl⁻¹) and between 50 and 55% at high food rations (100 to
300 cells µl⁻¹).

Assimilation efficiency (AE, Fig. 7), was inversely re-
teated to ingested ration, with a maximum of 80% at the
lowest food level and a minimum of 20% at the food level
which induced maximum ingestion (200 µl⁻¹).

The energy budgets of 200 and 240 µm-long larvae fed
at five Isochrysis galbana levels (Fig. 8) show that with
increasing size larvae require more food to achieve both
zero (maintenance) and maximum growth.

**Discussion**

Feeding rates

In contrast to later developmental stages, molluscan veli-
gers display an almost isometric relationship between feed-
ing rates and larval size, (preferably expressed as ash-free
dry weight, AFWD), yielding b-values approaching 1 in
the classic allometric equation (Y = aXᵇ). In Ostrea edulis
larvae, b-values for feeding rate include b = 1.1 (M. Helm,
personal communication, cited by Bayne 1983), b = 0.97
(Gerdes 1983a), and b = 1.02 (Beiras et al. 1990); and in
Kuditapes decussatus b = 1.00 (Beiras et al. 1994). Ve-
gers of Mytilus edulis have often displayed b-values of 0.8
(b = 0.85, Risgård et al. 1981; b = 0.82, Jespersen and Ol-
sen 1982; b = 0.77, Sprung 1984 b).

Many investigators have described the behavioural
changes of late pediveliger larvae, which spend increasing
amounts of time crawling on the bottom with the velum re-
tracted in search of a suitable substratum on which to met-
amorphosis. Therefore, in premetamorphic pediveligers, a
decrease in the feeding rate per gram is to be expected.
Low b-values are expected when late pediveligers are in-
cluded in the size range of larvae used to measure feeding
rates.

The effect of particle concentration upon ingestion rate
has been comprehensively studied not only in adult bi-
valves (e.g. Walne 1972; Foster-Smith 1975, 1976; Schulte
1975; Widdows et al. 1979; Navarro and Winter 1982;
Gerdes 1983a, b; Navarro et al. 1992), but also in other
phytoplanktophagous organisms such as copepods (Frost
1972; Mullin et al. 1975; Lam and Frost 1976; Lehman
1976; Kiorboe et al. 1982). In summary, ingestion increases
with particulate food concentration up to a critical level of
saturation above which ingestion remains fairly constant.
Finally, at very high particle concentrations ingestion de-
creases. The "functional response" (Lam and Frost 1976;
Winter 1978), consisting of a fall in clearance rate, which
is responsible for a constant ingested ration within a rela-
tively broad range of food concentrations, implies an ac-
tive control mechanism that responds to elevated concen-
trations of food particles. Such mechanism could be either
regulation of the cilia beat or partial closing of the shell
Fig. 8 Ostrea edulis. Partitioning of energy for larvae of 200 and 240 μm mean shell length as a function of algal food concentration

whereas in the curvilinear model, clearance rate is maximum at the minimum concentration and steadily decreases with increasing particle levels. In both models, the decrease in food uptake may be a response by the organism to a progressive saturation of its physical mechanism of capture, ingestion and/or digestion of the particulate food. For example, the rate of food processing in the digestive tube could limit food ingestion, and thus ingestion rate would be determined by egestion rate. On a practical basis, considering the natural variability in feeding rates, particularly under extreme particle concentrations, it is almost impossible to discern which model is more suitable. In fact, both have yielded comparable adjustments of experimental data (Mullin et al. 1975; and present study).

For bivalve veliger larvae, the response of ingestion rate to variable particle concentration has been fitted to curvilinear models, because of the limited ability of these organisms to regulate (maintain constant) ingestion (Wilson 1979, 1980; Jespersen and Olsen 1982; Crisp et al. 1985; Riisgård 1988; and present study). Several functions, such as the asymptotic (see Ivlev 1945), hyperbolic (Kjørboe et al. 1982) and parabolic (Crisp et al. 1985) equations, have been used to explain larval feeding response to concentration. A partial lack of regulated ingestion rates in veligers compared to adult bivalves may be due to the much lower efficiency of the particle-capturing mechanism of the former; i.e., only a very low percentage of the particles in the stream originated by the velar cilia are actually captured and ingested (Gallager 1988; and our own microscopical observations; see also review on larval feeding by Strathmann 1987). For the same reason, clearance rate (defined as the volume of water cleared per unit time) in veliger larvae has very limited biological meaning, and is inappropriate for adult—larvae comparisons because the total volume of water actually pumped by the larval velum is in fact several times higher than the volume reflected by the clearance rate.

On the other hand, Wilson (1979) demonstrated a marked decrease in the grazing rate of Ostrea edulis veliger at concentrations of >300 Isochrysis galbana μl⁻¹. Gallager (1988) suggested that the sharp reduction in food uptake at high food levels may result from interference and clogging of the velar cirri or food groove. In the present study, we present limited evidence of a decrease in ingestion rate at the highest concentration assayed (300 I. galbana μl⁻¹). Among the mathematical models cited above, a parabolic function, which reflects this decrease, is preferred for describing the larval feeding response over the whole range of food concentrations.

Respiration

We have found an allometric exponent of 1.09 for the oxygen consumption rate of Ostrea edulis larvae. According to the "surface law" formulated in the last century, the metabolic rate of an organism is directly correlated to its body weight raised to the power of two-thirds (=0.67). Experimental evidence generally supports this. In a literature
review of fishes, Winberg (1956) obtained an average allometric exponent of 0.815±0.0105, while Glass (1969) found a value of 0.86±0.03. In crustaceans the exponent was 0.81 (Winberg 1956), in gastropods (Berg and Ockelmann 1959) between 0.7 and 1, and in bivalves (Bayne and Newell 1983) between 0.65 and 0.84 with a mean of 0.7. However, classic studies have already shown that early developmental stages have higher allometric exponents than adults. Winberg (1956) reported an exponent of 0.98 for carp fry and Palheimo and Dickie (1966) a value of b = 1.19 for trout fry, but a value of b = 0.8 for adults. In veliger larvae of mussels, Rissård et al. (1981) found an exponent of 0.90; for Crassostrea gigas, Gerdes (1983b) reported 0.96; and for Terebratulinae, Mann and Galler (1985) reported 1.07 and 1.18. The exponent found in the present study with O. edulis (1.09) is within the range previously reported. In conclusion, despite the high variability of the allometric relationships describing the metabolic rate of larval stages of molluscs and other marine animals, the weight-specific metabolic rate (per g) seems to be relatively independent of body size. As concluded by Zeuthen (1953) after a comprehensive review of this subject: “...for all the animals studied there would seem to be a period of (approximately) directly proportional growth of the metabolism and the whole body”; that is, a period during which the metabolic rate is isometric.

Growth

In this study, the growth rate of oyster larvae was directly correlated with the amount of food offered in suspension up to a maximum where saturation of both particle capture and ingestion occurred. Saturation of ingestion was achieved at ~200 cells μl⁻¹ in all larval stages (Fig. 4). A decrease in ingestion rate at higher concentrations suggests that some step of food-processing (i.e., food uptake, ingestion and digestion) was adversely affected. Previous papers regarding Mytilus edulis veligers have reported saturation of ingestion at lower food levels. Jespersen and Olsen (1982), working at 15°C, found a plateau in both the ingestion and growth rates at Isochrysis galbana concentrations of >40 to 60 cells μl⁻¹. The lower ingestion capacity and optimum food concentration for M. edulis compared to oyster larvae may be due to the low larval densities that Jespersen and Olsen used in their growth experiments (1 to 2 larvae per 10 ml) and to the smaller size of their larvae (100 to 160 μm). Sprung (1984b, d) found that at 18°C mussel veligers grew at a maximum rate at the highest food concentration tested (40 I. galbana cells μl⁻¹); however, at lower temperatures, both growth and maximum ingestion occurred at much lower algal concentrations (10 cells μl⁻¹). In this case again, different larval size partially explains the differences in the algal concentration that maximizes ingestion. When the maximum ingested rations of Sprung’s studies were expressed on a percentage weight basis (see below), they were comparable to the rations reported in the present study.

In agreement with previous investigations, the present study has demonstrated that food assimilation efficiencies of bivalve veligers, measured as (G+R)/I, reach maximum values of 80%, and thereafter decline with increased ration to 20–35% (Fig. 7; see also, Jespersen and Olsen 1982; Sprung 1984d; Crisp et al. 1985).

The maintenance ration (mR) has been defined as the amount of ingested food that meets only the metabolic requirements of an organism, thus supporting zero growth. According to our results, the mR for a newly released (200 μm) oyster larva was 30 ng of Isochrysis galbana ingested daily, which is equivalent to 2–3% DW (6% AFDW). Since the metabolic rate per gram larva did not significantly change during larval development (exponent = 1.09), neither did mR as a percentage (algal weight:larval weight). Crisp et al. (1985) also found a high maintenance ration (~50 Pavlova lutheri cells μl⁻¹) for newly released Ostrea edulis larvae. This agreed with Walne’s (1965) minimum food levels for good hatching growth. In all three studies, the seston loads (expressed as particulate organic matter per litre) necessary to support oyster larval growth were clearly higher than those present under average oceanic and estuarine conditions, indicating that either supplementary nutrient sources are used in the natural environment, or that synergistic effects occur between different kinds of food. Manahan and Crisp (1982) emphasized the higher weight-specific capacity (greater surface:volume ratio) for absorbing dissolved organic material of marine invertebrate larvae compared to adults as a possible explanation. Although net uptake of dissolved organic matter has been demonstrated in molluscan veligers (Rice et al. 1980), the amounts recorded would not meet the complete energetic demands by far, and further research is needed on this subject.

Optimum ration (OR), corresponding to maximum gross growth efficiency (Kᵣ), increased during larval development. The calculated daily ORs of 1.5, 2 and 2.5 μg DW larvae (6, 10 and 13 d old) were 5, 10 and 20% (70, 180 and 500 ng of Isochrysis galbana larva⁻¹ d⁻¹). Nevertheless, Kᵣ was maintained near maximum levels within a wide range of food concentrations (20 to 100 cells μl⁻¹). Other studies have reported similar ranges: 5 to 100 cells μl⁻¹ (Walne 1965); 5 to 60 cells μl⁻¹ (Jespersen and Olsen 1982); 2 to 40 cells μl⁻¹ (Sprung 1984d).

Maximum ration (MR, corresponding to the fastest growth rate) was limited by the maximum ingestion capacity, which was a fairly constant proportion of larval size (see first paragraph of “Results—Growth”). Hence, MR fluctuated between 15 and 20% DW (45 to 60% AFDW) within the total developmental period. Therefore, offered rations should be increased during larval development to sustain maximum growth. For example, larvae of 200 and 240 μm (1.5 and 2.4 μg DW) require a daily MR of 250 and 360 ng algae. A concentration of 200 cells μl⁻¹ supports such a ration. However, larvae of 270 μm (3 μg DW) require 300 cells μl⁻¹ to acquire their MR. Rhodes and Landers (1973) achieved maximum growth rates by feeding 140, 170 and 200 μm-long Crassostrea virginica larvae with increasing algal concentrations of 175, 225 and
325 Isochrysis galbana cells µl⁻¹ added every 2 d; higher algal concentrations did not support better growth, even for larger larvae. Sprung (1984b) described similar maximum ingestion capacities in mussel veligers when expressed as a daily percentage of body weight - 60 to 80% AFDW d⁻¹ at 18°C and 50 to 70% at 12°C.

Since maximizing growth rate is the main goal in a hatchery, we contend that MR should be provided to the veligers. In hatchery rearing, food is usually delivered with each water change in the same dose throughout the larval period, despite early observations by Rhodes and Landers (1973) who found that it was more efficient to increase the Isochrysis galbana concentration as larvae grow. In the present study, where larvae were fed at constant rates, optimum growth could be achieved by feeding larvae daily with 100 cells µl⁻¹. However, the largest larvae required higher rations to fully exploit their maximum growth rate. Therefore, our study emphasizes that a variable feeding pattern, of 50, 100 and 200 cells µl⁻¹ from Days 0, 5 and 10, respectively, is an effective way of maximizing oyster larval growth. Alternatively, if the volume of containers and water availability are not restrictive, MR can be achieved using a constant ration of 100 cells µl⁻¹ by reducing larval density by one-half and one-quarter on Days 5 and 10, respectively.

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