Feeding, physiology and growth responses in first-feeding gilthead seabream (*Sparus aurata* L.) larvae in relation to prey density

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**Abstract**

The effects of prey density (0.1, 1 and 10 rotifer ml⁻¹) on feeding, oxygen uptake, growth, survival and energetic efficiencies in *Sparus aurata* larvae were investigated. Dry weights and total lengths at day 15 after hatching were similar in larvae fed with 10 and 1 rotifer ml⁻¹ but were significantly higher than in larvae fed with 0.1 rotifer ml⁻¹. These differences were a consequence of a delay in starting feeding and growth in larvae fed with the lowest rotifer concentrations tested. Growth rates were similar in larvae fed on 0.1 and 1 rotifer ml⁻¹, while larvae fed with 10 rotifers ml⁻¹ showed the smallest growth rate. Survival decreased markedly (from 91 to 7%) when prey density decreased. Ingestion rates of the actively feeding larvae increased with age at the three prey densities but larvae fed with 0.1 rotifer ml⁻¹ showed lower ingestion rates. The specific oxygen uptake increased from hatching up to 35–40 μg dry weight; above this size the specific oxygen consumption remained almost constant. Survival at the end of the experimental period was closely related to the percentage of larvae able to start feeding at day 6. In larvae fed with 0.1 rotifer ml⁻¹, the energy ingested during the first days of feeding roughly met maintenance requirements. Therefore, the survival of larvae able to start feeding is not guaranteed at such low prey density. © 2000 Elsevier Science B.V. All rights reserved.

**Keywords**: Larval fish; First feeding; Food availability; Ingestion rate and respiration rate

**1. Introduction**

The gilthead seabream (*Sparus aurata* L.) is a sparid, occurring in the North Eastern Atlantic Ocean and the Mediterranean Sea (Bauchot and Hureau, 1986). The larvae of

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this species measure 2.5 mm at hatching and are very sensitive during the first stages of development. Due to its importance in the aquaculture of the Mediterranean countries, gilthead seabream has been profusely studied in the laboratory (Person-Le Ruyet and Verillaud, 1980; Tandler and Sherman, 1981; Pascual and Arias, 1982; Divanach and Kentouri, 1983; Tandler and Helps, 1985; Koven et al., 1990; Polo et al., 1992; Kolkowski et al., 1993; Mourente et al., 1993; Yúfera et al., 1993a; Koven et al., 1998). One point of prime interest, both in nature and in cultured populations, is the ability of larval fish to grow and develop in relation to the food available at first feeding. Yúfera et al. (1993b) found that, in the complete absence of food at 19.5°C, the gilthead seabream larvae reached the point of irreversible starvation by day 8 after hatching, and did not survive day 10. However, the consequences of a relative food restriction had not been examined and it was important to know whether such restriction reduces growth or survival, or both. The implications of this question in understanding recruitment of the natural fish population are evident, and several studies have been conducted on different species in the past, trying to find critical prey availability to maintain a normal recruitment (Houde, 1978; Werner and Blaxter, 1980). But there are also implications for fish cultivation in the laboratory. High prey concentrations are used to maximise ingestion, and consequently growth and survival, in intensive rearing tanks with a high larvae density and high food demand. Relatively high live-prey density is also being used in combination with inert diet when researching prepared feeds for larvae (Vergara-Marín et al., 1990; Holt, 1993; Bernabè and Guissi, 1994; Hayashi, 1995; Fernández-Díaz and Yúfera, 1997). Nevertheless, to evaluate the real contribution of the inert diet it is necessary to first know to what extent the presence of live prey supports larval growth and development.

The present study investigated the effect of prey concentration on growth, survival, ingestion, oxygen uptake and energetic efficiencies of *S. aurata* larvae. The aims were to find the minimum food ration that allows larval development, and to examine whether prey availability influences the timing of the commencement of feeding and body growth.

2. Materials and methods

*Sparus aurata* eggs were obtained by natural spawning from captive broodstocks and were incubated at 19.5°C. Newly hatched larvae were transferred to 300-l tanks with continuous illumination and a salinity of 33 g l⁻¹. Constant slight aeration was provided. Initial larvae density ranged from 50 to 70 larvae l⁻¹. From day 3 onwards, about 15–20% of the water volume was renewed daily. Live prey was added from day 4 after hatching. Two different *Brachionus* species were supplied: *B. rotundiformis* (= 0.2 μg mean dry weight) for larvae with a mean dry weight below 60 μg and *B. plicatilis* (= 0.4 μg mean dry weight) for larvae above 60 μg (Polo et al., 1992). Three prey densities, 0.1, 1 and 10 rotifer ml⁻¹, were tested. The highest prey concentration tested is the standard concentration used in normal culturing of *S. aurata* larvae.

Larval dry weights and total lengths were obtained from samples taken 4, 6, 9, 12 and 15 days after hatching. Three replicates per treatment were performed using different
egg batches. Total lengths were measured with an ocular micrometer on 20 larvae per sample. Dry weight was determined by drying samples of about 15–30 larvae at 85°C to constant weight. Specific growth rate ($G$) was calculated as the slope of the exponential regression of dry weight on time. The initial weight-decreasing period before the onset of growth were not taken into account in determining $G$ and only positive growth periods were considered. Larval density in the rearing tanks was estimated on day 4 (first feeding) and day 15 (end of the experiment) by counting larvae in ten 250 ml samples. Energy content was determined on freeze-dried larvae using a semimicro bomb calorimeter Parr 1421. Three sub-samples of 20 mg were used in each determination. The energy employed in growth ($G_v$) was calculated using larval caloric content and the daily dry weight increase. Production ($P$) has been estimated from the total increase in larval dry weight biomass per volume unit during the experimental time, assuming that mortality occurred only in non-growing starved larvae.

Ingestion experiments were carried out directly in the rearing tanks at 6, 9, 12 and 15 days after hatching. About 20–30 larvae were sampled periodically (every 5, 10 or 15 min) over a 2- or 4-h period depending on larval age, and then anaesthetised with ethyl-4-amino-benzoate. The larvae were then examined under a light microscope to examine the gut content. The method described by Yúfera et al. (1993a) is based on the use of green-coloured rotifers by means of short refeeding period in a dense suspension of microalgae cells. These green rotifers can be distinguished from those that have been in rearing tanks for several hours, because the latter look brown. The fullness of guts follows an asymptotic function

$$C = C_{\text{max}} (1 - e^{-bt})$$

where $C$ is the number of green rotifers (per larva showing gut content), $C_{\text{max}}$ is the asymptote of the curve (rotifers·larva⁻¹), $t$ is time (h), and $b$ is a regression parameter which indicates the instantaneous rate of gut filling (h⁻¹). This model was fitted by the iterative method to the asymptotic function. The ingestion rate ($I$) was calculated as the derivative of this function against time of this function at the starting point, when no green rotifers had yet been evacuated

$$I = C_{\text{max}}b$$

The daily specific ration (SR) was calculated as $SR = I \cdot M \cdot 24$ DW⁻¹, where $I$ is the ingestion rate (rotifer larva⁻¹ h⁻¹), $M$ is the average rotifer dry weight (μg) and DW is the larval dry weight (μg). When $I$ is multiplied by rotifer dry weight (μg), ingestion rate is expressed as dry mass ingested per larva per hour, $IR$ (μg larva⁻¹ h⁻¹). Rotifer dry weight and energy content values used for the calculations were determined as a function of the egg/female ratio observed in the larval gut (Yúfera et al., 1997). The energy intake ($I_e$) was calculated using the ingestion rates and the rotifer energy content. Percent of actively feeding larvae were determined by examining at least 100 larvae from the same samples used in determining the ingestion rate.

Oxygen consumption determinations were carried out in a respiratory chamber equipped with a polarographic oxygen sensor. The electrode was attached to a dissolved oxygen meter (Strathkelvin Instruments mod. 781b with 1302-oxygen electrode). Output
was wired via a data acquisition board (Metrabyte DAS8-PGA) to a PC program used for continuous data logging. The Weiss equation was used to estimate oxygen solubility in relation to temperature and salinity (Weiss, 1970). After a 5–15 min equilibration period, the electrode was stabilised and oxygen concentration declined at a constant rate. Oxygen uptake by the larvae was estimated as the slope of the regression line of oxygen concentration on time during 20–30 min following electrode stabilisation. Sterilised and air-saturated seawater (salinity 33 g l⁻¹) was used. The respiratory chamber was kept at a constant temperature (19.50±0.05°C). The water volume in the respiratory chamber was approximately 3 ml. The number of larvae in each experiment ranged from 5 to 9. The larvae were held without food in the chamber, but they had been held under normal rearing conditions in the tanks prior to measurements. When mortality occurred inside the chamber, the data were excluded. Oxygen uptake was calculated in nmol O₂ larva⁻¹ h⁻¹. After each experiment, larval dry weight was determined for calculation of specific oxygen consumption (nmol O₂ µg⁻¹ h⁻¹). Oxygen consumption (OC) for each prey density in relation to larval weight were fitted to a curve of the type

\[ OC = a \cdot DW^b \]

where DW is the larval dry weight, and a and b are regression parameters.

During the early development, the seabream larvae that starved for more than 12 h suffer serious damage and this period is insufficient to evacuate the gut content because the larvae tend to retain the ingested food within the gut in absence of prey in the medium. Consequently, it is not realistic to perform experiments using larvae with empty guts. Therefore, we assumed measurements represented routine metabolism plus the specific dynamic action. The energy expended in metabolic processes (\( M_e \)) was calculated using the oxygen uptake rates and the oxycaloric coefficient (13.56 J mg⁻¹ dry weight) from Brett and Groves (1979) for conversion into energy units. The energetic efficiencies were calculated using the energy intake (\( I_e \)), the energy employed in growth (\( G_e \)) and the metabolic energy (\( M_e \)) as is shown in Table 1.

Data from the different treatments were compared using one-way ANOVA and Student t-test for slopes comparison. When significant differences were detected, the Newman–Keuls multiple-range procedure was used to determine the statistical differences between treatments. Before the statistical analyses, the dry weight and total length data were log-transformed and the survival percentage values were arcsine transformed.

### 3. Results

Larval dry weights and total lengths attained on day 15 were similar when fed with 1
Table 2
*Sparus aurata*: total length (TL; mm), dry weight (DW; mg), percentage of survival, energy content (J mg⁻¹), growth rates (G; d⁻¹) and biomass net production (P; mg l⁻¹) in 15-day-old larvae under different prey densities

<table>
<thead>
<tr>
<th>Prey density (rotifers ml⁻¹)</th>
<th>0.1</th>
<th>1</th>
<th>10</th>
</tr>
</thead>
<tbody>
<tr>
<td>TL</td>
<td>4.77±0.24⁸</td>
<td>5.27±0.36⁸</td>
<td>5.38±0.28⁸</td>
</tr>
<tr>
<td>DW</td>
<td>61.17±11.84⁸</td>
<td>110.82±14.10⁸</td>
<td>107.10±22.30⁸</td>
</tr>
<tr>
<td>Survival</td>
<td>6.67±3.65⁸</td>
<td>39.31±16.74⁸</td>
<td>91.12±12.26⁸</td>
</tr>
<tr>
<td>Energy content</td>
<td>17.18±1.44⁸</td>
<td>17.19±0.98⁸</td>
<td>19.23±0.23⁸</td>
</tr>
<tr>
<td>G</td>
<td>0.198±0.048⁸</td>
<td>0.180±0.012⁸</td>
<td>0.146±0.020⁸</td>
</tr>
<tr>
<td>P</td>
<td>-1222±24⁸</td>
<td>866±631⁸</td>
<td>4223±1256⁸</td>
</tr>
</tbody>
</table>

*Data represent mean±SD of three replicates. Same superscript letter denotes no statistical differences (P<0.05).*

and 10 rotifer ml⁻¹, whereas when fed 0.1 rotifer ml⁻¹ the larvae showed a significantly lower dry weight (P>0.05) (Table 2). This was a consequence of the corresponding growth patterns (Fig. 1). From the onset of feeding (day 4), when the larvae weighed approximately 25 μg, the weight gained at day 15 with 0.1 rotifer ml⁻¹ was less than one-half of that obtained with 1 and 10 rotifer ml⁻¹. However, Fig. 1 shows that there was a 2-day delay in starting growth with 1 rotifer ml⁻¹, and a 5-day delay with 0.1 rotifer ml⁻¹. Considering from the start of growth, the specific growth rate (G) in larvae fed on 10 rotifers ml⁻¹ was lower than in larvae fed with 0.1 and 1 rotifer ml⁻¹ (P>0.05). Mortality increased strongly during the experimental period with decreasing rotifer concentration, and only 6.7% of larvae survived at day 15 when fed 0.1 rotifer ml⁻¹ (Table 2). Consequently, the total net production from first feeding to the end of the experiment increased with increasing prey density up to a maximum of 4223 μg dry mass per liter. The maximum total length observed just before first feeding on day 4 was 4.0 mm. Length frequency distribution of larvae (Fig. 2) revealed that on day 9, only 10% of larvae fed 0.1 rotifers ml⁻¹ exceeded 4.0 mm total length. On the other hand,
most larvae fed 10 rotifers ml\(^{-1}\) (≈90%) exceeded 4.0 mm on day 9, while larvae fed at 1 rotifer ml\(^{-1}\) showed an intermediate figure, with 42% of the population over 4.0 mm.

The proportion of actively feeding larvae during development is shown in Fig. 3. The percentages of larvae able to start feeding increased when the prey density increased. When larvae were fed with 10 rotifers ml\(^{-1}\), this percentage increased progressively from the first days of feeding, reaching a maximum of approximately 90% by day 12 after hatching (Fig. 3a). Conversely, when fed with 0.1 and 1 rotifer ml\(^{-1}\), the percentage of feeding larvae decreased during the first days, especially with 0.1 rotifer ml\(^{-1}\). Only beyond the point of irreversible starvation, after the starving larvae died, did this percentage increase to reach values similar to those observed at 10 rotifer ml\(^{-1}\) by day 15. Fig. 3b shows the relationships between the percentage of actively feeding larvae and the mean dry weight of the population. It is interesting to note that when the population grew above 35–40 μg most of the larvae (>60%) were actively eating, irrespective of prey density.

The ingestion rates (μg larva\(^{-1}\) h\(^{-1}\)) of the actively feeding larvae increased with age (Table 3), but ingestion rates were always lower when larvae, of the same age, were fed
Fig. 3. Percentage of the actively feeding *Sparus aurata* larvae under three different rotifer concentrations in relation to (A) larval age and (B) mean larval dry weight.

on 0.1 rotifers ml$^{-1}$ than 1 and 10 rotifers ml$^{-1}$. On day 6, when the larval size differences among treatments were still small, larvae fed 0.1 rotifers ml$^{-1}$ only ingested 30% of their dry weight per day, while at the other tested rotifer densities the specific daily rations (SR) were higher (70–80%) ($P<0.05$). The differences in SR tended to decrease with age, but larvae fed with 1 rotifer ml$^{-1}$ always showed the highest SR.

The oxygen uptake increased with larval weight (Fig. 4a). Power functions relating the oxygen uptake (CO; nmol O$_2$ larva$^{-1}$ h$^{-1}$) to dry weight (DW; µg) were fit for each prey. Regression functions are:

- 0.1 rotifer ml$^{-1}$: $CO = 0.083 \cdot DW^{1.418}$, $r = 0.830$, $n = 30$
- 1 rotifer ml$^{-1}$: $CO = 0.236 \cdot DW^{1.193}$, $r = 0.881$, $n = 20$
- 10 rotifer ml$^{-1}$: $CO = 0.116 \cdot DW^{1.350}$, $r = 0.872$, $n = 43$

No statistical differences were found among the slopes ($P<0.05$). The function calculated when considering only pooled values of larvae above 25 µg dry weight was:
Table 3

*Sparus aurata*: ingestion rate (\(I\); \(\mu\)g larva\(^{-1}\) h\(^{-1}\)) and specific daily ration (SR; %) observed in larvae under three different prey densities during experimental period. Daily energy ingested (\(I_1\)), energy employed in growth (\(G_1\)), energy expended in metabolism (\(M_1\)), gross growth efficiency (\(K_1\)), assimilation efficiency (\(A_1\)), and gross metabolic efficiency (\(M_2\)) are also included\(^a\).

<table>
<thead>
<tr>
<th>Age (days)</th>
<th>6</th>
<th>9</th>
<th>12</th>
<th>15</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.1 rotifer ml(^{-1})</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DW ((\mu)g)</td>
<td>20.8±0.9</td>
<td>20.5±4.4</td>
<td>37.9±12.8</td>
<td>61.2±11.8</td>
</tr>
<tr>
<td>(I) ((\mu)g larva(^{-1}) h(^{-1}))</td>
<td>0.28±0.17</td>
<td>0.44±0.11</td>
<td>1.65±0.37</td>
<td>4.74±2.89</td>
</tr>
<tr>
<td>SR (%)</td>
<td>30±19(^a)</td>
<td>43±7(^a)</td>
<td>105±13(^a)</td>
<td>224±123(^a)</td>
</tr>
<tr>
<td>(I_1) (ml larva(^{-1}) d(^{-1}))</td>
<td>151</td>
<td>237</td>
<td>887</td>
<td>1554</td>
</tr>
<tr>
<td>(G_1) (mJ larva(^{-1}) d(^{-1}))</td>
<td>63</td>
<td>117</td>
<td>189</td>
<td></td>
</tr>
<tr>
<td>(M_1) (mJ larva(^{-1}) d(^{-1}))</td>
<td>80</td>
<td>77</td>
<td>207</td>
<td>307</td>
</tr>
<tr>
<td>(K_1) (%)</td>
<td>-</td>
<td>26.58</td>
<td>13.22</td>
<td>7.42</td>
</tr>
<tr>
<td>(A_1) (%)</td>
<td>-</td>
<td>58.89</td>
<td>36.47</td>
<td>19.48</td>
</tr>
<tr>
<td>(M_2) (%)</td>
<td>52.74</td>
<td>32.31</td>
<td>23.25</td>
<td>12.05</td>
</tr>
</tbody>
</table>

| 1 rotifer ml\(^{-1}\) |    |    |    |    |
| DW (\(\mu\)g) | 23.2±1.6 | 33.3±8.0 | 67.2±8.1 | 110.8±14.1 |
| \(I\) (\(\mu\)g larva\(^{-1}\) h\(^{-1}\)) | 0.79±0.30 | 1.09±0.18 | 10.17±4.20 | 12.17±5.92 |
| SR (%) | 82±32\(^a\) | 119±43\(^a\) | 365±140\(^a\) | 358±148\(^a\) |
| \(I_1\) (ml larva\(^{-1}\) d\(^{-1}\)) | 425 | 586 | 5467 | 6542 |
| \(G_1\) (mJ larva\(^{-1}\) d\(^{-1}\)) | 72 | 105 | 219 | 327 |
| \(M_1\) (mJ larva\(^{-1}\) d\(^{-1}\)) | 103 | 179 | 327 | 433 |
| \(K_1\) (%) | 16.94 | 17.92 | 4.01 | 5.00 |
| \(A_1\) (%) | 41.18 | 48.46 | 9.99 | 11.62 |
| \(M_2\) (%) | 24.16 | 30.53 | 5.98 | 6.61 |

| 10 rotifer ml\(^{-1}\) |    |    |    |    |
| DW (\(\mu\)g) | 29.0±3.2 | 49.9±3.0 | 78.1±11.7 | 107.0±22.3 |
| \(I\) (\(\mu\)g larva\(^{-1}\) h\(^{-1}\)) | 0.83±0.16 | 1.60±1.01 | 5.82±4.52 | 10.06±5.77 |
| SR (%) | 74±16\(^a\) | 111±74\(^a\) | 181±63\(^a\) | 266±115\(^a\) |
| \(I_1\) (ml larva\(^{-1}\) d\(^{-1}\)) | 446 | 860 | 3129 | 5408 |
| \(G_1\) (mJ larva\(^{-1}\) d\(^{-1}\)) | 80 | 138 | 219 | 324 |
| \(M_1\) (mJ larva\(^{-1}\) d\(^{-1}\)) | 150 | 264 | 359 | 426 |
| \(K_1\) (%) | 17.94 | 16.05 | 7.00 | 5.99 |
| \(A_1\) (%) | 51.67 | 46.74 | 18.47 | 13.87 |
| \(M_2\) (%) | 33.57 | 30.72 | 11.46 | 7.86 |

\(^a\) Data represent mean±SD of three replicates. Same superscript letters indicate no statistical differences in SR for each larval age (\(P<0.05\)).

\[
CO = 0.398 \text{DW}^{1.044} \quad r = 0.813 \quad n = 60
\]

The specific oxygen uptake (nmol \(O_2\) \(\mu\)g\(^{-1}\) h\(^{-1}\)) showed minimum and maximum values of 0.09 and 0.79 nmol \(O_2\) \(\mu\)g\(^{-1}\) h\(^{-1}\), respectively (Fig. 4b). An initial increase in specific oxygen uptake occurred with larval dry weight up to 35 \(\mu\)g, however, above this size, the specific oxygen uptake remained almost constant (Fig. 4b).
Fig. 4. (A) Oxygen uptake as a function of dry weight of *Sparus aurata* larvae fed with three different prey densities. Vertical dashed line indicates mean dry weight at first feeding (Day 4). (B) Specific oxygen uptake (nmol O$_2$ μg$^{-1}$ h$^{-1}$) as a function of dry weight. Two straight lines have been fitted to data below and above 25 μg dry mass.

Gross growth efficiency ($K_g$) decreased with increasing age and dry weight under the three prey densities tested, reaching minimum values of around 4–7% (Table 3). Assimilation efficiency ($A$) showed the same tendency, showing minimum values of around 10–20% at the end of the experiment period. Gross metabolic efficiency ($M_g$) displayed a similar pattern with all prey densities tested. However, the initial value (on day 6) in larvae fed on 0.1 was higher (53%) than the values in later days and also higher than the values in larvae fed with 1 and 10, where $M_g$ was never over 32% (Table 3).
4. Discussion

The relationship between growth and age during the first stages of larval development is determined by the transition from endogenous to exogenous feeding. *S. aurata* larvae hatch at an approximate dry weight of 30 μg and decrease to 25 μg at the opening of the mouth. At this time the yolk reserves are practically exhausted (Yufera et al. 1993b), and the larvae need to start exogenous feeding in order to continue development and start growth. The commencement of feeding requires a learning process lasting a few days, during which the percentage of actively eating larvae increases progressively from the opening of the mouth to the point of irreversible starvation. This learning period varies with species. Tucker (1988) found that over 80% of black sea bass (*Centropristis striata*) larvae were able to eat on the first day of feeding, while bay anchovy (*Anchoa mitchilli*) larvae needed 5 days to reach this level. Likewise, above 90% of Senegal sole (*Solea senegalensis*) larvae eat on the first day of feeding (Yufera, unpublished). This differential feeding behaviour determines a particular bioenergetic pattern for each species during this period.

The present study shows that prey availability affects the duration of the transition period before growth commences, causing delays in starting growth. More specifically, it seems to be related to succeeding in starting to feed, which depends on encounter opportunity and on the particular ability of each larva to catch prey. From day 4 to day 6, only the part of population, probably the most vigorous larvae, start feeding. With 10 rotifers ml$^{-1}$ there is enough prey for the rest of the larvae with less ability to catch prey, so they can also start feeding during the following days. However, with 1 rotifer ml$^{-1}$, practically the same number of larvae able to eat on day 6 continue eating after the moment of irreversible starvation (day 9), while with 0.1 rotifer ml$^{-1}$ the number of eating larvae decreases. These patterns are reflected in the size-frequency distribution on day 9 (Fig. 2), and the most remarkable is the coincidence between percentage of larvae above 4 mm at day 9 and the survival results at the end of the experiments. Only at the lowest rotifer density, survival was lower than the percentage of larvae showing gut content on day 9. This means that a concentration of 0.1 rotifer ml$^{-1}$ does not warrant a continuous feeding for those larvae able to feed at the onset of exogenous feeding. Consequently, this low prey concentration does not warrant their survival. The estimates of the total biomass produced from first feeding to the end of the experiment were highly related with prey concentration. At 0.1 rotifer ml$^{-1}$, the net production balance resulted negative due to mass mortality of larvae unable to start feeding, although such value could be underestimated, because some mortality occurred also after the theoretic point of irreversible starvation.

During the first days of exogenous feeding, fish larvae increase their swimming activity and improve their feeding ability progressively. In our experiments with gilthead seabream, most larvae above approximately 35 μg are actively eating irrespective of prey density. At that mean dry weight practically no starved larvae remained alive in the populations, but it seems that larvae need to reach such a minimum size in order to eat and grow with reasonable efficiency. In addition, food restriction induces a selection of larvae that are able to eat at a higher rate. This is especially evident at 1 rotifer ml$^{-1}$ (Table 1). These differences in the feeding rate can explain why the larvae showed
higher growth rates at the lower prey densities (0.1 and 1 rotifer ml\(^{-1}\)). A compensatory growth response, after a food-limited period, has been reported for larvae of several species (Van der Meeren and Naess, 1993; Goticitas et al., 1996), although the higher growth rates observed in our study can be a consequence of the selection of most vigorous larvae. In our study, larvae mortality produced a progressive change in the larvae/prey ratio mainly at low prey density; however, prey density remained constant. Changes in prey accessibility during the experiment were due to the development of swimming and predatory capabilities beyond 35 \(\mu\)g dry weight (approximately 4.2–4.4 mm total length) as mentioned previously. This enhancement of the predatory ability justifies the increase in specific ingestion during the experimental period, even in the lowest prey density. Yufera et al. (1995) observed that this upward tendency in the specific ingestion changes above approximately 100 \(\mu\)g larval dry weight. A similar pattern was observed in Solea solea larvae during the first days of feeding (Day et al., 1996).

Gross growth efficiency and assimilation efficiency of S. aurata larvae fall below the range determined for growing larvae of marine fish in general (Houde and Zastrow, 1993; Letcher and Bengtson, 1993), although \(K_1\) values close to 10% and assimilation efficiencies close to 20% has been reported for Anchoa mitchilli (Houde and Schekter, 1983; Tucker, 1988). Such low efficiencies could be a consequence of a feeding strategy tending to maximise the ingestion with a low food residence time in the gut in presence of high prey density. In fact, it is usual to see rotifers and eggs still alive in the faeces. In addition, the particular conditions of the intensive culture procedure, with permanent illumination and 24 h feeding a day, contribute to maximise the larval growth but probably with low assimilation efficiency.

The oxygen uptake at first days of feeding ranged from 3 to 10 nmol ind h\(^{-1}\). These values match with the 6 nmol ind h\(^{-1}\) determined for yolksac larvae (Rønnestad et al., 1994) and with the 3.5 to 6.5 nmol ind h\(^{-1}\) for first feeding larvae (Quantz and Tandler, 1984) of this species. Exponents in the oxygen uptake vs. larval weight equations ranged from 1.2 to 1.4, although the slopes in our study are biased by larvae unable to start feeding which lost weight as well as by the narrow dry mass range tested. Anyway, when considering pooled data of larvae above 25 \(\mu\)g dry weight, that is, only growing larvae, the metabolism tend to increase isometrically (exponent: 1.04) with larval weight.

The methodology used in the present study has some limitations. Dry weight and metabolism has been determined in samples which grouped several larvae. Nevertheless, differences in length and dry weight on day 6 are still too small, while the larvae unable to start feeding did not survive to day 12 (Yufera et al., 1993b). Therefore, only samples at day 9 could accumulated large feeding and small starved larvae, although differences in total length are also small (Fig. 2). On the other hand, we did not found any group effect in the oxygen consumption determinations (Parra, 1998) as observed by Imabayashi and Takahashi (1987) working with larvae of Pagrus major.

The specific oxygen consumption rate strongly depends on body mass during early development. At first feeding, the weight lost by starved larvae account for the high variability observed at the lower body mass. The initial upward tendency changes above 35 \(\mu\)g approximately and kept almost constant above this size. A similar pattern was described in the first larval stages of Pagrus major by Oikawa et al. (1991). The rapid
increase in the metabolism at first feeding is considered as a consequence of the
development of the digestive tract and the increase of the larval activity searching for
food during the learning period. After some days, the organs with high metabolic
activity would have an isometric grow and the catch efficiency acquired by the larvae
would allow to maintain a constant searching activity. The metabolic rate appeared to be
similar and independent of food availability at the first developmental stages, although
the high variability of our data would prevent to detect the differences. Nevertheless, a
decrease in oxygen uptake with decreasing food ration has been reported in growing
Clupea harengus larvae (Kiorbøe et al., 1987).

Gross metabolic efficiency ($M_e$) showed similar decreases in relation to body weight1
in larvae fed with the three prey densities. Therefore, the energy used in metabolism
followed a similar pattern irrespective of prey density. Only at day 6 in larvae fed 0.1
rotifer ml$^{-1}$ did the $M_e$ value not follow this trend. In that case, the energy involved in
metabolism was approximately 80 mJ larva$^{-1}$ day$^{-1}$, while the ingested energy was 151
mJ larva$^{-1}$ day$^{-1}$. Metabolic energy represented more than 50% of ingested energy.
Taking into account that part of rotifer biomass cannot be assimilated (lorica and
maxtac), those larvae had little energy available for activities other than maintenance.
This energy restriction could explain why a percentage of larvae showing rotifers in the
gut on day 6 did not continue eating on day 9 and that they did not survive to day 15.
Such an energetic limitation was not observed at higher prey densities. $M_e$ reached a
value of close to 32% after day 9 because their predatory capacities increased and
consequently there was enough energy to allow growth.

The $M_e$ values obtained in the present study are close those reported by Yamashita
and Bailey (1989) in Theragra chalcogramma larvae. Larvae were reared with two prey
densities also close to our highest prey densities (10 and 1 rotifer ml$^{-1}$). The $M_e$ values
reported at the beginning of their experiment were 30 and 36%, for the two prey
densities. They concluded that there were no differences in growth, ingestion and
efficiencies among both prey densities. However, in the present study, the lowest prey
density is ten times smaller than lower density tested in Yamashita and Bailey study, and
we found differences in growth and survival between larvae fed on 0.1 rotifers ml$^{-1}$ and
1 and 10 rotifers ml$^{-1}$. In gilthead seabream larvae, low prey densities can delay growth
and affect survival rather than affect growth rate. This have been also reported in
Oncorhynchus mykiss, the larvae of which, under a delay in starting to feed, showed
lower weights but maintained the same growth rate (Kamler, 1992). The maximisation
of growth in early stages shortens the period during which larvae are highly vulnerable
to predation and disease (Houde and Zastrow, 1993; Cowan et al., 1996).

The experimental conditions used in the present study differed from nature, mainly in
both larvae and prey densities, as well as in the species diversity (considering fish larvae,
prey and predators). Therefore, it is difficult to know to what extent the results obtained
coincide with the actual values of feeding and metabolic activities in natural habitats, but
they are representative of physiological tendencies and responses. Mackenzie et al.
(1990) reported in natural areas a mean prey density of around 25 µg l$^{-1}$, which is close
to the lowest prey density tested in the present study (0.1 rotifer ml$^{-1}$). The concept of
critical prey concentration at first feeding of larval fish is an arbitrary criterion, generally
established at that concentration which allows at least 10% survival at first feeding.
(Houde, 1978). Following that criterion, 0.1 rotifer ml⁻¹ is lower than the critical prey concentration. From the point of view of seabream larvae reared under laboratory conditions (usually at a density ranging between 3 and 10 rotifer ml⁻¹), a concentration of 1 rotifer ml⁻¹ is sufficient for half of the population to succeed in starting to eat and grow. Therefore, above such live prey density a food restriction never occurs and larvae will grow continuously.

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References


