Effect of meal size modulation on growth performance and feeding rhythms in European sea bass (*Dicentrarchus labrax*, L.)

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**Abstract**

The combined effect of feeding time and meal size on the growth performance and feeding rhythms were studied in European sea bass maintained under natural summer–autumn conditions. Three feeding strategies were compared: a modulated automatic-feeding (MF), a fixed automatic-feeding (FF) and a free access to self-feeders (SF). Under MF, feed was supplied in meals of different size, three times a day (morning, afternoon and evening, 33.33:16.67:50% of daily feed ration, respectively) during the first (31 days) and second (35 days) period of the experiment, and twice a day (morning and evening, 33.33:66.67% of daily feed ration, respectively) during the third period (27 days). In FF feed was supplied in equally-sized meals, three times a day (morning, afternoon and evening, 33.33:33.33:33.33% of daily feed ration) in all three periods of the experiment. Under SF, fish showed a diurnal self-feeding pattern, with the greatest percentage of self-feeding activity concentrated in the evening. In MF and FF, although feed was delivered automatically, the trigger was left in the tank to register activations as an indicator of feeding activity. The trigger activation of both treatments MF and FF was associated with the time of feed delivery. Feeding strategies affected biomass increase, specific growth rate (SGR) and feed conversion ratio (FCR), the greatest biomass increase and highest SGR being obtained with MF and the poorest FCR with FF. The results demonstrate that automatic-feeding systems, in which the quantity of feed supplied is modulated in accordance with the natural feeding rhythms of sea bass, may improve growth and feed efficiency. © 1999 Elsevier Science B.V. All rights reserved.

**Keywords:** Feeding rhythms; Growth; Feed conversion; *Dicentrarchus labrax*; Sea bass

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1. Introduction

The cost of feed is one of the principal factors deciding the profitability of intensive fish farming. Many fish farms use automatic-feeding systems which are programmed to distribute fixed quantities of feed at regular times (Thorpe et al., 1990; Kadri et al., 1991). While the overall quantities of feed delivered tends to be strictly controlled, little attention has been paid to the optimal temporal distribution of feed. Consequently, feed conversion efficiency may be high because of feed wastage (Thorpe and Cho, 1995).

Studies on the influence of feeding strategies have concentrated on two principal aspects: feeding time and feeding frequency. To study the latter, fish are usually provided with a feed ration divided into a varying number of meals fed throughout the day, but it is difficult to draw any general conclusions because of the differences in the experimental protocols used, the species studied and the rearing conditions (Andrews and Page, 1975; Grayton and Beamish, 1977; Omar and Günther, 1987; Kaushik and Gomes, 1988; Kerdchuen and Legendre, 1991; Kayano et al., 1993; Webster et al., 1993). With regards to the influence of feeding time, several authors (Sundararaj et al., 1982; Noeske-Hallin et al., 1985; Reddy et al., 1994; Boujard et al., 1995; Gélineau et al., 1996) report that there are certain times of day at which feeding results in better growth and feed efficiency in some species of teleosts, such as rainbow trout and catfish which have relatively stable daily feeding habits. However, in other species, which show varying patterns of feeding rhythms such as sea bass (Anthouard et al., 1993; Sánchez-Vázquez et al., 1994; Bégout-Anras, 1995; Boujard et al., 1996; Sánchez-Vázquez et al., 1995, 1998), Atlantic salmon (Kadri et al., 1991; Jørgensen and Jobling, 1992; Smith et al., 1993; Fraser et al., 1995) or gilthead sea bream (Anthouard et al., 1996), it may be more difficult to establish an optimum feeding time.

Sea bass is one of the most interesting species for Mediterranean aquaculture, and one which can rapidly learn to feed from self-feeders (Anthouard et al., 1986; Hidalgo et al., 1988; Anthouard et al., 1993; Sánchez-Vázquez et al., 1994). Feed conversion of sea bass fed by self-feeders may be better than those fed by automatic-feeders, which dispensed the feed into equally sized-meals (Azzaydi et al., 1998). However, given the difficulty of using self-feeders in some fish farms, it would be of interest to study automatic-feeding systems in which the quantities of feed supplied were varied in accordance with the natural feeding rhythms of the sea bass.

The objective of the study described in this paper was to compare the growth, feed conversion and feeding rhythms of sea bass fed by an automatic system which mimicked the natural feeding rhythms of the species (modulated automatic-feeding, MF) with an automatic system in which the feed was divided into three equally sized-meals (fixed automatic-feeding, FF). A third feeding strategy where fish had free access to the self-feeder (SF) was also used to study daily self-feeding patterns.

2. Materials and methods

2.1. Fish and rearing conditions

A total of 180 European sea bass (Dicentrarchus labrax, L.) hatched in captivity and supplied by CULMAREX at Aguilas (Murcia, Spain), were used in the experiment.
which was carried out at ‘Centro de Recursos Marinos y Humedales del Litoral de San Pedro del Pinatar’ (Murcia) from August to October. The fish, body weight of 80.3 ± 1.2 g (mean ± SEM), were then divided into 12 groups with 15 fish in each, and placed into 460 l experimental tanks, supplied with running sea water (37%e salinity). Throughout the experiment, the fish were exposed to a natural photoperiod and water temperature, which ranged from 14 h 00 min (August) to 11 h 30 min (October), and from 27.4°C (August) to 20.8°C (October).

During both the adaptation and the experiment, the fish were fed with a commercial diet (EWOS, 2 mm standard pellet) of proximate composition 49% protein, 12% fat, 6.8% moisture, 11% ash and 21.2% NFE (nitrogen-free extract). Each tank was provided with an electronic self-feeder which delivered approximately 8–9 pellets (about 0.4 g of feed) each time a fish activated a trigger located 3 cm below the water surface as

![Feeding strategy diagram](image)

Fig. 1. Meal schedule of treatments fed automatically. FF: fixed automatic-feeding; MF: modulated automatic-feeding. The vertical bars represent the meals, the height and width of each bar are proportional to the size and duration, respectively, of each meal. Black and white bars at the bottom of the graphs represent the scotophase and photophase, respectively.
reported elsewhere (Sánchez-Vázquez et al., 1994). Feeders were checked, every other day, the feed remaining was weighed and the feed reservoir refilled.

2.2. Experimental design

All the fish had initially free access to the self-feeders for 20 days. Then, fish were weighed and three feeding strategies were established (4 replicates/treatment). In the first treatment, sea bass had free access to self-feeders (SF treatment). The self-feeders were connected to a computer which recorded the number of trigger activations in 10 min bins. In the second and the third treatments, sea bass were fed using automatically-triggered feeders according to the schedules shown in Fig. 1 (FF and MF). MF fish were fed in accordance with the self-feeding rhythms of sea bass observed at this time of the year (Sánchez-Vázquez et al., 1998). As in the SF treatment, an electronic feeder was used, but it was activated automatically by a timer. There was a pause between each feed delivery to permit that the pellets were consumed. Although feed was delivered automatically, the trigger was left in the tank to register trigger activations as an indicator of feeding activity. Except for SF, the daily feed rations were established in accordance with the feeding tables provided by the feed manufacturer (EWOS) (Fig. 1).

The fish were weighed at 31, 66 and 93 days, each time after 1 day of feed deprivation. These sampling times served to delimit three periods, at the beginning of which the daily feed ration for FF and MF was adjusted in accordance with the body weight recorded and water temperature, and the feeding time was shifted in relation to photophase. Photoperiod (light level) and water temperature were continuously registered every 15 min by means of a portable data logger (Logit SL, DCP Microdevelopments and SCC Research, UK).

2.3. Biological and feeding parameters

The parameters characterizing growth performance were calculated as follows:

Specific growth rate \( (SGR) = \left( \frac{\ln(\text{final biomass})}{\ln(\text{initial biomass}) - \text{days}} \right) \times 100 \)

Feed conversion ratio \( (FCR) = \frac{\text{weight of total feed delivered}}{\text{biomass gain}} \)

Initial and final coefficient of variation \( (CV_{\text{io rf}}) \)

\[ = \frac{\text{(standard deviation of the individual weight)}}{\text{mean weight}} \times 100 \]

2.4. Statistical analysis

Treatment means were compared by one-way ANOVA using the statistics program STATGRAPHICS 7.0 (Statistical Graphics, Bitstream, Cambridge, MA, 1993) after
log-transformation of indices and percentages. When significant differences were detected by ANOVA, Tukey’s multiple range test was used a posteriori. CVr and CVt were compared by sign-test. The peak of the daily feeding phase of fish in treatment SF was estimated as the time in which a moving average (3 h bins) of feed demands reached its highest value. To calculate the acrophase (the time in which a rhythmic variable reaches a maximum value) of water temperature, sinusoidal rhythms were determined by the cosine best-fit analysis (COSINOR), \( y(t) = M + A \cos(\omega t + \phi) \), where \( M \) is the mesor, \( A \) is the amplitude and \( \phi \) is the acrophase. Relationships between trigger activations in the self-feeding regime (SF) and in the automatic-feeding regimes (MF and FF) were analyzed by correlation analysis. In all tests, the significance level was set at \( P < 0.05 \).

3. Results

3.1. Feeding activity

The daily pattern of feeding activity in sea bass varied between periods: SF fish had a self-feeding activity which was affected more by photoperiod than temperature, there being a pronounced feeding peak in the evening and also one around dawn. Nocturnal self-feeding activity was low, and was confined to the end of the night (Fig. 2). In all periods of the experiment, the daily peak of feeding preceded the acrophase of water temperature. MF and FF fish had been adapted to using self-feeders before the experiment began, and during the experiment, the fish continued to activate the trigger in close relation with the times of feed delivery even though feed was provided automatically (Figs. 3 and 4). In MF fish, trigger activations were in similar proportions to the duration and size of the meals, except for the second period in which trigger activity was slightly higher in the second meal than in the first (Fig. 3). The analysis of trigger activity inside the last meal revealed a progressive reduction of trigger activations towards the end. Although the duration and size of the three daily meals was identical in the FF treatment, trigger activity peaked during the last meal (Fig. 4). Contrasting with MF, trigger activations by FF fish persisted even 20 min after the end of the meal.

The proportions of trigger activations made by fish in MF and FF treatments in the times of feed delivery and those made by SF fish are shown in Fig. 5. Trigger activations of SF were calculated from the times of feed delivery of MF and FF, respectively. For MF vs. SF, there was a lineal correlation with a slope close to 1 (MF = −0.18 + 1.05SF, \( P < 0.0001 \), \( R^2 = 95.08\% \)), while the relationship between FF and SF was best explained by a reciprocal model (\( 1/FF = +0.62 - 0.09SF, P < 0.001, R^2 = 82\% \)) due to the greater number of trigger activations made by FF fish during the last meal of the day.

Feed delivery, demanded by SF fish and supplied to MF and FF fish is shown in Table 1. Feed demanded by SF fish was significantly lower than that supplied to MF and FF fish.
Fig. 2. Mean daily profile of self-feeding activity during the first (A), second (B) and third (C) period in sea bass having free access to the self-feeder. Bars represent the mean values made each 10 min ± SEM (N = 4). The daily profile of water temperature (solid line) and photoperiod (dotted line) have been superimposed.
Fig. 3. Mean daily profile of trigger activity during the first (A), second (B) and third (C) period in sea bass fed with modulated automatic-feeding system. Bars represent the mean values made each 10 min ± SEM (N = 4). The daily profile of water temperature (solid line) and photoperiod (dotted line) have been superimposed. The black bars represents the periods of feed delivery.
Fig. 4. Mean daily profile of trigger activity during the first (A), second (B) and third (C) period in sea bass fed with fixed automatic-feeding system. Bars represent the mean values made each 10 min ± SEM (N = 4). The daily profile of water temperature (solid line) and photoperiod (dotted line) have been superimposed. The black bars represents the periods of feed delivery.
Fig. 5. Correlation between trigger activations made by MF and SF (A) and between trigger activations made by FF and SF (B). The number of trigger activations made by MF and FF was calculated from the time of feed delivery. The number of trigger activations made by SF was calculated from the times of feed delivery of MF in (A) and of FF in (B).
Table 1
Effect of feeding strategy on growth performance

<table>
<thead>
<tr>
<th>Feeding strategy</th>
<th>SF</th>
<th>MF</th>
<th>FF</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Feed delivered (g)</td>
<td>1864 ± 24^a</td>
<td>2364 ± 39^b</td>
<td>2319 ± 18^b</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Biomass increase (g)</td>
<td>754 ± 25^a</td>
<td>894 ± 24^b</td>
<td>716 ± 27^b</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>SGR (% b.wt./day)</td>
<td>0.52 ± 0.02^*a</td>
<td>0.62 ± 0.01^b</td>
<td>0.52 ± 0.02^*a</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>FCR</td>
<td>2.48 ± 0.10^b$</td>
<td>2.65 ± 0.11^b</td>
<td>3.25 ± 0.10^a</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>CV_i</td>
<td>19.10 ± 0.82^a</td>
<td>19.53 ± 1.58^a</td>
<td>17.73 ± 2.36^a</td>
<td></td>
</tr>
<tr>
<td>CV_f</td>
<td>14.29 ± 0.97^b$</td>
<td>15.48 ± 1.64^b</td>
<td>12.99 ± 0.91^b</td>
<td>&lt; 0.01</td>
</tr>
</tbody>
</table>

Means with different letters in the same line (in the same row for CV) are significantly different (ANOVA, Tukey HSD, N = 4, mean ± SEM).
SF: free access to the self-feeders.
MF: modulated automatic-feeding.
FF: fixed automatic-feeding.

3.2. Growth performance

Biomass increase, SGR, FCR and CV are shown in Table 1. Biomass gain and SGR were significantly greater in MF than in both FF and SF treatments. The poorest FCR was recorded for FF fish. Comparisons of CVs were used to assess the influence of the feeding strategy on the dispersal range of fish weights, CVs_f were significantly smaller than CVs_P (P < 0.01) in all treatments, indicating that all groups became more homogeneous in weight with the passage of time.

4. Discussion

Sea bass given free access to the self-feeder had a predominantly diurnal feeding pattern with the greatest activity being concentrated towards the end of the day. When fish were fed automatically, their trigger activity was associated with the time of feed delivery, but independent of feeding strategy and experimental period most activity being registered during the last meal of the day.

The self-feeding pattern seen in SF fish is similar to that described previously (Bégout-Anras, 1995; Madrid et al., 1997; Azzaydi et al., 1998; Sánchez-Vázquez et al., 1998). The peak of feeding preceded the acrophase of water temperature, which is in agreement with the phase relationship found by Sánchez-Vázquez et al. (1998), but differs from the findings of Anthouard et al. (1993), who noted a direct relationship between daily fluctuations in water temperature and feeding peaks. The fish in MF and FF treatments, continued to activate the trigger when subjected to a meal feeding cycle, so the information provided by trigger activations may be useful for adjusting feeding schedules. In MF and FF fish, trigger activity was not equally distributed through the meals, which is in agreement with previously obtained results (Madrid et al., 1997; Azzaydi et al., 1998).

If we consider trigger activity as an indicator of fish appetite (Madrid et al., 1997), the coincidence of the patterns of trigger activity between MF and SF treatments (Fig. 5)
suggests that the scheduled meal program of MF was in accordance with the natural feeding rhythm of SF fish. On the contrary, the fact that trigger activity of FF fish differed in the three meals indicates that fish appetite did not match the feeding schedule imposed.

Sea bass in the MF treatment had the greatest biomass gain and SGR, while FF fish had the poorest feed conversion ratio. The time of feeding has been shown to affect growth performance in several fish species (Noeske et al., 1981; Sundararaj et al., 1982; Noeske and Spieler, 1984; Noeske-Hallin et al., 1985; Kerdchuen and Legendre, 1991; Boujard et al., 1995), but the combined effects of both feeding time and meal size has not, to the best of our knowledge, been studied. In the study described in this paper, FF fish had a higher FCR than SF. Similar results have been obtained with gilthead sea bream (Divanach et al., 1986; Kentouri et al., 1993), rainbow trout (Alanara, 1992a) and European sea bass (Azzaydi et al., 1998). According to several authors, self-feeding systems may offer the best growth (Divanach et al., 1986; Alanara, 1992a,b; Kentouri et al., 1993; Boujard et al., 1996), but in our experiment SF fish had significantly lower growth than those in the MF treatment. This may have been due to (a) the fact that MF fish received more feed than SF, even though the level of reward for each trigger activation used in SF (8–9 pellets for 15 fish) was higher than used previously (Divanach et al., 1993; Boujard et al., 1996), (b) the supply of undemanded feed may reduce the energy expenditure associated with the biting on the trigger, which may permit the fish to receive slightly more feed than they would voluntarily demand. The fact that the sea bass in the MF treatment grew more and had a lower FCR than those of FF treatment, implies that the fish in the FF treatment had a lower feed intake (i.e., higher feed wastage) and/or poorer utilization of feed due to a lack of synchronization between the timing of feed distribution and the natural feeding rhythm. The daily patterns of trigger activity of MF and FF fish support the feed wastage hypothesis since the amount of feed supplied to FF during the second meal seemed excessive (overfeeding), while that provided during the third meal seemed insufficient (underfeeding). Moreover the differences in growth between the MF and FF fish, which were fed at the same times, suggests that the feeding time per se may not alone explain the poor performance of FF fish. This would agree with the previous observations made by Boujard et al. (1996) and Azzaydi et al. (1998) on the same species.

One argument used against the employment of self-feeding is that only one or a few fish may activate the trigger of feeder, so that just a few fish ‘control’ the feed supply. This is expected to lead to size heterogeneity within a group due to competition for feed (Brännås and Alanara, 1994). In our study, \( CV_f \) was lower than \( CV_r \) under all feeding regimes, implying that the level of reward for each trigger activation (8–9 pellets for 15 fish) was sufficient to allow all the fish access to some feed. Boujard et al. (1996) and Azzaydi et al. (1998), also found no significant differences in \( CV \) between groups of sea bass fed according to different feeding regimes.

The results of our study indicated that, despite having flexibility in feeding, the appetite of sea bass followed daily rhythms which were not totally overridden by rigid feeding strategies. Thus, the best results were obtained on a strategy which most closely reflected natural feeding rhythms. Further, our results suggests that automatic feeding systems in which the quantity of feed supplied is modulated in accordance with the
times of maximum appetite may produce comparable and sometimes even better results than self-feeding systems.

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References


