

Seasonal changes in the food quality, diel feeding rhythm and growth rate of juvenile leaping grey mullet *Liza saliens*

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Abstract — A population of leaping grey mullet *Liza saliens* was studied in order to test whether growth rates decrease in summer owing to a reduction in food quality. A total of 330 juveniles of the 2-year age group were collected for measuring monthly changes in standard length, total weight, length growth rate and weight growth rate. Another 160 fish of the same age were caught monthly in February, April, August and November to measure food quality and calculate energy intake. Food quality changed as predicted. The organic matter content of the diet on a dry matter basis was 9.7 % in April, 7.9 % in August and 11.7 % in November. The protein content of the diet on a dry matter basis was 9.0 % in April, 6.4 % in August and 9.3 % in November. The carbohydrate content of the diet on a dry matter basis was 0.6 % in April, 0.7 % in August and 1.8 % in November. The lipid content of the diet on a dry matter basis was 0.2 % in April, 0.2 % in August and 0.6 % in November. The energy content of the diet was 2.63 kJ·g⁻¹ in April, 2.21 kJ·g⁻¹ in August and 3.13 kJ·g⁻¹ in November. All the analysed mullet stomachs were empty in February, which suggests that they starve in winter. Daily rations increased when food quality decreased (4 % of body weight in April, 6 % in August and 1.4 % in November). This allowed mullet to show high growth rates from June to August and to overcome a possible food limitation in the warm season. However, we do not know whether they would have grown even faster if food with a higher quality had been available. © 1999 Ifremer/Cnrs/Inra/Ird/Cemagref/Éditions scientifiques et médicales Elsevier SAS

Mullet / feeding / daily ration / detritivores / coastal lagoons / Mediterranean

Resumen — Cambios estacionales en la calidad del alimento, el ritmo diario de alimentación y la tasa de crecimiento de los juveniles de galua *Liza saliens*. Se estudió una población de galua *Liza saliens* para determinar si la tasa de crecimiento descendía en verano debido a una reducción de la calidad del alimento. Se capturaron un total de 330 juveniles de la clase de edad 2 para medir las variaciones mensuales de la longitud estándar, el peso total, la tasa de crecimiento en longitud y la tasa de crecimiento ponderal. Otros 160 ejemplares adicionales de la misma edad se capturaron mensualmente en febrero, abril, agosto y noviembre para determinar la calidad del alimento y la ingesta energética. La calidad del alimento varió de acuerdo con lo previsto. El contenido en materia orgánica del alimento seco fue 9.7 % en abril, 7.9 % en agosto y 11.7 % en noviembre. El contenido proteico del alimento seco fue 9.0 % en abril, 6.4 % en agosto y 9.3 % en noviembre. El contenido en carbohidratos del alimento seco fue 0.6 % en abril, 0.7 % en agosto y 1.8 % en noviembre. El contenido en lípidos del alimento seco fue 0.2 % en abril, 0.7 % en agosto y 0.6 % en noviembre. El contenido energético de la dieta fue 2,63 kJ·g⁻¹ en abril 2,21 kJ·g⁻¹ en agosto y 3,13 kJ·g⁻¹ en noviembre. Los estómagos de los mugílidos permanecieron vacíos durante el mes de febrero, lo que sugiere que ayunaron durante el invierno. Las raciones diarias mostraron el patrón opuesto y se incrementaron al descender la calidad de la dieta (4 % del peso corporal en abril, 6 % en agosto y 1,4 % en noviembre). Gracias a ello, los peces mantuvieron una elevada tasa de crecimiento durante toda la estación cálida superando una posible limitación trófica. Ahora bien, no sabemos si con un alimento de mejor calidad hubieran podido crecer a mayor velocidad. © 1999 Ifremer/Cnrs/Inra/Ird/Cemagref/Éditions scientifiques et médicales Elsevier SAS

Mugílidos / alimentación / ración diaria / detritívoros / lagunas costeras / Mediterráneo

1. INTRODUCTION

The leaping grey mullet *Liza saliens* (Risso, 1810), hereafter referred to as mullet, is an abundant species in the mesotrophic estuaries of the central part of the western Mediterranean [12]. Fry shorter than 35 mm (total length) feed mainly on zooplankton [23] but older specimens feed mainly on detritus, although microalgae and infauna are also consumed [12, 18].

Detritus is very abundant in estuaries and forms the basis of a trophic web [21, 34, 38]. Immediately after production, detritus from vascular macrophytes is of poor quality because it is rich in lignin [32]. Only after partial degradation by bacteria and fungi does its protein content increase and it becomes profitable for detritivores [36].

In warm temperate estuaries, detritus is produced mainly in the autumn, after macrophyte senescence [21, 31, 34, 42]. Detritus is quickly degraded and only a small fraction remains in the summer [21, 33, 34]. Furthermore, the quality of the remaining detritus quickly decreases during spring and summer owing to an increase in ash contents [34]. Thus, it can be predicted that the quality and quantity of the food available for detritivores may be high in autumn and winter, moderate in spring and low in summer. The metabolic rate of poikilotherms increases with temperature, and this can lead to high energetic demand in summer [43], when food supply is low and of low quality. As a consequence, the growth rate of several poikilotherm detritivorous species is known to decrease in summer [22, 31]. The aim of this study was to test whether the quality of mullet food decreases in summer and hence fish growth rate is also reduced.

2. MATERIALS AND METHODS

The study was carried out in 1989 in Albufera des Grau, a 72 ha shallow brackish coastal lagoon located in Minorca (Balearic Islands) (39° 57' N, 4° 13' E). The mean depth is 1.2 ± 0.52 m and no tidal influence exists. The salinity level is highly variable, in agreement with rainfall variability, but throughout the study it ranged from 29 to 38 g·L⁻¹. The lagoon fluctuates between summer transparent waters, which allow the development of a dense meadow of *Ruppia cirrhosa* (Petagna) Grande, and eutrophic winter waters, with dense phytoplankton blooms dominated by *Prorocentrum scutellum* [41]. The fish community is dominated by the leaping grey mullet and includes other grey mullet species (*Chelon labrosus*, *Liza aurata*, *Liza ramada* and *Mugil cephalus*), eel (*Anguilla anguilla*), black goby (*Gobius niger*) and two banded sea bream (*Diplodus vulgaris*) [12]. A total of 970 mullet were used for this study.

2.1. Fish growth

Samples were collected monthly from January to December 1989 in a shallow area (average depth: 53.2

± 7.8 cm) using trammel nets of 25 mm stretched mesh size. After collection, fish were stored on ice and frozen at -20 °C in less than 3 h. Once in the laboratory, fish were defrosted, measured to the nearest millimetre (standard length) and weighed to the nearest milligram. Standard length–frequency distribution using the Bhattacharya method [6] was used for age group identification. Only juvenile specimens of the 2-year age group (standard length ranging from 9.1 to 14.3 cm) were used for the following calculations, because they represented the bulk of samples and the growth of adult fish was affected by summer spawning (Cardona, unpublished data). Sample size was standardised to 30 fish per month by randomly picking them from the pool of specimens of the 2-year age group.

Maximum and minimum water temperatures during a 24 h cycle were measured monthly with a special thermometer at a depth of 25 cm. Salinity was measured with a refractometer.

Following Busacker et al. [11], the specific growth rate was calculated for each month using the equation:

$$\text{SGR}_w = 100 \times (\ln W_2 - \ln W_1)/t$$

where SGR is the specific growth rate expressed as percentage increase per day, ln is the natural logarithm, W_1 is the initial average weight of the age group in g, W_2 is the final average weight in grams of the age group 1 month later and t is 30 days (samples were collected at this precise time interval). The specific growth rate of the standard length (SGR_l) was also calculated for each month in the same way using length information given in centimetres and supplying growth rates as percentage increase per day.

2.2. Energy contents of the diet and fish energy intake

Eight 24 h cycles were studied: two in February 1989, two in April 1989, two in August 1989 and two in November 1989. Two 24 h cycles were studied in each of those months in order to reduce error in the calculation of daily consumption caused by changes in the feeding chronology and intensity [22, 43]. The two cycles were on consecutive days. Each 24 h cycle was divided into eight 3 h intervals and fish were caught with a trammel net throughout those intervals [2, 13]. The stomachs were removed and frozen at -20 °C. A total of 640 fish was used for this calculations, 160 fish per month.

Fish that were collected at the same time interval in the two feeding cycles of the same month were pooled and 20 of them were randomly selected for further analysis. Ten fish from each time interval were used for measuring the fullness coefficient and another ten fish were used for measuring proximate chemical composition.

The fullness coefficient, i.e. the weight of the contents of the cardiac stomach expressed as a percentage of total body weight, was used as an indicator

of feeding intensity [7, 13, 16]. Only the cardiac stomach contents were used, because ingested material is continuously transferred from the cardiac stomach to the pyloric stomach, the feeding intensity being reflected by the amount of material present in the cardiac stomach [37]. Sampling size was ten fish per time interval of 3 h.

The Elliott-Persson equation [19] was used to estimate food consumption within any given time interval:

$$C_t = R t (S_t - S_0 \times e^{-Rt}) / (1 - e^{-Rt})$$

where C_t is the food consumption within the interval expressed as percentage of body weight, S_t is the average fullness coefficient ($N = 10$) at the end of the 3 h interval, S_0 is the average fullness coefficient ($N = 10$) at the beginning of the interval, R is the gastric evacuation rate and t is the interval length (3 h). R is calculated as the slope between the digestion rate (r) and the maximum average fullness coefficient [8, 30]:

$$R = r/S_{\max} \text{ and } r = (S_{\max+1} - S_{\max})/t$$

where S_{\max} is the largest observed average fullness index in the 24 h cycle and $S_{\max+1}$ is the average fullness index in the next 3 h interval. Daily consumption was obtained summing up the food consumption of the eight 3 h time intervals that formed a 24 h feeding cycle. R was calculated separately for each of the sampling months.

The amount of food present in the stomachs was usually too small to allow chemical analysis and hence the contents of the 80 stomachs obtained for the chemical analysis were mixed and divided into 20 subsamples of 800 mg. Only the contents of the cardiac stomach was used, because it was not enriched with mucus [36, 40]. In order to measure moisture contents, five subsamples were dried at 60 °C for 48 h. They were then burnt at 450 °C for 8 h in order to calculate the percentage of organic matter as loss on ignition. Five subsamples were digested with diluted NaOH. Then, they were mixed with concentrated SO_4H_2 , H_2O_2 and HgO , in order to transform into NH_4^+ the nitrogen present in the aminoacids. Phenol, NaClO and sodium nitroprussiate were then added in order to reveal the presence of NH_4^+ and the light absorption of the solution was measured at 630 nm. A $(\text{NH}_4)_2\text{SO}_4$ standard was used to calculate a linear regression between light absorption and the concentration of NH_4^+ . A conversion factor of $\times 6.25$ was used to transform the concentration of NH_4^+ into the amount of protein in the original samples [39]. A further five subsamples were dispersed in distilled water, treated with NaOH, mixed with a solution of 0.1% anthrone in SO_4H_2 and boiled. Carbohydrate concentration was calculated after measuring light absorption at 630 nm. A glucose standard was used to calculate a linear regression between light absorption and glucose concentration [39]. The remaining five subsamples were used for lipid extraction with ether. They were boiled with diluted HCl and the lipids were

extracted with a Soxhlet apparatus. The amount of lipid was calculated by weighing the sample before and after the extraction [39].

Gross dietary energy was calculated from the chemical composition using values of 27.8, 39.5 and 17.6 $\text{kJ}\cdot\text{g}^{-1}$ for protein, lipids and carbohydrates, respectively [28]. Daily energy intake was calculated from daily consumption and gross energy content of food and was expressed as $\text{kJ}\cdot\text{fish}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$.

2.3. Sediment quality

Ten sediment samples were collected with a plastic core (5 cm in internal diameter) in February, April, August and November. Samples were stored in ice and frozen at -20 °C in less than 3 h. Once in the laboratory, cores were defrosted and two subsamples of 800 mg were taken from the upper centimetre of each core and analysed in the same way as the stomach contents.

2.4. Statistical analysis

Results are given as the average followed by the standard deviation (avg \pm std).

Specific growth rate was calculated only when the Student's t -test [14] revealed significant differences ($P < 0.05$) between the average weight or the average length of the population in two consecutive months. If there was no difference between them, the specific growth rate was defined as zero.

A linear regression [14] was calculated between specific growth rates and water temperature.

ANOVA followed by Tukey's test [14] was used to test differences in the feeding intensity along 24 h feeding cycles. The fullness coefficients of the 3 h time intervals of the 24 h feeding cycles of the same month were compared. The same procedure was also used to test differences in the mean contents of moisture, proteins, carbohydrates, lipids, organic matter and gross energy between samples of stomach contents collected in different seasons and between samples of sediment.

3. RESULTS

The monthly values of the average standard length, weight and growth rates are shown in *figure 1*. No fish were caught in January. Average weight was 19.3 ± 2.3 g in February and decreased until April, when it was 15.2 ± 2.1 g (Student's t -test; $P < 0.05$). The weight growth rate became positive in early spring and the average fish weight measured in May was not significantly different from that recorded in February (Student's t -test; $P > 0.05$). The weight growth rate increased throughout late spring and early summer and reached a value of 1.5% increase in body weight per day in the July–August period. It quickly decreased in the following months and became slightly negative in the October–November period.

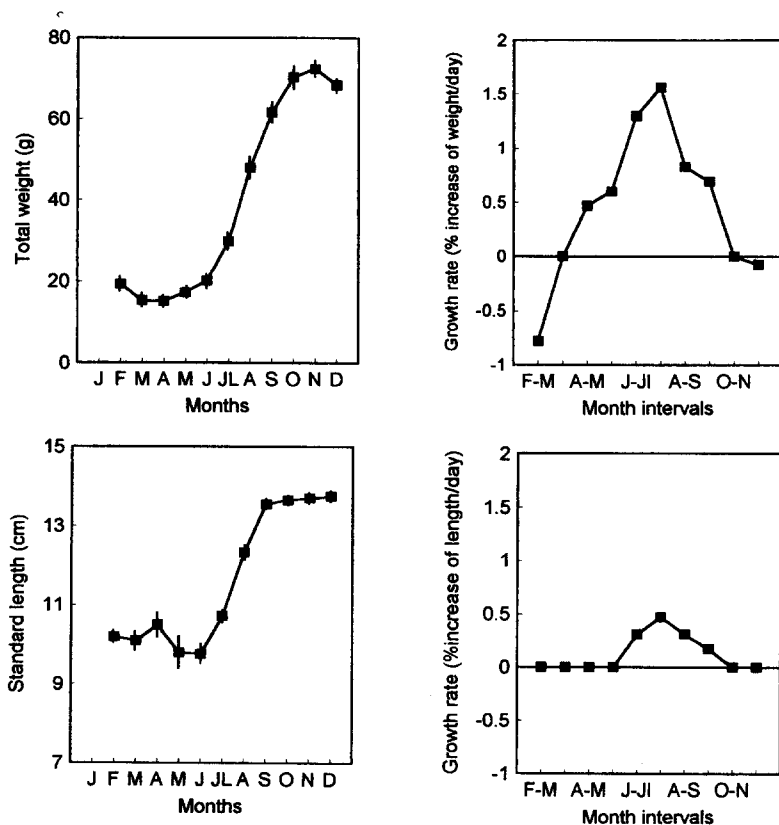


Figure 1. Monthly profile of the average weight, standard length, weight growth rate and length growth rate of the 2-year age group mullet from Albufera des Grau. Vertical bars show the standard deviation.

Average length was 10.2 ± 0.3 cm in February and remained constant until July, when increased to 10.7 ± 0.3 . This means that length growth started 2 months after the beginning of weight recovery. The growth rate peaked in the July–August interval, approaching 0.5 % increase in body weight per day, and then decreased throughout late summer and early autumn and became zero in October–November.

The monthly profile of the mean water temperature at the lagoon surface is shown in *figure 2*. The weight growth rate and water temperature (T) were significantly correlated:

$$\text{SGR}_w = 2.009 + 0.112 T \quad (P < 0.001; r = 0.902)$$

The same was true for the length growth rate and water temperature (T):

$$\text{SGR}_l = -0.435 + 0.026 T \quad (P < 0.002; r = 0.842)$$

The stomachs of mullet caught in February were empty and hence energy intake was nil. This corresponded with the high weight losses recorded that month (*figure 1*).

In April, an ANOVA test revealed the existence of significant differences between the fullness coefficients of two sets of time intervals ($P < 0.05$), which suggested that the mullet started feeding late in the

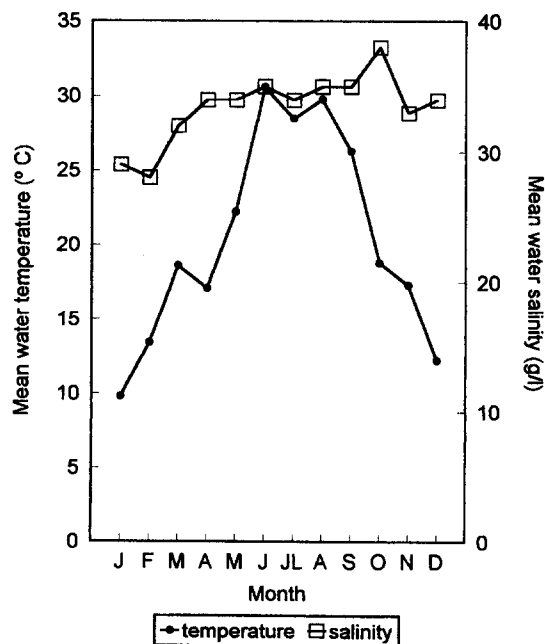


Figure 2. Monthly profile of the daily average water temperature and salinity in Albufera des Grau at a depth of 25 cm (depth of the sampling area: 53.2 ± 7.8 cm).

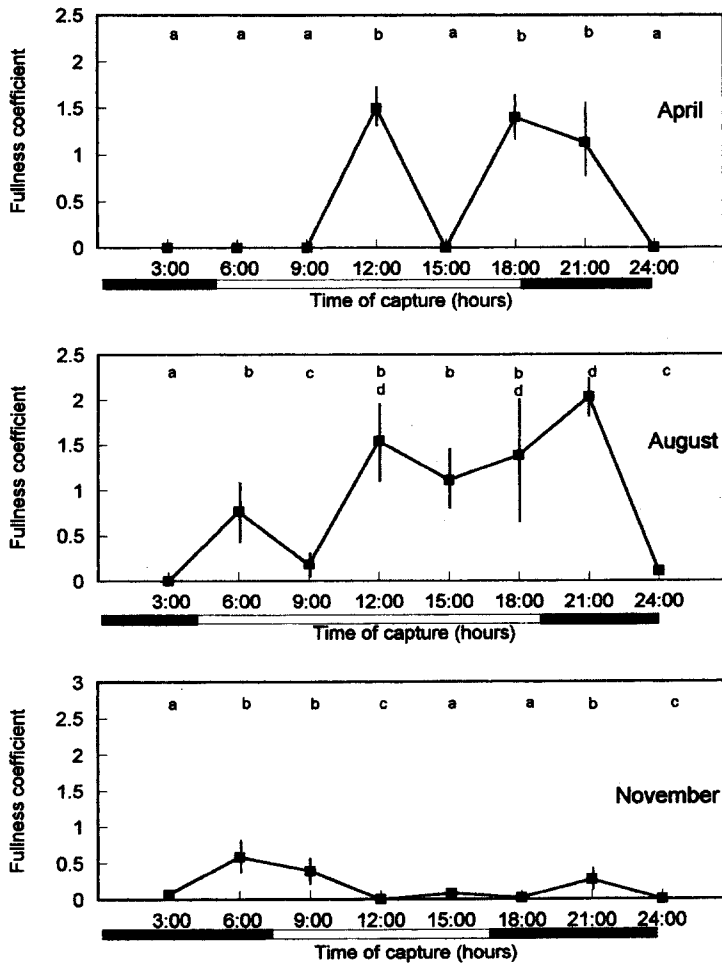


Figure 3. Mullet stomach fullness coefficient in relation to time of day (light and darkness cycles are indicated). Vertical bars show the standard deviation. The fullness coefficient of those time intervals of the same box with different superscripts (a, b, c or d) are significantly different (ANOVA; $P < 0.05$). Sample size was always 20 fish per time interval. The daily ration was 4 % of body weight in April, 6 % of body weight in August and 1.4 % of body weight in November.

morning, stopped in the afternoon, fed again at sunset and early evening and stopped eating at around midnight (figure 3). The daily ration was 4 % of body weight and food was relatively rich in organic matter

and gross energy (table I). The daily gross energy intake was $104.9 \text{ J} \cdot \text{fish}^{-1} \cdot \text{day}^{-1}$.

In August, food contained less organic matter, proteins and gross energy than in April (table I), but fish

Table I. Proximate chemical composition and energy content (mean \pm standard deviation) of the stomach contents of *Liza saliens* and of the top 1 cm of sediment from Albufera des Grau (values are on a dry matter basis, except moisture). Average values of the same sample type (stomach contents or sediment) in the same column and with different superscript are significantly different (ANOVA; $P < 0.05$). *N* is the number of analysed samples (see the text for explanation).

	N	Percentage moisture	Percentage proteins	Percentage carbohydrates	Percentage lipids	Percentage organic matter	Energy ($\text{kJ} \cdot \text{g}^{-1}$)
Stomach contents							
April	5	49.5 ± 2.4^a	9.0 ± 0.1^a	0.6 ± 0.5^a	0.2 ± 0.1^a	9.7 ± 0.4^a	2.6 ± 0.2^a
August	5	61.9 ± 9.0^b	6.4 ± 0.4^b	0.7 ± 0.5^a	0.7 ± 0.1^b	7.9 ± 0.1^b	2.2 ± 0.2^b
November	5	76.7 ± 1.2^c	9.3 ± 0.2^a	1.8 ± 1.1^b	0.6 ± 0.1^b	11.7 ± 0.9^c	3.1 ± 0.3^c
Sediment							
February	10	53.5 ± 3.4^a	16.7 ± 2.3^a	3.4 ± 0.5^a	0.6 ± 0.1^a	20.7 ± 3.5^b	5.5 ± 0.2^a
April	10	42.6 ± 3.4^b	11.1 ± 1.8^b	1.4 ± 0.23^b	0.7 ± 0.1^a	13.2 ± 2.0^a	3.6 ± 0.2^b
August	10	$56.3 \pm 5.2^{a,c}$	13.9 ± 1.7^b	0.8 ± 0.53^b	0.5 ± 0.2^a	15.2 ± 2.1^a	4.2 ± 0.4^b
November	10	63.4 ± 3.3^c	19.1 ± 3.8^a	5.4 ± 0.87^a	0.7 ± 0.2^a	25.2 ± 5.3^b	6.5 ± 0.7^a

foraged for most of the day and early evening (*figure 3*). An ANOVA test showed the existence of significant differences among the fullness coefficient of four sets of time intervals ($P < 0.05$), which suggested that feeding intensity increased throughout the day and that mullet did not feed from 21.00 to 03.00 hours (*figure 3*). The daily ration increased to 5.94 % of body weight and the daily gross energy intake increased to 128.7 J·fish⁻¹·day⁻¹.

In November, food quality was at a maximum (*table I*), but feeding intensity was very low. An ANOVA test revealed significant differences between the fullness coefficient of three sets of time intervals, which suggested that mullet foraged mainly before dawn and after dusk (*figure 3*) (ANOVA; $P < 0.05$). The daily ration decreased to 1.38 % of body weight and the daily gross energy intake fell to 43.3 J·fish⁻¹·day⁻¹. This low energy intake was consistent with a negative growth rate (*figure 1*).

The percentage of organic matter, the percentage of protein and the energy content of the sediment were high throughout the cold season and significantly lower in April and August (*table I*) (ANOVA; $P < 0.05$ for all parameters).

4. DISCUSSION

The method used to calculate the intake of energy available for growth probably resulted in an underestimate, as both the Elliott-Persson's method for calculating daily rations and the method used for transforming chemical composition to energy contents are known to underestimate values [19, 28]. Furthermore, the variance is usually high when the Elliott-Persson's method is used [9] and the daily rations are usually highly variable [25, 43]. Although this phenomenon does not usually affect fish growth rate, it can affect calculations based on the weight and rate of evacuation of gut contents [3]. Another problem is that the evacuation rate was measured with a method used for carnivorous fish [8], but no information exists about the suitability of this method for detritivores. In addition, an energy budget could not be calculated owing to some missing information. The metabolic rate of young leaping grey mullet at different temperatures may be calculated using the equation provided by Guinea and Fernández [27], but there is no information about the digestive assimilation efficiency in this species, although in other mullet species it is about 50 % [29, 40].

In spite of these shortcomings, the seasonal changes in calculated energy intake fit reasonably well with seasonal changes in growth rates and consequently results are useful for understanding the relationship among food supply, energy intake and growth rate in the population studied.

The percentage of organic matter, the percentage of protein and the energy content of the sediment changed throughout the study as expected, i.e. they were high in winter, decreased in the warm season and

peaked again in autumn. The proximate composition of stomach contents followed similar changes and decreased in the warm season, which supports the hypothesis that food quality was linked to the seasonal cycle of detritus production and degradation. Similar results were reported for other European mullet species [2, 31], although Hickling observed a fairly constant percentage of organic matter in the stomach content of British mullets throughout the year [29].

The only difference between the seasonal changes in the chemical composition of sediment and that of stomach contents was that summer food quality was lower than that of spring, whilst sediment quality did not change throughout the warm season. The stability of the percentage of the organic matter content in the sediment was due to the development of dense summer populations of benthic algae [12], thus partially compensating the organic matter loss due to detritus mineralisation. However, the mullet failed to collect most of them, probably owing to their coarse branchial filter [26]. Probably, they also had problems collecting particles remaining in the sediment after several months of degradation [34], which explains why the percentage of organic matter in the stomach contents was always smaller than that of the sediment. The opposite pattern has been reported for other mullet species with finer branchial filters [29, 36, 40].

Previous studies have reported a summer decrease in the growth rate of other detritivores due to food limitation [22, 31]. The studied population increased their foraging time in summer, a typical behaviour of most fish species when supplied with food of low energy content [15]. It should be noted that the quality of the sediment did not change from April to August, but that of the stomach content did decrease. The mullet reduced foraging time again in November, when food quality rose and energy demand decreased.

Strong correlation between fish growth and temperature suggests that the growth rate of mullet was not affected by the summer reduction in food quality, although we do not know whether the fish might have grown even faster if they could forage on more nutrient-rich food, because stomach filling capacity and the gastro-intestinal evacuation rate usually increase with temperature [10].

Mullet are believed to forage continuously owing to the small size of their cardiac stomach [18]. However, the studied population showed this pattern only in summer, when food quality was low. In spring and autumn, they foraged more intensely at dawn or dusk, as many other grey mullet species do [1, 2, 7]. The reduction in foraging time was probably due to an improvement in food quality, but this does not explain why mullet became more nocturnal in spring and autumn. Indeed, they may have achieved the same daily ration foraging at noon, for instance. Some salmonid are known to shift from diurnal to nocturnal feeding in cool water [4], in order to reduce predation risk [35]. It is possible that the above-mentioned changes were caused by the same reason, because the

main predator of the mullet in Albufera des Grau lagoon, the great cormorant (*Phalacrocorax carbo*), was only found from September to March (Cardona, unpublished data).

Juvenile mullet foraged almost continuously in summer because food quality was low. On the other hand, mullet fry smaller than 3 cm recruit in late summer but forage only for a few hours daily [24]. These differences exist because the small fry prey on the highly available summer zooplankton [23], while juveniles forage mainly on detritus, which are scarce in that season.

There is a last point that deserves discussion. Leaping grey mullet lost weight from February to March, when water temperature was below 20 °C. They gained weight again in April and their growth rate increased throughout late spring and early summer, to become negative in late autumn, when water temperature was again below 20 °C. Interestingly, leaping grey mullet are very scarce in the Atlantic north of the Tagus estuary [5, 17], where water temperature seldom rises above 20 °C [20]. This suggests that their penetration into the northern Atlantic is prevented by this phenomenon.

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