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Effects of starvation on swimming performance and body condition of pre-settlement *Sparus aurata* larvae

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ABSTRACT: Body condition in larval fishes is an important determinant of survival in the natural environment. However, few studies correlate body condition with behavioural traits critical for survival, such as swimming performance. In the present study, we compared normally fed larvae of gilthead seabream *Sparus aurata* Linnaeus, 1758, at various intervals post-hatch with larvae which were starved for 1 to 3 d (for U_{crit}) or 2 d (for swimming endurance). Feeding treatment (fed and or unfed) had no effect on the relationship between U_{crit} and larval size. However, in the endurance experiment, fed individuals swam twice as far as unfed larvae (19.7 km for fed larvae and 9.5 km for unfed larvae). The RNA/DNA ratio was higher in fed larvae in the U_{crit} experiment, but significant effects were only detectable after a 3 d period of starvation. Fulton's condition factor was significantly higher in fed larvae in the endurance trial, which suggests that growth (in weight) of starved larvae was affected by long-term swimming. Taken together, these results suggest that foraging and orientation behaviours (activities in which critical speeds might be involved) are not affected by reduced feeding over a few days, but that sub-lethal effects of starvation may affect dispersal potential (for which endurance swimming is critical) and therefore compromise subsequent recruitment to the adult population.

KEY WORDS: Gilthead seabream · Swimming performance · Nutritional condition · Sub-lethal effects · RNA/DNA ratio · Fulton's condition factor

INTRODUCTION

Early life stages of marine fishes typically experience high rates of mortality, with strong implications on future recruitment. Predation and starvation are considered to be the 2 major causes of mortality in larval fishes (Miller et al. 1988, Bailey & Houde 1989). These 2 factors can act together to increase mortality rates, as starved or underfed larvae may be more susceptible to predation (Neilson et al. 1986). Some evidence suggests that general activity or vertical migratory activity declines in starved larvae of several species (Laurence 1972, Blaxter & Ehrlich 1974). Moreover, starvation leads to decreased growth rates (Ehrlich et al. 1976, Yin & Blaxter 1986), slower development (Kamler et al. 1990), and changes in behaviour for energy-saving purposes (Munk 1995, Ross et al. 1996, Chick & Van den Avyle 2000, Skajaa et al. 2004). Thus it is expected that larvae with low nutritional condition will be smaller and less developed in sensory and locomotory capacities than well-fed larvae.

Despite several studies indicating that good body condition at the larval stage can be correlated with higher growth rate in larvae and enhanced recruitment or juvenile survival under natural conditions (Searcy & Sponaugle 2001, Bergenius et al. 2002, McCormick & Hoey 2004, Sponaugle et al. 2006), few attempts have been made to correlate larval condition

with any behavioural function critical for larval survival, such as swimming behaviour (e.g. Laurence 1972, Yin & Blaxter 1987, Chick & Van den Avyle 2000). Swimming is one of the most important behaviours in larval fish, determining to a large extent the success of predator avoidance, prey capture and dispersal potential (Reidy et al. 2000, Armsworth 2001, Plaut 2001, Fisher & Wilson 2004). It has been shown that larvae in good condition possess better swimming abilities and responsiveness to predators than larvae in poor condition (Chick & Van den Avyle 2000, Grorud-Colvert & Sponaugle 2006).

Larval condition may be estimated by a variety of morphometric, biochemical, histological, or otolith growth indices. Fulton's condition factor K is a morphometric index commonly used as an indicator of an individual's general well-being and is based on the assumption that heavier fish for a given length are in better condition (Ricker 1975, Suthers 1998). The RNA/DNA ratio is a widely used biochemical index of nutritional condition and recent growth of larval fishes (e.g. Clemmesen et al. 1997, Buckley et al. 1999, Esteves et al. 2000, Caldarone et al. 2003) and it reflects variations in protein synthesis rates (recent growth), as RNA concentration varies both with food intake and protein requirement, while DNA somatic content remains relatively constant (Bulow 1970).

In the present study, we examined the influence of starvation on the condition (measured through the RNA/DNA ratio and Fulton's condition factor) and swimming behaviour of gilthead seabream larvae *Sparus aurata*. We hypothesised that starved larvae would perform more poorly than fed larvae, using swimming abilities as a measure of behavioural performance. Two of the most common measures of swimming ability (critical speed and swimming endurance) were measured in larvae that had either been fed ad libitum or starved for 1, 2, or 3 d. Pre-settlement stages were chosen because this phase is often characterised by very high mortality rates (Almany & Webster 2005, Leis 2006), with obvious implications for the subsequent survival of and recruitment to the adult population (Searcy & Sponaugle 2001, Grorud-Colvert & Sponaugle 2006).

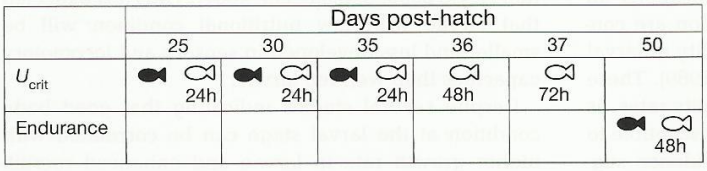

Fig. 1. *Sparus aurata*. Behavioural tests conducted on *S. aurata* larvae of different ages. Black fish represent larvae fed ad libitum; white fish represent unfed larvae. The hours noted below the white fish indicate the duration of the starvation period. U_{crit}: critical swimming speed

MATERIALS AND METHODS

Larvae. *Sparus aurata* Linnaeus, 1758 larvae were obtained from the fish hatchery TIMAR (Algarve, Portugal), at 22 d post-hatch (dph) and were maintained in 20 l aquaria, with constant slight aeration and a photoperiod of 13 h light:11 h dark. Larvae were raised in a semi-closed circuit of filtered natural seawater originating from the nearby coast. Salinity was kept constant at 37, and temperature ranged from 20.6 to 22.6°C.

Larvae were randomly distributed in 2 rearing aquaria: one aquarium with larvae fed ad libitum with *Artemia* sp. nauplii and the other aquarium with larvae deprived of food for a minimum of 24 h before experimental tests. The rearing aquaria were placed next to each other, with similar initial larval densities and the same light conditions and water quality, to minimise possible tank effects. Mortality did not differ between tanks.

Two behavioural tests were performed in order to evaluate the influence of feeding treatment on swimming performance: critical swimming speed (U_{crit}) and swimming endurance. For each experiment, fed and unfed larvae were tested (see Fig. 1). U_{crit} of fed and unfed (24 h of food deprivation) larvae was measured at 25, 30 and 35 dph. After perceiving that U_{crit} was not affected by a 24 h period of food deprivation, larvae were tested after starving for 48 h (36 dph) and 72 h (37 dph). U_{crit} was not measured on larvae older than 37 dph, because these were already post-flexion larvae, and, by this time, larvae had achieved the maximum flow speed of the swimming chamber (20 cm s^{-1}). Swimming endurance was measured on late-stage (50 dph) fed and unfed (48 h of food deprivation) larvae, since endurance experiments measure long-term swimming performance and provide data directly relevant to larval fish dispersal, which, in turn, becomes more important close to the settlement stage. Starvation in the experimental tank was thus sequential, and larvae were tested after each starvation episode. Space, time and logistic constraints prevented us from using an approach whereby all conditions were repeated once in each test to evaluate effects throughout ontogeny. Nevertheless, in spite of possible carry-on effects of each starvation period on the following ones, larvae in the wild will also probably face periods of starvation interspersed with periods of food abundance. Moreover, there were no significant differences in mortality rates or in the relationship between condition (both for RNA/DNA ratio and Fulton's K) and size between treatments. Therefore, a word of caution is needed when interpreting the results of ontogenetic effects.

For each experiment, 8 to 12 larvae were tested. After the experiment, larvae were put in liquid nitrogen and stored at −80°C for subsequent RNA/DNA analysis. The larvae were freeze dried and weighed on an ultra-balance with a precision of 1 µg (Mettler Toledo MX5) before the biochemical analysis.

Critical swimming speed. U_{crit} (cm s^{-1}) was measured using a swimming chamber, following the protocols of Stobutzki & Bellwood (1994, 1997). The chamber was made of clear Perspex with 6 parallel swimming lanes, each 30 mm wide, 50 mm high and 180 mm long. A removable lid allowed introduction and removal of fish from the lanes. A strip of black tape on the top of the lid provided fish with a visual reference to maintain position in the flow, and a mesh screen was placed at the upstream and downstream ends of each lane to retain larvae. A section of flow straighteners, 40 mm long, was placed at the upstream end of each lane to minimise turbulence. Previous work demonstrated that, at the typical U_{crit}, water velocity was not significantly different between the centre of the lane and 5 mm from the wall (Stobutzki & Bellwood 1997, Stobutzki 1998, Fisher et al. 2000). Experimental observations also confirmed that larvae did not show a depth preference in the chamber. The maximum flow speed was 20 cm s^{-1}. For details on the swimming chamber characteristics see Faria et al. (2009).

One hour after feeding, larvae were carefully removed from the rearing tank using a small container and were placed individually in large Petri dishes and left undisturbed for 1 h to allow recovery from handling (Fuiman & Ottey 1993). After this period, larvae were transferred to the swimming chamber, 1 in each lane, and allowed to acclimate for 5 min at a flow speed of 1 cm s^{-1}. If any behavioural symptoms of stress, such as lying on the bottom or clinging to the sides, were observed after this acclimation period, the individual was removed and replaced by another fish. Water temperatures in the chamber over the study period varied from 20.5 to 23°C. To measure U_{crit}, water velocity was increased by approximately 1.2 cm s^{-1} every 2 min until the larva was unable to swim against the current for 2 min. Calculation of U_{crit} followed Brett (1964) such that:

$$U_{crit} = U + (t/t_i \times U_i) \quad (1)$$

where U is the speed of the penultimate increment, U_i is the velocity increment, t is the time swum in the final velocity increment and t_i is the time interval for each velocity increment (2 min). After the test, fish were immediately put in liquid nitrogen for condition analysis.

Swimming endurance. Swimming endurance was measured by swimming larvae at a single speed until exhaustion. The speed of 12 cm s^{-1} (approximately 50% of the maximum U_{crit}) was chosen as a reference. During daylight hours, larvae were constantly observed, and the exact time to fatigue was recorded. At night, larvae were observed every 6 h, and the time to fatigue was calculated as the midpoint between when the larva was last seen swimming and when it was found no longer swimming. Only 1 larva stopped swimming during the night period. The swimming duration was converted in distance swum (km) using the flow speed. The values are therefore given as kilometres swum.

Condition indices. RNA and DNA were measured with the microplate fluorescent assay (MFA) of Wagner et al. (1998). The MFA assay is a modification of the sequential fluorometric method of Bentle et al. (1981), in which DNA and RNA in a single sample are determined sequentially by the addition of DNase and RNase, using ethidium bromide (EB) as a fluorescent dye (see Caldarone et al. 2001 for details). Wagner et al. (1998) modified the sequential fluorometric method of the MFA with 96-well microtiter plates by adopting a sarcosyl extraction technique and eliminating the DNase step. The larvae were individually homogenised by sonication (3 pulses 50 A during 1 min) with cold sarcosyl extraction buffer. The volume of extraction buffer was 500 µl (0.5%). The samples were then shaken for 1 h at room temperature on a vortex mixer equipped with a multiple-vial head. Next, they were centrifuged (12 000 ×g) for 15 min to separate insoluble larvae remains. The samples were subsequently diluted 1:10 with Tris buffer to reduce the sarcosyl concentration to 0.05%. In each run, duplicates of 50 µl aliquots of the samples' supernatants, in addition to duplicates of 0, 0.6, 1.1, 1.7, and 2.3 µg ml^{-1} of DNA standard solutions (λ-phagus, 0.25 µg $µl^{-1}$ from Roche), 16s to 23s *Escherichia coli* RNA (4 µg $µl^{-1}$ from Roche) and 0, 3.6, 7.3, 10.9 and 14.6 µg ml^{-1} of RNA standard solutions (16s to 23s *E. coli*, 4 µg $µl^{-1}$ from Roche) were transferred to 96-well microplates (type nuclon black round bottom). The average slope ratio of DNA and RNA (slope of DNA standard curve/slope of RNA standard curve) was 5.5 ± 0.8; this ratio can be used to compare RNA/DNA ratio results determined by other protocols (Caldarone et al. 2006). EB solution (30 µl) was added to each well, and the plates were shaken gently at room temperature for 15 min. The EB fluorescence was then scanned on a microplate reader (Biotek synergy HT Model SIAFRTD) with 360 nm (excitation) and 590 nm (emission) (first scan: total fluorescence of RNA + DNA). Following the first scan, RNase solution (30 µl, 0.12 µg ml^{-1}) was added to each well, and the concentration of DNA was calculated directly from the standard curve. The concentration of RNA was determined indirectly by subtraction of DNA fluorescence (second scan) from total fluorescence (first scan).

Fulton's condition factor was directly determined from morphometric data using the formula:

were treated as a single unfed group. U_{crit} of the unfed group revealed a significant relationship with length ($F_{1,46}$ = 58.5, p < 0.0001; Fig. 3), ranging from 1.1 to 18.9 cm s^{-1} (1.5 to 20.2 bl s^{-1}) over the size range of from 6.1 to 12.9 mm (SL). In both feeding treatments, there was large variation in performance among individuals, at any size (Fig. 3).

There was no difference between the slopes of the regressions of U_{crit} on the size of fed and unfed larvae (ANCOVA: $F_{1,75}$ = 0.39, p = 0.53), indicating that U_{crit} did not differ between feeding treatments.

To test endurance 10 fed and 10 unfed larvae were stimulated to swim at a constant speed of approximately 12 cm s^{-1}. The fed group swam for a significantly longer period than the unfed group (t = −5.16, df = 18, p < 0.0001), with fed larvae swimming about twice as long as unfed larvae (mean ± SD: swimming duration of fed larvae = 42.2 ± 11.1 h; swimming duration of unfed larvae = 20.4 ± 7.4 h). Fed fish swam an equivalent mean distance of 19.7 km (range: 10.3 to 23.9), whereas unfed fish swam an equivalent mean distance of 9.5 km (range: 4.4 to 14.1) (Fig. 4).

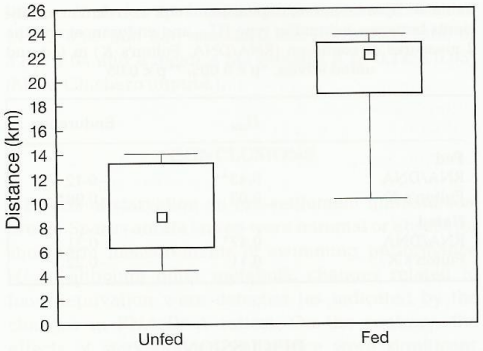

Fig. 4. *Sparus aurata*. Comparison of distance travelled (km) between fed and unfed larvae of *S. aurata* in endurance tests. Small squares represent the median, box values represent 25 to 75% percentiles and whiskers represent minimum and maximum distances swum by the larvae (see 'Results' for statistical results)

Effect of feeding treatment on body condition

RNA/DNA ratio and Fulton's K were both highly correlated with length (SL) and age, in both feeding treatments (Table 1). Both condition indices were significantly higher for fed larvae than for unfed larvae (RNA/DNA ratio: Mann-Whitney, U = 1418.0, p < 0.001; Fulton's K: Mann-Whitney, U = 4612.0, p = 0.003; Table 2). When analysing all data pooled together, the RNA/DNA ratio was the only condition measure affected by the duration of the starvation period (Kruskal-Wallis, H [2, N = 80] = 8.27, p = 0.016), but only after 3 d of food deprivation.

When investigating whether the condition indices were correlated with the type of swimming measured (U_{crit} or endurance), in each feeding treatment, the results showed that the RNA/DNA ratio is positively correlated with U_{crit} in both fed and unfed larvae, and Fulton's K is highly correlated with endurance in fed larvae (Table 3).

Table 1. *Sparus aurata*. Spearman rank correlation coefficients between length (standard length) and age (days post-hatch) and the 2 measures of condition (RNA/DNA, Fulton's K) in fed and unfed larvae. $^{*}p < 0.005$; $^{**}p < 0.05$

	Length	Age
Fed		
RNA/DNA	0.53*	0.40*
Fulton's K	0.31**	0.35**
Unfed		
RNA/DNA	0.50*	0.32*
Fulton's K	0.31**	0.35*

Table 2. *Sparus aurata*. Nucleic acid content and Fulton's K factor of analysed larvae for the fed and unfed groups in the U_{crit} and endurance experiments (average ± standard deviation). N: number of larvae; SL: standard length; DW: dry weight

	N	SL (mm)	Weight (mg)	RNA $larva^{-1}$ (µg)	RNA mg^{-1} DW (µg)	DNA $larva^{-1}$ (µg)	DNA mg^{-1} DW (µg)	RNA/DNA	Fulton's K
U_{crit}									
Unfed	48	9.07 ± 1.75	1.82 ± 1.50	134.95 ± 188.50	82.55 ± 95.39	75.03 ± 89.30	49.93 ± 46.96	1.89 ± 1.10	0.22 ± 0.16
Fed	30	9.13 ± 1.98	2.31 ± 1.97	471.39 ± 934.48	160.78 ± 175.17	122.03 ± 209.93	46.97 ± 47.12	3.31 ± 1.59	0.28 ± 0.24
Endurance									
Unfed	9	11.70 ± 1.22	3.67 ± 1.82	248.13 ± 171.81	74.54 ± 44.78	383.04 ± 605.97	142.89 ± 281.14	2.64 ± 2.34	0.21 ± 0.05
Fed	6	12.44 ± 1.28	5.88 ± 1.74	717.93 ± 670.43	114.28 ± 89.87	335.16 ± 416.92	52.22 ± 59.28	2.66 ± 1.69	0.30 ± 0.05

Table 3. *Sparus aurata*. Spearman rank correlation coefficients between swimming type (U_{crit} and endurance) and the 2 measures of condition (RNA/DNA, Fulton's K) in fed and unfed larvae. $^{*}p < 0.005$; $^{**}p < 0.05$

	U_{crit}	Endurance
Fed		
RNA/DNA	0.43**	−0.12
Fulton's K	0.03	0.98*
Unfed		
RNA/DNA	0.47*	0.31
Fulton's K	0.11	−0.22

DISCUSSION

Sparus aurata larvae became more competent swimmers with size. U_{crit} increased throughout ontogeny, for both fed and unfed larvae. Nevertheless, variation at any size was large, and size itself only explained 46 and 56% of the variation in critical swimming performance for fed and unfed groups, respectively. Similar results have been documented in other experimental works with other species (e.g. Clark et al. 2005, Faria et al. 2009, Leis et al. 2009) and suggest that other factors in addition to size are important in influencing swimming speed, such as larval condition (Leis & McCormick 2002).

The U_{crit} recorded for gilthead seabream larvae in the current study ranged from 1.7 to 19.3 cm s^{-1}, which falls within the range of critical speeds found in other studied Sparidae larvae. A recent study by Koumoundouros et al. (2009) also examined the ontogeny of the U_{crit} of pre-metamorphic (13.7 to 18.7 mm total length, TL) *Sparus aurata* larvae at different temperatures. At 20°C, a temperature similar to the one used in the present study, average U_{crit} of larvae was 10 cm s^{-1}. Pattrick & Strydom (2009) examined U_{crit} and endurance of late-stage wild larvae of 2 other temperate Sparidae, *Diplodus capensis* and *Sarpa salpa*, and reported maximum U_{crit} values of 35 and 33 cm s^{-1}, respectively. Clark et al. (2005) studied the ontogeny of U_{crit} of 2 warm-temperate Sparidae, *Acanthopagrus australis* and *Pagrus auratus*, over a size range similar to that used in the present work, and U_{crit} speeds varied between 2 and 27 cm s^{-1}.

Critical swimming speed did not differ between fed and unfed treatments, suggesting that the starvation period used (3 d) is not sufficent to induce changes at the level of maximum attained speed of pre-settlement *Sparus aurata* larvae. The greatest impact of starvation on performance was seen in the endurance experiment: fed larvae swam twice as long as unfed larvae, with an average of 42.2 h and 19.7 km, at 12 cm s^{-1}. During swimming trials, lipids, carbohydrates and proteins are all used (Stobutzki 1997). Larvae that were fed ad libitum prior to the experiment clearly had more energy reserves than the ones that were starved for a 2 d period. These results suggest that reserves of unfed larvae were depleted faster than reserves of fed larvae and indicate that endurance is less limited by fatigue than by energy supplies. Other studies support this evidence. For example, Fisher & Bellwood (2001) examined the effect of food on the sustained swimming ability of late-stage *Amphiprion melanopus* at 7 cm s^{-1} and reported an increased swimming distance from around 6.9 to 12.2 km when feeding larvae during the trial. Leis & Clark (2005) also found that swimming endurance of late-stage larvae of 6 pomacentrid species was greatly increased by feeding; fed larvae were able to swim at least twice as long as unfed larvae.

The mean endurance results found are higher than values reported for settlement-stage larvae of other Sparidae: *Pagrus auratus*, 9.9 km at a speed of 10 cm s^{-1} (Clark et al. 2005) and *Sarpa salpa* and *Diplodus capensis*, 8 and 6 km, respectively, at a speed of 18 cm s^{-1} (Pattrick & Strydom 2009). These differences might be related to the speed chosen for the endurance experiments, but can also be attributed to the ontogenetic stage itself.

The lack of food deprivation effects on short-term swimming behaviours, such as U_{crit}, has been reported in other studies. Laurence (1972) studied sustained swimming abilities and activity level of fed and starved largemouth bass *Micropterus salmoides* larvae at 19°C and found that differences in swimming activity were only notable after a period of 4 d of starvation. Similarly, Yin & Blaxter (1987) reported decreased responsiveness and escape speed for starved herring, cod and flounder, reared at 9 to 10°C, but the effects of starvation were not evident until larvae had been starved for several days. Chick & Van den Avyle (2000) observed a similar pattern when examining the effects of feeding ration on the routine swimming speed of larval striped bass *Morone saxatilis*. More recently, Skajaa & Browman (2007) concluded that escape responses in food-deprived cod larvae *Gadus morhua* were not, in general, affected by 3 d of food deprivation at 10°C. These studies support the evidence that short-term swimming behaviours are conserved and even prioritised in food-deprivation scenarios. On the contrary, long-term performance, such as endurance swimming, is affected by short periods of starvation, which suggests that, in terms of dispersal potential (for which endurance swimming is critical), starving larvae may not succeed.

The RNA/DNA analysis confirmed differences in nutritional status between groups, but only after a 3 d period of food deprivation, which seems to indicate that this is the minimum starvation period necessary to

induce changes in the RNA/DNA ratio for this species in these conditions. The RNA/DNA ratio has been shown to respond to changes in feeding conditions and growth in periods as short as 1 to 3 d in a variety of fish species (Clemmesen 1994, Rooker & Holt 1996) and is a reliable growth rate estimator, which has been applied in numerous field assessments (Buckley et al. 1999, Gwak & Tanaka 2001, Chícharo et al. 2003). Therefore, one might expect that a condition-related effect on behaviour might have been apparent if the larvae had been food-deprived for a longer period.

Grorud-Colvert & Sponaugle (2006) studied the influence of condition on behaviour and survival potential of newly settled bluehead wrasse *Thalassoma bifasciatum* and reported that recruits fed for 1 wk grew faster, had a greater Fulton's condition factor, swam faster and avoided simulated predators at faster speeds than recruits starved for the same period. Similar results were found in the present study, as fed larvae had higher Fulton's K and higher endurance performance when compared to larvae deprived of food. A link between starvation, condition and behaviour is thus evident in these studies, although other possible explanatory factors exist, such as a change in the way larvae allocate energy for growth and swimming, but this is beyond the scope of the present study. Future work may supply further evidence in this regard.

The possible use of condition indices (RNA/DNA ratio and Fulton's K) as a proxy for swimming performance was also investigated. The results show that the RNA/DNA ratio is positively correlated with U_{crit}, which indicates that larvae with higher condition are capable of attaining higher U_{crit}. Moreover, the measured morphometric index, Fulton's K, was highly correlated with endurance abilities. Despite this high correlation, care should be taken when extrapolating the attributes of laboratory-reared larvae to ocean-caught larvae (Ferron & Leggett 1994). Larvae reared in the laboratory are usually fatter, exhibit less shrinkage, have less histological variation, less RNA and DNA relative to length (Ferron & Leggett 1994) and may require prey concentrations 2 to 3 orders of magnitude greater than larvae in the field to survive (Suthers 1998). The mean (±SD) RNA/DNA ratio in the present study was 3.31 ± 2.28 for fed larvae and 2.21 ± 1.71 for unfed larvae; the mean (±SD) Fulton's K was 0.28 ± 0.13 for fed larvae and 0.24 ± 0.20 for unfed larvae. The critical value of condition indices for survival is species specific, and, to our knowledge, no reference studies presently exist on the RNA/DNA ratio or Fulton's K of wild-caught *Sparus aurata* larvae or any other sparid that could be used for comparison. Nevertheless, unpublished data on the nucleic acid content of wild-caught sparid larvae (*Diplodus* sp., M. A. Chícharo unpubl.) seem to be comparable to the values reported in the present study for fed larvae. *Diplodus* sp. larvae with a mean ± SD size of 11.7 ± 0.68 mm had a mean ± SD RNA/DNA ratio of 3.8 ± 1.04 and a mean ± SD Fulton's K of 0.17 ± 0.05) (M. A. Chícharo unpubl.).

CONCLUSIONS

Effects of starvation on pre-settlement gilthead seabream *Sparus aurata* larvae were minimal or absent for short-term measurements of swimming performance (U_{crit}), although other metabolic changes related to food deprivation were detected (as indicated by the changes in RNA/DNA ratios). On the contrary, the effects of starvation on endurance were significant. These results suggest that larvae may be capable of performing escape and foraging behaviours even in poor nutritional condition (activities in which critical speeds are involved), but sub-lethal effects of starvation may affect dispersal potential by greatly reducing endurance swimming, hence, compromising subsequent survival and recruitment to the adult population.

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