



ELSEVIER

Aquaculture 205 (2002) 89–102

www.elsevier.com/locate/aqua-online

Aquaculture

Survival, growth and feeding in early life stages of European sea bass (*Dicentrarchus labrax*) intensively cultured under different stocking densities

A. Hatzithanasiou^{a,*}, M. Paspatis^a, M. Houbart^b, P. Kestemont^b,
S. Stefanakis^a, M. Kentouri^{a,c}

^a*Institute of Marine Biology of Crete, PO Box 2214, GR-71003 Heraclion, Crete, Greece*

^b*Unité de Recherches en Biologie des Organismes, Facultés Universitaires Notre-Dame de la Paix, rue de Bruxelles, 61, B-5000 Namur, Belgium*

^c*University of Crete, Department of Biology, PO Box 2208, GR-71409 Heraclion, Crete, Greece*

Received 30 August 2000; accepted 12 May 2001

Abstract

Two experiments were conducted in triplicate in order to study the effect of stocking densities on survival (highlighting sibling cannibalism), growth and feeding of intensively cultured sea bass larvae (50, 100, 150 and 200 fish l⁻¹) and post-larvae (5, 10, 15 and 20 fish l⁻¹). Experimental populations were reared under controlled conditions in 50-l cylindroconical tanks. Dead fish were counted daily and classified into cannibalised and non-cannibalised. Total length and weight were measured weekly. Results indicate that stocking density did not affect survival and growth of larvae. No cannibalistic phenomena were observed at this stage. On the other hand, survival of post-larvae was higher at 5 and 10 fish l⁻¹ than at 15 and 20 fish l⁻¹, while growth performance fluctuated between the lowest value recorded in the group of 10 fish l⁻¹ and the highest value in that of 5 fish l⁻¹. Feed intake in post-larvae was independent of stocking density. Cannibalism was the main cause of death in post-larvae. Two types of cannibalism were detected: type I, attack from tail (observed at the beginning of this stage) and type II, attack from head (observed at the end of the stage). © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Stocking density; Growth; Feeding; Cannibalism; Survival; Larval stages; European sea bass; *Dicentrarchus labrax*

* Corresponding author. Tel.: +30-81346860; fax: +30-81241882.

E-mail address: antigoni@imbc.gr (A. Hatzithanasiou).

1. Introduction

In intensively cultured fish species, there are demands for more efficient early stages production due to low survival rates (Baras et al., 1999; Baskerville-Bridges and Kling, 2000). To meet current needs, farmers resort to increasing stocking density. Density is one of the most deterministic factors in larviculture, affecting social interactions such as aggressiveness (Kaiser et al., 1995; Sakakura and Tsukamoto, 1999), hierarchical phenomena (Schreck, 1981) and cannibalism (Katavic et al., 1989; Moore and Prange, 1994), resulting in variations in size, survival and growth performance in fish populations (Sheikh-Eldin et al., 1997).

Cannibalism is the limiting factor in larviculture for a variety of fish species (Van Damme et al., 1989; Kestemont et al., 1995; Stephanou et al., 1995; Morrow et al., 1997; Baras, 1999; Baskerville-Bridges and Kling, 2000). Sibling cannibalistic phenomena are strongly related not only to stocking density, as stated above, but also the nutritional state of fish (Baras, 1999), population weight variation (Mélard et al., 1996), and to non-biological parameters such as water temperature (Mélard et al., 1997) and light (Baras et al., 1999), significantly increasing fish mortality in early stages and contributing to higher production cost.

The European sea bass (*Dicentrarchus labrax*) is one of the most popular cultured species in the Mediterranean region. All growth stages take place in intensive conditions and sea bass culture is profitable for the aquaculture industry. However, difficulties mainly in the early stages of its cultivation relating to skeletal deformities (Chatain, 1994; Boglione et al., 1995; Divanach et al., 1997), feeding (Cahu and Zambonino Infante, 1994) and rearing conditions (Barahona-Fernandes, 1979; Cerqueira and Chatain, 1991) restricted the number of available fish for further development. Nowadays, most of these difficulties have been overcome. However, to our knowledge, the common practice of the very high densities and their effects on sea bass larviculture has not been adequately studied, though preliminary attempts in lower densities have been performed (Barahona-Fernandes, 1981) and cannibalism is present in some of these stages affecting their survival, as Katavic et al. (1989) stated in their work.

In the present study, two critical phases of sea bass development (larval and post-larval stages) were examined under intensive rearing conditions, in order to determine the effects of stocking density on survival rate (highlighting sibling cannibalism), growth performance, weight variation and feeding status of fish.

2. Materials and methods

Experiments were conducted at the Institute of Marine Biology of Crete, Greece, in two subsequent phases, larval and post-larval rearing.

2.1. Phase 1: larval rearing

Sea bass eggs obtained from a captive broodstock well acclimated to rearing conditions were counted and separated into experimental tanks in order to have final

four stocking densities: 50, 100, 150 and 200 larvae l^{-1} . All treatments were conducted in triplicate for 30 days. Incubation, hatching and pre-larval stage were carried out under total darkness in 50-l cylindroconical tanks connected to an open water system. Larvae were reared in the same tanks using the reliable “clean water” technique (Divanach and Kentouri, in press) which, for this species, gives the best results in terms of survival and quality. Water circulation from the bottom provided by an airlift system and aeration ensured a gentle homogenisation (Divanach et al., 1998). Both the rate of water circulation (from days 1 to 30) and water renewal (started on day 10 until day 30) were gradually increased from 5% to 40% h^{-1} . During the experimental period, light intensity was gradually increased from 5 to 100 lx and the light phase was regulated to last 14 h (08:00 to 22:00 h). At the same time, ambient temperature increased gradually from 16 to 23 °C, salinity was $40 \pm 0\text{‰}$, and oxygen level was maintained at $6.0 \pm 0.5 \text{ mg } l^{-1}$. Larvae were fed live prey enriched with Selco (Artemia Systems, Belgium): *Brachionus plicatilis* (Br), *Artemia* nauplii (A0) and 1-day-old *Artemia* (A1), according to the feeding schedule (from days 1 to 10 of exogenous feeding, 5–8 *Brachionus* $ml^{-1} h^{-1}$ was distributed; from days 11 to 20, *Brachionus* was decreased gradually and *Artemia* A0 and A1 was increased up to 1–2 individuals $ml^{-1} h^{-1}$; from days 21 to 25, *Artemia* A0 and A1 were supplied; from days 26 to 30 only, *Artemia* A1 was supplied) as proposed by Divanach et al. (1998).

2.2. Phase 2: post-larvae rearing

Post-larvae originated from the same batch of eggs and were reared in the early stages under similar conditions described for phase 1. At 35 days, post-hatching (17.05 mm in length), they were transferred to 50-l cylindroconical tanks and divided into four groups according to the following stocking densities: 5, 10, 15 and 20 post-larvae l^{-1} . Each group was tested in triplicate and the experiment lasted 22 days.

During the experiment, light intensity was 100 lx (daily light phase from 08:00 to 22:00 h), temperature and salinity were $23 \pm 2 \text{ °C}$ and $40 \pm 0\text{‰}$, respectively, and the oxygen level was maintained at above 6 $mg l^{-1}$. At the beginning of the experiment, water circulation and water renewal was 50% and 10% h^{-1} , respectively, and both gradually increased to 80% h^{-1} at the end. Post-larvae were fed with live 1-day-old *Artemia* (A1) enriched with Selco (1–2 individuals ml^{-1} gradually decreased until day 11) and artificial food (Af) (Lansy A2, Lansy W3) gradually increased and distributed ad libitum (reaching 10% of biomass $l^{-1} day^{-1}$) throughout the experiment.

2.3. Parameters studied and data analysis

Temperature, dissolved oxygen, salinity, pH and light intensity were monitored daily for both phases.

Total length and individual wet weight were measured in order to determine growth performance. Therefore, samples consisting of 30 individuals per tank were taken on days 1, 10, 20 and 30 for the larvae phase and 5% of the initial stocking density per population was sampled on days 1, 8, 15 and 22 for the post-larvae phase. All samples were taken at 08:00 h before food supply and measured in vivo under a stereoscope and a Mettler AT

201 balance (accuracy of 0.01 mm and 0.01 mg for the larvae, and 0.1 mm and 0.1 mg for the post-larvae, respectively).

In order to study individual food consumption for the post-larval phase on the same days mentioned and 30 min after the first feeding, 5% of each initial stocking density was sampled.

Behavioural observations (events of aggressiveness between siblings, the way of population dispersion, attacks due to cannibalism) were made early in the morning before the first food supply and during photophase before and after feeding. In case of morphological abnormalities or lesions indicating cannibalism, photos were taken of live and dead fish under an Olympus SZH stereoscope with an Olympus Om-4 camera.

Mortality was estimated daily by counting all dead fish removed from the tanks during surface and bottom cleaning.

Final observed survival (S_o) estimation was based on the formula of Bergot et al. (1986), which takes into account the daily counting of the dead fish and the number of fish removed for sampling purposes:

$$S_o (\%) = \left[\frac{(n_0 - d_1)}{n_0} \frac{(n_0 - d_1 - s_1 - d_2)}{(n_0 - d_1 - s_1)} \frac{(n_0 - d_1 - s_1 - d_2 - s_2 - d_3)}{(n_0 - d_1 - s_1 - d_2 - s_2)} \right] \times 100$$

where: n_0 was the initial number of fish; d_1 was the number of dead fish during the first period (between the first and the second sampling); s_1 was the number of fish sampled in the second sampling; d_2 was the number of dead fish during the second period (after the second and before the third sampling); s_2 was the number of fish sampled in the third sampling; and d_3 was the number of dead fish during the third period.

Cannibalism was estimated in two ways: directly, by enumeration of cannibalised dead fish (characterised by heavy damage to dorsal, anal and mainly to the caudal fin) removed from the rearing tanks; and indirectly, by the number of missing fish at the end of the experiment that we assumed were victims completely ingested and digested as already reported by Katavic et al. (1989) and Van Damme et al. (1989). The percentage of missing fish over the final number of live fish was evaluated by the following equation:

$$M (\%) = \left[\frac{n_m}{(n_f - s)} \right] \times 100$$

where n_f was the final number of fish counted at the end of the experiment, s was the total number of fish sampled and n_m was the missing fish due to cannibalism.

Specific growth rate was evaluated by the following formula:

$$SGR (\% \text{ day}^{-1}) = \left(\frac{\ln W_f - \ln W_i}{t} \right) \times 100$$

where W_i and W_f were mean initial and final individual weight, respectively, at time t . Population variation was estimated using weight variation:

$$CV (\%) = \left(\frac{S.D.}{m} \right) \times 100$$

where S.D. was the standard deviation of individual weight and m was the mean individual weight.

Food consumption in sea bass post-larvae was estimated by a method based on the constant relationship between head weight (x) and total body weight (y) of unfed fish (Person Le Ruyet et al., 1993). A calibration curve between these two variables was determined using data collected from individual post-larvae sampled on days 8, 15 and 22. After feeding, samples of fed fish were collected from each tank, fish were weighed individually, dissected and their head weight used to estimate their theoretical body weight before feeding, based on the calibration curve formed by the equation:

$$y = 0.039x^2 + 1.95x + 5.83.$$

For each fish weighed individually, the head was dissected behind the skull perpendicular to the longitudinal axis and weighed with a precision of 0.1 mg. Individual feed intake was calculated as the difference between measured and estimated weights. It was expressed in absolute (mg of food ingested) or in relative values to the body weight (% of body weight). Inter-individual coefficient of feed intake or of relative feed intake was calculated.

Data were compared by one-way analysis of variance (one-way ANOVA) followed by the least square difference multiple range test (Tukey) when differences between means were significant ($P < 0.05$).

3. Results

3.1. Larval phase

Biological parameters concerning the larval stage of sea bass are shown in Table 1. The initial stocking density did not affect survival, which ranged from 52.6% to 60.7%. No cannibalism was observed at this development stage. Percentage of missing fish was similar in all groups. These fish were not counted and deducted with the dead larvae from the tank bottom at the end of the experiment. It was assumed that these fish were lost due to disintegration. Repeated direct observations during the day, especially when fish were

Table 1

Mean values (\pm S.D.) of the biological parameters during the larval stage of sea bass kept in different stocking densities ($n=3$)

	50 larvae l^{-1}	100 larvae l^{-1}	150 larvae l^{-1}	200 larvae l^{-1}
Final observed survival (So, %)	53.68 \pm 8.01	56.31 \pm 2.27	52.63 \pm 3.75	60.71 \pm 5.05
Missing fish (M , %)	5.67 \pm 1.22	5.16 \pm 0.34	4.92 \pm 0.50	4.20 \pm 0.43
Initial individual weight (W_i , mg)	0.45 \pm 0.00	0.45 \pm 0.00	0.45 \pm 0.00	0.45 \pm 0.00
Final individual weight (W_f , mg)	6.21 \pm 0.26	6.22 \pm 0.24	5.77 \pm 0.50	5.85 \pm 0.87
Initial total length (L_i , mm)	5.12 \pm 0.00	5.12 \pm 0.00	5.12 \pm 0.00	5.12 \pm 0.00
Final total length (L_f , mm)	12.03 \pm 0.19	12.08 \pm 0.29	11.84 \pm 0.35	11.87 \pm 0.63
Initial coefficient of weight variation (CV _i)	15.6 \pm 0.00	15.6 \pm 0.00	15.6 \pm 0.00	15.6 \pm 0.00
Final coefficient of weight variation (CV _f)	45.90 \pm 5.34	45.68 \pm 3.63	36.90 \pm 8.36	36.78 \pm 9.35
Specific growth rate (SGR, % day ⁻¹)	8.75 \pm 0.14	8.76 \pm 0.13	8.50 \pm 0.28	8.53 \pm 0.50

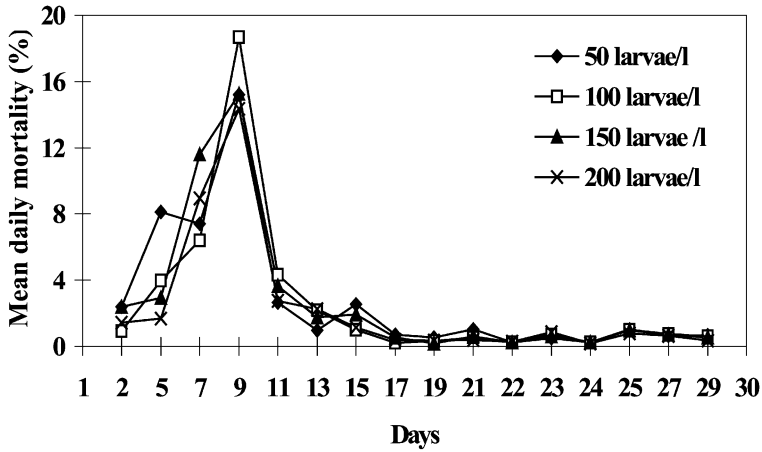


Fig. 1. Observed daily mortality during rearing of sea bass larvae under four different stocking densities.

unfed, did not reveal any cannibalistic phenomena (attacks between siblings). Even dead fish collected from the tanks did not have any sign of cannibalism. Most deaths were recorded between days 6 and 10 (Fig. 1) and coincided with the onset of exogenous feeding. A percentage of 10–20% of dead fish collected during the first 10 days of the experiment were found not to have absorbed their lipid drop. After this period, the mortality rate decreased. Dead fish were mostly unfed (80–85%) or suffered from swim bladder hypertrophy (10–15%).

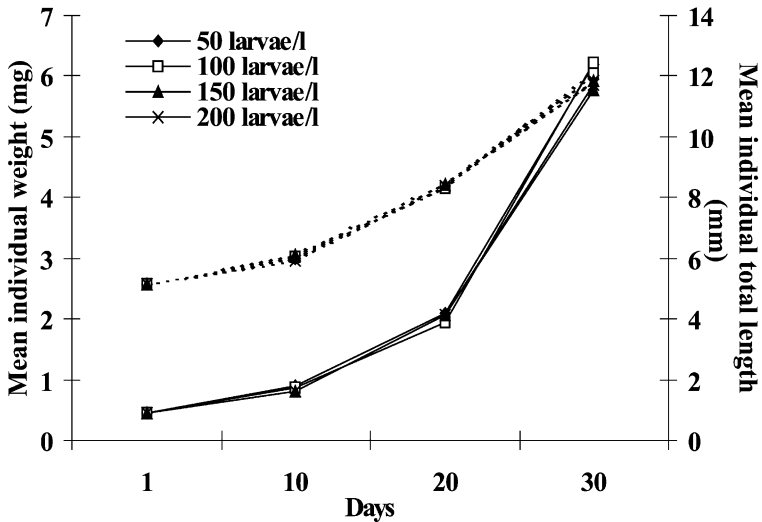


Fig. 2. Mean individual weight (solid lines) and total length (broken lines) of the experimental populations of sea bass larvae reared under four different stocking densities.

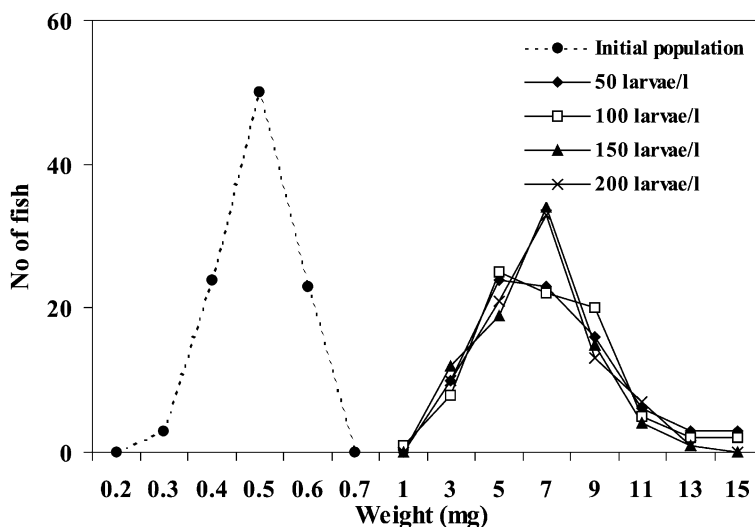


Fig. 3. Individual weight distribution of sea bass larvae kept in four different stocking densities. Broken line refers to the distribution of the overall initial population and solid lines to the distribution of the respective larval populations at the end of the experimental period.

No significant differences among the four fish groups were found in terms of body weight and total length (Fig. 2). Specific Growth Rate proved rather to be stable varying between 8.5% and 8.8% of body weight. A tendency towards better growth was observed in groups of 50 larvae l^{-1} and 100 larvae l^{-1} but this is not confirmed by the statistical test applied.

Individual weight distribution of final populations is presented in Fig. 3. The coefficient of weight variation was estimated to be 15.6% at the beginning of the experiment and increased in all treatments up to 36.8–45.9% at the end. There was no significant difference among treatments.

3.2. Post-larval stage

In Table 2, the mean values of biological parameters estimated for the post-larval stage of sea bass are presented. Survival was significantly higher in low stocking densities (5 and 10 post-larvae l^{-1}). In all treatments, missing fish were recorded at the end of the experiment. Since cannibalistic behaviour was observed from the first day of the experiment and all dead fish could be found at the tank bottom, it was considered that the missing fish were lost due to cannibalism. The number of missing fish in the highest density (20 post-larvae l^{-1}) differed significantly from the missing fish found in densities 5 and 15 post-larvae l^{-1} . Many deaths were recorded during the first 5 days but most were recorded after day 13 when the fish were fed exclusively with artificial food (Fig. 4). Daily observations showed that dead fish removed from the rearing tanks were all cannibalised and the typical symptoms were heavy damage to dorsal, anal and mainly to the caudal fin. Cannibals often remained in the lower part of the tank while swimming and attacked their

Table 2

Mean values (\pm S.D., $n=3$) of the biological parameters during the post-larval stage of sea bass kept in different stocking densities

	5 post-larvae l^{-1}	10 post-larvae l^{-1}	15 post-larvae l^{-1}	20 post-larvae l^{-1}
Final observed survival (S_o , %)	63.65 \pm 2.84 _a	60.20 \pm 3.30 _a	44.69 \pm 2.81 _b	48.35 \pm 2.73 _b
Missing fish (M , %)	0.90 \pm 1.13 _a	3.06 \pm 0.87 _{ab}	1.44 \pm 1.13 _a	5.25 \pm 1.21 _b
Initial individual weight (W_i , mg)	25.56 \pm 0.00	25.56 \pm 0.00	25.56 \pm 0.00	25.56 \pm 0.00
Final individual weight (W_f , mg)	60.54 \pm 6.13 _b	40.42 \pm 8.11 _a	51.46 \pm 4.51 _{ab}	58.23 \pm 6.77 _b
Initial total length (L_i , mm)	17.05 \pm 0.00	17.05 \pm 0.00	17.05 \pm 0.00	17.05 \pm 0.00
Final total length (L_f , mm)	21.53 \pm 0.41 _b	19.60 \pm 1.59 _a	20.44 \pm 0.35 _a	21.10 \pm 0.53 _{ab}
Initial coefficient of weight variation (CV_i)	44.20 \pm 0.00	44.20 \pm 0.00	44.20 \pm 0.00	44.20 \pm 0.00
Final coefficient of weight variation (CV_f)	54.78 \pm 7.67	62.62 \pm 11.38	54.22 \pm 10.45	57.77 \pm 3.63
Specific growth rate (SGR, % day^{-1})	3.90 \pm 0.45 _b	2.02 \pm 0.97 _a	3.17 \pm 0.41 _{ab}	3.72 \pm 0.52 _{ab}

Means with different subscript letters in the same line differed significantly ($P < 0.05$).

victim catching them by the caudal fin. The head or the rest of the body with skeletal remains was rejected but some cannibals suffocated with the prey in the mouth (Fig. 5). An abandonment of prey caused other attacks to wounded fish and even same size individuals could become cannibals. After the second week of the experiment, the biggest members of each population caught their prey from the head and swallowed it whole or progressively.

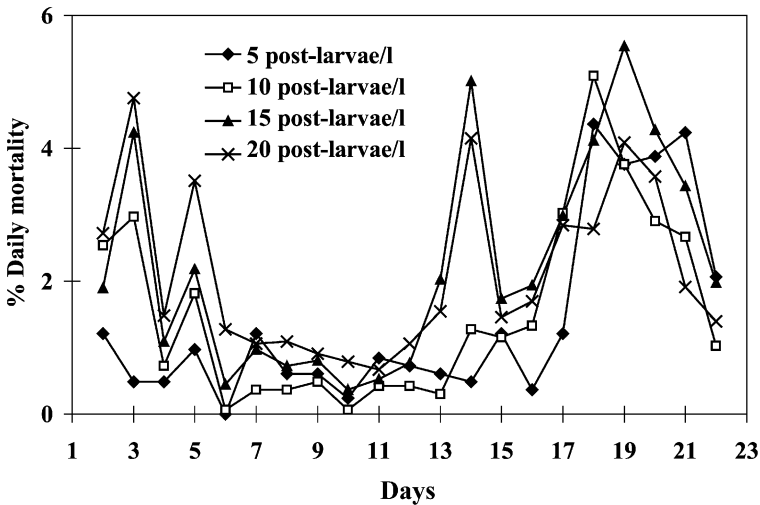


Fig. 4. Observed daily mortality per treatment during the rearing of sea bass post-larvae under four different stocking densities.

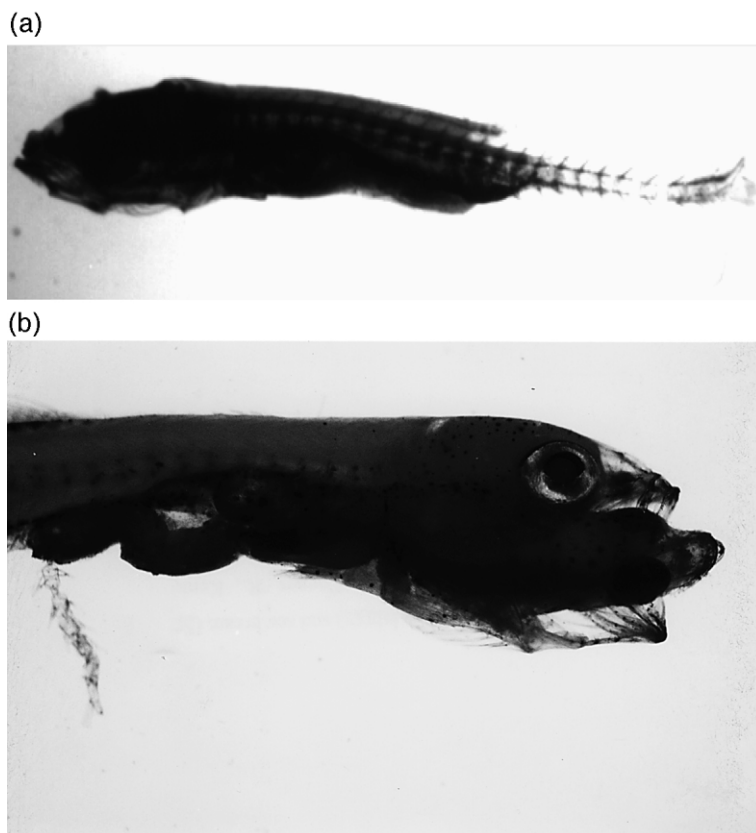


Fig. 5. Cannibalism during sea bass post-larval rearing. (a) The predator caught the prey from the caudal region. (b) Predator suffocated with the victim in mouth. Skeletal remains of the spinal column of a previous victim can be seen at the anus.

Examinations of stomach content of such cannibals showed that the unique food was other siblings. No dead fish sinking slowly or lying on the tank bottom were attacked or ingested.

Mean body weight and total length fluctuation throughout the experiment is presented in Fig. 6. Final body weight was equivalent at the densities of 5, 15 and 20 post-larvae l^{-1} but higher than the group of 10 post-larvae l^{-1} (Table 2). Specific growth rate in the density of 10 post-larvae l^{-1} was significantly lower compared to the density of 5 larvae l^{-1} . The coefficient of weight variation (CV) increased from 44.2% at the beginning of the experiment to 54–62%. The final CV was independent of stocking density (Table 2). Fig. 7 presents the weight distribution of populations, which altered from a peaked profile to a flat one with a positive skewness to bigger fish over the experiment.

Correlation between head weight and body weight of post-larvae was high ($r^2=0.96$) and provided an estimation of theoretical body weight from which feed intake could be estimated. Because of an accidental desiccation, all the samples for the 15 larvae l^{-1}

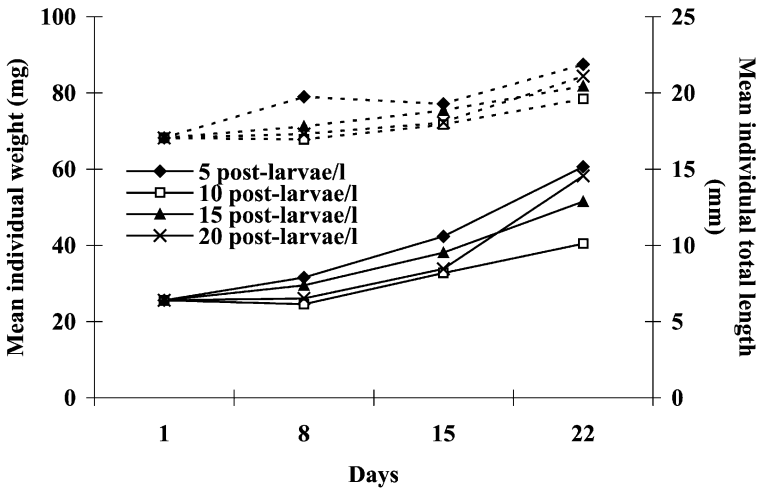


Fig. 6. Mean individual weight (solid lines) and total length (broken lines) of sea bass post-larvae kept in four different stocking densities.

could not be used for the calculation of feed intake. In the samples taken on day 8, no significant relation ($P > 0.05$) was found between density and feed intake. It is worth noting that a high percentage (64.7%) of unfed fish was noticed in the lowest stocking density (5 post-larvae l^{-1}). No such phenomenon was observed in the stocking densities of 10 and 20 post-larvae l^{-1} (30% and 45% of unfed fish, respectively). On day 22, feed

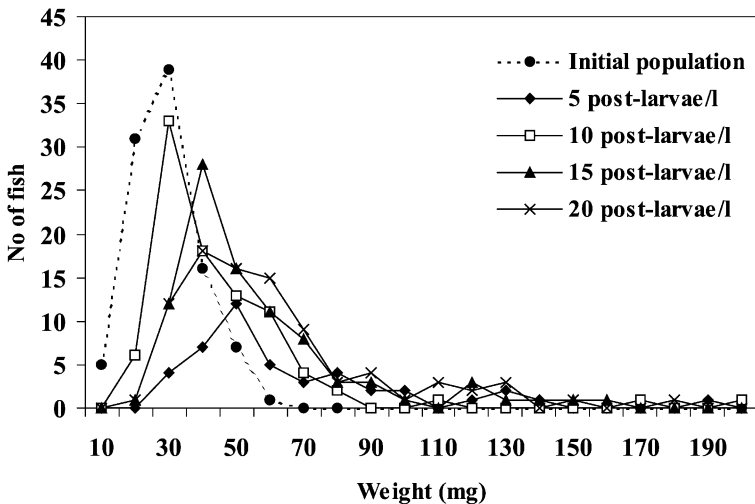


Fig. 7. Individual weight distribution of sea bass post-larvae kept in four different stocking densities. Broken line refers to the distribution of the overall initial population and solid lines to the distribution of the respective post-larval populations at the end of the experimental period.

intake and relative feed intake increased with stocking density, although this relation was not significant ($P > 0.05$). Inter-individual coefficient of variation for feed intake and inter-individual coefficient of variation for relative feed intake decreased non-significantly with density ($P > 0.05$).

4. Discussion

The present study shows that the stocking densities examined did not affect the survival of sea bass larvae. The observed mortality was likely due to the adaptation to exogenous diet. Sea bass larvae do not consume exogenous food as soon as their mouths open (Deplano et al., 1991). Their growth is supported by the assimilation of oil globule reserves progressively replaced by continuously larger amounts of live prey. The rate of oil globule assimilation depends on the quality and quantity of prey consumed (Divanach and Kentouri, 1983). In the present study, the maximum mortality recorded during the larval stage from days 6 to 10 of exogenous feeding seems to be due to the exhaustion of energy resources because of unknown reasons as already stated by Person Le Ruyet et al. (1993). Daily observations of dead fish showed that most of them had empty stomachs even if plenty of food had been added hourly during daylight. Others had intact oil globules.

After day 10, larval development was based only on exogenous food. Larvae fed efficiently and their mortality rate decreased significantly. Dead fish were found mainly with empty stomachs and sly with swim bladder hypertrophy. No cannibalistic behaviour of sea bass larvae was observed and no signs of cannibalistic attacks were deducted from the dead fish collected daily. No cannibalistic attack was recorded in the larvae of other species such as red porgy, *Pagrus pagrus*, (Stephanou et al., 1995) and marine silverside, *Odontesthes argentinensis* (Sampaio and Phonlor, 1996), but it was not the rule as larval cannibalism was described in Koi carp, *Cyprinus carpio* (Van Damme et al., 1989) and vundu, *Heterobranchus longifilis* (Baras, 1999). Missing fish calculated at the end of the experiment were probably the result of disintegration.

At the end of larval rearing, mean total length, growth rate, body weight and coefficient of weight variation were similar in all treatments, indicating that stocking density was not a limiting factor during the intensive larval rearing period. Similar findings were recorded in other reared species (Kaiser et al., 1995; Duray et al., 1996; Sampaio and Phonlor, 1996; Baskerville-Bridges and Kling, 2000). The applied rearing methodology (Divanach et al., 1998) on sea bass larvae seemed reliable and not limited by high stocking densities. Population weight distribution was similar in all treatments throughout the larval period.

In sea bass post-larvae, survival was strongly affected by stocking density. Results revealed that survival significantly improved at the densities of 5 and 10 post-larvae l^{-1} . Cannibalism was identified as the most important factor inducing mortality during this stage. It was dependent on the population density, increasing drastically during the transition period from live to artificial feed. Timing of transition in rearing and its effects on mortality and cannibalism have already been described for other species (Paller and Lewis 1987; Folkvord, 1991). Daily observations showed that all dead fish removed from

the rearing tanks over the experimental period had been cannibalised. The increased mortality recorded in the first 5 days of this experiment was probably due to the adaptation of the fish to experimental conditions. The second increment was observed after complete weaning when live food was totally replaced by artificial dry food.

Sea bass post-larvae exhibited two types of cannibalism: (I) attack and ingestion from the tail and (II) attack and whole ingestion from head. At the beginning of the experiment, most of the cannibalised fish were damaged in the caudal fin and a few days later, they were half eaten from the tail to the body. In the last week of the experiment, as the differences in size increased, prey were caught from the head and completely ingested and digested by the largest fish of each population. The shift from the first to the second type was achieved when the predators reached a capable size and capture ability to consume their prey's head. Once begun, cannibalism continued even after food was given. Two types of cannibalism were also distinguished during the early life stage of African catfish *Clarias gariepinus* (Hecht and Appelbaum, 1988), Koi carp (Van Damme et al., 1989) and vundu (Baras, 1999). Literature relating to cannibalism in the early life stages of sea bass is extremely poor. Katavic et al. (1989) examined the cannibalism among sea bass fingerlings and found a head-first cannibalism, which could be considered as the second step in our findings. In contrast to the present study, the above authors recorded that heavy damage to caudal fins was not a typical sign of cannibalism. Rather, they identified large individuals with expanded abdomens or, more frequently, swimming with smaller-size prey caught by head and half swallowed as presence of cannibals.

Present results revealed that the density of 10 post-larvae l^{-1} negatively affected the growth rates in weight and length. Population weight distribution indicated that the frequency of smaller fish increased in this fish group compared to the other groups. It is not clear why this intermediate density influenced fish growth although in other species such as Macquarie perch, *Macquaria australasica* (Sheikh-Eldin et al., 1997), similar densities presented the best growth. It is known that density reduces fish growth due to social interactions (mainly dominance), but in some species, very high densities in larval stages (Macintosh and De Silva, 1984) or larger fish (Jobling, 1995) have the opposite effect. In the present study, fish groups up to the density of 10 post-larvae l^{-1} followed the principle of negative correlation between density and growth performance, but the higher densities of 15 and 20 post-larvae l^{-1} seemed to promote fish growth. Coefficient of weight variation merely supports these findings. The tendency of higher CV in the density of 10 post-larvae l^{-1} was expected to increase population interactions.

Feed intake in post-larvae was not affected by stocking density though there was a non-significant positive relation between these two parameters. In all cases, individual feed intake variation was very high. The percentage of unfed individuals in density 5 post-larvae l^{-1} increased in the beginning (on day 8) compared to the other groups, but this difference was not found later on (on day 22).

In conclusion, this study showed the different rearing response of larvae and post-larvae of sea bass held in different stocking densities. Larval stage was independent of density as growth and survival rates were similar in all groups. No cannibalism appeared. Post-larval stage was negatively affected by stocking density. Cannibalism was the main cause of death in this stage. The way of catching prey changed from tail-first to head-first. Ten individuals per liter was the critical density for decreasing growth rate of post-larvae.

Acknowledgements

We would like to thank L. Anezaki, V. Bengoa for their assistance in the maintenance of fish populations during the trials, and M. de Wilde for her contribution to the English manuscript. This study has been carried out with financial support from the Commission of the European Union, Agriculture and Fisheries (FAIR) specific RTD programme CT96-1572. It does not necessarily reflect its view and in no way anticipates the Commission's future policy in this area.

References

- Barahona-Fernandes, M.H., 1979. Some effects of light intensity and photoperiod on the sea bass larvae (*Dicentrarchus labrax* (L.)) reared at the Centre Oceanologique de Bretagne. *Aquaculture* 17, 311–321.
- Barahona-Fernandes, M.H., 1981. Problèmes liés au sevrage du bar (*Dicentrarchus labrax*): 1. Influence de la charge dans le bac de sevrage. *La Piscic. Fr.* 65, 5–7.
- Baras, E., 1999. Sibling cannibalism among juvenile vundu under controlled conditions: I. Cannibalistic behaviour, prey selection and prey size selectivity. *J. Fish Biol.* 54, 82–105.
- Baras, E., Tissier, F., Philippart, J.-C., Mélard, C., 1999. Sibling cannibalism among juvenile vundu under controlled conditions: II. Effect of body weight and environmental variables on the periodicity and intensity of type II cannibalism. *J. Fish Biol.* 54, 106–118.
- Baskerville-Bridges, B., Kling, L.J., 2000. Larval culture of Atlantic cod (*Gadus morhua*) at high stocking densities. *Aquaculture* 181, 61–69.
- Bergot, P., Charlon, N., Durante, H., 1986. The effect of compound diets feeding on growth survival of coregonid larvae. *Arch. Hydrobiol., Beih. Ergeb. Limnol.* 22, 265–272.
- Boglione, C., Marino, G., Fusari, A., Ferreri, F., Finioia, M.G., Cataudella, S., 1995. Skeletal anomalies in *Dicentrarchus labrax* juveniles selected for functional swimbladder. *ICES Mar. Sci. Symp.* 201, 163–169.
- Cahu, C.L., Zambonino Infante, J.L., 1994. Early weaning of sea bass (*Dicentrarchus labrax*) larvae with a compound diet: effect on digestive enzymes. *Comp. Biochem. Physiol.* 109, 213–222.
- Cerqueira, V.R., Chatain, B., 1991. Photoperiodic effects on the growth and feeding rhythm of european sea bass, *Dicentrarchus labrax*, larvae in intensive rearing. In: Lavens, P., Sorgeloos, P., Jaspers, E., Ollevier, F. (Eds.), Larvi '91-Fish and Crustacean Larviculture Symposium. Gent, Belgium, EAS Spec. Publ. No. 15, pp. 304–306.
- Chatain, B., 1994. Abnormal swimbladder development and lordosis in sea bass (*Dicentrarchus labrax*) and sea bream (*Sparus aurata*). *Aquaculture* 119, 371–379.
- Deplano, M., Diaz, J.P., Connes, R., Kentouri-Divanach, M., Cavalier, F., 1991. Appearance of lipid absorption in larvae of the sea bass *Dicentrarchus labrax* during the exotrophic phase. *Mar. Biol.* 108, 361–371.
- Divanach, P., Kentouri, M., 1983. The influence of initial trophic condition on oil globule resorption, growth and survival of gilt head sea bream *Sparus aurata* larvae in extensive breeding. *Aquaculture* 35, 43–55.
- Divanach, P., Kentouri, M., 2000. Hatchery techniques for specific diversification in Mediterranean finfish larviculture. *Cah. Options Mediterr.* pp. 1–12.
- Divanach, P., Papandroulakis, N., Anastasiadis, P., Koumoundouros, G., Kentouri, M., 1997. Effects of water currents on the development of skeletal deformities in sea bass (*Dicentrarchus labrax* L.) with functional swimbladder during postlarval and nursery phase. *Aquaculture* 156, 145–155.
- Divanach, P., Papandroulakis, N., Kentouri, M., 1998. Bases techniques de l'élevage larvaire de la daurade (*Sparus aurata*). *La Piscic. Fr.* 134, 61–69.
- Duray, M.N., Estudillo, C.B., Alpasan, L.G., 1996. The effect of background color and rotifer density on rotifer intake, growth and survival of the grouper (*Epinephelus suillus*) larvae. *Aquaculture* 146, 217–224.
- Folkvord, A., 1991. Growth, survival and cannibalism of cod juveniles (*Gadus morhua*): effects of feed type, starvation and fish size. *Aquaculture* 97, 41–59.

- Hecht, T., Appelbaum, S., 1988. Observation on intraspecific aggression and coeval sibling cannibalism by larval and juvenile *Clarias gariepinus* under controlled conditions. *Zoology* 214, 21–44.
- Jobling, M., 1995. Feeding of charr in relation to aquaculture. *Nord. J. Freshwater Res.* 71, 102–112.
- Kaiser, H., Weyl, O., Hecht, T., 1995. The effect of stocking density on growth, survival and agonistic behaviour of African catfish. *Aquacult. Int.* 3, 217–225.
- Katavic, I., Jug-Dujakovic, J., Glamuzina, B., 1989. Cannibalism as a factor affecting the survival of intensively cultured sea bass (*Dicentrarchus labrax*) fingerlings. *Aquaculture* 77, 135–143.
- Kestemont, P., Fioqbe, E.D., Parfait, O., Micha, J.C., Mélard, C., 1995. Relationship between weaning size, growth, survival and cannibalism in the common perch larvae, *Perca fluviatilis*: preliminary data. In: Lavens, P., Jaspers, E., Roelants, I. (Eds.), Larvi'95. Fish and Shellfish Larviculture Symposium. Ghent, Belgium, EAS Spec. Publ. No. 24, pp. 285–288.
- Macintosh, D.J., De Silva, S.S., 1984. The influence of stocking density and food ration on fry survival and growth in *Oreochromis mossambicus* and *O. niloticus* female X *O. aureus* male hybrids reared in a closed circulated system. *Aquaculture* 41, 345–358.
- Mélard, C., Baras, E., Mary, L., Kestemont, P., 1996. Relationship between growth, cannibalism and survival rate in intensively cultured larvae and alevins of perch (*Perca fluviatilis*). *Ann. Zool. Fenn.* 33, 643–651.
- Mélard, C., Baras, E., Kestemont, P., 1997. Does low temperature rearing of Eurasian perch larvae (*Perca fluviatilis*) limit the incidence of cannibalism without significantly reducing growth rate. In: Crewell, L., Herache, Y. (Eds.), Proceedings of Martinique '97. Island Aquaculture and Tropical aquaculture. Oostende, Belgium, EAS, pp. 347–348.
- Moore, A., Prange, M., 1994. Influence of stocking densities on walleye fry viability in experimental and production tanks. *Prog. Fish-Cult.* 56, 194–201.
- Morrow Jr., J.V., Miller, G.L., Killgore, K.J., 1997. Density, size, and food of larval northern pike in natural and artificial wetlands. *North Am. J. Fish. Manage.* 17, 210–214.
- Paller, M.H., Lewis, W.M., 1987. Effects of diet on growth depensation and cannibalism among intensive cultured larvae striped bass. *Prog. Fish-Cult.* 49, 270–275.
- Person Le Ruyet, J., Alexandre, J.C., Thebaud, L., Mugnier, C., 1993. Marine fish larvae feeding: formulated diets or live prey? *J. World Aquacult. Soc.* 24, 211–224.
- Sakakura, Y., Tsukamoto, K., 1999. Ontogeny of aggressive behaviour in schools of yellowtail, *Seriola quinqueradiata*. *Environ. Biol. Fishes* 56, 231–242.
- Sampaio, L.A., Phonlor, G., 1996. Effects of stocking density on growth and survival of the marine silverside, *Odontesthes argentinensis* (Pisces: Atherinidae), larvae. *Arq. Biol. Tecnol.* 39, 443–449.
- Schreck, C.B., 1981. Stress and compensation in teleostean fishes; response to social and physical factors. In: Pickering, A.D. (Ed.), *Stress and Fish*. Academic Press, London, pp. 295–321.
- Sheikh-Eldin, M., De Silva, S.S., Ingram, B.A., 1997. Effects of diets and feeding rate on the survival and growth of Macquarie perch (*Macquaria australasica*) larvae, a threatened Australian native fish. *Aquaculture* 157, 35–50.
- Stephanou, D., Georgiou, G., Shoukri, E., 1995. Reproduction and larval rearing of the common sea bream (*Pagrus pagrus*), an experimental culture. Proceedings of the seminar of the CIHEAM Network on Socio-economic and Legal Aspects of Aquaculture in the Mediterranean (SELAM), Zaragoza, Spain. *Cah. Options Mediterr.* 16, pp. 79–87.
- Van Damme, P., Appelbaum, S., Hecht, T., 1989. Sibling cannibalism in Koi carp, *Cyprinus carpio* L., larvae and juveniles reared under controlled conditions. *J. Fish Biol.* 34, 855–863.