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Embryonic and larval development of Corsican brown meagre, *Sciaena umbra* (Linnaeus 1758), rearing in captivity from the Mediterranean Sea

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Abstract
The brown meagre, *Sciaena umbra*, is a Sciaenid fish of patrimonial and fisheries interest in the Mediterranean and North East Atlantic. Sciaenids species are new to aquaculture and present high potential for aquaculture, demonstrating fast growth and an efficient feed conversion. Hence, this study documents early ontogeny from fertilized eggs to 40 days post-hatching (DPH) in order to assess the culture potential of brown meagre. Eggs were collected from spontaneous spawning of captive broodstocks and incubated at 18.5 ± 0.5 °C and 38 ppt of salinity for about 42 h post fertilization (hpf). Fertilized eggs were pelagic, transparent, and spherical, measuring 1.254 ± 0.026 mm. The eggs were characterized by a narrow perivitelline space, smooth and thin chorion and carried a non-segmented yolk with a single lipid globule. Embryonic development consisted of four consecutive periods: the cleavage period (0–2:38 hpf), the blastula period (2:38–3:52 hpf), the gastrulation period (3:52–17:20 hpf), and the segmentation period (17:20–41:20 hpf). Thereafter, the eggs hatched (41:20–43:20 hpf) into yolk sac larvae, measuring from 3.139 ± 0.132 mm (total length, TL). Larval development of brown meagre was divided into four periods: yolk sac until complete absorption (0–3 DPH, $TL_{3DPH} = 3.649 \pm 0.119$ mm), pre-flexion (4–14 DPH, $TL_{14DPH} = 4.996 \pm 0.300$ mm), flexion (15–17 DPH, $TL_{17DPH} = 5.387 \pm 0.381$ mm), and post-flexion (18–35 DPH, $TL_{35DPH} = 16.450 \pm 1.012$ mm). After 35 DPH, the larval metamorphosis was complete as larvae were transformed into juveniles. Our results emphasize the high potential of brown meagre for aquaculture either in restocking programs or mariculture projects.

Keywords Sciaenidae · *Sciaena umbra* · Embryogenesis · Larval development · Aquaculture

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Introduction

The brown meagre (*Sciaena umbra,* L. 1758), is a member of the Sciaenidae family (croakers and drums) encompassing 70 genera and 270 marine, brackish, and freshwater species distributed worldwide (Nelson et al. 2016). The brown meagre is a coastal nectobenthic fish species present from the eastern Atlantic Ocean (from the English Channel to Senegal, including the Canary Islands) to the Mediterranean Basin, the Black Sea, and Sea of Azov (Chao 1986). It is generally a sedentary and gregarious fish, gathering in schools, living in shelters on rocky bottoms, or hidden within seagrass meadows (Mayol et al. 2000; Grau et al. 2009). The adults are found in inshore waters down to about 180 m depth, while juveniles, more cryptic, seem to inhabit shallower habitats (0–30 m depth; Harmelin 1991; Grau et al. 2009). This gonochoristic species reaches sexual maturity at age 3 to 4 years, equivalent to 20–30 cm of total length (TL) (Chakroun-Marzouk and Ktari, 2003; Grau et al. 2009; Harmelin-Vivien et al. 2015) and spawning occurs during the summer, between May and August (Fiorentino et al. 2001; Ragonese et al. 2002; Grau et al. 2009).

Brown meagre is a valuable commercial fish species in the Mediterranean harvested by artisanal fishery using gill net and trammel net. It does not constitute an important component of the catches except for Southern and Eastern regions (i.e., Algeria, Tunis, Egypt, Turkey) (Harmelin 1991; Chakroun et al. 1982). One of the main fishing pressures on brown meagre is recreational fishing through spearfishing. Currently, due to its biological and behavioral characteristics, the brown meagre is considered a near threatened species (IUCN red list for the Mediterranean) (Chao 2020) for which protection measures have been proposed (Harmelin 1991; Mayol et al. 2000). The brown meagre can therefore be the object of fishing regulations, for instance in France there is a regulation banning recreational fishing on since 2013.

Sciaenids are generally considered efficient aquaculture species because they prove to be relatively easy to raise considering their high fecundity, their fast growth rate, their high food conversion rate, their adaptation to salinity variations, and the quality of food preservation on the market (Silberschneider and Gray 2008). Thus, the rearing of brown meagre could provide a source of commercial food as well as could support conservative actions of enhancement and restocking.

In aquaculture, gathering knowledge of the early development of a species is a main issue to understand physiological features and to provide useful clues for developing rearing techniques (Divanach et al. 1996). For example, developing accurate knowledge is an essential prerequisite to detect and remove early morphological abnormalities that can be common under rearing conditions and, hence, can significantly reduce the effectiveness of hatcheries. Furthermore, a detailed knowledge of the early development of a species is very important also for fisheries biology and aquaculture and not only from the embryological point of view. For example, the identification of the early life stages in ichthyoplankton surveys is based on a developmental series of specimens, particularly in the case of families or species with close morphology and overlapping spawning seasons and habitat (Blaxter 1984).

Despite its potential aquaculture value, the early development of brown meagre is poorly documented, except for Chatzifotis et al. (2006) who documented brown meagre growth under culture conditions using different diets and for Hamzaçebi and Can (2021) who investigated larval rearing using green water technique. The majority of related studies describe a few biological features of brown meagre into the wild such as the reproductive biology, age and growth, the diet, or movements (Harmelin 1991; Chakroun-Marzouk

and Ktari 2003; Derbal and Kara 2007; Grau et al. 2009; Alós and Cabanellas-Reboredo 2012). Until this work, current articles were carried out on other Scianidae species such as shi drum *Agyrosomus hololepidotus* (Battaglene and Talbot 1994), mulloway *Argyrosomus japonicas* (Musson and Kaiser 2014), *Atractoscion nobilis* (Orhun 1989; Moser et al. 1983), and meagre *Argyrosomus regius* (Pastor et al. 2013).

The aim of this study is to provide a detailed documentation of brown meagre embryonic development and to characterize its early life stages. Knowledge regarding the embryonic and larval development metamorphosis is essential to develop appropriate and specific techniques and procedures in aquaculture production. To this end, our experiment investigated the embryonic and larval development of brown meagre under hatchery conditions where, first, eggs were fertilized and hatched under artificial conditions and then, larvae were reared and fed in captivity until the juvenile stage.

Material and methods

Broodstock maintenance

The eggs used in this study were obtained by spontaneous spawning of the broodstocks kept in captivity at the Stella Mare platform (In Corsica Northwestern Mediterranean). The broodstock was composed of seventeen wild breeders captured between 2018 and 2019 (4 females: 775.5 ± 375.0 g; 13 males: 714.8 ± 265.9 g (mean ± SD)) and stocked under natural photoperiod and temperature condition in a 12 m^3 circular tank connected to a recirculation unit. Dry fish food, frozen shrimp (*Penaeus notialis*), and frozen clam (*Ruditapes philippinarum*) were provided three times a week as primary food source. To collect the eggs immediately after fertilization, the collector was checked every 2 min between 1 h before and after sunset. Following the spawning, buoyant (viable) eggs were collected from the collector with 100 µm net; dead sinking eggs were used later for the egg viability value.

Eggs incubation conditions

Fertilized eggs were collected and incubated, immediately after spawning, in complete darkness into two 0.2 m^3 black cylindrical-conical tanks connected to an open circulation system (10–15% water exchange per day) with initial concentration of 170 eggs·L^{-1}. During incubation, water temperature was 18.5 ± 0.5 °C, oxygen saturation was over 80%, salinity was 38 ppt, pH was around 7.1 ± 0.2, and ammonia never exceeded 0.05 mg·L^{-1}.

Larval rearing

After hatching, larvae were transferred into two 0.2 m^3 black cylindrical-conical tanks at a density of 150 larvae·L^{-1}. During larval rearing, tanks connected in a semi closed circuit were supplied from 10 to 50% of filtered seawater. Water temperature was 20 ± 1 °C, oxygen saturation ranged from 65 to 95%, salinity remained stable at 38 ppt, pH was 7.1 ± 0.2, and ammonia never exceeded 0.05 mg·L^{-1}. Illumination was first set up on dark until 3 days post-hatching (DPH), and then, supplied by white led power at 30 lx for 10 h a day until 40 DPH. From day 4, food was supplied into the larval tank and food size was adjusted gradually in accordance with the fish development, from micro-diet to small

crustaceans (Gemma micro 75 grain size 50–100 µm; Gemma micro 150 (100–200 µm); Gemma micro 300 (200–500 µm); Gemma wean 0.3 (350–500 µm); and Gemma wean 0.5 (500–800 µm) SKRETTING, France)). Brown meagre were fed with both dry food and living food. Living food concentration was adjusted two to six times a day: (i) *Artemia* nauplii were supplied from the 7 to 20 DPH, (ii) *Artemia* enriched metanauplii were used from 18 to 30 DPH.

Sampling

During embryonic stages, subsamples of eggs ($n = 10$) were randomly collected from the tank every hour into a beaker (1 L). Eggs were characterized and photographed every 15 min during the first 24 h and every hour thereafter under a ZEISS Discovery V.20 stereomicroscope coupling with a color video camera Sony XCD-U100CR. The embryonic stages of eggs were identified using Kimmel et al. (1995). Next, the diameters of eggs and lipid globules ($n = 100$) were measured based on the photographs using an image-analysis system (ImageJ software, *v.1.52*). Based on these diameters, the volume of eggs and lipid globules were estimated, using the equation of the sphere $(4/3)\ \pi\ (LD/2)^3$.

During larval stage, subsamples of larvae ($n = 10$) were randomly collected from the tank into a beaker (1 L) every day from 0 to 15 DPH and then, at 17, 20–21, 23, 25–26, 30, 35, and 40 DPH. All samples of larvae were first anaesthetized (ethylenglycol-monophenylether), then observed and photographed under a ZEISS Discovery V.20 stereomicroscope coupling with a color video camera Sony XCD-U100CR. Early life stages of brown meagre were characterized according to Kendall et al. (1984) and separated into five stages I: yolk sac larva, II: pre-flexion larva, III: flexion larva, IV: post-flexion larva and V: juvenile. Next, larvae were measured using an image-analysis system (ImageJ software, *v.1.52*). Four measurements were made on brown meagre larvae: the total length (TL), yolk sac length, width and lipid globule diameter.

Data analysis

The growth pattern during the developmental stages of brown meagre was estimated as power function of the TL (Fuiman 1983; Koumoundouros et al. 1999; Peña and Dumas 2009) using log-transformed data: $TL = a.e^{SGR-DPH}$ (Gisbert et al. 2002), where TL is the mean total length of each sample of 10 larvae (mm), a is the TL at the onset of the stage occurring (mm), SGR is the specific growth rate (d^{-1}), and DPH the number of days post hatch.

Results

Brown meagre eggs

Newly released and fertilized eggs

Details of embryonic development stages of brown meagre, *S. umbra*, are given in Table 1 and Figs. 1 and 2. The fertilization rate and hatching rate of *S. umbra* eggs were 95% and 64%, respectively. The newly released and fertilized eggs of brown meagre

Table 1 Embryonic development of *Sciaena umbra* at 18.5 °C

Development stage	Time post fertilization	Characteristics	Figure
Zygote period			
1 cell	30 min	One-cell stage, cytoplasm accumulated at animal pole and forms the blastodisc	a
Cleavage period			
2 cells	50 min	First mitotic division, blastodisc divided via meridional cleavage to form two equal blastomeres	b
4 cells	1 h 15 min	Second cleavage, blastodisc divided into four blastomeres arranged horizontally	c
8 cells	1 h 37 min	Third cleavage, division parallel to the second to form eight blastomeres	d
16 cells	1 h 58 min	4th cleavage, 16 blastomeres	e
32 cells	2 h 19 min	5th cleavage, 32 blastomeres	f
64 cells	2 h 38 min	Sixth cleavage, 64 blastomeres and the end of the cleavage period	g
Blastula period			
128 cells	2 h 59 min	Early blastula period (5 tiers of blastomeres)	h
256 cells	3 h 18 min	Blastomeres continued to divide but they were less synchronously and between the periblast the yolk syncytial layer was discernible (7 blastomere tiers)	i
512 cells	3 h 34 min	Yolk syncytial layer more visible (9 blastomere tiers)	j
1024 cells	4 h 30 min	11 tiers of blastomeres	k
High stage	5 h 20 min	The end of period during which the blastodisc perches « high» upon the yolk cell (> 11 tiers of blastomeres)	l
Dome or start gastrulation	8 h 15 min	Yolk cell bulging toward animal pole as epiboly begins	m
Gastrula period			
30% epiboly	10 h 20 min	Epiboled 30% of yolk sac	n
Germ ring	11 h 20 min	Germ ring visible from animal pole	o
50% epiboly	12 h 29 min	Epiboled 50% of yolk sac	a
60% epiboly	13 h 26 min	Epiboled 60% of yolk sac and beginning the neurulation	b
80% epiboly	14 h 25 min	Epiboled 80% of yolk sac	c
Bud stage	16 h 34 min	Vitelline cell completely covered by the blastoderm	d

Table 1 (continued)

Development stage	Time post fertilization	Characteristics	Figure
Segmentation period			
4 somites	17 h 20 min	Beginning of the segmentation, optic vesicle was clearly visible	e
5 somites	18 h 20 min	Kupffer's vesicle and pigmentation appeared	f
11 somites	21 h 20 min	Heart appeared	g
14 somites	23 h 20 min	The formation of the primordial fin	h
15 somites	24 h 20 min	Kupffer's vesicle disappeared, lenses appeared	i
19 somites	27 h 20 min	First muscle contraction observed in embryos, otic vesicle appeared	j
Heartbeat	28 h 20 min	Weak heartbeat observed	k
Embryo 3/4	30 h 20 min	Embryo occupied approximately 3/4 of the vitellus circumference	l
Increasing pigmentation	35 h 20 min	The pigmentation expanded	m
Hatching period			
Start hatching (20%)	41 h 20 min	Embryo began to spin	n
End hatching (100%)	43 h 20 min	Newly hatched larvae with a huge yolk sac, a single lipid globule	o

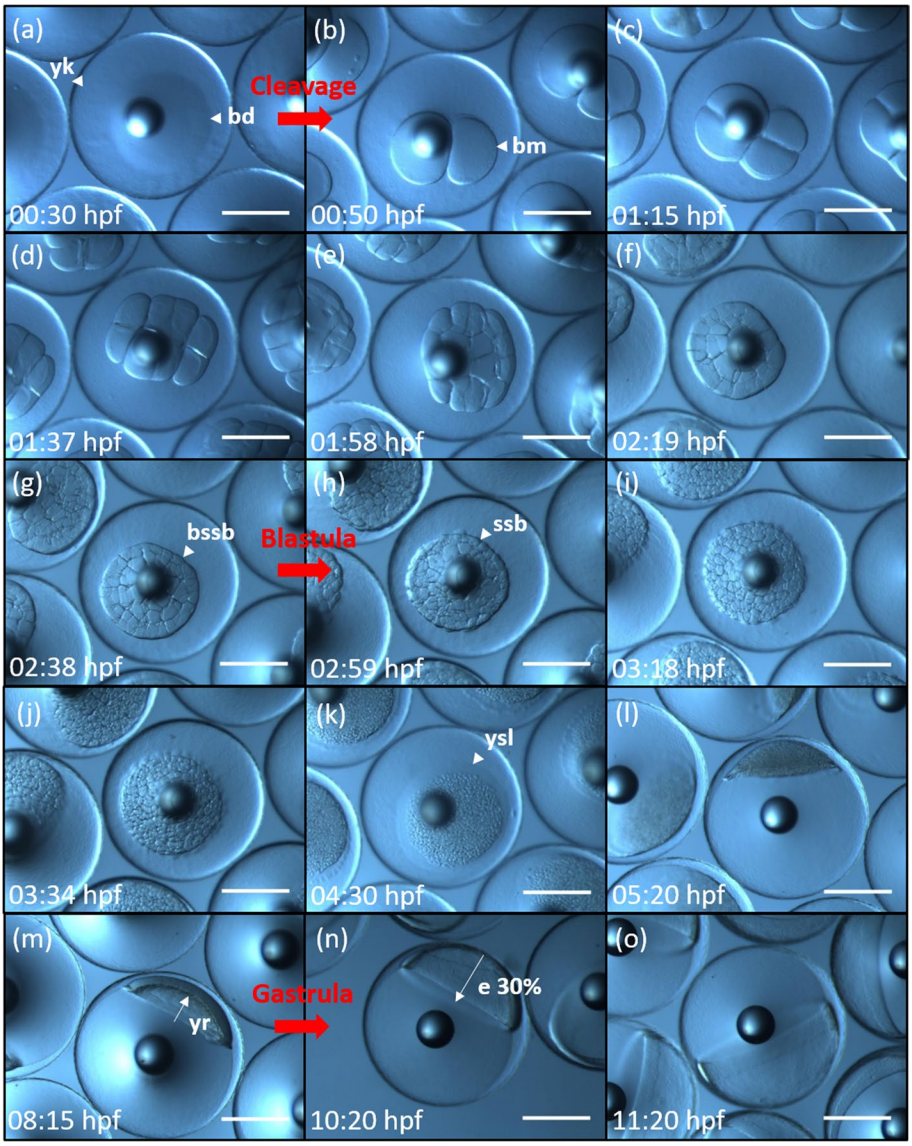


Fig. 1 *Sciaena umbra* embryonic developmental stages at 18.5 °C. hpf, hours post fertilization. Scales 500 micron (×50). (**a**) 1-cell stage; (**b**) 2-blastomere stage; (**c**) 4-blastomere stage; (**d**) 8-blastomere stage; (**e**) 16-blastomere stage; (**f**) 32-blastomere stage; (**g**) 64-blastomere stage; (**h**) 128-blastomere stage; (**i**) 256-blastomere stage, (**j**) 512-blastomere stage; (**k**) 1024-blastomere stage; (**l**) high stage; (**m**) dome or start gastrulation; (**n**) 30% epiboly; (**o**) germ ring. bd, blastodisc; bm, blastomere; bssb, beginning spherical shape blastodisc; e 30%, epiboly 30%; ssb, spherical-shape blastodisc; yr, yolk rise in animal pole; ysl, yolk syncytial layer. The red arrows indicate the transition periods

exhibited a transparent outer shell, a spherical structure, a homogenous (unsegmented) vitellus that fills the shell completely and a smooth and thin chorion. Fertilized eggs had a diameter of 1.254 ± 0.026 mm (mean ± SD), with a volume of 1.033 ± 0.064 mm^3

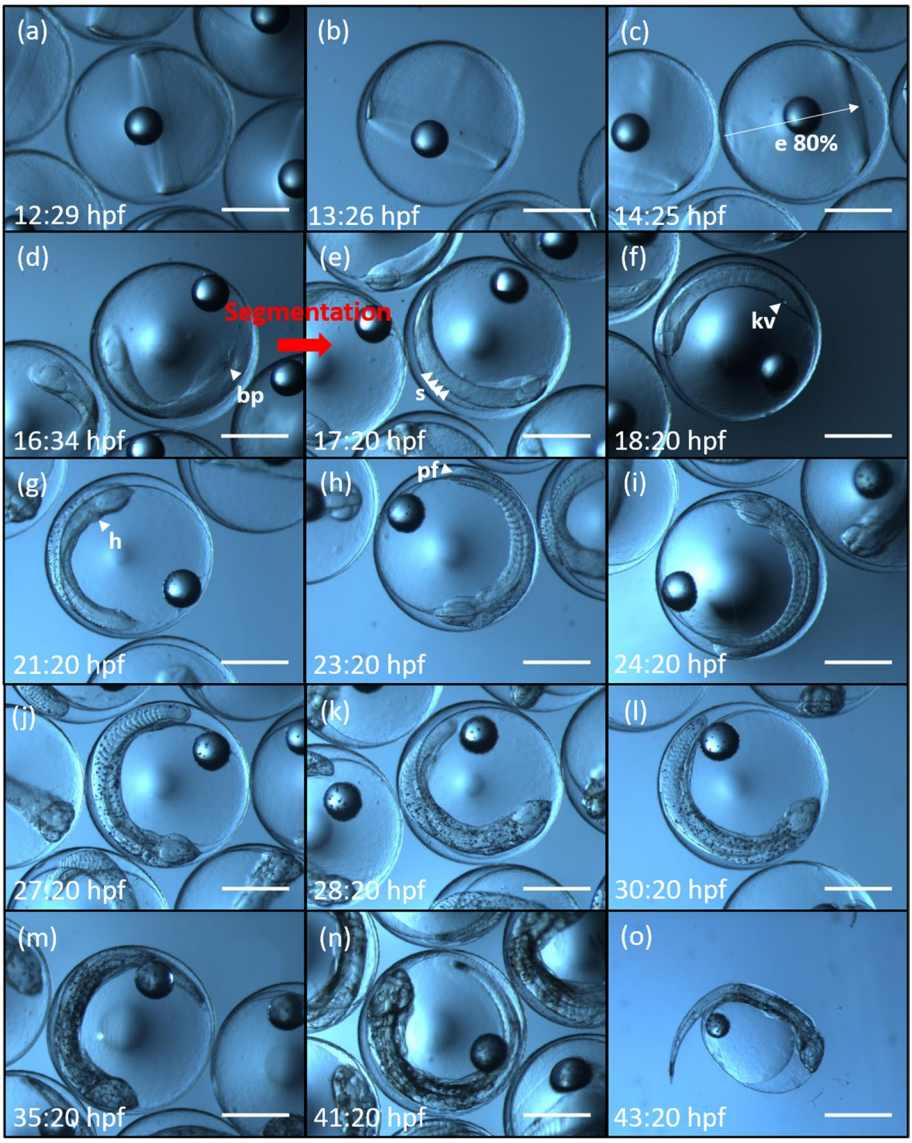


Fig. 2 *Sciaena umbra* embryonic developmental stages at 18.5 °C. hpf, hours post fertilization. Scales 500 micron (×50). (**a**) 50% epiboly; (**b**) 60% epiboly; (**c**) 80% epiboly; (**d**) bud stage; (**e**) 4-somite embryo stage; (**f**) 5-somite embryo stage; (**g**) 11-somite embryo stage; (**h**) 14-somite embryo stage; (**i**) 15-somite embryo stage; (**j**); 19-somite embryo stage; (**k**) heartbeat stage; (**l**) embryo ¾ stage; (**m**) increasing pigmentation; (**n**) 20% hatching; (**o**) 100% hatching. bp, blastopore; e 80%, epiboly 80%; h, heart; kv, Kupffer's vesicle; pf, primordial fin; s, somites. The red arrows indicate the transition periods

($n = 100$). All newly fertilized eggs usually contained a single and unpigmented lipid globule positioned at the center of the egg. The mean diameter of the globule measured 0.278 ± 0.015 mm, i.e., a volume of 0.011 ± 0.002 mm^3. Unfertilized eggs were opaque and settled at the bottom.

The zygote period

At 00:30 h after fertilization (hpf), the fertilized egg initiated the zygote period until the first cleavage occurred (Fig. 1a). The one-cell zygote showed visible cytoplasmic movements. The formative cytoplasm began to accumulate toward the animal pole, forming the blastodisc and the perivitelline space. The accumulation of formative cytoplasm continued during early cleavage stages.

The cleavage period

The cleavage period is defined as the phase of embryogenesis consisting in a cascade of mitotic divisions from one-cell zygote egg until reaching the morula stage. During the cleavage period, the cells or blastomeres divided sequentially so, for each division, the cell numbers double until the blastodisc was formed of 64 cells (Fujimoto et al. 2004)**.** The telolecithal eggs of brown meagre exhibited meroblastic discoidal cleavage as the common pattern of other Teleost embryos. The first cleavage occurred 00:50 hpf, culminating in two large equal cells located at the animal pole (Fig. 1b). During the second cleavage of cells, the blastomere divided meridionally into four equal cells (01:15 hpf, Fig. 1c). During the third cleavage (01:37 hpf), we observed eight cells which were arranged horizontally in a 2×4 formation (Fig. 1d). During the fourth cleavage, the embryo was divided into 16 cells, arranged in 4×4 formation (01:58 hpf, Fig. 1e). The fifth cleavage took place at 02:19 hpf when the meridionally cleavage of blastoderm formed 32 cells. From this stage, the cell divisions pattern became irregular (Fig. 1f). At 02:38 hpf, the sixth cleavage led to the formation of 64 cells (i.e., morula stage) (Fig. 1g). Then, the next mitotic division led to the beginning of the blastula period.

The blastula period

The blastula period is the phase of embryogenesis when the blastodisc begins to look sphere-like in the animal pole (Fujimoto et al. 2004; Kimmel et al. 1995). This period began from the seventh cleavage when 128 cells were formed until the time of the onset of gastrulation (Fig. 1h). During the blastula period, important processes occurred: the yolk syncytial layer formation and the start of the epiboly (Kimmel et al. 1995). For brown meagre, it is more appropriate to use the term of "stereoblastula" as the blastula presented no clear cavity, contrasting to the usual blastula shape. Each stage was distinguished from the previous stage based on the tiers number of blastomere. We observed 128 cells and 5 blastomere tiers at 02:59 hpf (Fig. 1h), 256 cells and 7 blastomere tiers at 03:18 hpf (Fig. 1i). At 03:34 hpf, we observed 512 cells and 9 blastomere tiers and the yolk syncytial layer formation between the periblast border and the blastodisc border was already visible (Fig. 1j). At 04:30 hpf, we observed 1024 cells and 11 blastomere tiers (Fig. 1k). At 05:20 hpf, we observed more than 11 tiers of blastomeres corresponding to the end of the blastula period during which the blastodisc perches "high" upon the yolk cell. This shape is called the "high stage" (Fig. 1l). The blastula period was completed at 08:15 hpf when the yolk rises toward the animal pole to form the dome marking the beginning of epiboly (Fig. 1m).

The gastrula period

The gastrula period consists of a set of movements of cells which set up the layers of the embryo during morphogenesis. The start of involution defines the onset of gastrulation, starting at about 10:20 hpf for brown meagre. At this stage, the process of epiboly was still engaged leading to the blastoderm spreading and to the covering of nutritive cytoplasm (or yolk) approximately 30% (Fig. 1n). Then, the blastoderm approximately covered: 40% of the yolk at 11:20 hpf and the germ ring appeared clearly (Fig. 1o), 50% at 12:29 hpf (Fig. 2a), 60% at 13:26 hpf and neurulation began leading to the establishment of the neural plate (Fig. 2b). At 14:25 hpf, 80–90% of epiboly was achieved and the bit of uncovered yolk cell protruding in the vegetal pole formed a yolk plug (Fig. 2c). Blastoderm was thicker on the dorsal side compared to the ventral side. At 16:34 hpf, the yolk was fully covered, marking the end of epiboly (i.e., 100% of the epiboly) and the closure of the blastopore. This state of embryonic development was defined as the bud stage (Fig. 2d). At this stage, embryos presented a thickened neural plate along the embryonic axis which was more prominent in the animal pole where the head will form. The bud stage marked the end of gastrulation stage and the onset of the segmentation period.

The segmentation period

The segmentation period consists of a wide variety of morphogenetic movements related to the establishment of the somites, the rudiments of the primary organs, the tail-bud development and the elongation of embryo (Kimmel et al. 1995). Thus, the appearance of the somites marked the beginning of the segmentation period during which process of somitogenesis continued until hatch. For brown meagre, the segmentation period began at 17:20 hpf with the closure of the blastopore and the development of four pairs of somites located in the middle of the future vertebral column (Fig. 2e). At this state, the embryo occupied approximately half of the circumference of the vitellus and the contrast between the cephalic and caudal tail regions of the embryonic axis became clearer. Furthermore, the optic vesicle appeared for the first time as two rounded vesicles located in the cephalic region. The first signs of embryonic pigmentation appeared after 18:20 hpf at the dorsal anterior of the body (Fig. 2f). At this state, we also observed five pairs of somites and the Kupffer's vesicle near the base of the tail. After 21:20 hpf, embryos were characterized by 11 pairs of somites, pigments on the lipid globule and the heart first appeared (Fig. 2g). At 23:20 hpf, embryos displayed 14 pairs of somites and first signs of the primordial fin (Fig. 2h). After 24:20 hpf, the lenses vesicles were formed and the Kupffer's vesicle disappeared (Fig. 2i). About 27:20 hpf, the muscle contraction of embryos was observed for the first time (Fig. 2j). At this state, the otic vesicle emerged and held pairs of otoliths in the posterior position of the optic primordium. At 28:20 hpf, the rudimentary heart displayed peristaltic movements, which promoted the axial artery dilation, suggesting that the embryos were on the verge of hatching (Fig. 2k). At 30:20 hpf, the embryo was surrounded approximately by three quarters of the circumference of the vitellus (Fig. 2l). Just before hatching, the embryo pigmentation and size developed until the embryo was integrally surrounded by the circumference of the vitellus (Fig. 2m). The hatching of brown meagre eggs occurred from 41:20 hpf to 43:20 hpf. The spontaneous myotomal contractions produced dechorionation responsible for the hatching (Fig. 2n and o).

Brown meagre larvae

Complete exogenous feeding

At 0 DPH, the average length of yolk sac was 1.257 ± 0.070 mm. From 0 to 1 DPH, the average length of yolk sac was halved: 0.586 ± 0.032 mm, decreasing to 0.430 ± 0.062 mm at 2 DPH until the sac was completely resorbed at 3DPH. Similarly, the average length of lipid globule was 0.269 ± 0.010 mm at 0 DPH, 0.127 ± 0.015 mm at 4 DPH, and completely absorbed at 7 DPH (Table 2).

Larval development

The onset of hatching initiated from 41:20 hpf and all larvae were hatched in the 2 h following. TL of newly hatched larvae was 3.139 ± 0.132 mm ($n = 10$). Brown meagre larvae floated in the surface layer and were transparent, laterally compressed and initially elongated (Fig. 3a). Larvae were characterized by a huge ovoid yolk sac extending from the tip of the snout to the middle of the body which usually contained a single lipid globule pigmented located at the posterior end of the yolk sac. Thus, at this early stage, brown meagre larvae fed exclusively on endogenous reserve of nutrients containing in the yolk sac and lipid globule. Newly hatched larvae were primitive and surrounded by a transparent primordial fin. This primordial fin extended from the dorsal part of the head to the ventral limit of the stomach and was cut locally at the anus. Yolk sac larvae of brown meagre showed unpigmented eyes and both mouth and anus were closed. Besides, the acoustic vesicles were distinguished regarding the held otoliths forming two blackish spots. At the yolk sac stage, the digestive tract was still an undifferentiated tube and the notochord straight. The yolk sac larvae had a pigmentary pattern, with dentritic melanophores distributed on the ventral surface from the back of the eye to the anus, distributed on the head, thus at notochord tip. Also, three characteristic spots appeared on the 1–3 somites, at 9–11 somites and 21–22 somites.

At one-day post hatching (1 DPH), the average TL was 3.575 ± 0.076 mm and their yolk sacs were still resorbing, represented 20% of the TL of larvae (Fig. 3b). The pectoral fin bud began to form by 24 h of post-hatch but remained difficult to observe because of its transparence, except from ventral and dorsal viewing angle. One-day larvae showed first retinal pigmentation and both mouth and anus remained closed. Their digestive systems

Table 2 Consumption of the yolk sac and lipid globule (mean ± SD) in *Sciaena umbra* reared at 20 °C

Days post-hatching	Yolk sac length (mm)	Lipid globule length (mm)
0	1.257 ± 0.070	0.269 ± 0.010
1	0.586 ± 0.032	0.236 ± 0.013
2	0.430 ± 0.062	0.217 ± 0.019
3	Yolk sac resorbed	0.178 ± 0.015
4	/	0.127 ± 0.015
5	/	0.100 ± 0.012
6	/	0.021 ± 0.035
7	/	Lipid globule resorbed

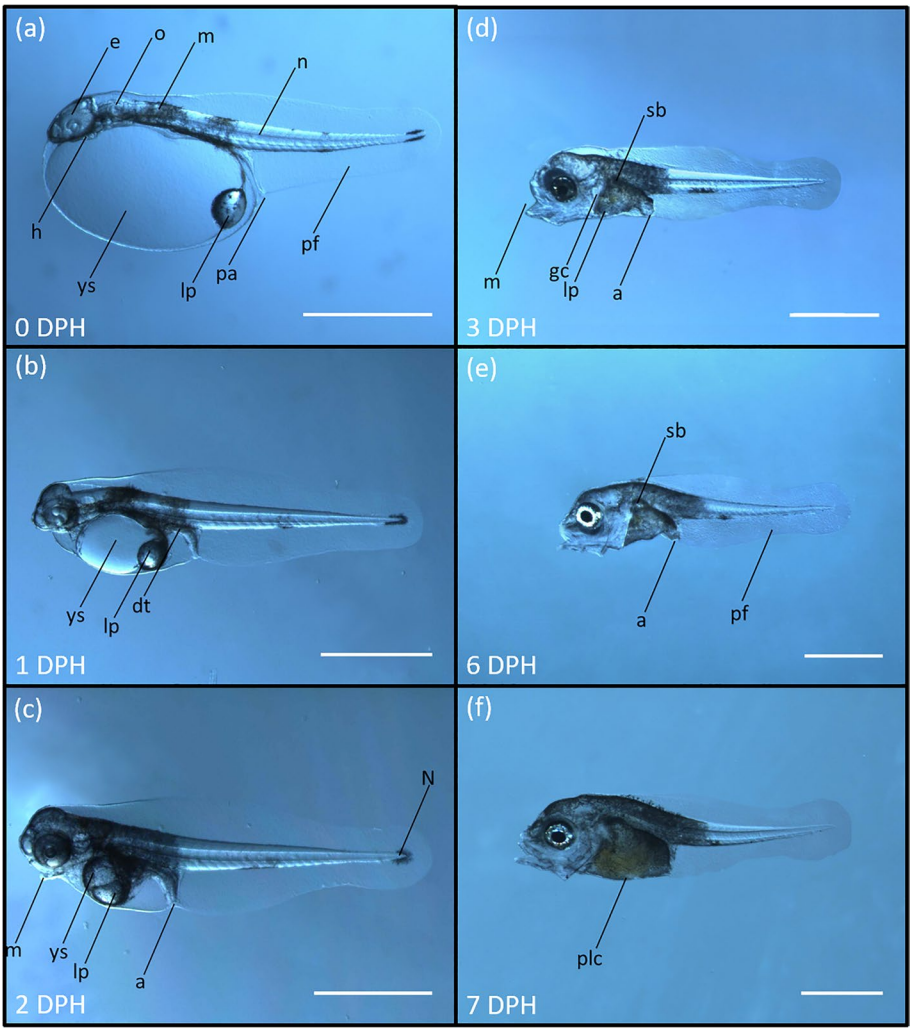


Fig. 3 *Sciaena umbra* larval developmental stages reared at 20 °C. DPH, days post-hatching. Scale 1 mm. (**a**) Larva (0 DPH, × 32), 2 h after hatching; (**b**) pigmentation started in the eyes and pectoral bud appeared (1 DPH, × 32); (**c**) retinal pigmentation completed and mouth opened (2 DPH, × 32); (**d**) swim bladder occurred and the yolk sac is completely consumed (3 DPH, × 20); (**e**) lipid globule disappeared (6 DPH, × 20); (**f**) pigment body evolved (7 DPH, × 20). a, anus; dt, digestive tract; e, eye; gc, gill-cover; lp, lipid globule; m, mouth; mp, melanophore pigments; n, notochord; N, tip of notochord; o, otocyst and otoliths; pa, primordial anus; pf, primordial fin; sb, swim bladder; ys, yolk sac

could be thought of as a differentiated straight tube. The pigment pattern remained the same as before.

At 2 DPH, larvae had almost completely resorbed their yolk sacs and the ratio between the yolk sac length and TL decreased to 10%. Besides, the retinal pigmentation of larvae was completed, the mouth started to open and the anus to became functional (Fig. 3c). Indeed, the digestive tract was opened to the exterior via the anus. The pigment pattern distinguished in the area of the two vertical anterior spots (1–3 and 9–11 somites): a kind

of homogenization had taken place forming a unique spot and the pigmentation at the tip of the notochord decreased until disappearing. The tip of notochord was not flexed.

At 3 DPH, the average TL was 3.649 ± 0.119 mm and larvae had begun exogenous feeding as yolk sac was resorbing and the pre-flexion period started (Fig. 3d). However, larvae continued to feed on endogenous reserve contained in the remaining lipid globule. The mouth was functional, and small crustaceans (*Artemia* spp.) were even observed along the digestive tract of some larvae. Furthermore, the swim bladder of larvae was inflated and gill-cover appeared. Although the primordial fin was still undifferentiated, the pectoral fins were completely shaped and functional.

At 6 DPH, the average TL was 3.729 ± 0.094 mm and the lipid globule was completely absorbed at 6–7 DPH (Fig. 3e). Hence, we identified the critical period of feeding transition after larvae completely absorbed their yolk and initiated exogenous feeding from 3 to 7 DPH. Larvae showed an undifferentiated primordial fin and a swim bladder elongated toward the posterior. The pigmentation of larvae evolved beyond the anus and larvae displayed a straight notochord.

At 7 DPH, the average TL was 3.922 ± 0.118 mm and the width of larvae' head, trunk and mouth began to increase (Fig. 3f). Their pigmentation continued to increase as the two third of the body was now pigmented, reaching the third vertical spot.

At 10 DPH, although the pelvic fin bud began to shape, both the dorsal, caudal, and anal fins remained undifferentiated. The pigmentation of brown meagre was still expanding.

At 11 DPH, larvae started to widen and we observed the emergence of caudal fin rays in the ventral region of the notochord tip (4.277 ± 0.165 mm; Fig. 4a). Furthermore, the head and trunk became relatively robust and teeth were developed on the upper maxilla.

At 13 DPH, the average TL was 4.709 ± 0.372 mm (Fig. 4b). The state of larva development was close to the beginning of the flexion of the notochord and primordial fins began to evolve to dorsal, anal and caudal fins. The pelvic fins were still developing but remained transparent. Brown pigments started to be visible at the end pigmentation.

At 15 DPH, the melanophores began to exhibit a typical "honey-comb" structure on the body and a pigmentation on the pelvic fin was observed for the first time.

At 17 DPH, the average TL was 5.387 ± 0.381 mm and dorsal, anal and caudal fins rays became more perceptible. The pigmentation was still increased, covering three quarter of larva's body. In our experiment, the complexion of notochord flexion was observed from 15 to 17 DPH (Fig. 4c).

At 20 DPH, the average TL was 6.585 ± 0.749 mm (Fig. 4d). Larvae reached the post-flexion stage and notochord was bended in the caudal region. The primordial fin of 20 DPH larvae was almost resorbed. Thus, dorsal, anal and caudal fins with rays were readily distinguishable compared to previous days. However, the pelvic fin was still developing and now completely pigmented. Brown pigments were more noticeable along the body, especially in the tail area.

At 21 DPH, pigments were found for the first time on the first dorsal and the pigmentation of pelvic fins was completed. Although the primordial fin had almost disappeared, caudal fin was not fully separated from the median primordial fin.

At 22–23 DPH, the average TL was 9.228 ± 0.472 mm (Fig. 5a). At this stage, resorption of the primordial fin was completed and hence, the dorsal, anal and caudal fins fully shaped. The first dorsal and pelvic fins exhibited pigmentation while other fins remained transparent. Fin formula of the larvae was: D_XI + 25; A_II + 7–8. The structure of melanophores organized in "Honey-comb" was more pronounced.

At 25–30 DPH, larvae began metamorphosis into the juvenile shape, i.e., into small adult (Fig. 5b) and by 35 DPH, larvae had metamorphosed. This last transformation marked the

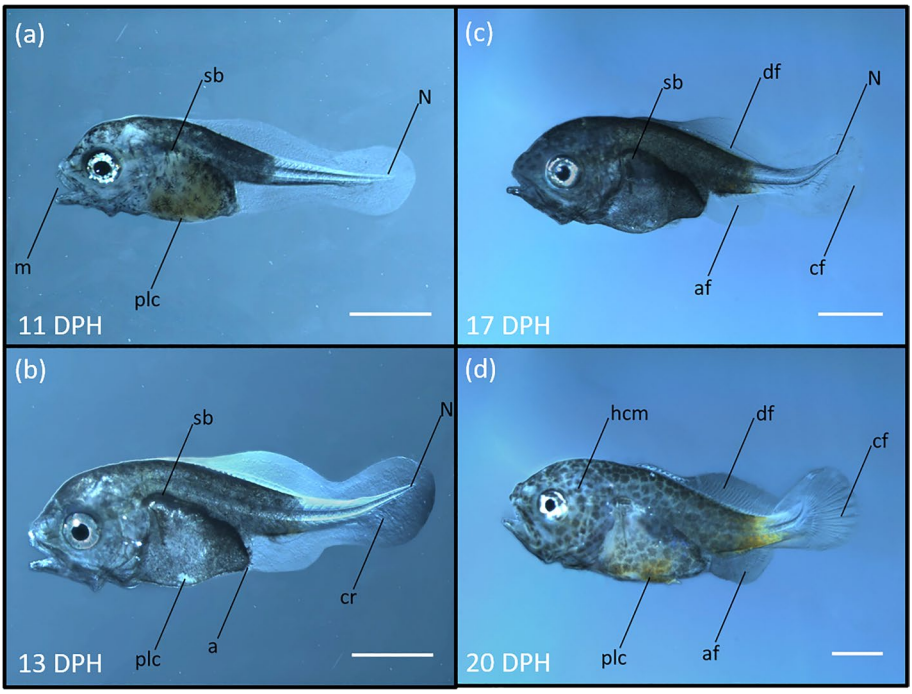


Fig. 4 *Sciaena umbra* larval developmental stages reared at 20 °C. DPH, days post-hatching. Scale 1 mm. (**a**) Emergence of caudal fin rays (11 DPH, × 20); (**b**) primordial fins began to evolve to dorsal, anal, and caudal fins (13 DPH, × 20); (**c**) flexion completion (17 DPH, × 16); (**d**) the post-flexion stage reached (20 DPH, × 12.5). a, anus; af, anal fin; cf, caudal fin; cr, caudal rays; df, dorsal fin; hcm, honey-comb melanophore; m, mouth; N, tip of notochord; plc, pelvic fins; sb, swim bladder

end of the larval phase at about 35 DPH for an average TL of 16.450 ± 1.012 mm. Brown meagre was colored in brown-yellow, except for anal and second dorsal fin areas, had a hyper-development of the first dorsal and their pelvic fins were disproportionate, contrasting with younger translucent larvae (Fig. 5c). Afterwards, few morphological changes will continue to occur for *S. umbra* juveniles (Crec'hriou et al. 2015). Key steps highlighted during the larval development of *S. umbra* are synthetized in Fig. 6.

Growth

Brown meagre measured in average 3.139 ± 0.132 mm following hatch and grew fast to 19.720 ± 1.656 mm after 40 DPH. Growth rate followed an exponential rate described by the equation of $TL = 2.5757e^{0.0515DPH}$ ($R^2 = 0.9619$) (Fig. 7).

Discussion

This study aims to describe the full sequential events of embryonic and larval development of the brown meagre, *Sciaena umbra*, reared in controlled laboratory conditions. Embryonic development of brown meagre eggs was completed after 43 h 20 min following the

fertilization and led to the hatch of yolk sac larvae. Metamorphosis, corresponding to the transition from larvae to the juvenile stage, occurred at 25–30 DPH.

Spawning of brown meagre began straightaway after sunset as observed in many egg fish scatterers. In aquaculture, eggs development is an important stage as its size mainly reflect the quality of the eggs and its potential for larval survival (Hinckley 1990; Ojanguren et al. 1996). Larger eggs of larger yolk sac are able to allocate more energy for growth and development (Hempel 1979) and hence, are able to produce larvae of higher survival potential compared to lower-sized eggs. These larvae from larger eggs hold a competitive advantage under unfed conditions (Hempel 1979; Hunter 1981; Lagomarsino et al. 1988), because their endogenous reserve allow then to extend their search of preys before starvation (Hinckley 1990). In natural environment, it is known that egg stage encompasses a critical period in the life-history of fish subject to a high mortality rate during early life (Hirst and López-Urrutia 2006). In this study, the egg diameter of brown meagre measured 1.254 ± 0.026 mm and ranged from 1.200 to 1.310 mm. Brown meagre eggs were larger compared to other Sciaenidae species, except for *Atractoscion nobilis* which measured 1.270 ± 0.020 mm, ranging from 1.240 to 1.320 mm (Moser et al. 1983). As summarized in Table 3, the egg diameters of the other Sciaenidae species are smaller and fluctuated between 0.800 and 1.100 mm (for *Argyrosomus hololepidotus*, Battaglene and Talbot 1994; for *A. regius*, Gamsiz and Neke 2008; Klimogianni et al. 2013; Pastor et al. 2013; for *Leiostomus xanthurus*, Powel and Gordy 1980; for *Sciaenops ocellata*, Holt et al. 1981; for *Genyonemus lineatus*, Watson 1982; for *Totoaba macdonaldi*, Escuredo-Vielba et al. 2018).

Moreover, several studies highlighted the influence of salinity on the size of the eggs (Thomas et al. 1995; Pastor et al. 2013). Most of Sciaenidae are euryhaline species, and hence, their eggs are suitable to be exposed to a wide fluctuation of salinities (Silberschneider and Gray 2008). In captivity, eggs of *A. regius* incubated at 39 ppt measured 0.857 ± 0.010 mm while eggs incubated at 37 ppt salinity measured 0.904 ± 0.049 (Pastor et al. 2013, Table 3). Similarly, Thomas et al. (1995) observed in laboratory conditions that the size of *S. ocellatus* egg decreased with salinity, having diameter of 1.001 mm at 24 ppt salinity and 0.920 mm at 37 ppt salinity.

In this study, the completion of embryonic development of brown meagre that corresponds to eggs hatching after fertilization until the beginning of the larval stage lasted for 41–43 h at 18.5 ± 0.5 °C and 38 ppt salinity. Other Scianidae species exhibits similar hatching times, ranging from 24 to 72 h (Table 3). Several studies emphasized that water temperature influence the metabolic rate of Teleost fishes (Clarke and Johnston 1999) and then, that water temperature also affects the hatching development times (Kupren et al. 2008). In captivity, eggs of *A. regius* incubated at 19–23 °C hatched approximately after 33 h of incubation, while the eggs kept at 21–25 °C hatched at 27 h (Pastor et al. 2013; Table 3). Thus, the duration of embryonic development is greatly influenced by water temperature (Kupren et al. 2008; Table 3). In the present study, the cleavage, blastula, and gastrula periods of brown meagre at similar hpf compared to *A. regius* (Gamsız and Neke 2008, respectively at 02:30, 04:15, and 03:25 hpf), *T. macdonaldi* (Escuredo-Vielba et al. 2018, at 02:00, 04:00, and 6:30 hpf), *A. hololepidotus* (Battaglene and Talbot 1994, at 02:18, 05:10, and 07:05 hpf), and *S. ocellata* (Holt et al. 1981, at 02:30, 03:30, and 06:00 hpf). In addition, embryonic period occurred during the same range of times among Sciaenidae species, i.e., during 2–3 h for the cleavage period, during 4–6 h for the blastula period and during approximately 3–8 h for the gastrula period. However, the segmentation period differed among Sciaenidae species. Indeed, the segmentation period lasted for 25 h for brown meagre while Gamsiz and

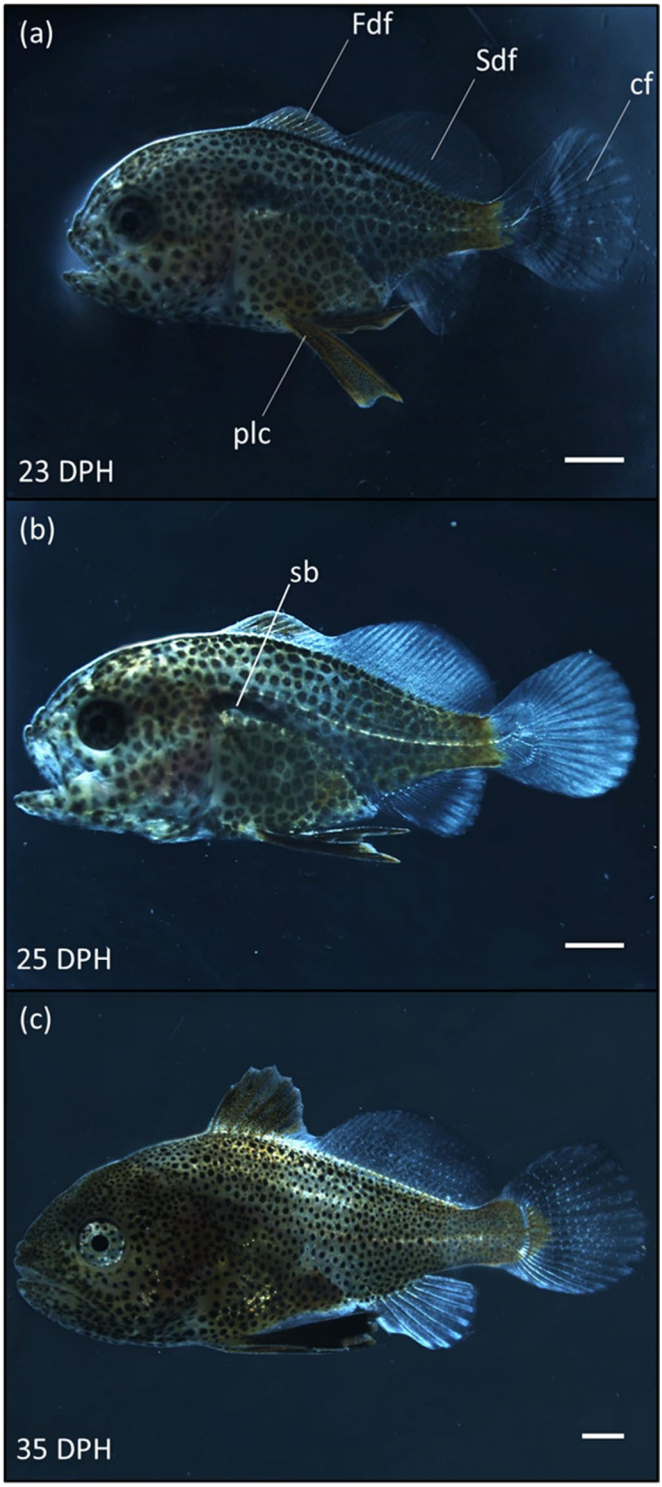
Fig. 5 *Sciaena umbra* larval developmental stages reared at 20 °C. Scale 1 mm. (**a**) Resorption of the primordial fin was completed (23 DPH, × 10); (**b**) metamorphosis began (25 DPH, × 10); (**c**) juvenile stage (35 DPH, × 7.5). af, anal fin; cf, caudal fin; Fdf, first dorsal fin; hcm, honey-comb melanophore; plc, pelvic fins; sb, swim bladder; Sdf, second dorsal fin

Neke (2008), Escuredo-Vielba et al. (2018), Holt et al. (1981) and Battaglene and Talbot (1994) reported that the period occurred from 12 to 17 h. In addition, our results suggest that the cell division pattern and the further embryonic development stages are mostly similar among Sciaenidae species.

During the resorption of the yolk sac, the pattern of larval development we observed for brown meagre was similar to other Mediterranean aquaculture species such as the common dentex (*Dentex dentex*, Jug-Dujaković et al. 1995; Koumoundouros et al. 1996), common pandora (*Pagellus erythrinus*, Klimogianni et al. 2004), or red porgy (*Pagrus pagrus*, Mihelakakis et al. 2001). In agreement with the other marine larvae carrying visible lipid globule (Koumoundouros et al. 1999; Williams et al. 2004; Bustos et al. 2007; Mendonça et al. 2019), larvae of brown meagre are characterized by a faster consumption of vitelline reserve allocated for early growth compared to the consumption of lipid globule. After resorption of the yolk sac, energy contained in the lipid globule promotes the transition from the endogenous feeding to the onset of exogenous feeding (Parra and Yúfera 2000; Moteki et al. 2001; Klimogianni et al. 2013). The yolk sac consumption pattern we observed for brown meagre was similar to other Sciaenidae species (Holt et al. 1981; Watson 1982; Moser et al. 1983; Orhun 1989; Battaglene and Talbot 1994; Gamsız and Neke 2008; Klimogianni et al. 2013; Pastor et al. 2013; Escuredo-Vielba et al. 2018; Table 3).

Mouth opening was completed at 3 DPH, which also corroborates with the observations for *A. regius* (Gamsiz and Neke 2008: Papadakis et al. 2013; Pastor et al. 2013), *G. lineatus* (Watson 1982), *S. ocellata* (Holt et al. 1981) and *U. cirrosa* (Cardellini et al. 1998; Zaiss et al. 2006). However, this action occurred slightly earlier than other Mediterranean aquaculture fishes except for the common pandora (*Pagellus erythrinus*) which also occurred at 3 DPH (18.5–20 °C) (Micale et al. 2006) or the greater amberjack (*Seriola dumerili*) which occurred at 2 DPH (23.5 °C) (Papandroulakis et al. 2005). The mouth opening occurs for the common dentex (*Dentex dentex*) at 4 DPH (16–20 °C) (Koumoundouros et al. 1996; Santamaría et al. 2004) similarly to the gilthead seabream (18–20 °C) (*Sparus aurata*) (Elbal et al. 2004) and at 4–5 DPH for the turbot (16–20 °C) (*Psetta maxima*) (Segner et al. 1994) and the European seabass (19.5 °C) (*Dicentrarchus labrax*) (Deplano et al. 1991). Simultaneously with the opening of the mouth, the yolk sac absorption is depleted and the larvae start to feed.

The length of newly hatched larvae of brown meagre was similar to *A. regius* larvae observed at IFAPA with the average TL of 3.19 ± 0.09 mm (Pastor et al. 2013). Brown meagre displayed a larval development in rearing conditions that fulfill many prerequisites of aquaculture species: easy to reproduce, having a large mouth, a fast growth and a high rate of survival (Hamzaçebi and Can 2021). These characteristics are common for a numerous Sciaenidae species farmed in aquaculture as *A. regius* (Pastor et al. 2013) and *U. Cirrosa* (Cardellini et al. 1998; Mylonas et al. 2000; Zaiss et al. 2006). The growth rate of brown meagre was similar to *A. nobilis* (Moser et al. 1983; Orhun 1989), but slightly lower compared to other aquaculture Sciaenidae species. For example, at 30 DPH, brown meagre measured 13.050 ± 1.189 mm whereas *A. regius* reached 15.11 ± 3.49 mm (Pastor et al. 2013). Yet, 30-day brown meagre were larger compared to gilthead seabream (Zaki et al. 2007) or seabass (Hatziathanasiou et al. 2002).


(a)
Fdf
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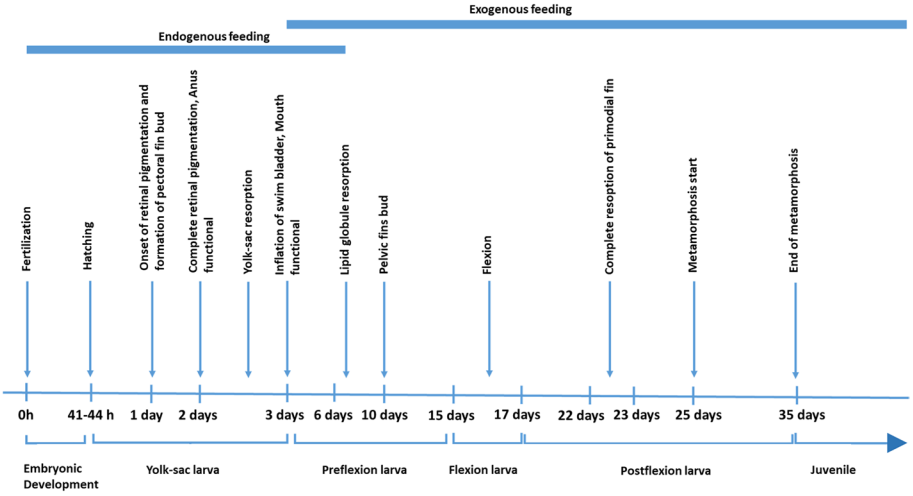

Fig. 6 Principal steps during the larval development of *Sciaena umbra* at 20 °C

Furthermore, in the present study, brown meagre is one of the few Sciaenidae species along with weakfish (*Cynoscion squamipinnis;* Abarca et al. 2017) which spawn spontaneously in captivity. On the contrary, the reproduction of most Scianidae species, despite excellent aquaculture conditions, requires hormonal injections (Thomas and Boyd 1988; Thomas et al. 1995; Tucker 2000; Koumoundouros et al. 2005; Duncan et al. 2008; Mylonas et al. 2013a, b; Musson and Kaiser 2014) and hand stripping to collect eggs and sperm (Battaglene and Talbot 1994). These different techniques are time-consuming, difficult to achieve and stressful for the fish because it also requires to examine males for free milt and to perform an ovarian biopsy on females. Moreover, hand stripping significantly influences the success of fertilization and the eggs viability (Bromage et al. 1994; Cejko et al. 2016).

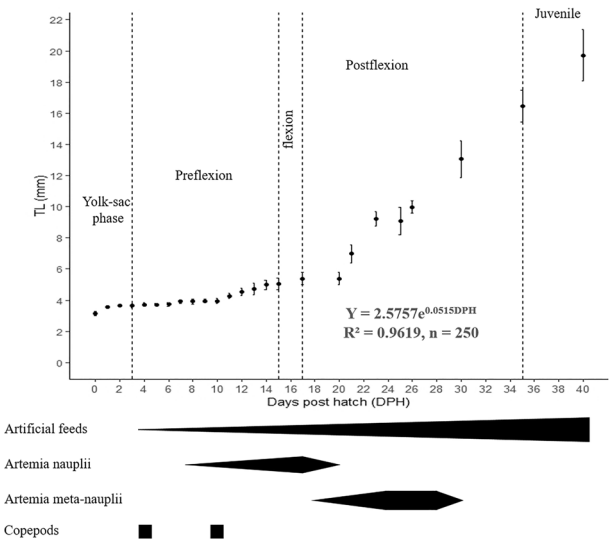

Fig. 7 Growth and development of *Sciaena umbra* larvae in TL (mean ± SD) during larval rearing a 20 °C, in relation to time (days post-hatching). The type and relative amount of different feeding items offered during rearing are shown schematically below the graph. The vertical dashed lines on the graph indicate the four periods of larval development

Table 3 Comparison of egg and larva characteristics with Sciaenidae species. *LT* total length, *SL* standard length

Species	Egg diameter (mm)	Time of hatching (water temperature and salinity)	Length of newly hatched larvae (mm)	Yolk sac completion (day)	References
Sciaena umbra	1.254 ± 0.026 (1.200–1.310)	41–43 h (18.5 ± 0.5 °C, 38 ppt)	TL: 3.139 ± 0.132	3	Our study
Sciaena umbra	1.457 ± 0.047 (1.380–1.530)	39–40 h (20.5 ± 0.5 °C)	TL: 4.860 ± 0.260	-	Hamzaçebi and Can (2021)
Argyrosomus hololepidotus	0.938 ± 0.024	28–30 h (23 ± 0.5 °C, 35 ppt)	TL: 2.250 ± 0.090	3	Battaglene and Talbo (1994)
Atractoscion nobilis	1.270 ± 0.020 (1.240–1.320)	72 h (16–20 °C, 30 ppt)	TL: 2.490	3–6	Mosser et al. (1983); Orhun (1989)
Argyrosomus regius	At IFAPA: 0.850 ± 0.020 At LIMIA: 0.904 ± 0.049	At IFAPA: 27 h (21–25 °C, 39 ppt) At LIMIA: 33 h (19–23 °C, 37 ppt)	At IFAPA, TL: 3.190 ± 0.090 At LIMIA, TL: 2.200 ± 0.020	3	Pastor et al. (2013)
Argyrosomus regius	0.857 ± 0.010 (0.825–0.910)	24 h (22.5 °C, 38 ppt)	TL: 2.593 ± 0.055 TL	3	Gamsiz and Neke (2008)
Argyrosomus regius	1.056 ± 0.010	27 h (19 ± 0.2 °C, 35 ppt)	TL: 2.621 ± 0.037	3	Klimogianni et al. (2013)
Leistomus xanthurus	0.800 (0.720–0.870)	48 h (20 °C, 30–35 ppt)	SL: 1.600–1.700	5	Powel and Gordy (1980)
Scianops ocellata	0.950	28–29 h (22–23 °C)	SL: 1.710–1.790	3	Holt et al. (1981)
Genyomus lineatus	0.850 ± 0.020	52 h (20 °C)	SL: 1.570	3	Watson (1982)
Totoaba macdonaldi	0.800–0.900	28 h (21 °C)	-	-	Escuredo-Vielba et al. (2018)

Brown meagre larvae exhibit an ontogenic development similar to *A. regius*, *A. hololepidotus*, *A. nobilis*, and *S. Ocellatus* (Holt et al. 1981; Moser et al. 1983; Battaglene and Talbot 1994; Papadakis et al. 2013). Hence, these similarities will assist in the development of aquaculture techniques for *S. umbra* by allowing the adaptation of techniques developed for other sciaenids. Since 2019, the brown meagre larvae reared at Stella Mare platform show a survival rate which range from 20% in the 0.2 m^3 tank with 100 larvea·L^{-1} to 63% in the 2 m^3 tank with 25 larvae·L^{-1} at 45 DPH. This difference between rates might be induced by an effect of larval density. Indeed, intensive aquaculture production of larvae enhances both interspecific competition and cannibalism (Soletchnik et al. 1988; Orhun 1989; Hamzaçebi and Can 2021), reducing significantly the survival rate and increasing the size heterogeneity of larvae (Soletchnik et al. 1988). Although larval mortality is not assessed in this study, cannibalism issue appeared since day 30 onwards when reducing (then stop) the living prey feeding. This problem may be reduced by either increasing the density of preys or by reducing the concentration of larvae (Soletchnik et al. 1988; Dou et al. 2000). For example, the rate of cannibalism for *S. Ocellatus* was reduced by a reduction in density (Soletchnik et al. 1988).

In conclusion, the present study emphasizes that brown meagre is an easy species to rear and has the advantage, over the other Sciaenidae species, of spontaneous spawn. Thus, brown meagre species is a relevant species to farm in captivity for restocking programs regarding its declining stocks list (Abdul Malak et al. 2011; Chao 2020) or for mariculture as a productive alternative for fishermen (Abarca et al. 2017). Following this study, we recommend to conduct further experiments in order to assess the optimal condition in terms of abiotic and biotic factors to enhance brown meagre rearing.

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Author contribution All authors contributed to the study conception and design. Material preparation, data collection, and analysis were performed by Rémi Millot, Mikaël Demolliens, Sally Pugliese, Alban Delmas, and Alizée Boussard. The conceptualization of the research and the writing of the original manuscript were carried out by Salomé Ducos, Lucie Vanalderweireldt, Antoine Aiello, and Eric Dominique Henri Durieux. The first draft of the manuscript was written by Rémi Millot and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding authors, Rémi Millot and Dr Eric Dominique Henri Durieux, on reasonable request.

Declarations

Ethics approval The authors confirm that the ethical policies of the journal, as noted on the journal's author guidelines page, have been adhered to and the appropriate ethical review committee approval has been received. The European Directive 2010/63/EU guidelines for the Care and Use of Laboratory Animals were followed. Reference of ethics committee file: APAFIS23731-2020012211568209v3 and UMS 3514 Stella Mare-UCPP-CNRS animal health approval number: A.2B.001.

Conflict of interest The authors declare no competing interests.

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