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Ontogenetic differentiation of swimming performance in Gilthead seabream (*Sparus aurata*, Linnaeus 1758) during metamorphosis

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ABSTRACT

The critical swimming speed (U_{crit}) of gilthead seabream (*Sparus aurata*, Linnaeus 1875) was studied in two ontogenetic phases, early (13.7-18.7 mm total length, TL) and late metamorphosis (20.4-34.3 mm TL, after the full development of fin meristics and during squamation ontogeny), under four exercise temperatures (15, 20, 25 and 28 °C). Both the exercise temperature and the ontogenetic stage had a significant effect on the relative U_{crit} (RU_{crit}) of *S. aurata*, with the fish of early metamorphosis phase (E group) presenting significantly higher RU_{crit} than those of the late metamorphosis stage (L group). This ontogenetic shift in swimming performance was accompanied by significant ontogenetic shifts of body shape and of muscle anatomy. Compared to the L group, *S. aurata* of the E group were characterized by a streamline body shape and significantly higher relative contribution of the slow-red muscle to the cross-sectional area of the body (31.0±1.3% vs 12.0±1.2% in the L group).

1. Introduction

In most marine demersal fish, ontogeny involves a planktonic larval phase before transition to demersal juvenile habitats (a process called settlement) (Leis, 2006). This transition is often characterised by mortality rates of up to 85% (Van der Veer and Bergman, 1987; Tanaka et al., 1989; Carr and Hixon, 1995; McCormick, 1998; Almany and Webster, 2006; Leis, 2006), thus underlining the importance of fish capabilities at the time of settlement for the population structure. To a large extent, settlement is strongly related to the ontogenetic phase of metamorphosis from larva to juvenile (Kendall et al., 1984; McCormick et al., 2002; Ditty et al., 2003), as individuals maximise their survival in the new environment by developing juvenile characters.

Swimming performance is one of the most important functional characteristics in fish, determining to a large extent the success of predator avoidance, prey capture, migration etc (Videler, 1993; Reidy et al., 2000; Armsworth, 2001; Hunt von Herbing et al., 2001; Plaut, 2001; Fisher and Wilson, 2004; Green and Fisher, 2004). In the case of developing fish, the importance of swimming performance is furthermore underlined, as the development of the different anatomical characters is related in each ontogenetic stage to different swimming abilities and modes (Fuiman and Webb, 1988; Patruno et al., 1998; Osse and van den Boogaart, 1999; Sagnes et al., 2000; Johnston et al., 2001; Koumoundouros et al., 2001a,b; Guan et al., 2008). Therefore, understanding this phenotypic and functional variation between ontogenetic stages is critical, because it is related to profound demographic consequences in populations. Most research on fish swimming during ontogeny has focused on the stages up to settlement, in order to understand how morphology serves function and contributes to survival, dispersal and recruitment of early life stages (Clark et al., 2005; Leis et al., 2007; Guan et al., 2008). In most fish species however, the transition from the pelagic-larval to the demersal niche takes place well before the full attainment of juvenile characteristics (Clark et al., 2005; Fisher et al., 2005), thus raising questions about the ontogeny of swimming performance during metamorphosis.

Gilthead seabream (*Sparus aurata*, Linnaeus 1758) is a valuable species for fisheries, and a major marine fish of European aquaculture. Its natural distribution extends from the Eastern Atlantic (British Isles, Strait of Gibraltar to Cape Verde and around the Canary Islands), to Mediterranean Sea and the Black Sea (Bauchot and Hureau, 1990). Like many marine fish species, *S. aurata* is demersal during the juvenile and adult phase, but planktonic during the early life stages (Divanach, 1985). It is a well studied organism with respect to the ontogeny of the features that contribute to the function of swimming, such as muscles (Rowlerson et al., 1995; Patruno et al., 1998; Ayala et al., 1999), skeleton (Koumoundouros et al., 1997; Faustino and Power, 1998, 1999, 2001) and body shape (Koumoundouros et al., 1995).

In the present study, we examined swimming performance of *S. aurata* with respect to the ontogenetic state of the individuals near

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settlement (early or late metamorphosis phase). As temperature exerts a significant effect on fish swimming performance (Beamish, 1978; Videler, 1993; Fuiman and Batty, 1997; Johnson et al., 1998), the swimming performance of *S. aurata* was studied at each ontogenetic phase at different water temperatures. To explain any potential differences in the swimming performance between the two ontogenetic phases, body shape, ontogenetic state of the fins and squamation, as well as muscle structure were compared.

2. Materials and methods

2.1. Fish origin

Two batches of 200 individuals each were randomly taken from a reared fish population at 40 (early metamorphosis, group E) and 50 days (late metamorphosis, group L) post-hatch. Both batches were acclimated for 8 days at 20 °C in the facilities of the Biology Department (University of Patras, Patras, Greece), and subsequently tested for their swimming performance.

Larval rearing was performed in the hatchery facilities of Andromeda SA (Greece, Vonitsa), according to the standard methodology for the intensive larval rearing of *S. aurata*. In particular, the autotrophic and larval phases were carried out in an indoor tank of 16 m^3 volume, at an initial stocking density of 125 eggs L^{-1}. Larvae were reared in the presence of background phytoplankton (*Isochrysis galbana* and *Nannochloropsis occulata*, 3.5-8.5 mm total length, TL) with initial feeding on rotifers (3.5-8.5 mm TL), followed by gradual provision of Artemia nauplii instar I (5.8-6.5 mm TL) and II (6.0-11.0 mm TL), and finally weaning and pre-growing on inert diets (Caviar Bernaqua, Perla Plus Truvit). Commercial emulsion oils were used for the enrichment of the rotifers (DHA Protein Selco, INVE SA) and instar II Artemia nauplii (Easy DHA Selco, INVE SA). Throughout the entire rearing phase, tanks were supplied with borehole seawater. Photoperiod was initially 24:0 light:dark and 16:8 during the pre-growing phase. Water temperature was 19.0-20.0 °C, salinity was 35 ppt and oxygen saturation 90-95%.

Fish transportation from Andromeda SA to the laboratory facilities lasted 2 hours, and took place in plastic bags of 30 L volume, filled with seawater (20 °C) and O_2. In the laboratory, fish were kept in two aquarium tanks of 100 L volume, which were equipped with a biological filter (EHEIM, model 2217), a protein skimmer, chiller (Flite, Sfiligoi) and continuous aeration through a diffuser. During the period prior to the swimming tests, water temperature was 20 °C, salinity 35 ppt (Tropic Marin), O_2 saturation 85-95%, and photoperiod 14:10 light:dark. Fish were fed with inert diet 5 times per day (MeM, Bernaqua).

2.2. Swimming performance

Swimming performance tests were carried out at 15, 20, 25 or 28 °C water temperature, i.e. the thermal range of coastal areas during settlement and early juvenile stages of the species (Arias 1980, Kissil et al., 2001, Akin et al., 2005, Craig et al., 2008). The swimming apparatus consisted of a 70.0 X 10.0 X 5.0 cm deep swimming channel (plexiglas), and two holding tanks (Fig. 1). Water was pumped from one holding tank (EHEIM pumps, model 2217) and returned to the other, thus forming the necessary water current in the swimming channel (Fig. 1). The rectilinear flow regime was obtained by adjustable valves, and water velocity was calibrated by means of an electromagnetic flow-meter (Valeport, Model 801). Fish forward escape was prevented by a screen of straws (8 cm long), which was located at the upstream end of the channel. A homogenous current velocity throughout the whole depth and length of the channel was verified by visualisation of dye injected into the water stream. Temperature was maintained constant at the desired experimental levels by the combined use of a cooling (Super-Flite, Sfiligoi) and a heating system (Fig. 1). Water salinity was 35 ppt and oxygen saturation was 95-100% (achieved by means of an air-diffuser).

At eighteen hours prior to the swimming tests, 15-20 fish were transferred from the stock population to a 100 L holding tank (with biological filter, chiller and air diffuser), where they were kept in the dark and at 35 ppt salinity, starved and acclimated to the test temperatures (at a rate of ca 5 °C hr^{-1}). For the swimming tests, one fish was placed in the swimming channel for 10 min at 2 TL s^{-1} water velocity. Subsequently, the water velocity was increased at a rate of 1 TL s^{-1} every 10 min until fish were fatigued and left the swimming channel, without being able to react to visual and acoustic stimuli from the side or behind. Side visual and acoustic stimuli were proven adequate to prevent most of the fish from swimming near the wall boundary layer. Although given swimming data concern only the individuals swimming near the centre of the channel, the influence of the wall boundary-layer cannot completely been eliminated. Therefore, reported swimming speeds might be slightly faster than they would be in the absence of the wall boundary layer (Guan et al., 2008).

Critical swimming speed was estimated according to the formula

$$U_{crit} = U_i + (U_{ii} t_i t_{ii}^{-1}) \quad \text{(Brett, 1964)}$$

where U_i is the highest swimming velocity (mm s^{-1}) maintained for the entire 10 min interval, U_{ii} the velocity increment (15, 20, 25, or 30 mm s^{-1}, depending on the class of fish size tested), t_i is the time interval (min) that each individual swam at the fatigue velocity, and t_{ii} the time interval (10 min) between velocity changes. No correction for blocking effects was made (Bell and Terhune, 1970), as the maximum

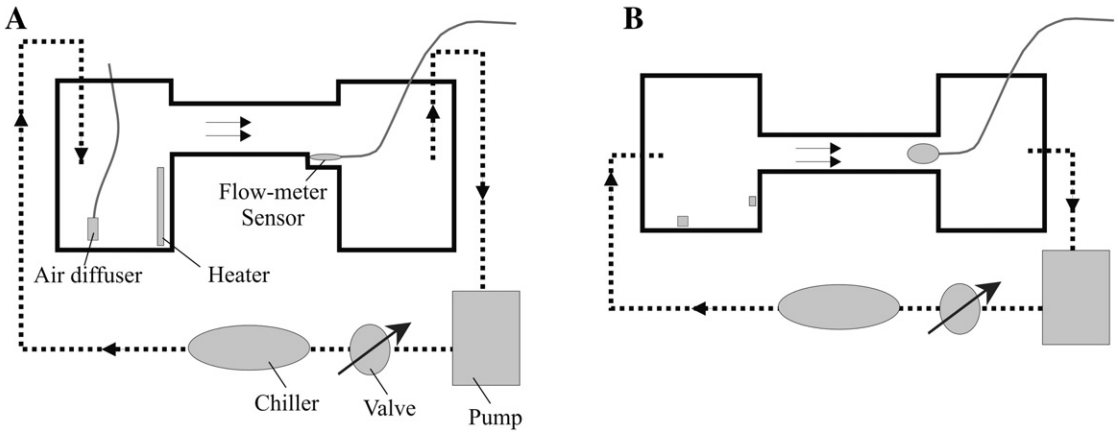

Fig. 1. Swimming apparatus used in the present study. (A) Lateral view; (B) top view. Arrows indicate the direction of water circulation.