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Updating control of puberty in male European sea bass: A holistic approach

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ABSTRACT

Puberty is the process by which an immature animal acquires the ability to reproduce for the first time; its onset occurs soon after sexual differentiation and is characterized by the beginning of gametogenesis in both sexes. Here we present new insights on when and how the onset of puberty occurs in male European sea bass, its dependence on reaching a critical size, and how it can be controlled by photoperiod, revealing the existence of a photolabile period with important applications in aquaculture. Regarding size, apparently only European sea bass above a certain size threshold attain the ability to carry out gametogenesis during their first year of life, while their smaller counterparts fail to do so. This could imply that fish need to achieve an optimal threshold of hormone production, particularly from the kisspeptin/Gnrh/Gth systems, in order to initiate and conclude puberty. However, a long-term restricted feeding regime during the second year of life did not prevent the onset of puberty, thus suggesting that the fish are able to maintain the reproductive function, even at the expense of other functions. Finally, the study of daily hormonal rhythms under different photoperiod regimes revealed the equivalence between their core values and those of seasonal rhythms, in such a way that the daily rhythms could be considered as the functional units of the seasonal rhythms.

1. Introduction

Puberty can be defined as the process by which an immature animal acquires the ability to reproduce for the first time (Okuzawa, 2002); its onset occurs soon after sexual differentiation (Strüssmann and Nakamura, 2002), and in male teleosts it is characterized by the beginning of spermatogenesis (Schulz and Goos, 1999; Schulz and Miura, 2002). A more precise knowledge of fish puberty will allow more effective control over the time of its onset and even make it possible to inhibit this process. But how is this control achieved? In general, it is known that in order to reach puberty, a sufficient number of germ cells need to be activated, and it is also necessary to achieve a certain energy threshold during the initial period of gametogenesis. Age and size at puberty is species-specific and can be modulated by genetic and environmental factors. In addition, in nature, puberty in fish may occur either early or late in the life cycle, and in both cases it may inflict many problems in farmed fish species (Taranger et al., 2010). The onset of puberty is controlled by the activation of the brain-pituitary-gonad (BPG) axis, and a series of internal (i.e. kisspeptins) and external (i.e. photoperiod) factors stimulate and/or modulate this activation. Kisspeptins are essential agents in the regulation of key aspects of reproductive physiology, including the proper timing of puberty and the control of reproductive function by photoperiod cues. The comparative analysis of essential aspects of the evolution and conserved functions of kisspeptins and their receptors in the control of reproduction have been recently reviewed (Tena-Sempere et al., 2012). Furthermore, the occurrence of an effective environmental factor is required to initiate the process of puberty. In temperate fish species, among all the known factors, the photoperiod has emerged as the most predictable cue for the regulation of physiological events, including sexual cycles, and is the only signal that can provide accurate messages to entrain daily and seasonal cycles involved in the synchronization and timing of reproduction (Migaud et al., 2010). However, other methodologies, including genetics as well as hormonal and nutritional approaches, could be also very effective and/or complementary to this control (Taranger et al., 2010). Finally, a very important aspect of fish

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photo-transduction, namely the mediation of melatonin on the effects of photoperiod on crucial functions and behaviors, particularly on the circannual clock and annual cycle of reproduction, has also been reviewed (Falcón et al., 2010). In any case, puberty control may imply techniques to both delay/arrest and advance/induce puberty, according to the reproductive pattern of a given species. The implementation of one monitoring strategy or another is critical in intensive fish farming. For example, some fish species, such as groupers, tunas and sturgeons, attain puberty at a later age and larger size. Keeping them in captivity entails an important investment in terms of food, facilities and management, which translates into the cumulative costs of long-term maintenance. Breeding or studying the hormonal regulation of these species' reproduction would require extensive facilities to keep breeders in captivity for a long period of time, which would be too costly. Thus, in this case, it is advisable to advance the process of puberty through environmental and/or hormonal manipulation. Other species, such as *Sparus aurata*, *Perca flavescens, Atlantic salmon*, *Gadus morhua*, *Hippoglossus hippoglossus* and, in particular, *Dicentrarchus labrax*, may exhibit early puberty without having attained marketable size, and consequently their premature reproduction results in growth well below that required for marketing, producing serious losses for the aquaculture sector. A suitable strategy for studying the hormonal mechanisms involved in the onset of puberty in these species, and more specifically, in European sea bass, would be inhibiting anticipated puberty, or at least delaying its onset, through photoperiodic manipulation. The latter would provide the additional benefit of somatic growth as a result of delayed gonadal growth, and will be analyzed in detail in the present review. Since the last review of the environmental and hormonal control of puberty in male European sea bass (Carrillo et al., 2009), there have been many breakthroughs made regarding the endocrine regulation of this process and its photoperiodic control in this species. The aim of this review is to update this knowledge and to identify new research trends that should be pursued.

2. Sex differentiation, anticipated puberty (precocity) and puberty

Fish species show a wide range of ages and sizes at puberty. In farmed fish, the growth rates are normally higher than in wild fish, due to greater feed availability. This is also accompanied by higher levels of adiposity, which in combination lead to a reduction in the age of puberty when fish are reared in captivity (Taranger et al., 2010). In European sea bass, males can attain precocious puberty during their first reproductive cycle (Carrillo et al., 2009). Different studies (Begtashi et al., 2004; Felip et al., 2008; Bayarri et al., 2009; Rodríguez et al., 2012b) have shown that fish which mature precociously are larger than non-precocious specimens, and in fact a significant positive correlation was observed between the spermiation rate and the weight and length of one-year-old male European sea bass (Rodríguez et al., 2012b). The basis for this observation is the high energy demands of the first gonadal maturation, which only occurs in fish that have attained a certain size, as they have enough reserves to engage in this process with any certainty of success (Rowe et al., 1991). However, in male European sea bass, the consequence of this early maturation during the first year of life is an 18% lower growth rate in the second year of life with respect to their non-precocious counterparts, probably due to a redirection of energy towards gonadal development at the expense of somatic growth (Felip et al., 2008). In terms of the different sexes, males reach normal puberty at an earlier size and age than females (two versus three years), and the difference between male and female growth rates becomes more pronounced with age (Carrillo et al., 1995). Accordingly, during the first year of age, precocious males are the largest males (Begtashi et al., 2004), but their growth rate decreases during the second year, when the rest of the males attain puberty at the normal time (Felip et al., 2006). Towards the third year of age, the reduction in the somatic growth rate of males becomes very evident, as compared to that of females (Carrillo et al., 1995). Finally, at the end of the third year, once females have also reached puberty, the growth rate reduction in already adult European sea bass becomes more marked in both sexes (Carrillo et al., 2009). Moreover, in fish reared to a larger size than the normal portion-size, the presence of precocious females at two years of age has also been observed (Zanuy et al., 2008), although this phenomenon and its relation to body size have yet to be studied, as in the case of males.

It has been shown that the gonads of European sea bass remain undifferentiated during the first 5 months of life, with females differentiating before males, at 150 days post-fertilization (dpf) and 200 dpf, respectively. At 250 dpf, gonad differentiation has been completed in both sexes (Papadaki et al., 2005). After fertilization, and generally under intensive culture conditions, as much as 20–30% of the male population can attain anticipated puberty or precocity (Begtashi et al., 2004); in this case, gonad size does not exceed 1.5% of the GSI. By the second year of life, 100% of the male population will have reached puberty, and the GSI may be as high as 3.5% (Carrillo et al., 2010). Under intensive culture conditions, precocious females start to appear at this time, and their GSI does not exceed 9% (Zanuy et al., 2008; Zanuy and Carrillo, unpublished observations). By the third life cycle, 100% of the females will have reached puberty, and the GSI may reach levels of around 16% (Rocha et al., 2009). The value of the GSI for pubertal fish is approximately twice as high as that of precocious fish (Zanuy and Carrillo, unpublished observation). At this point, the question would be: Is there any relevant factor that determines whether a fish becomes precocious? Previous studies have shown that under intensive farming conditions, precocious male European sea bass can be 1.28 and 1.06 times heavier and longer, respectively, than non-precocious fish at the peak breeding time during their first year of life. Similarly, the condition factor of precocious fish was 1.02 higher than that of non-precocious (Begtashi et al., 2004). Furthermore, a significant positive correlation was found between the rate of spermiating males and their weight ($x = 60.140 + 4.472y$; $r = 0.753$; $P = 0.012$) or size ($x = 17.296 + 0.213y$; $r = 0.708$; $P = 0.022$) during this period of maximum spermiation (Rodríguez et al., 2012b). All this evidence suggests that in male European sea bass, a critical size may certainly be required at the onset of puberty in order to initiate gametogenesis for the first time. However, the hormonal mechanisms mediating this effect of size on male fish precocity during their first sexual cycle are unknown. Very recently, Espigares et al. (2015a) reported that only larger male European sea bass of less than a year of age were able to attain puberty, while smaller fish of the same age remained immature. It was proposed that during their first year of life, male European sea bass need to reach a critical size (about 50 g) at the start of gametogenesis (September) in order to progress to the gonadal recrudescence stage and successfully attain puberty. Moreover, it has been found that fish weighing less than 50 g do not develop gonads, and therefore do not enter puberty. Although hormonal profiles of both large and small fish were similar, the amplitude of the hormonal rhythms in the small fish was significantly lower than that of the large specimens. This may explain why small fish fail to achieve full reproductive competence at the level of the BPG axis, thus establishing that male size is a permissive condition to ensure full effectiveness of key hormonal actions (Espigares et al., 2015a). This is in agreement with the gating theory that states that fish must have a critical size at a specific stage of maturational development in order to be able to respond to proximal cues (Bromage et al., 2001). Considering that the