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Effects of genetic and environmental factors on sex differentiation in the European sea bass (*Dicentrarchus labrax*)

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Abstract

One of the major problems in the mariculture of the commercially important European sea bass, *Dicentrarchus labrax*, is that females grow 20-50% more rapidly than males. For that reason, farmers are interested in developing female monosex populations. Studies on evolution, genetics, and physiology have been conducted during the last decade to solve this problem. This review summarizes the latest data related to the effects of evolution, genetics, physiology, and environment on sex determination and differentiation in the European sea bass.

Genetic Effects

A differentiated gonochoristic marine teleost, *Dicentrarchus labrax* L. (1758), Teleost: Perciformes: Moronidae, is comparable to most marine bony fishes. It does not have specialized hetero-chromosomes or sex-linked markers, however, there are noticeable parental effects on the sex ratios of progeny (Gorshkov et al., 2003). Current data indicate that the percentage of females ensuing from individual crossings varies 1-70%. Sex differentiation begins when fish reach 8-9 cm standard length, about 200 days after hatching. Females differentiate before males.

In European sea bass, the consequence of evolution in diverse zones is manifested in its dispersion throughout the coastal waters of the Atlantic Ocean from Scandinavia to Western Sahara and through the Mediterranean Sea to the Black Sea. Genetic investigations on *D. labrax* populations using an assortment of molecular markers revealed that there is scattered mixing between Atlantic and Mediterranean populations as well as within the Atlantic and within the Mediterranean. Time and again, genetic divergence is associated with hydrographical characteristics of the marine environment. Yet many times build-ups of this kind of data do not support and/or elucidate the genetic differentiation seen in an organism. Genetic disparity at nuclear and cytoplasmic loci in *D. labrax* populations permits us to deduce that the Atlantic Ocean vs. Mediterranean Sea seg-

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regation is probably related to the fish reproductive isolation which might be tracked to ancient barriers during glacial eras. Many investigators tried to characterize genetic affinities among *D. labrax* populations. Some proposed the existence of an Atlantic/ Mediterranean division, others of a division between eastern and western Mediterranean populations (Castilho and McAndrew, 1998; Bahri-Sfar et al., 2000; Castilho and Ciftci, 2005).

In the eastern Mediterranean, Bahri-Sfar et al. (2000) showed significant divergence between samples from the Adriatic, Ionian, and north Aegean Seas and samples from the Libyian-Tunisian Gulf. Castilho and Ciftci (2005) investigated sea bass from the Levantine basin in the Mediterranean Sea, where genetic data on marine teleosts are scarce. Their work revealed that although current patterns do not prevent intermixing, they do not aid in mixing the two populations in the eastern Mediterranean.

Differentiation at nine microsatellite loci discovered in Levantine *D. labrax* specimens most likely characterize an additional subdivision of this fish in the eastern Mediterranean (Castilho and McAndrew, 1998; Lemaire et al., 2005; Castilho and Ciftci, 2005). There are considerable discrepancies among loci for traits of financially important characteristics among and within strains and their crosses, indicating good prospects for mariculture of *D. labrax* strains derived from the southeastern part of the Mediterranean (Gorshkov et al., 2004a; Mylonas et al., 2005).

A good example of a non-mixed *D. labrax* population in one of the many habitats around the Mediterranean Basin was found by Gorshkov et al. (2003) and Mylonas et al. (2005). In 1995, about 60 *D. labrax* juveniles (30-50 g) were fished out of the brackish Lake Edku in the estuarine region of the Nile River (Egypt) and transported to the National Institute for Mariculture in Eilat, Israel, where they were reared under controlled conditions (Gorshkov et al., 1999). During the following years, fully developed and mature *D. labrax* were used as broodstock for experiments and production.

Recent efforts to understand the sex determination machinery in *D. labrax* have been unsuccessful. Neither research to classify sex chromosomes or sex-specific DNA sequences (Sola et al., 1993; Cano et al., 1996; Martinez et al., 1999) nor progeny analysis by means of steroid sex-reversed *D. labrax* or production of gynogenetic fish have achieved anything beyond a merely genetic scheme of sex determination (Blázquez et al., 1999; Zanuy et al., 2001). Nevertheless, inconsistent sex ratios are produced by individual crosses (Blázquez et al., 1999; Gorshkov et al., 1999; Saillant et al., 2003a).

Environmental Effects

Evidence is mounting that sex differentiation in *D. labrax* may be influenced by multifaceted genetic and environmental interactions involving light, salinity, pH, and temperature.

The photoperiod is an important signal for the control of reproduction in teleosts (Bromage et al., 1993; Carrillo and Zanuy, 1993). Custom-made photoperiod regimes have been used to modify the rate of sexual maturation and occurrence of spawning in cultured teleost species such as the rainbow trout (*Oncorhynchus mykiss;* Bromage et al., 2001), gilthead sea bream (*Sparus aurata*; Ron and Okimoto, 1999; Kissil et al., 2002; Zilberman-Peled et al., 2004; Naor and Ron, unpubl.), and Atlantic salmon (*Salmo salar*; Taranger et al., 1995, 1998, 1999). Ron (2004) demonstrated that the pineal gland in *D. labrax* is photosensitive, can be trained, and contains an internal circadian oscillator that regulates the production of melatonin. Although photoperiod did not seem to affect the sex ratio and density in *D. labrax* (Blázquez et al., 1998; Saillant et al., 2003a; Bayarri et al., 2004), long-term exposure to continuous light inhibits precocity in juvenile males (Begtashi et al., 2004).

Using constant salinities, Saillant et al. (2003c) were unable to influence the *D. labrax* sex ratio. However, abrupt alteration of the salinity created stress that may affect the course of sexual differentiation.

While pH was able to affect sex differentiation in a number of teleosts (Rubin, 1985;

Roemer and Beisenherz, 1996), it did not affect the sex ratio in *D. labrax* (Saillant et al., 2003a).

Temperature undoubtedly influences the sex ratio in *D. labrax*. When high temperature was applied during larvae and juvenile rearing protocols, the fish more often than not developed as males. Most recent results found that the rearing temperature throughout the labile period of gonad development significantly affects the sex ratio in progeny (Blázquez et al., 1998; Pavlidis et al., 2000; Saillant et al., 2001ab, 2002, 2003a; Ben-Atia et al., 2002; Koumoundouros et al., 2002; Gorshkov et al., 2004ab; Mylonas et al., 2005).

Genetic-Environmental Interactions

Fertilization, survival, and hatching during the larvae rearing stages of *D. labrax* are extremely interconnected and were thought to be influenced by the female parent and, to a lesser degree, the interaction between the female and male parents (Saillant et al., 2001ab, 2002). Although the female has more parental effect on early performance in *D. labrax*, the influence of the male can be seen in the rate of egg fertilization, egg survival, and early development (Saillant et al., 2001a), while the female/male interaction affects the length of the larvae. In the last few years, confirmation of the female and male effects on sex ratios was shown by Saillant et al. (2003a) and, with the addition of strain, by Gorshkov et al. (2003).

In many gonochoristic fishes, including *D. labrax*, phenotypic sex reflects the effect of environmental and genetic factors (Devlin and Nagahama, 2002). However, our knowledge of parental effects on the sex ratio in progeny of *D. labrax* is incomplete and acknowledged only to some extent (Blázquez et al., 1999; Saillant et al., 2002; Gorshkov et al., 2003; Saillant et al., 2003ab). The combined effects of temperature, dam, sire, or strain on the sex ratio in *D. labrax* progeny was studied by Ben-Atia et al. (2002), Saillant et al. (2002), and Mylonas et al. (2003).

In our recent work using the SE Mediterranean-Egyptian *D. labrax*, the average percent of females in four tested families was around 50 (Gorshkov et al., 2003). During our earlier *D. labrax* studies, we infrequently found a comparable sex ratio in single-pair crossings (Gorshkov et al., 1999). From our records, however, we were unable to determine a single genetic and/or environmental cause for the difference in sex ratio. The results of the above diallel crossing trial demonstrate substantial parental effects on the sex ratio. Similar results were obtained from a more complex diallel crossing experiment using a strain of *D. labrax* from the western Mediterranean region, with a noteworthy dam-temperature and sire-temperature interaction on the sex ratio (Saillant et al., 2002). Others also obtained sex differentiation by temperature manipulations (Blázquez et al., 1998; Pavlidis et al., 2000, Ben-Atia et al., 2002; Koumoundouros et al., 2002; Saillant et al., 2002), while Gorshkov and co-workers (2003) suggested that genotype-temperature interactions are the most likely factors responsible for sex determination in *D. labrax*. Therefore, it is most important to take into consideration the genetic make-up of different *D. labrax* strains as they can react differently to identical temperature management.

Gorshkov et al. (2003) found that the sex ratios of progeny families significantly diverged from a 1:1 ratio, demonstrating that Mendelian segregation of heteromorphic sex chromosomes is not responsible for sex determination in this species (Gorshkova et al., 1996). It could mean that polygenic and/or genotype-environmental relationships have an effect on the sex determination mechanism (Baroiller et al., 1999; Devlin and Nagahama, 2002). Notwithstanding, the reality is that, owing to its faster growth rate, it is more advantageous for commercial operations to raise *D. labrax* females while most fish farms in the Mediterranean area end up with a higher proportion of males (Zanuy et al., 2001; Mylonas et al. 2005; Piferrer et al., 2005).

In contrast to the morphological aspects of sex differentiation, the genetic, physiological, and chemical aspects managing this course of action are somewhat ambiguous. Differentiation in *D. labrax* gonads takes place 130-250 days after hatching at 21-26°C.

Dicentrarchus labrax females differentiate earlier than males. Mylonas et al. (2005) showed that it is possible to influence the sex phenotype by temperature manipulations months before the stage of sex differentiation. Consequently, it seems improbable that temperature is the main cause for alteration in sex steroids throughout the period of induction and the questions asked by Mylonas et al. (2005) remain unanswered: what and how does the temperature regime during early development in *D. labrax* affect its sex many weeks later?

As seen in Table 1, no one has yet been

Table 1. Temperature, period during which temperature applied, and resulting mean percentage of females among European sea bass.

Temperature (°C)	Age (days after fertilization)	Mean % females	Reference
13	1-93	73	Pavlidis et al. (2000)
13	11-51	50	Mylonas et al. (2005) NW
13	11-51	38	Mylonas et al. (2005) SE
13	55-95	65	Mylonas et al. (2005) NW
13	55-95	52	Mylonas et al. (2005) SE
13	0-346	11	Saillant et al. (2002)
15	1-11	38	Koumoundouros et al. (2002)
15	1-38	47	Koumoundouros et al. (2002)
15	1-64	66	Koumoundouros et al. (2002)
15	1-74	69	Pavlidis et al. (2000)
15	0-120	35	Navarro et al. (unpubl.)
17	11-51	51	Mylonas et al. (2005) NW
17	11-51	28	Mylonas et al. (2005) SE
17	55-95	68	Mylonas et al. (2005) NW
17	55-95	28	Mylonas et al. (2005) SE
20	1-65	26	Pavlidis et al. (2000)
20	1-56	18	Koumoundouros et al. (2002)
20	19-149	33	Saillant et al. (2002)
21	11-51	31	Mylonas et al. (2005) NW
21	11-51	8	Mylonas et al. (2005) SE
21	55-95	54	Mylonas et al. (2005) NW
21	55-95	38	Mylonas et al. (2005) SE
21	15-120	12	Navarro et al. (unpubl.)
22	15-57	6	Blázquez et al. (1998)

NW = northwestern Mediterranean Sea strains
SE = southeastern Mediterranean Sea strains

able to produce a 100% female although different time windows were experimented. Thus, additional research is required to scrutinize the most favorable temperature-exposure combination for obtaining a 100% female population. It seems, though, that a significant genetic sex determination constituent within *D. labrax* overcomes environmental pressure.

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