

Gametogenesis correlated with steroid levels during the gonadal cycle of the sea urchin *Paracentrotus lividus* (Echinodermata: Echinoidea)

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Abstract

The specific mechanism regulating reproduction in invertebrates is a field of topical interest which needs to be explored in detail considering also the intriguing possible comparison with vertebrates. In this paper levels of Testosterone (T) and Estradiol (E2) and their reciprocal ratios were determined in ovaries and testis of the echinoid model species *Paracentrotus lividus* during the year 2004 by taking into account a putative relationship between steroid levels and reproductive cycle. T levels appeared to significantly vary during male reproductive cycle, thus suggesting a possible role of this hormone in regulation of spermatogenesis as demonstrated for other echinoderms. E2 levels were lower in males with respect to females; consequently E2 involvement in oogenesis is hypothesized. In parallel with steroid levels evaluation, variations in P450-aromatase activity and its possible role on regulation of gametogenesis were also considered. Clear correlations between steroid levels and gonad index (GI), as well as between GI and reproductive cycle were not detected, suggesting that GI alone is not a reliable parameter in describing the reproductive status of the gonads. Altogether the results obtained so far confirm the presence of a relationship between steroid levels and reproductive cycle as suggested by previous results on different echinoderm species.

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1. Introduction

Reproductive physiology of echinoderms has been frequently investigated in terms of both their anatomical features and biochemical variations occurring in hormonal levels during gametogenesis. Although factors such as age, size, photoperiod, nutritional state and water temperature (Pearse and Cameron, 1991; Pearse and Bosch, 2002) were taken into account in order to define the roles of the different variables on echinoderm reproductive biology, convincing experimental evidence reported that typical hormones, particularly steroids, can have a specific role in echinoderm reproduction as well as in other physiological processes of these animals (Schoenmakers and Dieleman, 1981; Xu and Barker, 1990; Voogt et al., 1991; Hines et al., 1992; Watts et al., 1994; Wasson et al., 2000a). Different

methods, namely bioassays, chromatography, radioimmunoassay, gas chromatography–mass spectrometry (GC–MS) and NMR spectroscopy, revealed the presence of sex steroids in several echinoderm classes (Dieleman and Schoenmakers, 1979; Voogt et al., 1992; Watts et al., 1994). In particular cholesterol, progesterone, androstenedione, testosterone, 17 β -estradiol and estrone were detected in starfishes, sea urchins and in a few species of other echinoderm classes (Schoenmakers and Dieleman, 1981; Voogt and Dieleman, 1984; Xu and Barker, 1990; Wasson et al., 2000a), most of the studies being referred to asteroids (Watts et al., 1994; Barbaglio et al., 2006; Georgiades et al., 2006; Lavado et al., 2006a,b). In the seastars *Asterias rubens*, *Sclerasterias mollis* and *Asterias vulgaris*, progesterone, estrone and testosterone levels appeared to vary according to the reproductive cycle with a sex-specific relationship (Voogt and Dieleman, 1984; Xu and Barker, 1990; Hines et al., 1992).

Further laboratory tests demonstrated the ability of various echinoderms (mainly asteroids and echinoids and a few

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ophiuroids, holoturoids and crinoids) to synthesize sex steroids through metabolic pathways comparable to those characteristics of vertebrates. In particular, the activity of Δ^5 - Δ^4 -isomerase, 17 β -hydroxysteroid dehydrogenase, 5 α -reductase, 3 β - and 3 α -hydroxysteroid dehydrogenase, 11 β -hydroxylase and 11 β -hydroxysteroid dehydrogenase was demonstrated with a tissue-, and sometimes sex-specific pattern (Schoenmakers and Voogt, 1981; Voogt et al., 1990; Hines et al., 1992, 1994; Watts et al., 1994; Janer et al., 2005a). At present just a few studies reported a P450-aromatase activity in echinoderms (Den Besten, 1998; Lavado et al., 2006a,b). Enzymes responsible of phase II metabolism were also identified in asteroids and echinoids (Voogt and van Rheenen, 1986; Janer et al., 2005b). As in other invertebrates, such as molluscs (gastropods and bivalves), phase II metabolism might play a key role in the metabolism and/or excretion of endogenous steroids (Gooding and LeBlanc, 2001; Janer et al., 2005b).

Although sex steroids and steroid-metabolizing enzymes were detected in echinoderms, the relationship between steroids and reproduction was not yet completely demonstrated. Nevertheless, a series of investigations reported that dietary administration of steroids to experimental animals may produce physiological effects *in vivo* on different reproductive parameters (Wasson et al., 2000b). Moreover, in *A. rubens* and in *Asterina pectinifera* an increase in oocyte diameter and in lipid amount *in vivo*, as well as an increase in RNA levels *in vitro* was detected following exposure of ovarian fragments to estradiol (Schoenmakers et al., 1981; Takahashi and Kanatani, 1981; Van der Plas et al., 1982).

With regard to sea urchins, data on steroid levels and metabolism are scarce and limited to a restricted number of species. A historical pilot-test realised by Donahue and Jennings (1937) showed that extracts from the echinoid *Lytechinus variegatus* could induce estrogen-like responses in the reproductive tracts (vagina and uterus) of ovariectomized rats. Later on, other authors (Botticelli et al., 1961) demonstrated for the first time the presence of progesterone-like substances in another sea urchin (*Strongylocentrotus franciscanus*). According to Wasson et al. (2000a), steroid levels measured in *L. variegatus* (testosterone: 60 to 320 pg/g – estradiol: 5 to 160 pg/g) were much lower than levels in asteroids (testosterone: 140 to 5500 pg/g gonad – estradiol: 4 to 460 pg/g gonad; Hines et al., 1992), probably due to different regulation mechanisms of gamete nutrition in the two echinoderm groups (Walker, 1982; Pearse and Cameron, 1991; Wasson et al., 2000a).

With regard to steroid metabolism, Watts et al. (1994) demonstrated in three echinoid species that androstenedione was primarily metabolized into testosterone through the activity of 17 β -hydroxysteroid dehydrogenase in gut and gonads, the conversion rate being higher in intestinal tissues. The presence of 5 α -androstenedione as a secondary metabolite of androstenedione suggested a competition between 17 β -hydroxysteroid dehydrogenase and 5 α -reductase, with a sex-specific difference in the respective activities recorded in ovaries and testes. The activity of 11 β -hydroxylase and 11 β -hydroxysteroid dehydrogenase related to production of 11-oxygenated androgens was detected in testes of *L. variegatus* (Watts et al., 1994). 11 β -keto

testosterone and 11 α -keto testosterone have been identified previously in other echinoderm species (Watts et al., 1993). More recently, tissue-specific differences in steroid metabolic pathways were detected in *Paracentrotus lividus* (Janer et al., 2005a): in gonad tissues testosterone was primarily transformed to dihydrotestosterone by 5 α -reductase, whereas in gut it was transformed to 4-androstene-3 β ,17 β -diol by 3 β -hydroxysteroid dehydrogenase. Interestingly, from a comparative point of view, 11-keto testosterone represent the bioactive androgen in teleost fishes (Fostier et al., 1983), whereas dihydrotestosterone is a potent androgen in humans (Wilson, 2001) and in most vertebrates (Sperry and Thomas, 1999a,b). Sex-specific differences in androstenedione metabolism have been demonstrated in *L. variegatus* (Wasson et al., 1998). The production of 5 α -diols reported above for *L. variegatus* and *P. lividus* resulted to be an intriguing aspect taking into account the physiological role of these hormones in vertebrates: 3 α ,5 α -diols appear to control the sperm fertilizing capacity in male rats (Lubicz-Nawrocki, 1973). Lavado et al. (2006a,b) reported the presence of aromatase activity in digestive tube and gonads of *P. lividus* according to the stereospecific loss of hydrogen from the C-1 β position of 1 β -[3H]androstenedione during aromatization and the formation of tritiated water. Aromatase activity showed up to 20-fold higher activity in digestive tube than in gonads, and no sex related differences were detected in *P. lividus*. These data suggest that the biosynthesis of E2 from T could have occurred in digestive tube of *P. lividus* (Lavado et al., 2006a,b). Furthermore, as reported above, *L. variegatus* was shown to be able to metabolize estrogens to esters and secondarily to aqueous-soluble products (Hines et al., 1994).

Finally, both gonad index and gametogenesis were demonstrated to be influenced by the experimental dietary administration of progesterone, testosterone and estradiol in *Pseudocentrotus depressus* (Unuma et al., 1999; Wasson et al., 2000b) and *L. variegatus* (Wasson et al., 2000b).

The action mechanism of steroids in echinoderms is still to be explained. Wasson et al. (2000a) suggested a receptor-mediated effect for these hormones. Although no definitive evidence was obtained on the existence of steroid receptors in echinoderms, recently radioreceptor assays showed the presence of testosterone and estradiol binding sites in *P. lividus* (Lutz et al., 2004). Taking into account the results reported above, a possible role for sex steroids on reproductive physiology is further suggested by past and recent available data regarding effects of *endocrine disruptors* on gametogenesis, fertilization and development in this and other echinoderm species (Wasson and Watts, 1998; Moschino and Marin, 2002; Novelli et al., 2002; Pesando et al., 2004; Candia Carnevali, 2005; Roepke et al., 2005, 2006; Barbaglio et al., 2006; Kiyomoto et al., 2006; Lavado et al., 2006a,b).

The present study focuses on variation of steroids level during *P. lividus* reproductive cycle. *P. lividus* is a common sea urchin species along the Mediterranean coasts. It is found in the lower rocky shore, in the shallow sublittoral areas (at depth of 3 m or more) and in beds of seagrass (Riedl, 1991). The ecological relevance of this echinoid is related to its impact on the algal community as well as to its common employment as

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