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Prostaglandins and its Role in Aquatic Reproduction: A Review

Maysa Enayatmehr[1], Shahla Jamili[2]

[1]Phd student in Marine Biology, Department of Marine Biology, Science and Research Branch, Islamic Azad University, Tehran, Iran

[2] Iranian Fisheries Science Research Institute, Agricultural Research Education & Extension Organization

Abstract: ***Prostaglandins (PGs) are a group of biologically active compounds that play major roles inmammalian andnon-mammalian physiology in both health and disease. They function in many different ways and in all major organs. This article reviews the basic physiology of prostaglandins in marine organismand major focus is their application in aquaticreproduction. Present study indicates prostaglandin E2 (PGE2) has been detected in reproductive organs, and may play a role in the control of ovarian maturation in teleost and crustacean.Moreover, we found that administration of PGE2 stimulated the ovarian maturation in these species by shortening the length of the ovarian cycle, increasing ovarian-somatic index.***

Keywords: Prostaglandins**;** aquatic reproduction**;** maturation

1. Introduction

Prostaglandins (PGs) are physiologically active substances occurring primarily in human and sheep seminal plasma. They are also present in lesser amounts in uterus, lungs, brain, iris, thymus, pancreas and kidney tissues. Prostaglandins are biosynthesized from C20 polyunsaturated fatty acids and, widely distributed in mammalian tissues. In contrast to hormones, PGs neither circulate in the body nor stored in tissues. Rather they are synthesized locally on demand, perform a tissue-specific function and then rapidly inactivated by metabolic enzymes. They act in Nano gram quantities on reproductive, gastrointestinal, respiratory and cardiovascular systems to produce physiological effects. Their importance in therapeutic abortion and regulating menstruation, fertility and conception is well established. Their use in prevention and treatment of peptic ulcers, thrombosis and control of blood pressure is envisaged. Due to their pivotal role in the biological system and application in pharmaceuticals use, extensive work has been done in this area. Prostaglandins are biosynthesized from the essential polyunsaturated fatty acids (unpublished data), such as 8,11,14-icosatrienoic acid (dihomolinolenic acid (Legler et al., 2010); 5,8,11,14-eicosatetraenoic acid [arachidonic acid (Harizi et al., 2008)] and 5,8,11,14,17- eicosapentaenoic acid (Legler et al., 2010). Van Drop et al 26, 27 have demonstrated that the fatty acids (Bouarab et al., 2004), (Harizi et al., 2008) and (Legler et al., 2010) are precursors of the prostaglandins PGE1, PGE2 and PGE3, respectively. Arachidonic acid (Harizi et al., 2008) in mammalian system is converted into the prostaglandins (PG2 series, (unpublished data) by various enzymes via endoperoxide route. The enzyme phospholipase-A releases the precursor such as arachidonic acid (Harizi et al., 2008) which exists in tissues as phospholipids. It is then acts upon by other prostaglandin synthesizing enzymes.

In 1969, Weinheimer and Spraggins reported the first high yield isolation of non-mammalian type, (15*R*)-PGA2 (Ogiwara et al., 2010) and its methyl ester acetate (Weinheimer et al., 1969) from the Caribbean gorgonea*Plexaurahomomalla*(Esper). This report stimulated a worldwide search of PGs in marine life. Subsequently it was found that some forms of *P. homomalla*contained various mammalian-type PGs, such as (15*S*)-PGA2 (Gregson et al., 1979), PGE2 (Sorbera et al., 2001), 13-14-*cis*-PGA2, 15-acetate, 13,14- dihydro-PGA2. Later on by monitoring the activity towards isolated guineapig ileum, PGF2 (Honda et al., 1991) was isolated from the Japanese coastal gorgonean, *Euplexauraerecta*. The occurrence of PGs in marine life other than gorgonians was also reported, PGE2 (Sorbera et al., 2001) and PGF2 (Honda et al., 1991) are even isolated from the Australian red alga *Gracilaria lichienoides.*31 This was the first report of the occurrence of PGs in plant. The red soft coral *Lobophytondepressum* was found to contain PGF2 (Honda et al., 1991) 11-acetate methyl ester and its 18-acetoxy derivative as well as their two corresponding free carboxylic acid. The Hawaiian octocoral*Telestoriisei*, which lacks symbiotic photosynthetic algae, yielded a series of highly functionized halogenated prostaglandins named punaglandins. The Okinawan soft coral *Clavulariaviridis*Guoy and Gaimard (*Stoloniferaclavulariidae*) afforded a number of prostaglandins name claviridenones.

2. Role of Prostaglandins in Fish Reproduction

Knowledge the roles of prostaglandins (PGs) in mammalian reproduction have expanded dramatically over the last decade (Legler et al., 2010). Although PG involvement in reproduction of non-mammalian vertebrates has received considerably less attention, these compounds apparently play important roles in oviposition in birds (Hertelendy and Biellier 1978), ovulation in fish (Sumpownon et al., 2015), and female sexual behavior in fish and amphibian(Stacey 1976. 1981**)**. In this report we review what is known of PG functions in fish reproduction and relate these findings to what we believe to be relevant studies in other vertebrate classes.

3. Prostaglandins and Reproduction in Male Teleost

In male teleost, PGs were first identified in testes of a flounder (PGE,). *Plrobichfhkaysolivac.cus.*andbluefin tuna (PGE2 And PGF2α), *jrhunnlrs t11ynnu.s.* and in semen of chum salmon (PGE,), *Ovzcorhynchuskefa*(Nomura et al. 1973). Bouffard (1979) used radioimmunoassay to measure both blood and gonadal levels of PGF, PGE, and PGB during gonadal recrudescence in male goldfish, *Carcsssius 6durcdPz~s.* Changes in blood and testicular PG levels were not obviously con-elated with specific stages of gonadal inaturation in untreated males. However, plasma levels of PGE, but not PGF or PGB. Were significantly elevated 10 h following injection of human chorionic gonadotropin (KG).Bouffard (1979) suggests that PGE, known to stimulate vasodilation and increase vascular permeability in mammals (Legler et al., 2010), may mediate the effect of gonadotropin on testicular hydration in goldfish (Clemens and Grant 1964).

4. Prostaglandins and Reproduction in Female Teleost

There is much evidence that in the rat PG (particularly PGE,) stimulates luteinizing hormone release (Ojeda et al. 1979). Indeed, the recent work of Ojeda et al. (1979) indicates that stimulation of LH-RH release by catecholamines in the rat is mediated by PGE2 acting directly on, and perhaps synthesized within, LH - WH neurons. There are few published accounts of PG effects on GtH secretion in fish. Peter and Billard (1976) found that injection of PGF2, or PGE2, but not PGE,into the third ventricle of the brain decreased immune-reactive serum GtH 30 min postinjection in mature female goldfish. In contrast, Singh and Singh ***6*** 1976) have shown that daily intraperitoneal (ip) injections of PGF2, or PGE, induce ovulation within 2-6 **d** in the catfish, *Heteropnerastefossilus.* Ashypophysectomy blocks this ovulatory response, and PGs stimulated both serum and pituitary GtH activity (measured by ovarian "P bioassay in hypophysectornized*Heteropneuste)* Singh and Singh suggest PG exerts this ovulatory action by stimulating GtH release. The 2-6 d latency to PG-induced ovulation (Singh and Singh 1976) is considerably in excess of the 18 h (maximum) latency to ovulation in *Heteropneustes*following GtH injection at similar temperatures (Sundararaj et al. 1976). Indicating PGs did not induce rapid release of ovulatory levels of GtH. Whether PGs affect GtH secretion in *Carassius*nd*Heteropneustes*by an action on the hypothalamus or the pitknitary is not known. The apparent use of hypophysectomized recipients to assay hypothalamic extracts (Singh and Sinph 1979) makes it difficult to accept the claim of Singh and Sinph (1979) that PG exerts its action on the pituitary.

Kapur and Toor(1979) demonstrated that a single injection of indomethacin (Id) blocked ovulation for up to 12 d in carp *Cjprinus*carpio, held in conditions in which controls ovulated spontaneously within 24 h. As clonaiphene citrate, which induces GtH release in carpand ovulation in intact but not in hypophysectomized goldfish (Pandey et al. 1973), restored ovulation in Id-treated carp, it seems likely that Id blocked preovulatoryGtH release.

5. PGS and ovulation

Many studies of a wide variety of mammalian species have demonstrated an obligatory role for PG in ovulation (Legler et al., 2010). Generally, ovulation (follicular mature) is blocked if BG synthesis is inhibited in mature follicles exposed to ovulatory levels of GtH, although oocyte final maturation and follicle luteinization arc not impaired. Exogenous PG (especially KF2) is usually effective in restoring ovulation of GtH-stimulated follicles in which the normal preovulatory increase in follicular PG has been blocked by PG synthesis inhibitors. Similarly in teleost, there is considerable evidence that PGs arc involved in ovulation.

5.1 PGS and female sexual behavior

PGs have been implicated in the control of female sexual behavior in rats (Buntin and Lisk1979), guinea pigs (Marrone et al. 1979), and amphibians, (Didcow and Nemiroff 1981) and teleosts, (Sumpownon et al., 2015). In mammals and teleost PGs apparently act on the brain to induce these behavioral changes and, unlike estrogen may be effective within minutes (Stacey and Peter 1979). In goldfish PG appears to mediate the stimulatory effect of intraovarian ovulated oocytes on female spawning behavior (Stacey 1976). Female sexual behavior in goldfish is normally dependent on the presence of ovulated oocytes but can be induced in non-ovulated females when ovulated oocytes (from donor females) are injected through the cvipore and into the ovarian lumen (Stacey and Liley 1974). In non-ovulated females injected with ovulated oocytes, spawning behavior is completely inhibited by Hd and restored in Id-treated fish by injection of PGs (especially PGF) (Stacey 1976). As well, female goldfish perform progressively less spawning behavior when they are tested immediately, 1h or 2 h following injection of PGF2α suggesting the PG-sensitive substrate: regulating spawning behavior is activated only when circulating PC3 levels are sufficiently high.

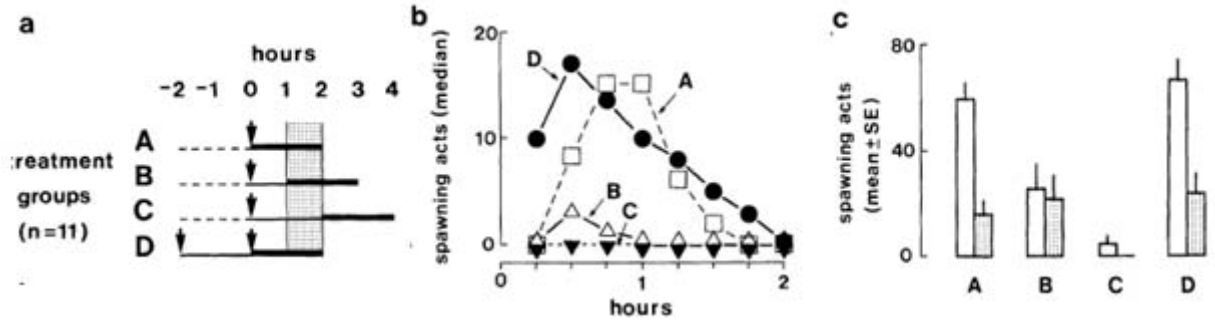

Figure 1: Effect of delay between PGF2, injection and behavioral testing, and of a second PGF,, injection, on spawning behavior in female goldfish. (a) arrows indicate times of PGF,, injections (intnamuscular, 0.1 pg - g I) and horizontal bars indicate tirile of 2 h behavioral test; (b) median number of female spawning acts per 15-min interval of 2 h test; (6) total number of spawning acts (mean 2 SE) performed during thc 2 & test period (clear bars) or during the second hour (stippled bars) following the single (groups A and B) or the second (group D) XF2, injection (group C not tested during the second hour postinjection

They recently demonstrated that prostaglandin E2 (PG2) increases osteoclastic activity and induces bone resorption in both *in vitro* and *in vivo* experiments using goldfish. In the fish reproductive period, the plasma calcium (Ca) level in female teleosts increases remarkably to make vitellogenin, which is a major component of egg protein and a Ca–binding protein. In this period, however, there is no reported relationship between PGE2 and Ca metabolism in fish. To clarify the Ca metabolism in fish reproduction, they examined plasma PGE2 and Ca levels and measured tartrate–resistant acid phosphatase (TRAP) activities as an indicator of osteoclastic activity in goldfish. Plasma PGE2 levels in the reproductive stage significantly increased as compared with those in non–reproductive stages. Also, both plasma Ca and TRAP increased in the reproductive stage. Using the goldfish scale *in vitro* assay system, they recently demonstrated that PGE2 acts on osteoblasts and then increases the osteoclastic activity in the scales of goldfish as it does in the bone of mammals (Omori *et al*., 2012). Prostaglandin E2 (PGE2) functions to bone metabolism and is an important hormone in bone and promoter ofosteoclastogenesis (Kaneko *et al*., 2007).

5.2 Changes in GSI, plasma PGE2 levels, Ca levels, andTRAP activities of female goldfish in reproductiveand non-reproductive stages

There was a significant difference in the values ofGSI between goldfish in March and August (Fig. 2). In addition, the plasma PGE2 levels, Ca levels, and TRAP activities of female goldfish in March were significantly higher than those in August (Figs. 3, 4, and 5).

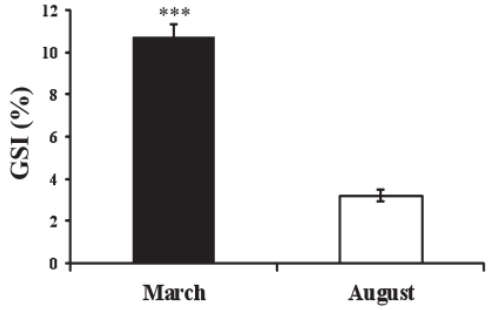

Figure 2: GSI values of female goldfish in the reproductive (March) and non–reproductive (August) stages. *** indicates a statistically significant difference at $p<0.001$ in the values of the reproductive and non– reproductive stages.

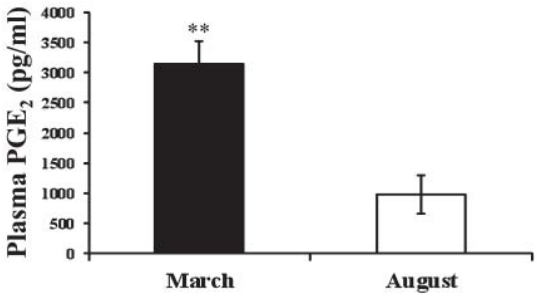

Figure 3: Plasma PGE2 values of female goldfish in the reproductive (March) and non–reproductive (August) stages. ** indicates a statistically significant difference at $p<0.01$ in the values of the reproductive and non–reproductive stages

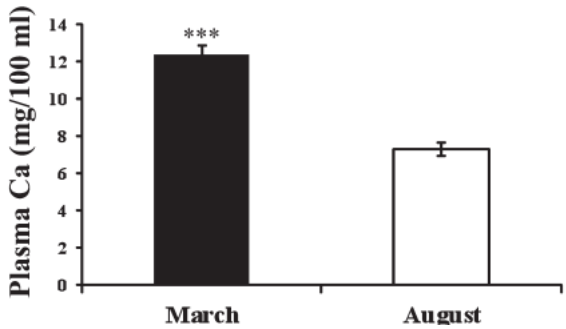

Figure 4: Plasma Ca values of female goldfish in the reproductive (March) and non–reproductive (August) stages. *** indicates a statistically significant difference at $p<0.001$ in the values of the reproductive and non– reproductive stages.

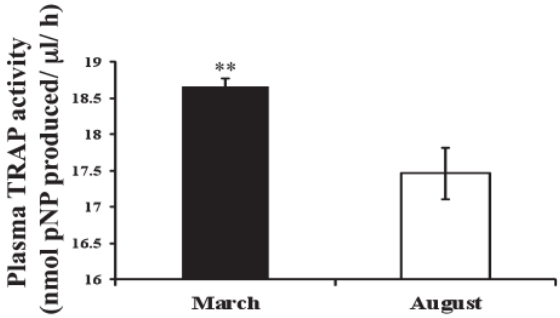

Figure 5: Plasma TRAP activity (nmolpNP produced/μl/h) values of female goldfish in the reproductive (March) and

non–reproductive (August) stages. ** indicates a statistically significant difference at $p<0.01$ in the values of the reproductive and non– reproductive stages.

The results of correlation among GSI, plasma PGE2 levels, Ca levels, and TRAP activities are indicated in Table 1.

Table 1: Correlation among GSI, plasma Ca levels, PGE2 levels, and TRAP activities (n=14).

Table 1. Correlation among GSI, plasma Ca levels, PGE_2 levels, and TRAP activities (n=14).

	r values	*p* values
GSI vs Plasma PGE_2	r=0.790	p=0.0007
GSI vs Plasma Ca	r=0.813	p=0.0004
GSI vs Plasma TRAP	r=0.631	p=0.015
Plasma Ca vs Plasma PG_{E2}	r=0.635	p=0.014
Plasma Ca vs Plasma TRAP	r=0.584	p=0.028
Plasma PGE_2 vs Plasma TRAP	r=0.514	p=0.058

In an *in vivo* experiment, furthermore, hypercalcemia was induced as a result of osteoclastic bone resorption after an intraperitoneal injection of PGE2 into goldfish (Omori *et al*., 2012). Taking these results into consideration together with the present study, they have concluded that PGE2 acts as a calcemic hormone in fish reproduction.

In the present study, the highest correlation between GSI and plasma Ca was recognized. They think that several hormones, with the exception of PGE2, are involved in Ca metabolism during fish reproduction. The candidate for this hypercalcemic hormone is estrogen. In female teleosts, estrogen enhances the synthesis of vitellogenin, which is a major component of egg protein and a Ca–binding protein (Tinsley, 1985; Kwon *et al*., 1993). At the same time, estrogen promotes Caresorption from the scales by activating osteoclasts (Persson*et al*., 1995; Suzuki *et al*., 2000; Suzuki and Hattori, 2003; Suzuki *et al*., 2009). Consequently, plasma vitellogenin and Ca levels increase corresponding to the increase in estrogen level (Norberg*et al*., 1989). PGE2 is closely related to ovulation (late stage of fish reproduction) (for a review, see Takahashi *et al*., 2013), suggesting that in the early stage of fish reproduction, estrogen acts as a hypercalcemic hormone, and then PGE2 plays roles in both ovulation and Ca metabolism . However, it should be noted that there are clear differences in the architecture of ovarian follicles in mammalian and non-mammalian species. The large follicle in mammals consists of a round oocyte and two types of somatic cells, granulosa cells and theca cells. Some of the granulosa cells surround the oocyte and form the COC, which protrudes toward the interior of an antrum filled with follicular fluid. The remainder of the granulosa cells are positioned just below the basement membrane in multiple cell layers known as the membrane granulosa. Theca cells, which are present on the outside of the basement membrane, also exist in multiple cell layers with rich extracellular matrix (ECM) components. On the other hand, the large follicle of non- mammalian species (from Pisces to Aves) consists of a single layer of granulosa cells surrounding an oocyte, a single layer of theca cells, and a basement membrane between the two layers (Fujimori et al., 2012). PGE2 has been reported to be involved in reproductive processes including ovarian-follicular function, ovulation, luteolysis and parturition in many species (Armstrong, 1981; Sirois et al., 2004). Several studies reported that in invertebrates PGs are also involved in controlling reproduction, including the egg-laying and associated behaviors in insects and mollusks (Stanley, 2006; Ono et al., 1982). In the crayfish, *Procambaruspaeninsulanus*, ovarian PGE2 increased through all of vitellogenic stages, while prostaglandin F2a (PGF2a) did not significantly increase until the late vitellogenic stage (Spaziani et al., 1993). In Kuruma prawn, the amount of PGE2 and PGF2a reached their highest levels at stage I followed by marked decrease in stage IV and V ovaries, which attest to their roles in early oogenesis (Tahara and Yano, 2004). These studies provide evidence that PGs are involved in the regulation of ovarian maturation in crustaceans. Key enzymes for PGs biosyntheses, cyclooxygenase (COX) and prostaglandin G/H synthase (PGHS) were found to be most abundant in the nuclear envelope and endoplasmic reticulum of cells that produce PGs in insects and some crustaceans (Varvas et al., 2009). COX is present in all vertebrates and has been used as a marker enzyme for the synthesis of PGs (Smith et al., 2000). The COX-mediated pathway of PG biosynthesis in non-vertebrate animals was first detected in the arctic soft coral, *Gersemiafruticosa* (Varvas et al., 1994). Subsequently, COX enzymes were cloned from this coral (Koljak et al., 2001) and also from Plexaurahomomalla. Several putative genes associated with eicosanoids biosynthesis are reported in Daphnia pulex (Heckmann et al., 2008). In the freshwater field crab, *Oziotelphusasenexsenex*, there was a significant increase in activity of prostaglandin synthase enzymes during the late vitellogenic stages compared to the early non vitellogenic stage ovaries (Reddy et al., 2004). Moreover, injections of PGE2 or PGF2a into these crabs stimulated the ovarian maturation. Recently, the expression of several genes involved in the biosynthetic pathways of PGF2a and PGE2 were detected in the ovaries of Penaeusmonodon (Wimuttisuk et al., 2013).

The length of ovarian maturation cycle and the ovarian-somatic index. The length of the ovarian maturation cycle of prawns injected with PGE2 at 10^{-7}, 10^{-8} and 10^{-9}mol/prawn were shortened to 20.33 $\pm$ 3.51, 23.08 $\pm$ 3.77, 24.28 $\pm$ 2.35 days which were significantly different when compared with the control group (34.08 $\pm$ 5.76 days) (Fig. 6). The effects of PGE2 administrations on ovarianmaturation as determined by the ovarian somatic index (OSI) were presented in Fig. 7. The OSI values of PGE2-treated and control prawns were not significantly different up to days 16 post-injection. At day 20 the OSI values of all PGE2-treated prawns (5.7 $\pm$ 0.7%, 6.5 $\pm$ 0.6%, and 7.2 $\pm$ 0.9%, respectively) were significantly higher than that of the control (2.0 $\pm$ 0.2%).

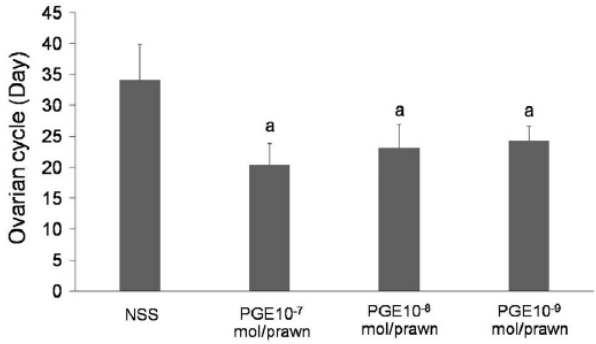

Figure 6: The induction of ovarian maturation cycle by injecting PGE2 at the doses 107, 108 and 109 mol/prawn at days 0, 4, and 8. The values are the lengths of ovarian cycle expressed as mean ± S.E., and ''a'' indicate significant differences when compared with the control $P < 0.05$. The ovarian cycle is shortened in all PGE2-treated groups.

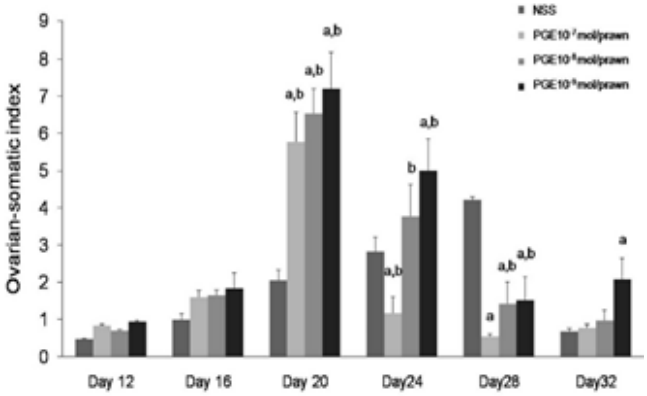

Figure 7: Ovarian-somatic index (OSI) values at day 12 to day 32 after PGE2 injections: at day 20 the OSIs significant increase in all PGE2-treated groups when compared with the control. At day 24 all PGE2-treated groups show significantly decreased OSIs when compared with the same groups on day 20. However, when compared with the control at the same day (24) the PGE2 10^{-7}-treated group shows lower OSI while the remaining groups show higher OSI values ($P < 0.05$). There were no significant differences between the OSI values between the PGE2-treated and the control groups at days 0, 4, and 8 (data not shown). n = 48 prawns per group. Values are mean ± S.E., and ''a''indicates significant difference when compared with the control group at the same day while ''b'' indicates significant difference when compared with the same groups at the preceding day ($P < 0.05$).

5.3 Oogonia and oocyte proliferations

The proliferations of oogonia and oocytes in the ovaries of each group were estimated by BrdU-labeling method which detected dividing cells that incorporated into their newly synthesized DNA. When observed under a light microscope, the BrdU-labeled cells in the ovarian sections showed distinct purple nuclei, and the labeled cells appeared to be mostly oogonia (Og) and some early oocytes (Oc1) (Fig. 8A(ii)). The numbers of labeled cells were counted in all groups (Fig. 8A(i–v)) and presented as the histograms showing BrdU-labeled nuclei/mm2 (Fig. 8B). All PGE2-treated groups showed significantly higher numbers of cell division than the control group at day 12, while at days 16 the numbers of cell division in the treated groups appeared to decrease but still higher than the control. At days 20 and 24 the numbers of dividing cells in the treated groups were not different from that of the control group (data not shown).

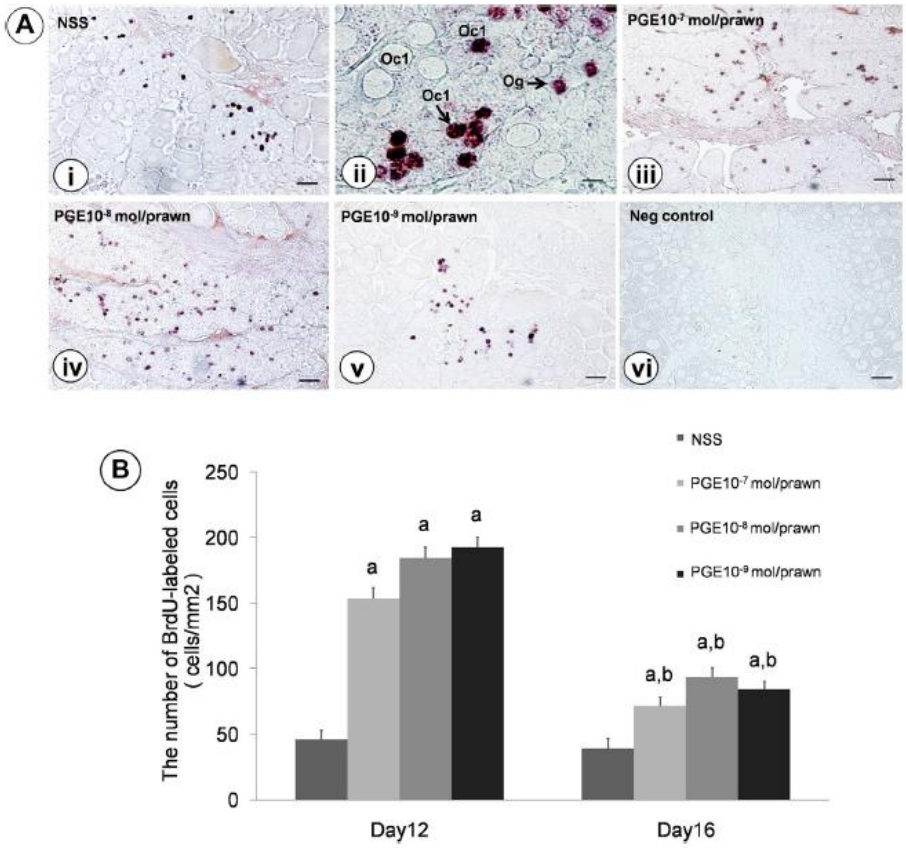

Figure 8: (A) Estimations of oocyte proliferation in the control group (NSS) and PGE2-treated groups, using BrdU labeling, at days 12. The labeled (dividing) cells showed dark purple-colored nuclei. Neg control = negative control, scale bars = 50 lm. (B) The numbers of BrdU-labeled nuclei per mm2. At day 12, a low number of BrdU-labeled nuclei were detected in the ovarian sections of the control group (46.0 ± 6.93 cells/mm2), while the numbers of BrdU-labeled nuclei in all PGE2-treated groups are significantly increased: PGE 10-7 mol/prawn at 153.16 ± 8.61 cells/mm2, PGE 10-8 mol/prawn at 184.5 ± 8.05 cells/mm2, and PGE 10-9 mol/prawn at 192.54 ± 7.96 cells/mm2. At day 16, BrdU-labeled nuclei in all treated groups markedly decrease compared to day 12: PGE 10-7 mol/prawn at 71.5 ± 6.82 cells/mm2, PGE 10-8 mol/prawn at 93.5 ± 7.27 cells/ mm2, and PGE 10-9 mol/prawn at 84.12 ± 6.36 cells/mm2, but the numbers of labeled cells are still significantly higher than in the control group (39.25 ± 7.53 cells/mm2). Histograms show mean number ± S.E. of BrdU-labeled nuclei/mm2 area in three nonconsecutive sections per prawn (n = 8 animals). Values are mean ± S.E., and ''a'' indicates significant difference when compared with the control group at the same day while ''b'' indicates significant difference when compared with the same groups at the preceding day ($P < 0.05$).

Apart from other functions, it is well known that PGs are key mediators of reproductive processes in mammals, including follicular development, ovulation, luteolysis, and parturition (Flores and Barlund, 2009). In fish PGs was reported to be involved in ovarian maturation, ovulation (follicular rupture), and secretion of gonadotropin in females (Lister and Van Der Kraak, 2008; Fujimori et al., 2012). For invertebrates there have been many reports on the existence of PGs in a few mollusks, and it has been proposed that they are associated with gonadal maturation, egg production, and spawning in freshwater snails and bivalves. In insects such as the cricket, Teleogrylluscommodus, PGE2 injection increased the number of eggs production (Watzer et al., 2009). It has also been reported that PGs signaling is involved in the regulation of vitellogenesis in Rhodniusprolixus (Medeiros et al., 2002), and ovarian follicle development in Bombyxmori (Machadoa et al., 2007). In a study, we have detected PGE2 in the early oocyte stages (Oc1 and Oc2) in the ovaries of M. rosenbergii as defined by Meeratana and Sobhon (2007). Correspondingly, COX1 and PGES, the key enzymes involving in the biosyntheses of PGE2, could also be detected in these previtellogenic oocyte stages and vitellogenic oocyte Oc3, with the highest immunoreactivity appearing in Oc1 and Oc2. These data strongly support the notion that PGE2 is present and synthesized locally in the fresh water prawn ovaries. These findings are similar to the situation in the penaeid shrimp, P. monodon, in which Wimuttisuk et al. (2013) could detect nine putative genes of the enzymes associated with eicosanoid biosyn thesis pathways from P. monodon EST Project (Tassanakajon et al., 2006) and transcriptomic data of marine organisms from Marine Genomics Project (McKillen et al., 2005), including the terminal enzymes prostaglandin E synthase (PmPGES), prostaglandin D synthase (PmPGDS), and prostaglandin F synthase (PmPGFS).

The actual detection of PGE2 by immunohistochemistry in pre vitellogenic oocytes and the finding that its levels were high in ovarian stages I and II strongly indicated that PGE2 may be involved in stimulating proliferation, development and differentiation of early stage oocytes before the onset of vitellin synthesis. Additionally, PGE2 may also stimulate vitellogenesis process as it was found that in M. rosenbergiivitellin protein was synthesized in late oocyte stages (Oc3 and Oc4) (Soonklang et al., 2012) following the appearance of the peak level of PGE2 in stage II. These propositions are supported by their in vivo bioassays where they have demonstrated the effect of PGE2 by directly injecting this hormone at the dose 10^{-9}–10^{-7}mol/prawn, which could accelerate the ovarian maturation by shortening the length of the ovarian cycle by at least one week. Additionally, the OSIs of the PGE2-treated prawns were markedly increased between 16 and 20 days then suddenly decreased at 24 days, which corresponded with the changing of ovarian maturation from the middle phase to the late phase that eventually lead to an early spawning. This was also supported by the simultaneous rise and fall of the hemolymphvitellogenin levels during the same period. Presumably, Vg is released from both the hepatopancreas and ovaries into the hemolymph (Soonklang et al., 2012). Furthermore, PGE2 was demonstrated to stimulate cell division in the proliferative zone of oogenetic pouch, and the labeled cells were mostly oogonia and primary oocytes (Meeratana and Sobhon, 2007). The active cell proliferation in the ovaries of the treated groups, as demonstrated by BrdU labeling, occurred during early phase of ovarian cycle (12 days) but started to decline in middle phase of ovarian cycle (16 days) when most of the oocytes had differentiated into vitellogenic stages, i.e. Oc3. In late the phases (stage IV) of the ovarian cycle the numbers proliferating cells were extremely low as most oocytes became the fully mature Oc4 which were not dividing.

6. Conclusion

Taken together the data from the present study provide strong evidence that PGs, especially PGE2, is an important molecule in reproduction cycle specially signaling the ovarian maturation, oocytes's proliferation and differentiation in females of marine organism. Its exploitation in aquaculture with regards to promoting GSI in male and also female fecundity, gamete and larval productions should be further explored as this molecule is quite stable when incorporated in feed that can be fed to animals or in bio plastic microcapsules that can be directly administered to the female broodstock. These are the topics of their current research which, if successful, will help to increase the productivity of these species by aquaculture.

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