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Deviation of habitat salinity during seasonal gonad recrudescence affects plasma sex steroid levels and suppresses gonadal maturation in an euryhaline fish *Etroplus suratensis*

Babita Mandal[1] | Paramita Banerjee Sawant[1] | Subrata Dasgupta[1] | Narinder Kumar Chadha[1] | Jitendra Kumar Sundaray[2] | Bhawesh T. Sawant[3] | Aritra Bera[1]

[1]Division of Aquaculture, Central Institute of Fisheries Education Versova, Mumbai, India

[2]Central Institute of Brackishwater Aquaculture, Kakdwip Research Centre, West Bengal, India

[3]Fisheries Resource Management, Taraporevala Marine Biological Research Station, Dr. Balasaheb Sawant Konkan Krishi Vidyapeeth, Mumbai, India

Correspondence
Paramita Banerjee Sawant, Division of Aquaculture, ICAR - Central Institute of Fisheries Education, Versova, Mumbai, India.
Emails: aquaparo@gmail.com; paromita@cife.edu.in

Present addresses
Babita Mandal and Aritra Bera, Central Institute of Brackishwater Aquaculture, R. A. Puram, Chennai, India.
Jitendra Kumar Sundaray, Central Institute of Freshwater Aquaculture, Kausalyaganga, Odisha, India.

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Abstract

Impact of osmoregulation on plasma sex steroid levels and gonadal histo-architecture was monitored to elucidate the effects of deviation from habitat salinity on gonadal recrudescence in an active reproductive season of an euryhaline fish *Etroplus suratensis* (pearlspot). Fish were maintained in three different salinities of 0 ppt Fresh Water (FW), 15 ppt Brackish Water (BW) and 30 ppt Sea Water (SW) for a period of 60 days. Plasma osmolality values were found to be significantly highest in SW-acclimated fish accompanied by highest levels of plasma K^+ and Cl^- ions. The progress of gonadal recrudescence was higher in BW followed by FW and SW as evident from the cellular features of gonads and increased level of plasma sex steroids, such as, in case of female and 11-keto Testosterone and Testosterone in case of males. Plasma cortisol levels were comparatively higher in fish of both sexes in SW group. Significantly high levels of cortisol in SW suggest its role in hypo-osmoregulation and associated stress. This study clearly reveals that salinity changes during the active reproductive phase can suppress the steroid-mediated gonad recrudescence maximally under hypo-osmoregulation in an euryhaline fish.

KEYWORDS
cortisol, *Etroplus*, gametogenesis, osmoregulation, sex steroids

1 | INTRODUCTION

The green chromid or pearlspot, *Etroplus suratensis* is a brackish water cichlid fish that is widely distributed in the estuaries of peninsular India and Sri Lanka (Padmakumar, Bindu & Manu, 2009). Being an euryhaline fish, it can survive in both fresh and brackish water salinities (Ward & Wyman, 1977). Salinity tolerance, ability to breed in confined waterbodies, good growth rate and omnivorous feeding habits makes *Etroplus suratensis* a candidate species for brackish water aquaculture (Padmakumar et al., 2009). In spite of that, lack of required quantities of seed has been a serious constraint in intensive farming of this species. Reproduction in fish involves complex processes, regulated by the integration of endogenous neuroendocrine, endocrine and autocrine/paracrine signals with environmental factors (Baroiller & Guiguen, 2001; Bromage, Porter & Randall,2001; Segner, Eppler & Reinecke, 2006). Although very little published data exist on effects of salinity on reproductive development, it appears that salinity may act as a subsidiary or permissive cue to other environmental factors in some species (Magwood, Bromage, Duncan & Porter, 1999; Tamaru, Lee, Kelley, Miyamoto & Moriwake, 1994). Moreover, cichlid parental strategy attempts to imbricate the spawning (with period of the year) when physical factors like salinity and

temperature facilitate the maximum survival and growth of the young ones (Faunce & Lorenz, 2000). During gonadal growth phase, teleost fish spend enormous amount of energy for reproduction (Williams, 1966). Roff (1982) proposed that in the face of energy crisis, trade-off may result in atresia of oocytes and subsequent resorption during vitellogenesis. In nature, estuarine fish are faced with such situations during wide salinity fluctuations in nature, during which, energy partitioning for reproduction may be curtailed for maintaining ionic homoeostasis under hypo-osmoregulation. (Evans, Piermarini & Choe, 2005). Chandrasekar et al. (2014) found that pearlspot, alike other euryhaline teleost fish (*Oryzias dancena*, *Plactichthys flesus*, *Oreochromis mossambicus*, *Poecilla reticulate*, *Oryza latipes* and *Dicentrarchus labrax* etc.), has an efficient capacity of acclimation of osmoregulatory function in different salinities. However, an effect of various salinities on gonadal recrudescence in pearlspot is not yet elucidated. Thus, the present study attempts to elucidate the effect of high and low salinity on gonadal recrudescence of broodstock collected from brackish water by assessing macro and microscopic gonadal growth and associated changes in plasma levels of cortisol, 17 β-Estradiol (E2), Testosterone (T), 11-keto Testosterone (11-kT).

Pearlspot exhibits natural spawning during December-January (De Silva, Parakum & Cumaranatunge, 1984) in estuaries and brackish water in India. Even though the fish has established itself well in fresh water systems, its gonadal recrudescence in response to salinity changes is yet unknown, particularly in higher salinity. The present study is the first experimental evaluation of the changes in plasma sex steroid levels in relation to seasonal gonadal recrudescence under environment of varying salinities of a euryhaline system.

2 | MATERIALS AND METHODS

2.1 | Experimental fish

The adult fish (125 ± 25 g; >1 Year age) were collected in the month of September from brackish water pond (salinity 15 ppt) of Kakdwip Research Centre (KRC) of ICAR—Central Institute of Brackishwater Aquaculture, India and were stocked randomly in FRP tanks at 15 ppt salinity (Brackishwater). The fish were maintained at average temperature of 25°C ± 1.5°C under a photoperiod regime of 12L:12D with adequate good water quality parameters throughout the experimental period. The fish were fed commercial diet containing 35% crude protein, ad libitum, during the 15 days of acclimation period.

2.2 | Experimental design and adjustment of salinity

After 15 days acclimation period, adult fish were randomly distributed in three experimental groups in triplicate following a completely randomized design. Adult, male and female fish were selected and distributed equally (n = 15 of each sex) in each FRP tank of 2000 L capacity and maintained at 15 ppt (habitat salinity). Thereafter, salinity was either increased or decreased at a rate of 2.5 ppt day^{-1} until it reached at 1 ppt (68.43 mOsm. kg^{-1}, denoted FW) and 30 ppt (850.0 mOsmol kg^{-1}, denoted SW), respectively, for the above two experimental groups, whereas salinity remained same (15 ppt) for BW group. The salinities were increased or decreased either by diluting with filtered freshwater or exchanging with filtered seawater (35 ppt) (Seo, Lee & Kaneko, 2009). After reaching the required salinity for the individual treatment groups, fish were reared for 60 days with ad libitum feeding twice a day at the rate of 2% body weight. Fish excreta and uneaten feed were removed by siphoning twice a day after feeding. Water was exchanged and again replenished with maintained salinity after every third day.

2.3 | Sampling protocol

On 30^{th} day and 60^{th} day of the experiment, six fish from each tank were anaesthetized with MS-222 (Sigma, USA) and blood samples were collected from caudal vein with the help of heparinized syringe followed by centrifugation at 3,000 rpm at 4°C for 10 min to collect the plasma and stored at −20°C until analysis. Tissues such as gonad (Ovary and testis) and liver were dissected out carefully. Body weight, total length and liver weight were recorded for each fish. Later on gonads were fixed in 10% neutral buffer formalin (NBF) for further histological observations. Hepatosomatic index (HSI) and Gonadosomatic index (GSI) were computed for both the sexes as described earlier (Abdel-Tawwab, Ahmad, Khattab & Shalaby, 2010; Biswas & Takeuchi, 2003).

2.4 | Plasma Analysis

Plasma cations (Na^+, K^+) and anion (Cl^-) concentrations (mmol l^{-1}) were determined by flame photometry (Digimed NK-2004; Brazil) and colorimetric titration (Chloridometer PLM3 Jenway Ltd., England) respectively. Plasma osmolality was determined with Vapour Pressure Osmometer, Wescor 5100B (Wescor Inc., USA).

Concentrations of plasma steroids, such as, Testosterone (T), 11-keto Testosterone (11-kT), 17-β estradiol (E2) were analysed according to the manufacturer's instructions provided with the commercial competitive enzyme immunoassay kits (Cayman Chemical, MI, USA), specific to each hormone. Cortisol was estimated with the help of EIA kit from Diagnostic Systems Laboratories, Inc. (DSL, Texas, USA).

2.5 | Histological analysis of gonad

Gonads were fixed in 10% NBF for at least 24 hr. After proper fixation, gonads were dehydrated in graded ethanol series and embedded in paraffin. Embedded gonad samples were sectioned to 5 μm, stained with haematoxylin-eosin and mounted on slides for further examination. Slides were examined under a Motic B5 compound microscope with Motic Images Advanced 3.2 software

(Motic Electric Group Co., Canada). Maturity stages of gonads and oocytes were determined by following Diwan and Krishnan (1986).

2.6 | Statistical analysis

All values are expressed as mean ± SE. Data were analysed by two-way analysis of variance (ANOVA) and the significant differences in mean values were determined by Tukey's test using the software program SPSS 16.0 for Windows (SPSS Inc. 2008; Norušis, 2008). The significant level for all statistical analyses was set at $p < .05$.

3 | RESULTS

3.1 | Plasma osmolality and ionic concentrations

Initial values of plasma osmolality showed almost same levels in all the groups. After 30 days, these levels significantly ($p < .001$) increased in SW and BW group, whereas it dipped low in FW group. Furthermore, these levels persisted at almost the same level in all the groups till the end of experiment (Table 1).

Plasma Na^+ values were increased significantly ($p < .001$) in SW group after 30 days, whereas the values decreased in BW and FW groups and remained same till 60 days of experiment. After 60 days, however, concentrations of the same decreased significantly in SW group and were almost similar to BW group on 60th day. Contrary to plasma Na^+, the plasma Cl^- concentrations on 60th day decreased in BW group and increased in FW and SW groups from initial concentrations on 0 day. The K^+ concentrations in plasma significantly ($p < .001$) increased in SW group and reduced in BW and FW groups on 30thday. Furthermore, these levels remained same till the 60th day of study in BW and FW groups and significantly ($p < .001$) decreased in SW group (Table 1).

TABLE 1 Plasma osmolality and ionic concentrations in pearlspot at varying salinities.

	Days of salinity exposure		
	0 day	30th day	60th day
Plasma osmolality (mmol L^{-1})			
FW	319.17 ± 10.1	307 ± 17.6^{a}	310 ± 17.4^{a}
BW	314.5 ± 10	329.5 ± 14.9^{ab}	326.1 ± 16.2^{ab}
SW	318.33 ± 8.8	355.5 ± 14.7^{b}	345.5 ± 7.9^{b}
Plasma (Na^+) (mmol L^{-1})			
FW	176.55 ± 28.65^{b}	153.2 ± 13.78^{a}	150.1 ± 15.01
BW	176.08 ± 31.01^{b}	162.5 ± 19.76^{a}	164.8 ± 11.11
SW	174.73 ± 20.99^{ab}	186.6 ± 15.31^{c}	162 ± 18.41
Plasma (Cl^-) (mmol L^{-1})			
FW	153.07 ± 11.11	170.5 ± 9.01^{ab}	161.8 ± 13.18^{ab}
BW	151.82 ± 10.12	146 ± 20.15^{a}	141.8 ± 13.09^{a}
SW	153.29 ± 8.19	190.2 ± 12.2^{b}	170.6 ± 13.31^{ab}
Plasma (K^+) (mmol L^{-1})			
FW	5.36 ± 0.29	5.01 ± 0.21^{a}	4.96 ± 0.23^{a}
BW	5.41 ± 0.31	5.17 ± 0.25^{a}	5.18 ± 0.21^{a}
SW	5.41 ± 0.25	5.54 ± 0.12^{b}	5.32 ± 0.28^{ab}

Values are mean ± SEM ($N = 18$). Different superscript indicates significant difference ($p < .05$)

3.2 | Progress of gonadal recrudescence

3.2.1 | Changes in GSI and HSI

The GSI and HSI values increased gradually in both sexes over the period of rearing under different salinities. After 30 days of rearing, mean GSI value was 0.65 ± 0.11% in BW females, which was significantly higher ($p < .001$) compared to that in SW groups (0.37 ± 0.1%) (Figure 1a). On the 60th day, BW group attained highest GSI values of 1.40 ± 0.2%, which were significantly different from SW group, whereas FW group showed moderate growth. Female HSI values in BW and FW groups on 30th day were significantly higher than that of SW group and mean female HSI values were recorded as 4.48 ± 0.52%, 4.0 ± 0.33% and 3.5 ± 0.32% for BW, FW and SW, respectively, at the end of experiment (Figure 1a). There was no significant difference in HSI between FW and SW groups. The BW males showed highest mean GSI values of 0.022 ± 0.001% and the mean GSI values were found significantly lower ($p < .05$) in FW- and SW-acclimated males on the 60th day (Figure 1c). Male HSI followed a similar increasing trend as exhibited by male GSI; BW group showed highest value (2.07 ± 0.24%) followed by FW (1.8 ± 0.36%) and SW groups (1.67 ± 0.22%) at the end of experiment (Figure 1d).

3.2.2 | Changes in gonad histo-architecture

At the beginning, mainly perinucleolar (PNS) oocytes along with few cortical alveolus stage (CAS) occupied entire ovaries in all the groups (Figures 2a, b and c). On the 30th day, oocytes at primary yolk stage (PYS) appeared and showed higher percentage among other oocyte groups which mainly comprised of CAS and few secondary yolk stage (SYS) in the ovary of BW females (Figures 1b and 2d). Highest percentage of CAS oocytes followed by PNS and PYS oocytes were present in FW females at 30 days, whereas at the same time, highest number of PNS oocytes accompanied by few CAS were recorded in SW group (Figure 1b and Figures 2e and f). On the 60th day, ovaries were mostly occupied by tertiary yolk stage oocytes (TYS) in BW females (Figure 2g), while in FW group, TYS oocytes were present in less numbers (Figure 2h). On the same day, numerous CAS oocytes along with a low percentage of PYS oocytes were observed in SW females (Figures 1b and 2i).

Testicular histology showed occurrence of few spermatids in the beginning of experiment in all males (Figures 3a, b and c). At the 30th day, highest occurrence of spermatids was noticed in BW group followed by FW and SW males (Figures 3d, e and f). In BW males, lumens of testes were filled with spermatozoa on the 60th day with few early spermatogenic stages (Figure 3g). In contrast, early

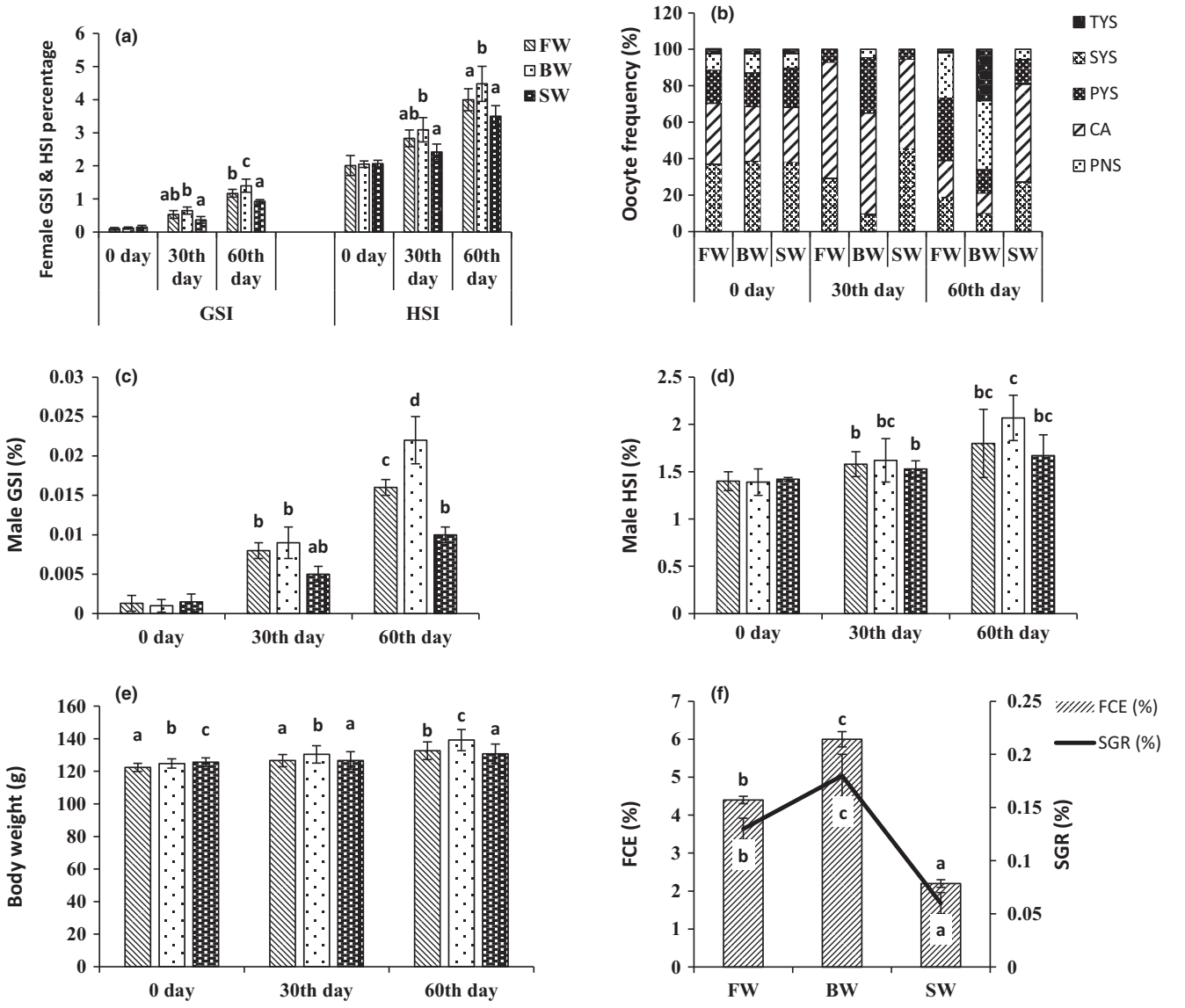

FIGURE 1 Gonadal development and hepato-somatic index in pearlspot in different salinities. a) GSI and HSI percentage of female fish. b) Percentage of different oocyte stages in female fish. c) Gonado-Somatic Index of male fish in different salinities. d) Hepato-somatic index of male fish in different salinities. e) Body growth of adult Pearlspot during experimental period. f) Feed conversion efficiency (FCE) of adult Pearlspot during experimental period. Values are mean ± SEM ($N = 9$). Different superscript indicates significant difference ($p < .05$)

spermatogenic stages were dominant in testes of SW group. FW males showed intermediate phase of spermatogenesis at the same time (Figures 3h and i).

3.2.3 | Changes in plasma sex steroid levels

Initially, there were no significant differences in plasma levels of 17 β-estradiol (E2) among females in all groups. Plasma E2 concentrations increased significantly ($p < .05$) with the progression of time and BW females showed highest levels of E2 (2.16 ± 0.14 ng ml^{-1}) followed by FW (2.27 ± 0.11 ng ml^{-1}) and SW (1.92 ± 0.19 ng ml^{-1}) females on the 60th day (Figure 4a). Plasma T concentrations significantly increased with progress of time in females irrespective of groups. The highest mean value was recorded in BW group (1.5 ± 0.24 ng ml^{-1}), followed by FW (1.3 ± ng ml^{-1}) and SW (1.1 ± ng ml^{-1}) acclimated females (Figure 4a). Plasma 11-kT concentrations were not found significant during this period (Fig. 5a).

Mean plasma 11-kT and T concentrations in males showed similar increasing trend exhibited by plasma E2 levels in females on 60th day of experiment. Plasma 11-kT concentrations increased irrespective of groups on 30th day and found significantly ($p < .05$) highest in BW group (7.11 ± 0.96 ng ml^{-1}) and lowest in SW group (Figure 4b). Plasma T level in males were found 8.07 ± 0.52 ng ml^{-1}, 6.39 ± 0.28 ng ml^{-1} and 4.88 ± 0.18 ng ml^{-1} at the end of experiment in BW, FW and SW groups respectively (Figure 4b). Plasma concentrations of E2 were not significantly different during experimental duration. (Fig. 5b)

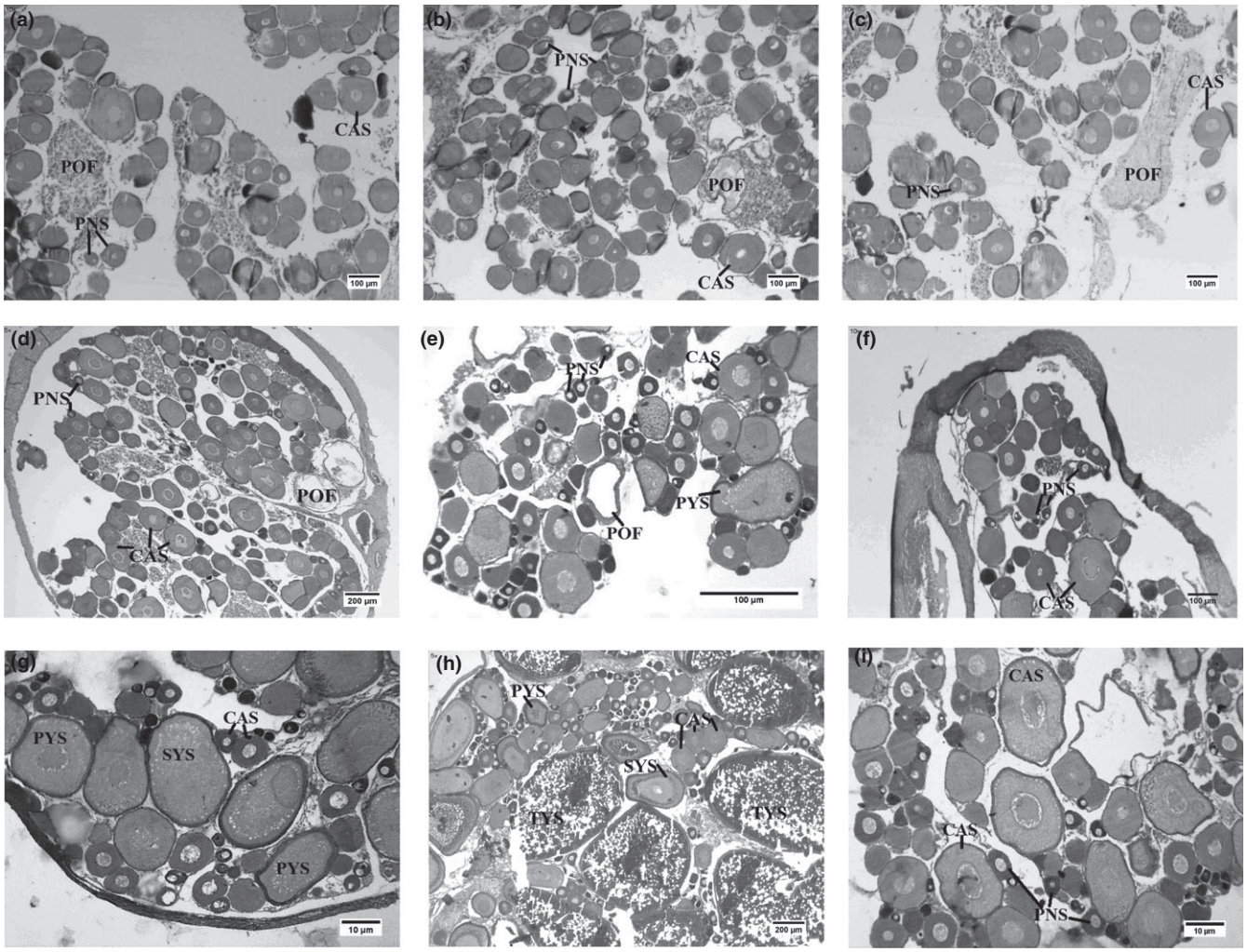

FIGURE 2 Transverse sections of ovary of pearlspot under different salinities showing oogenesis in female fish reared in different salinities. a), b) and c) Gonads of fish in BW, FW and SW groups at 0 day showing oocytes in PNS and CAS stages with POF bodies. d) BW group on the 30th day showing oocytes in PNA, CAS and PYS stages of oocytes. e & f) FW and SW group, respectively, on the 30th day, showing oocytes in PNS and CAS stages. g) On the 60thday of rearing in the BW group female fish showing oocytes in TYS, SYS and PYS stages with few CAS oocytes. h) FW group on the 60th day showing oocytes in PYS, SYS and CAS stages. i) SW group on the 60th day showing oocytes in CAS and PNS stage. PNS, Perinucleolus stage; CAS, Cortical alveolus stage; PYS, Primary Yolk stage; SYS, Secondary Yolk stage; TYS, Tertiary Yolk stage; POF, Post Ovulatory Follicle

3.2.4 | Changes in plasma cortisol level

Plasma cortisol concentrations sharply declined in females on the 30th day irrespective of groups, (35.5 ± 2.04 ng ml^{-1}, 30.3 ± 1.41 ng ml^{-1} and 49.8 ± 1.19 ng ml^{-1} in FW, BW and SW groups respectively (Figure 4c). Plasma cortisol levels were significantly ($p < .05$) higher in SW females compared with other fish in FW and BW groups, whereas the levels significantly attenuated in BW females than that of FW group on the 30th day. On the 60th day, plasma cortisol levels in females showed marked variations among the groups, wherein, levels remained elevated in SW group (even though an overall declining trend was recorded in all groups from initial levels) and were significantly different ($p > .05$) from the other two groups (FW and BW) (Figure 4c). Male plasma cortisol concentrations exhibited similar pattern of changes as observed in females up to 30th day. Thereafter, it decreased in a similar fashion as in females up to 60th day. However, there were no significant differences in cortisol levels among groups in males ($p > .05$) on 60th day (Figure 4d).

3.2.5 | Growth and Feed efficiency

Improvement of fish body weight was observed clearly in BW and FW groups throughout the experiment period. On the 30th day, weight gain in BW treatment group (130.4 ± 2.35 g) was significantly higher than FW and SW. Rearing upto the 60th day revealed significant ($p < .05$) highest weight gain in BW (139.2 ± 5.6 g) followed by FW (132.6 ± 3.2 g) group (Figure 1e). Percentage of Specific Growth Rate (SGR) increased significantly ($p < .05$) in BW group, whereas it was decreased in SW treatment groups. Feed

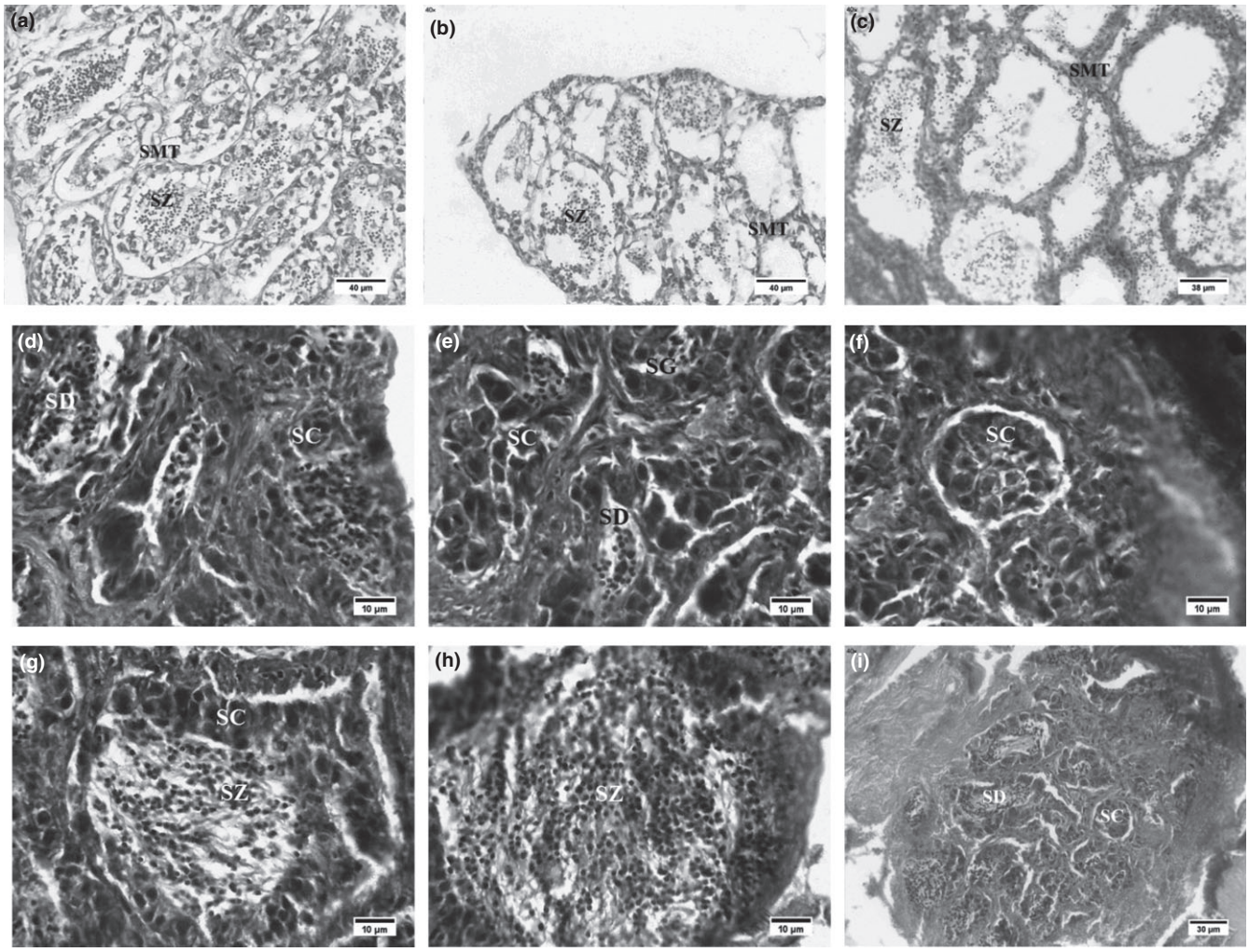

FIGURE 3 Maturation stages of male pearlspot acclimatized in different salinities. a), b) and c) BW, FW and SW groups, respectively, at 0 day showing spent stage of testes with presence of Vacuoles and SZ. d) BW group showing SC, SG and SD on the 30th day of acclimation. e) FW group showing SC and SD on the 30th day. f) SW group on the 30th day showing SC. g) BW group, 60th day showing SZ stage (X100). h) FW group on the 60th day showing SC and SZ. i) SW group, on the 60th day showing SC and SD. SC, Spermatocyte; SD, Spermatid; SG, Spermatogonia; SZ, Spermatozoa

Conversion Efficiency (FCE) (%) followed the same trend as SGR (Figure 1f).

4 | DISCUSSION

Effect of various stressors was reported on gamete production during prespawning and spawning phases by Contreras-Sanchez, Schreck, Fitzpatrick and Pereira (1998); Campbell, Pottinger and Sumpter (1992); Campbell, Pottinger and Sumpter (1994); and Morehead, Ritar and Pankhurst (2000). However, few studies have been carried out to elucidate salinity as a stressor during gametogenesis in euryhaline fish. According to Schreck (2000), osmoregulatory consequences produce an allostatic load which reduces reproductive fitness in fish. Thus, seasonal reproduction and gonadal growth may be heavily affected by variations in osmoregulatory activities in euryhaline fishes (Haddy & Pankhurst, 2000; Sherwood & Backhouse, 1982). Effects of salinity on gonadal growth appear to be mediated by changes in circulating levels of reproductive hormones. There is a close association between decreased plasma sex steroid concentrations and gonadal growth. Estradiol has been shown to regulate vitellogenesis and thereby influence ovarian growth in teleosts (Hiramatsu, Matsubara, Fujita, Sullivan & Hara, 2006), whereas T and 11-kT increase gradually as spermatogenesis proceeds and decreases at spermiation (Schulz et al., 2010).

Generally, in a normal reproductive phase, process of gonadal growth is accompanied by increased GSI and HSI. Relative gonad growth (GSI) was significantly less in SW- acclimated females may be linked to 26% lower plasma E2 level compared to BW females, even though concentrations of the precursor hormone T were unchanged. Histological examination of developmental stages of oocytes revealed that there was a reduction in the percentage of secondary and tertiary yolk oocytes in SW group compared to BW and FW groups. Such retardation in oocyte growth clearly suggests

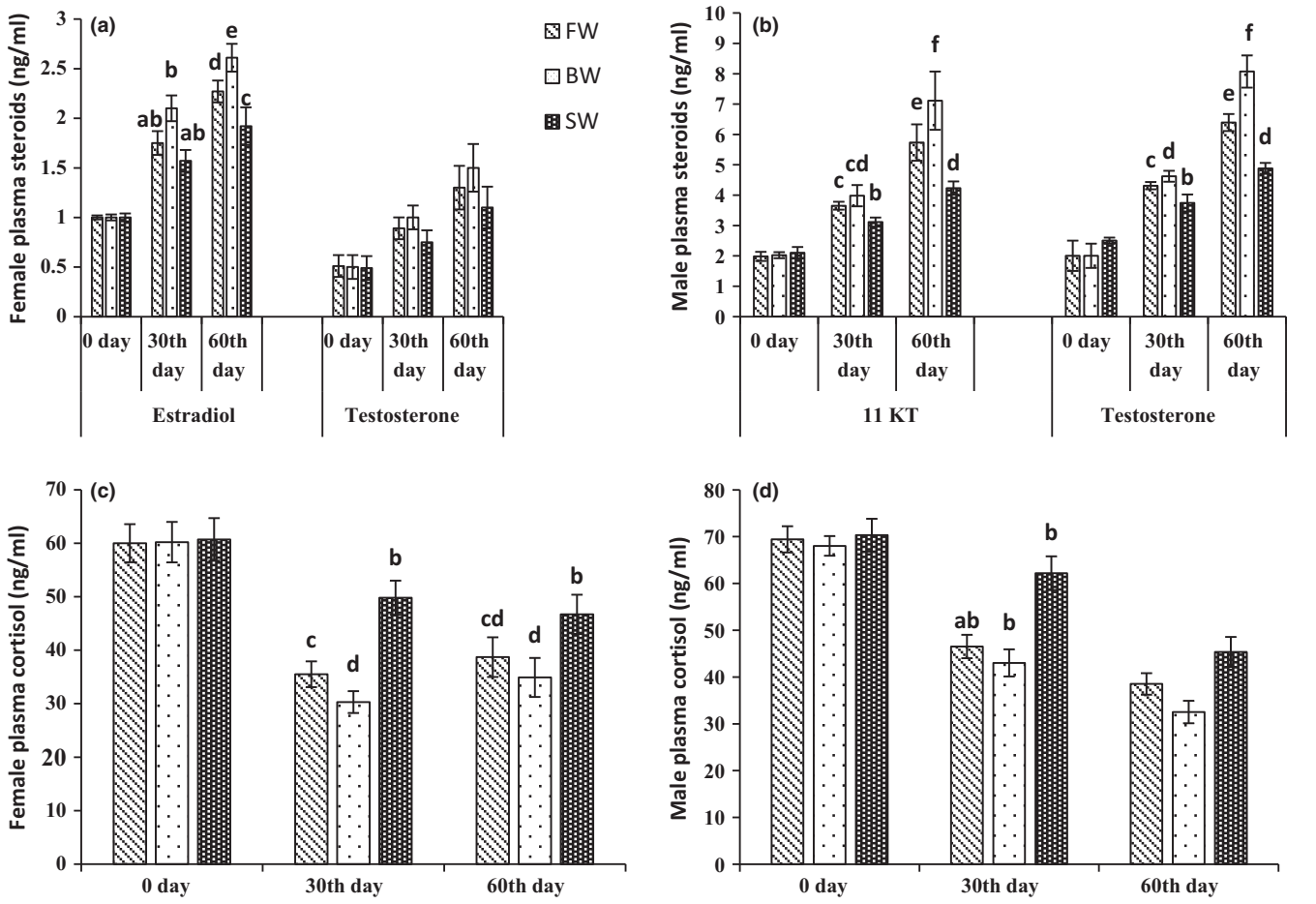

FIGURE 4 Changes in plasma steroid levels during ovarian recrudescence acclimatized under various salinities. a) Plasma Estradiol (E2) and Testosterone levels in female pearlspot. b) 11-keto Testosterone and Testosterone levels in Male pearlspot. c) Cortisol levels in Female fish. d) Cortisol levels in Male fish. Values are mean ± SEM ($N = 9$). Different superscript indicates significant difference ($p < .05$)

sensitivity of the process to extreme alteration in ambient salinity even in euryhaline species, such as the pearlspot. In males, GSI significantly decreased in both FW and SW environments, which may be attributed to plasma 11-kT, which is critical for spermatogenesis and development of secondary sex characteristics in male fish (Devlin & Nagahama, 2002). Decrease in 11-kT levels by 19% and 40% in FW- and SW-acclimated males, respectively, may be associated with inhibition of transformation of spermatogenic cells towards final maturation as revealed by the presence of a less number of spermatozoa and spermatids in testicular lobules in SW males. The GSI values, HSI values, plasma E2, Testosterone, 11-kT concentrations and histological architecture of gonads indicate that reproductive endocrine function and ovarian growth in female pearlspot are significantly altered under changes in ambient salinities mimicking FW and SW environments compared to natural habitat salinity (BW). Exposure to SW caused a greater suppression of ovarian growth than exposure to FW, which suggests that exposure to higher salinities causes greater disruption of reproductive processes in pearlspot than exposure to a lower salinity. Similar observations were also recorded in males wherein, testicular growth was highly suppressed at SW than FW environment. In earlier studies, differential reproductive responses under various salinities were recorded for different euryhaline teleosts. The present study provides insight that, salinity affects plasma sex steroid levels associated with gonadal development in both sexes of pearlspot. Tamaru et al. (1994) reported changes in salinity suppressed vitellogenesis and oocyte growth in female *Mugil cephalus*. In contrast, Zanuy and Carrillo (1985) did not find such a difference in gonadal recrudescence in seabass (*Dicentrarchus labrax*) reared at 3.5 ppt and 37.8 ppt salinities. We found that pearlspot maintained the plasma osmolality between 307.83 mM and 355.5 mM during active reproductive phase under hypo- and hyper-osmoregulation, respectively, which is similar to the ranges of osmolality reported by Chandrasekar et al.(2014) in case of immature pearlspot. Plasma osmolality is considered as a key indicator for monitoring osmoregulatory ability of fish (Evans et al., 2005) which remains in the range of 285–320 mOsm kg^{-1} in most of the euryhaline teleost fish (Kang, Tsai, Lee & Hwang, 2008). Regulation of osmolality is mostly dependent on species (Varsamos, Nebel & Charmantier, 2005) and its habitats (Lee, Hwang, Shieh & Lin, 2000; Lin, Chen & Lee, 2003). Our results are also within the osmolality ranges of an earlier study by Nordlie (2009) for 20 different diadromous teleost

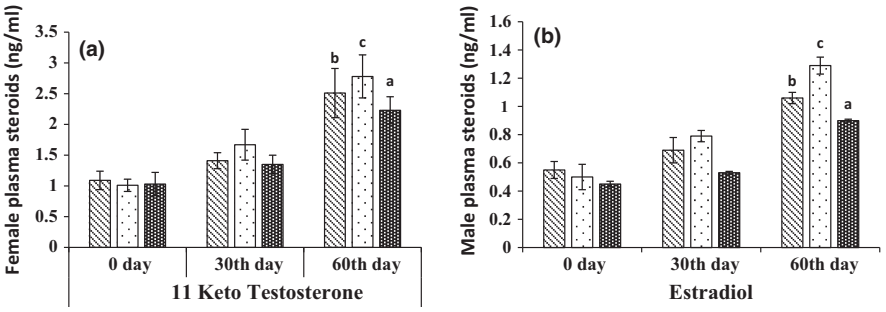

FIGURE 5 Changes in plasma steroid levels during acclimatiztion under various salinities. a) Plasma steroid 11-keto Testosterone levels in female pearlspot. b) Plasma steroid Estradiol (E2) levels in Male pearlspot. Values are mean ± SEM (N = 9). Different superscript indicates significant difference ($p < .05$)

species. Plasma Na^+ levels in the present study were within the range of 150.0 ± 3.9 mmol L^{-1} in FW to 173.8 ± 3.8 mM in SW, in accordance with Nordlie (2009), whereas significant increase in plasma Na^+ level above the range was noticed only during SW acclimation on the 30th day. Bystriansky, Richards, Schulte and Ballantyne (2006) reported that plasma levels of Na^+ remained high after SW transfer for 30 days in Arctic char, 10 days in *O. mykiss* and up to 4 days in *S. salar*. It is known that the gills of euryhaline teleosts normally absorb and secrete Cl^- in order to maintain constant plasma Cl^- concentrations in various saline environments (Evans et al., 2005). The pearlspot, being an euryhaline teleost cichlid, is therefore, an efficient osmoregulator and possesses ability to maintain ionic homoeostasis under varying salinities even during gonadal recrudescence phase.

Cortisol plays a key role in osmoregulatory process largely through its effect in stimulating gill Na^+/K^+ -ATPase activity (McCormick, 1995) at lower levels. This hormone also has permissive effects on female reproductive activities during the pre-ovulatory period (Milla, Wang, Mandiki & Kestemont, 2009). Besides regulating a wide range of physiological functions under normal conditions, cortisol also allows for rapid physiological re-adjustments in the face of exposure to stressors (Mommsen, Vijayan & Moon, 1999). Initially, plasma cortisol levels were high in both sexes owing to capture and handling stress (Carragher & Pankhurst, 1991; Haddy & Pankhurst, 2000), and gradually declined with acclimation in the confinement. As cortisol is known for maintaining ionic homoeostasis for both hyper and hypo-osmoregulatory function (Madsen, 1990; Pickford et al., 1970; Richman, Nishioka, Young & Bern, 1987; Sakamoto & McCormick, 2006), its increased level in the SW-acclimated pearlspot at 30 days supports its established role in hypo-osmoregulation (McCormick, 2001). In males, its concentrations were gradually attenuated in all groups in due course of acclimation. It can therefore be concluded that initial increase in cortisol levels in *Etroplus suratensis* under salinity changes may be attributed to pre-acclimation stress, which decreased afterwards in all the groups suggesting acclimation under various salinities. However, compared to other groups, elevated levels in SW group may be attributed to hypo-osmoregulatory adaptation under the control of cortisol, which is known to be responsible for cellular differentiation of chloride cells for enhancing branchial Na^+/K^+-ATPase activity reported in SW-acclimated pearlspot and other teleosts (Chandrasekar et al., 2014; McCormick, 1995). This, being an energy expensing event, may lead to low leftover energy for other metabolic actions. After long acclimation, decrease in cortisol level was seen in all the groups. This explains differential responses of the piscine system to a particular stressor, wherein, energy rebudgeting may be different in case of emergency response situations and situations where fish can cope with a stressor (Schreck Carl, 2010). In cases where energy rich environment prevails (i.e. in cases where FCE is higher as in case of BW and FW acclimated fish as shown in Figure 1f), coping with allostatic load is better. Hence, cortisol levels declined in FW and BW groups compared with SW group. Again, energy repartitioning or rebudgeting in reproductively active females may occur as a trade-off between homoeostasis and gametogenesis, causing elevated stress in females, resulting in comparatively higher levels of cortisol up to 60th day, in females, compared with males. (Figures 4c and d).

In the present study, fish resumed normal feeding (2% body weight) within 3 days of acclimatization to respective tank salinity from habitat salinity (15 ppt). Salinity did not affect feeding activity and feed intake in any treatment group. Specific growth rate of fish in SW treatment groups were observed to be slowest compared to BW and FW. This indicates major utilization of feed energy towards somatic growth and gonad maturation in BW and FW groups as compared to SW. We have found highest SGR and FCE in 15 ppt salinity. Habitat salinity of pearlspot environment was found between 15 and 20 ppt, which explains the low energetic cost of osmoregulation than other lower (0 ppt) and higher (30 ppt) salinities in present study. Isoosmotic environment would be helpful in saving energy leading to weight gain and gonad maturation in active reproductive season in BW treatment groups (Boeuf & Payan, 2001; Brett & Groves, 1979; Kirschner, 1995). This is again in conformity with studies of other researchers on different euryhaline species such as Seabream, *Sparus sarba* (Woo & Kelly, 1995), Grey Mullet, *Mugil cephalus* (De Silva & Perera, 1976), Tilapia, *Oreochromis mossambicus* (De Silva & Perera, 1985), Atlantic cod, *Gadus morhua* (Lambert, Dutil & Munro, 1994) and Turbot, *Scopthalmus maximus* (Imsland et al., 2001) where body growth was found optimum at 10–15 ppt water salinity. Earlier studies on euryhaline fish revealed that during

acclimatization to non-habitat salinity, fish mostly expend feed energy towards metabolic cost of ionic and osmotic regulation which affects growth and food conversion (Brett, 1979; Jobling, 1994). FCE was found largely affected in SW treatment group which is in agreement with findings of Imsland et al., 2008; elucidated improved FCE in Atlantic halibut (*Gadus morhua*) cultured in intermediate salinities (15–20 ppt). Transient changes in gill chloride cell dynamics including sodium—potassium pump (Na^+-K^+-ATPase) and $Na^+/K^+/2Cl^-$ co-transporter (NKCC) activities play a key role in the ion regulation process after SW or FW exposure in this species (Chandrasekar et al., 2014). Specific estimates of this osmoregulatory cost (based on salinity-related differences in metabolism) in *Oreochromis niloticus* is 19% and 29% of the total body metabolism in FW and SW respectively (Farmer & Beamish, 1969), whereas Morgan, Sakamoto, Grau and Iwama (1997) recorded it as 20% in case of SW acclimation. Thus, a reduction in gonadal growth when reared in non-habitat salinities, could be due to an increase in channel proteins activity and concomitant energy expenditure, similar to that which happens in case of growth reduction under environments of varying salinities (Boeuf & Payan, 2001; Sampaio & Bianchini, 2002).

Besides, extra energy expenditure owing to osmoregulatory acclimation in non-habitat salinity and stress during chronic exposure to such salinities may inhibit reproductive process in fish due to interactions of Hypothalamus Pituitary Interrenal (HPI) axis with Hypothalamic-pituitary-gonadal (HPG) axis. In fish, cortisol plays a dual role (positive and negative) in the final reproductive process depending on species, sex, stages of reproductive phase, magnitude and duration of plasma hormonal levels (Gennotte et al., 2012; Wendelaar-Bonga, 1997). Cortisol inhibits 11-kT production (Carragher & Sumpter,1990; Consten, Lambert, Komen & Goos, 2002), but does not affect estradiol production in fish (Pankhurst, Van Der Kraak & Peter, 1995). However, cortisol treatment inhibited hepatic expression of oestrogen receptors, vitelline envelope, protein-b and vitellogenin (Aluru & Vijayan, 2007; Lethimonier, Flouriot, Valotaire, Kah & Ducouret, 2000). In this study, cortisol has been possibly responsible for attenuation of 11-kT levels in males, whereas the reason behind the decreased estradiol levels in spite of having higher plasma levels of cortisol in SW-acclimated females indicates possibility of stress activated HPI axis suppressing estradiol levels as earlier reported in zebra fish ovary by Alsop, Ings and Vijayan (2009).

5 | CONCLUSION

Although pearlspot thrives well in a wide range of salinity; steroidogenesis and gametogenesis get differentially suppressed during hypo- and hyper-osmoregulation. During active reproductive phase, changes in salinity increases cortisol levels in blood plasma of fish leading to sizeable amounts of stress. High osmoregulatory acclimation along with stress utilizes most of the metabolic energy which eventually retards gonadal growth in SW-acclimated groups in the present study. The study elucidates that an euryhaline fish faces stress during gametogenesis under various modes of osmoregulation which certainly interferes with maturity of eggs and spawning time. As the fish naturally thrive in estuaries, acclimation in BW did not show any inhibition in reproduction. Although the fish native to brackish water has been reported to thrive well in FW, this study conclusively, proved that, in the absence of habitat salinity of BW, this fish could be matured and bred in alternative environment of FW, (which exhibited marginal retardation in progress of gonadal growth) better than SW, wherein, SW-acclimated fish could not maintain same accelerated gonadal growth as noticed in case of FW acclimation. So, it is clearly evident that salinity variations during the active reproductive phase suppress gametogenesis, which, however, varies with modes of osmoregulation. The higher retardation in progress of gonadal recrudescence in the SW-acclimated fish may be attributed to maximum energy trade-off during hypo-osmoregulation. Therefore, the present study clearly indicates better adaptability of pearlspot under hyper-osmoregulation during the active reproductive phase and therefore can form an important advisory for stakeholders who are interested in breeding this fish but may have limited or no access to BW.

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CONFLICT OF INTEREST

The authors also declare that they have no conflict of interest.

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