Coral Reefs (2021) 40:1757–1767
https://doi.org/10.1007/s00338-021-02183-x

REPORT

Physiological effects of the lunar cycle on the spawning of a coral reef fish, *Abudefduf Vaigiensis*: in vivo and in vitro trait

Asma Golmoradizadeh[1] · Ahmad Noori[1] · Bagher Mojazi Amiri[2]

Received: 2 December 2020 / Accepted: 17 September 2021 / Published online: 27 September 2021

Abstract The aim of the present study was to investigate the lunar cycle effects of the spawning of *Audefduf vaigiensis* through in vivo and in vitro analysis. For this purpose, the indices of GSI, serum levels of sex steroids, including testosterone (T), 17α-hydroxyprogesterone (OHP), 17α, 20β-dihydroxyprogesterone (DHP), and 11-keto-testosterone (11-KT) as well as the germinal vesicle breakdown (GVBD) were measured. The sampling pattern was weekly, based on the moon cycles as the new moon (NM), the first quarter (FQ), the full moon (FM), and the last quarter (LQ). In females, the highest in vivo values of the GSI index were obtained in FQ and LQ, and in males, this value was significantly higher in LQ than NM. The highest in vivo level of OHP in females was observed in FQ, whereas in males was obtained in FM. In both sexes, the in vivo serum levels of DHP were obtained in LQ. In males, the level of 11-KT were at the peak in NM. In vitro analysis showed the highest rate of GVBD in LQ. Moreover, the in vitro levels of T, OHP, and DHP were significantly higher in LQ compare to NM in both sexes. However, in males, the in vitro levels of 11-KT was significantly higher in NM than LQ. These cyclical changes obtained from in vivo plasma steroid hormones and in vitro data on GVBD suggested that lunar periodicity is a major external regulator that synchronized ovarian and testicular activity of *A. vaigiensis* with emphasis on spawning phenomenon.

Keywords Coral reef fish · GVBD · Indo-Pacific sergeant fish · Lunar cycle · Sex steroids · Spawning cycle

Topic Editor Morgan S. Pratchett

✉ Ahmad Noori
nooryahmad@gmail.com

[1] Department of Fisheries Science, Faculty of Marine Science and Technology, University of Hormozgan, 3995 Bandar Abbas, Iran

[2] Department of Fisheries, Faculty of Natural Resources, University of Tehran, 31585-4314 Karaj, Iran

Introduction

In teleost fishes, almost all steps of the reproductive cycle, from initiation of gametogenesis until spawning time, are indirectly affected by different external stimuli. These environmental factors mediate the reproductive stages by affecting different effectors and pathways, including enhancing or inhibiting the related hormones (Lam 1983; Sumpter 1997; Bhattacharya et al. 2007; Falcón et al. 2007; Cardinaletti et al. 2010; Carnevali et al. 2010; Fukushiro et al. 2011; Pankhurst and Munday 2011; Kashiwagi et al. 2013; Chakraborty 2018; Burgerhout et al. 2019; Fukunaga et al. 2019). However, the intensity of the influence is greatly variable, depends on different parameters, including the fish species, developmental stage, and the nature of the factor. Water temperature (Van Der Kraak and Pankhurst 1997; Donelson et al. 2010; Dadras et al. 2017; Fraser et al. 2019), photoperiod (Baggerman 1980; Bayarri et al. 2004; Borg et al. 2004; Fiszbein et al. 2010; Wang et al. 2010; Maitra and Hasan 2016), and physicochemical parameters (Craig and Baksi 1977; Brummett 1995; Edwards et al. 2006; Wu 2009; Sarkar et al. 2018) of the habitat are the well-studied ones. Nevertheless, some less understood environmental factors like lunar phases seem to be the most prominent external stimuli that influence some marine species behavior inhabiting shallow waters in tropical and subtropical zones. Although the synchronization of different reproductive stages, especially the spawning time, with lunar periodicity is a common phenomenon in some marine teleost families, the effects of this factor are not well-understood.

Some studies demonstrated that the main sex steroids which manage the final sexual maturation are effectively affected by lunar phases. Oliveira et al. (2010) showed significantly higher levels of sex steroid concentrations in females *Solea senegalensis* during the full moon compared to the new moon. Weekly changes in plasma sex steroid hormones in relation to lunar periodicity phases were observed in forktail rabbitfish, *Siganus argenteus* (Rahman et al. 2003a, b, c) and golden rabbitfish, *Siganus guttatus* (Rahman et al. 2000b, a, 2001, 2002). Wang et al. (2008) revealed a variation with semilunar periodicity of plasma sex steroids in mudskipper, *Boleophthalmus pectinirostris*.

Indo-Pacific sergeant fish, *Abudefduf vaigiensis* inhabits shallow water and coral reef areas. Although this fish is found in a vast area of the indo-pacific region, including the red sea, and is considered as an aquarium fish, few studies are done to elucidate the different aspects of the reproductive characteristics of this valuable species. Few conducted studies like the research done by Soltanzadeh et al. (2013) restricted to the annual fluctuation in plasma testosterone in this species. Some species of these valuable fishes have a lunar-dependent reproductive pattern. Foster (1987) showed that *A. troschelii* followed a lunar periodicity, whereas the pattern of reproduction in *A. saxatilis* demonstrated no lunar-dependent manner, as this fish spawned throughout the month. This study clearly showed that not all the species of this fish adopt the same reproductive strategy. Whether *A. vaigiensis* possesses a lunar periodicity in reproduction or not, is not been investigated so far.

The objective of the present study was to examine the possible cognition of the lunar cycle clue by *A. vaigiensis*. To this end, the influence of this environmental stimulus was investigated on plasma sex steroid levels to determine the physiological effects of the lunar cycle on the regulation of spawning time.

Materials and methods

Experimental fish

Indo-Pacific sergeant fish, *A. vaigiensis*, was captured by hook and line from the coral reefs around the east coast of Qeshm Island. One hundred and three fish, including 51 males (55.25 ± 1.88 g) and 52 females (50.50 ± 1.49 g), were captured in May 2018. The spawning season of this species in this region was demonstrated from March to May and September to November, with the former as the main period (Soltanzadeh et al. 2013). The specimens were caught weekly on the dates corresponding to the lunar phases. All the captured fishes were sexed according to the shape of their genital papilla before any further analysis.

Blood and gonad sampling procedure

The specimens were anesthetized with clove oil before biometry and sampling. The blood samples were withdrawn from the caudal vein using a sterile syringe equipped with a 25-gauge needle. The collected blood from each fish was immediately transferred into a separate sterile microtube and kept on ice and sent to the laboratory. Then the fish was dissected, and the gonad was removed carefully. The weight of the gonad of each specimen was recorded to the nearest 0.01 g for further gonadosomatic index (GSI) calculation through the formula of GSI = (gonad weight/body weight) × 100 (Noori et al. 2015). Biopsy from the gonads was performed on those with fully developed gonads. The taken samples were immediately transferred to a sterile container filled with Leibovitz L-15 medium (Sigma, USA) and sent to the laboratory in cool condition for further in vitro analysis. This sampling was performed for each lunar phase separately.

In vitro assessment of gonadal maturation in different lunar phases

In the laboratory, the preserved fully developed gonads in the Leibovitz L-15 medium were rinsed thoroughly with fresh pre-cooled Leibovitz15 (L15) medium. Approximately 30 intact oocytes from female ovaries with the fully developed stage (somewhat around 30 mg), and 20 mg of the full matured testis from males, in triplicates, were sampled from each lunar phase and transferred to the wells of 24-well tissue culture plates (SPL life science, South Korea). Each well filled with culture medium composed of 1 ml of L15, 100 IU/ml human chorionic gonadotropin (hCG), 1 µg/ml progesterone, 1 µg/ml testosterone, 5 mM Hepes (to adjust the pH as 7.5), 70 µg/ml penicillin, and 100 µg/ml streptomycin (Mojazi Amiri et al. 2001). The culture plates were incubated at 27 °C for 24 h. After incubation, the medium was removed and preserved at − 80 °C for further hormone analysis. The oocytes were fixed by adding one ml of Bouin's solution to each well. The state of the oocyte maturation was evaluated externally using a stereomicroscope based on the appearance of the germinal vesicle.

Measurement of hormones concentrations in the serum and the medium

Blood samples were centrifuged at 2500 g for 5 min, and the separated serum was collected for hormone assay. The serum hormones concentrations, including OHP, DHP, 11-KT, and T were measured by commercial kits (Hangzhou Eastbiopharm Co., China) through Enzyme-Linked Immunosorbent Assay (ELISA), based on the method of Asahina et al. (1995).

The collected culture medium was also used to measure the concentration of these hormones through the same method.

Statistical analysis

All data were checked for normality and homogeneity of variance by Shapiro–Wilk and Leven's test, respectively. In cases that the assumptions of the parametric tests were met, one-way ANOVA followed by Duncan's multiple range test was administered. Otherwise, Kruskal–Wallis and Mann–Whitney U tests, the proper non-parametric substituted tests, were applied. Mean values were considered significantly different at $P< 0.05$. Bonferroni correction was considered to keep the type 1 error (α) equal to 0.05. The data in percentage were arcsin transformed before any analysis. Data are expressed as mean values ± S.E. All statistical analyses were conducted using the statistic software SPSS version 16.0 (SPSS Inc., Chicago, IL, USA).

Results

Changes in GSI during lunar phases

The fluctuations in the values of GSI in the females were significant in different lunar phases (Fig. 1a). The lowest values of the GSI were observed in the new moon (1.73 ± 0.28) and full moon (1.60 ± 0.27), whereas the highest values were recorded in the last quarter (3.61 ± 0.41) and first quarter (3.37 ± 0.31), with no significant differences between them.

The GSI of males demonstrated somewhat less fluctuation than the females (Fig. 1b). These values, with a significantly lower mean of 1.2 ± 0.17 in the new moon, demonstrated a gentle ascending trend toward the last quarter, reaching a significantly higher value of 1.85 ± 0.19 in this phase.

Changes in plasma steroid hormones during lunar phases

In different lunar phases, the plasma levels of testosterone in the females of *A. vaigiensis* demonstrated a plateau trend, with no significant difference (Fig. 2a). The same picture was observed in males, with no significant variation throughout the different lunar phases (Fig. 2b).

In females, the levels of OHP demonstrated a higher value (0.081 ± 0.001) in the first quarter, whereas no significant fluctuations were observed in the rest of the lunar phases (Fig. 2c). In males, the highest level of OHP (0.067 ± 0.001) was recorded in the full moon, with no significant changes in the other phases (Fig. 2d).

The plasma levels of DHP showed more fluctuations in females (Fig. 2e). Although the plasma level of this hormone in the first quarter (31.80 ± 1.80) did not show any significant difference with the other lunar phases, the levels of this steroid in the last quarter (34.95 ± 0.92) was significantly higher than the new moon (27.13 ± 2.87) and full moon (27.25 ± 0.91). In males, the last quarter revealed the highest value of DHP (23.05 ± 1.21). In the other lunar phases, with no significant difference within these phases, the lowest levels of DHP were displayed (Fig. 2f).

The plasma levels of 11-KT in males exhibited the highest value in the new moon (Fig. 2 G). The levels of this

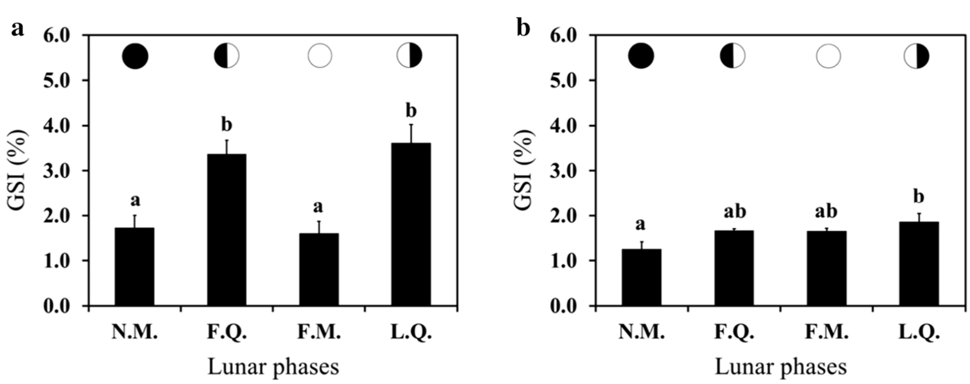

Fig. 1 Lunar-dependent variation in the GSI of female (**a**) and male (**b**) Indo-Pacific sergeant fish, *A. vaigiensis*. Each bar represents the mean value from four replicates with the standard error. The bar assigned with different letters are significantly different ($p < 0.05$). Lunar phases are indicated as new moon (●; N.M.), first quarter (◐; F.Q.), full moon (○;F.M.), and last quarter (◑; L.Q.)

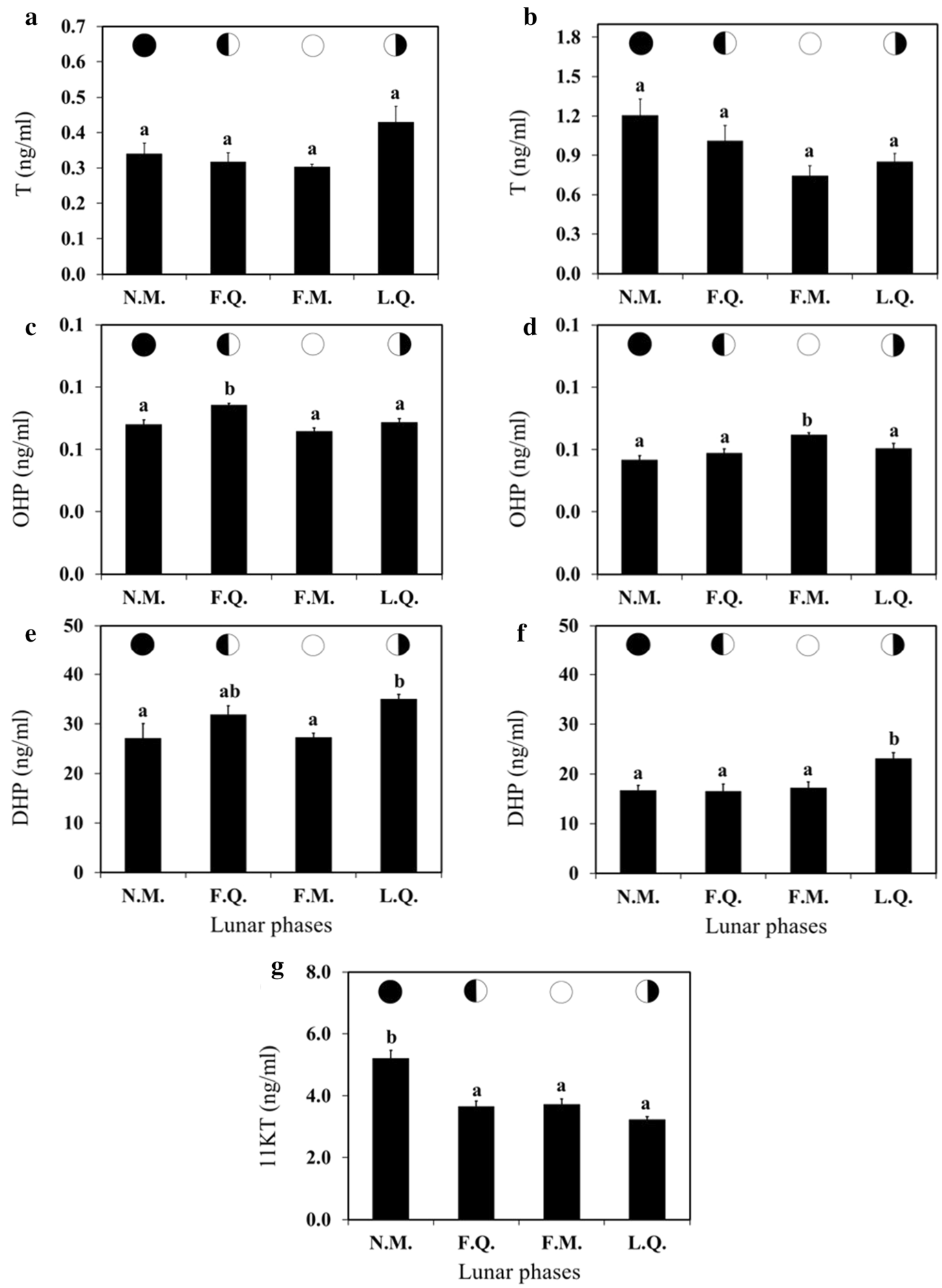

Fig. 2 Lunar-dependent variation in the plasma T (testosterone; ng/ml), OHP (17α-hydroxy progesterone; ng/ml), DHP (17α, 20β-dihydroxy progesterone; ng/ml), and 11-KT (11-keto-testosterone; ng/ml) of female (**a**, **c**, **e**) and male (**b**, **d**, **f**, **g**) Indo-Pacific sergeant fish, *A. vaigiensis*. Each bar represents the mean value from four replicates with the standard error. The bar assigned with different letters are significantly different ($p < 0.05$). Lunar phases are indicated as new moon (●; N.M.), first quarter (◐; F.Q.), full moon (○; F.M.), and last quarter (◑; L.Q.)

hormone in the other three lunar phases were significantly lower, with no significant difference between them.

Effect of the different lunar phases on the oocyte maturation (in vitro assessment)

Induction of GVBD in *A. vaigiensis* oocytes by hCG treatment was compared between the last quarter with the full moon, first quarter, and new moon (Fig. 3). Addition of hCG to the culture medium significantly induced GVBD in the oocytes from last quarter. Although hCG administration induced the GVBD phenomenon in the other lunar phases, these values were significantly lower than that of the last quarter.

Effect of the different lunar phases on sex steroids concentrations (in vitro assessment)

In vitro production of steroids was compared between two lunar phases (Fig. 4). In different lunar phases, the medium levels of testosterone in the ovaries of *A. vaigiensis* demonstrated the highest value around the last quarter,

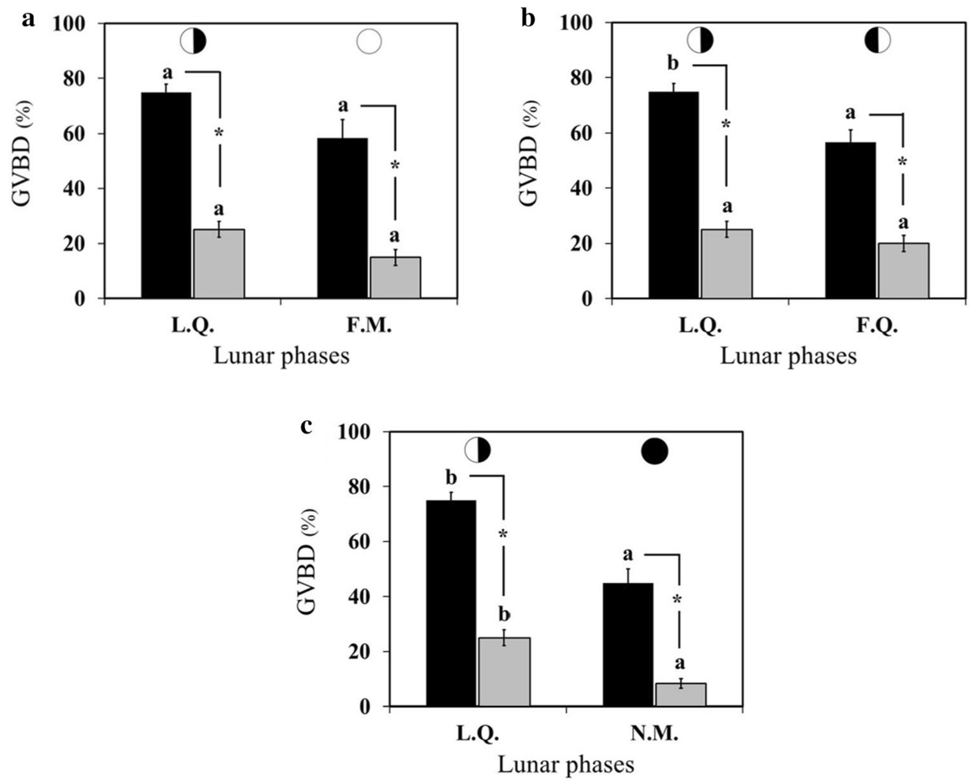

Fig. 3 Lunar-dependent effects of hCG on GVBD induction in oocytes of Indo-Pacific sergeant fish, *A. vaigiensis*. Comparison between different lunar phases (**a, b, c**) showed as bars, which each represent the mean value from three replicates with the standard error. Statistical comparison between different lunar phases is assigned with letters. Statistical comparison within each lunar phase is shown with an asterisk. The bar assigned with different letters or an asterisk is significantly different ($p < 0.05$). Black columns are hormone treatments and grey columns are controls. Lunar phases are indicated as new moon (●; N.M.), first quarter (◐; F.Q.), full moon (○; F.M.), and last quarter (◑; L.Q.)

with a significant difference (Fig. 4a). The same picture was observed in the testis in testosterone, with significant variation throughout different lunar phases (Fig. 4b).

In ovaries, the levels of OHP demonstrated higher value in the last quarter (Fig. 4c). In this lunar phase was a significant difference between two lunar phases. In the last quarter, testicular fragments exhibited significantly higher OHP production than the new moon (Fig. 4d).

In the ovaries, DHP levels showed a higher value in the last quarter (46.07 ± 1.55) than in the new moon (25.27 ± 1.89) (Fig. 4e). In the testicular fragments, the last quarter revealed the highest value of DHP (Fig. 4f).

In the testis fragment, levels of 11-KT exhibited the highest value in the new moon (11.30 ± 0.28) (Fig. 4g). The levels of this hormone in the last quarter (10.07 ± 0.09) were significantly lower.

Discussion

Assessment of the in vivo results obtained from different indicators revealed a lunar-dependent spawning in Indo-Pacific sergeant fish, *A. vaigiensis*. In females, the highest values of the GSI index were obtained in FQ and LQ, and in males, this value was significantly higher in LQ than NM. The gonadosomatic index is a commonly used indicator not only for annual reproductive period assessment but for determining the spawning time too. Babatunde et al. (2018) used different indicators, including GSI, for assessment of the gonadal maturation and spawning time in Cobia, *Rachycentrum canadum*, and found the highest value of GSI coincided with the highest percentage of matured females based on the histological analysis. Zhang et al. (2019) also found the average GSI peaks at the spawning months in *Johnius taiwanensis*. Similar results have been shown in other species of Perciformes with different lunar spawning periodicities, such as *Epinephelus polyphekadion* (Teruya et al. 2008), *Pomacentrus taeniometopon* (Pisingan et al. 2006), *Apogon amboinensis* (Pisingan and Takemura 2007), *Pterapogon kauderni* (Ndobe et al. 2013), *Abudefduf troschelii* (Foster 1987), *Siganus canaliculatus* (Hoque et al. 1999), *S. fuscescens* (Jumawan-Nanual and Metillo 2008), *S. doliatus* (Park et al. 2006b), *S. argenteus* and *S. spinus* (Harahap et al. 2001; Park et al. 2006a). As the index of gonadosomatic is evaluated through the ratio of the gonad weight to the body weight, the more mature the gonadal stage, the higher the index. The results from this study clearly showed that in *A. vaigiensis*, the spawning phenomenon occurred at FQ and LQ, with the latter as the main spawning time.

Assessment of the in vivo serum levels of OHP and DHP, the main sex steroids involved in final gonadal maturation, support these findings. These hormones in the females were at the highest levels in FQ and LQ. In the males also obtained the same situation in the case of DHP. This progesterone, which is synthesized from OHP as the

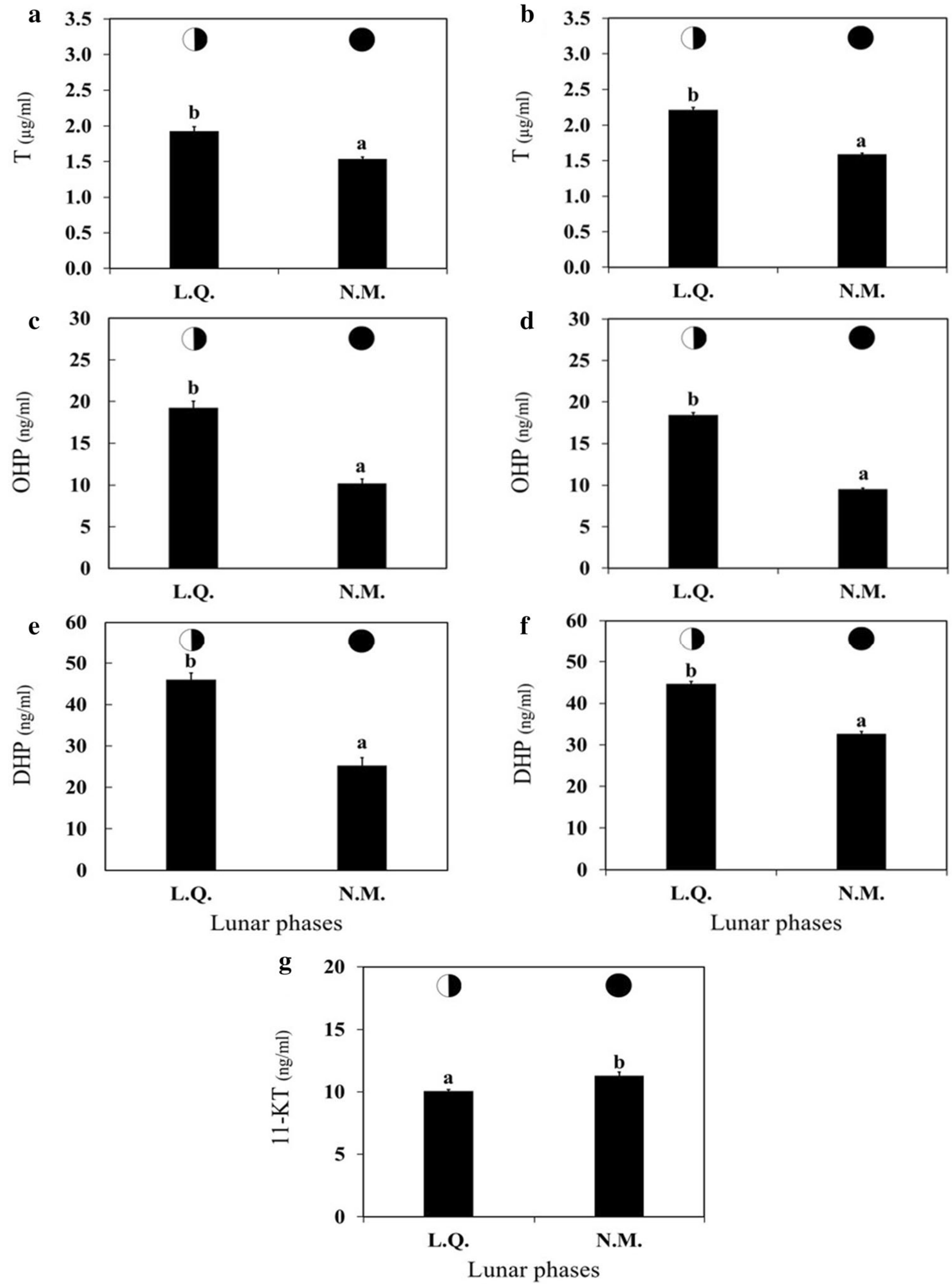

Fig. 4 Lunar-dependent variation in the levels of T (Testosterone) (µg/ml), OHP (17α-hydroxy progesterone) (ng/ml), DHP (17α, 20β-dihydroxy progesterone) (ng/ml), and 11-KT (11-keto-testosterone) (ng/ml) in the culture medium of ovary fragments (**a, c, e**) and testis fragments (**b, d, f, g**) of Indo-Pacific sergeant fish, *A. vaigiensis*. Each bar represents the mean value from four replicates with the standard error. The bar assigned with different letters are significantly different ($p < 0.05$). Lunar phases are indicated as last quarter (◐; L.Q.) and new moon (●; N.M)

main precursor, is the most potent steroid that induces the final maturation processes in many teleost fishes (Billard et al. 1982; Nagahama 1994; Nagahama et al. 1995; Agahama and Yamashita 2008; Schulz et al. 2010). Rahman et al. (2000a) demonstrated a lunar periodicity in sex steroids of *S. guttatus*, with significantly higher levels of plasma DHP in the first quarter, concomitant with the spawning time in this species. In other marine species like *S. argenteus* (Rahman et al. 2003c), *Chromis dispilus*, and *Hypsypops rubicundus* (Pankhurst 1990) also high levels of this steroid are obtained in the spawning time. When the germ cells are full-grown, a shift in steroid production will normally occur in teleost fish from C18 and C19 to C21 steroids (Kazeto et al. 2011). During this process, the somatic cells of the gonads, definitely theca and leydig cells in females and males, respectively, biosynthesize progestogens like OHP, which serves as a precursor for DHP production in both sexes (Sangalang and Freeman 1988; Mojazi Amiri et al. 1999; Ijiri et al. 2016). So in this stage of gonadal development, an increase of these hormones will be responsible for final maturation just prior to the spawning (Kazeto et al. 2001; Senthilkumaran et al. 2004). In the present study, the increment of OHP and DHP levels around the first and the last quarter showed that the physiological processes of the final maturation of oocytes and spermatozoa followed by spawning in *A. vaigiensis* are in agreement with the process found in other marine teleosts. Furthermore, synchronization of these physiological processes with different lunar phases revealed lunar spawning periodicity in this species.

Although the measurement of the in vivo serum levels of T revealed a plateau trend during the lunar phases in both sexes based on the statistical interpretation, the levels of this androgen were noticeable in both females and males. In females, the level of this hormone in LQ showed a value of approximately 43% more than that in FM. In males, the serum level of this androgen measured as much as 14% and 61% more in LQ and NM (7 days after spawning time), respectively, compared to the FM value. So, the peak of T in *A. vaigiensis* was concomitant with the spawning time that was indicated by the changes in the GSI. The results are in agreement with those obtains from the studies on *Fundulus grandis* (Greeley JR. et al. 1988; Emata et al. 1991), *F. heteroclitus* (Cochran et al. 1988), *Siganus guttatus* (Rahman et al. 2000a, 2000b), *S. argenteus* (Rahman et al. 2003c; Takemura et al. 2004), *Solea senegalensis* (Oliveira et al. 2009), *Boleophthalmus pectinirostris* (Wang et al. 2008), and *Plectropomus leopardus* (Frisch et al. 2007). Lunar spawning periodicity relies on daily gonadal development that needs proper hormonal fluctuations to manage these different developmental stages. The daily maturation cycle is shown in some Perciformes like *Lutjanus campechanus* (Jackson et al. 2006), *Sparus aurata* (Meseguer et al. 2008), *Pagrus major* (Matsuyama et al. 1988) as well as lunar periodicity spawners like *Solea senegalensis* (Oliveira et al. 2009) and *Fundulus heteroclitus* (Shimizu 1997). Testosterone not only acts as the main precursor for E_2 and 11-KT production in females and males, respectively, but induces maturation processes of post-vitellogenic oocytes (Iwamatsu 1978; Greeley et al. 1986). Campbell et al. (1976) found higher levels of T in winter flounder females at the spawning period. The same results were obtained in female rainbow trout by Campbell et al. (1980). In males, T was not only noticeable in LQ but, along with 11-KT, demonstrated prominent values in NM (7 days after spawning). Elevated levels of 11-KT were observed in plainfin midshipman, *Porichthys notatus*, not only at spawning time but after spawning and during the pre-nesting period (Knapp et al. 1999; Sisneros et al. 2004). Cunha et al. (2019) demonstrated that 11-KT implantation in bluegills, *Lepomis macrochirus*, resulted in more aggressive and parental care behavior in males. The paternal care behavior is shown in damselfishes like *A. sordidus* (Kerr Lobel and Lobel 2013; Kerr Lobel et al. 2019), *A. abdominalis* (Maruska and Peyton 2007), and *A. vaigiensis* (Allen 1991). High levels of 11-KT in NM and after spawning time suggested the possible role of this androgen in mediating the male secondary sexual characters related to territoriality and the expression of the reproductive behavior in parental males.

In vitro assessment was performed to have an elaborate picture of the lunar effects on *A. vaigiensis* reproductive physiology. Around the last quarter, GVBD was significantly induced by the addition of hCG, whereas the lowest percentage of GVBD was obtained around the new moon. Analyzing the produced hormones in the media revealed that the concentrations of OHP and DHP around the LQ were significantly higher than these levels around the NM. Mojazi Amiri et al. (1999) confirmed the role of DHP, a C21 steroid, as the most potent maturation-inducing hormone (MIH) on the induction of GVBD in vitro in Bester. Rahman et al. (2000a) demonstrated DHP as the most effective steroid with the highest levels at the spawning time in *S. guttatus*. Matsuyama et al. (1998) founded diurnal changes of the serum levels of MIH with peaks coincided with GVBD in *Pseudolabrus japonicas*. In the present study, in vitro GVBD induction was significantly performed in the samples from LQ. A suggestion reason for this influence may be attributed to the possible effects of lunar phases as an external stimulus on the activity of 20β-HSD enzyme biosynthesized in the follicular layers as well as the increment of the sensitivity of the oocytes to the triggered MIH production through this steroidogenic enzyme toward LQ as the specific lunar phase for this species. It has been proved that high activity of 20β-HSD as the main steroidogenic enzyme has a critical role in initiating the maturational events including GVBD in teleosts (Nagahama 1994, 1997; Agahama and Yamashita 2008). In *S. guttatus*, a species with a lunar spawning periodicity characteristic with first lunar quarter considered as a species-specific time that triggers spawning in this marine fish, a significant conversion rate of OHP to DHP occurred around this lunar phase (Harahap et al. 2002; Rahman et al. 2002; Takeuchi et al. 2018). The same results were shown in *S. argenteus* (Rahman et al. 2000a, 2003b), *Apogon amboinensis* (Pisingan and Takemura 2007), *Fundulus heteroclitus* (Petrino et al. 1993; Hsiao et al. 1996), and *Haliochoeres trimaculatus* (Leatherland et al. 2003) with high activity of 20β-HSD and peaks in MIH near the spawning time. In males also the high levels of OHP and DHP in the culture media supported the role of these hormones as MIH in this species. However, further research will be needed to determine the predominant C21 steroid acts as MIH in this species. Studies on spotted seatrout, *Cynoscion nebulosus* (Thomas and Trant 1989), Atlantic croaker, *Micropogonia sundulatus* (Trant and Thomas 1989), Turbot, *Scophthalmus maximus* (Mugnier et al. 1997), and yellowfin porgy, *Acanthopagrus latus* (Jeng et al. 2012), provided evidence that 20β-S acts as the major MIH in these marine teleosts.

In stripped seabass, *Morone saxatilis* (King et al. 1994) and bambooleaf wrasse, *Pseudolabrus japonicas* (Matsuyama et al. 1998), both DHP and 20β-S play as potent inducers of MIH. However, in the most studied teleosts DHP was identified as the principal MIH (Scott et al. 1990; Suzuki et al. 1991; King et al. 1995; Todo et al. 2000; Inbaraj et al. 2001; Rahman et al. 2002, 2003b; Hachero-Cruzado et al. 2013). Based on the present results obtained from both the in vivo and the in vitro analysis, it is supposed that DHP acts as the main MIH in *A. vaigiensis*. However, supplementary analysis is needed to elucidate whether the final maturation processes in this fish is induced only by this hormone or other kinds of progesterone concomitant with this C21 steroid are effective.

In males, the testis fragments sampled in NM (7 days after spawning time) significantly produced higher levels of 11-KT in comparison to those sampled in LQ (spawning time). 11-oxygenated androgens, like 11-KT, that are generally effective not only in spermatogenesis but in stimulating secondary sexual characters and reproductive behavior, are biosynthesized through the activity of the 11β-HSD (Jiang et al. 1996; Young et al. 2005; Schulz et al. 2010). The essential role of this steroidogenic enzyme is shown in *Anguilla japonica* (Jiang et al. 2003), *Oreochromis niloticus* (Jiang et al. 2003), *Oncorhynchus maykiss* (Kusakabe et al. 2003), *Epinephelus coioides* (Lee et al. 2002), and *Amphiprion clarkii* (Miura et al. 2008). Jiang et al. (1996) found no 11β-hydroxylase expression in immature eel testes before hCG administration but detected high expression after hCG injection. High levels of in vitro production of 11-KT in NM could be postulated as the hCG-induced expression of the 11β-HSD in the testes fragments. However, further studies are needed to verify the presence of this steroidogenic enzyme in *A. vaigiensis* testis.

In conclusion, as this study was performed during a period covering all different lunar phases, reproductive indicators, as well as hormonal fluctuation revealed that spawning in Indo-Pacific sergeant fish, *A. vaigiensis*, is characterized by lunar periodicity. Lunar zeitgeber is likely recognized by this fish and the spawning time-synchronized, accordingly. In FQ and LQ, the peaks of different reproductive indicators are observed, with the LQ as the main spawning time. Based on the obtained results, it can be proposed that the spawning is controlled in semilunar manner. In general, the hormonal control process of oocyte maturation and spermiation to acquire fertile germ cells is similar to those seen in other teleost fishes. However, more studies are needed to elucidate the different aspects of reproductive physiology in *A. vaigiensis*. The obtained results can help a better understanding of environmental influence, with an emphasis on lunar regulatory effects on *A. vaigiensis* reproduction, which finally leads to better management of this fish.

Acknowledgements We are grateful to the editor and anonymous reviewers for their insightful comments, which greatly improved the manuscript. The authors are thankful to the University of Hormozgan for providing us with laboratory facilities. We are grateful to Alireza Razi for his assistance in the field. This work was performed according to the Iranian Society for the Animal Welfare.

Declarations

Conflicts of interest The authors claim that there is no conflict of interest in this manuscript.

Data availability statement The data that support the findings of this study are available from the corresponding author upon reasonable request.

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