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# The annual reproductive cycle and sex inversion of the Picnic seabream, *Acanthopagrus berda* (Forsskål 1775) from Indian waters: Histological and morphometric description

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## Abstract

The annual reproductive cycle of picnic seabream, *Acanthopagrus berda* (Forsskål, 1775), one of the potential aquaculture candidate from estuarine waters of Calicut, Kerala (India) was studied. Based on the morphological and histological studies, the ovotestes of *A. berda* were classified as active male, active female, inactive male, inactive female, transitional and undifferentiated. Histological observation of transitional gonads showed signs of degeneration in the testicular lobe, proliferation of connective tissue and empty sperm ducts indicating protandrous hermaphroditism in *A. berda*. Ovary was classified into seven maturity stages (virgin, developing virgin, developing, maturing, mature, running, spent) and testis into five maturity stages (resting, maturing, mature, running, spent). Gonadal development in *A. berda* indicated resting phase (February–July), pre-spawning phase (March–August) and spawning phase (August–December). Inactive (24.6%) and active males (21.6%) were observed as dominant in smaller length classes (140–250 mm TL), whereas inactive (18%) and active females (51%) were observed as dominant in larger length classes (251–450 mm TL). Few primary females (28.1%) were observed in smaller (below 250 mm TL) and few primary males (28.5%) were observed in larger length classes (above 250 mm TL). From the present study, it can be concluded that in *A. berda*, most of the individuals function first as males and then change sex to female, but few continue to function as either male or female throughout their lifespan indicating digynous protandrous hermaphroditism.

**KEYWORDS**
*Acanthopagrus berda*, gonad, histology, India, mariculture, reproductive cycle

## 1 | INTRODUCTION

Teleost fish shows a wide array of sexual patterns (Alonso-Fernández, Alos, Grau, Dominguez-Petit, & Saborido-Rey, 2011) and reproductive development. New accounts of hermaphroditism are continually being reported in certain families of teleost namely, Sparidae, Scaridae, Scarinae and Serranidae (Buxton, 1990). Diverse expressions of sexuality are found in Sparidae fishes, which exhibit protandry (Abou-Seedo, Dadzie, & Al-Kanaan, 2003), protogyny (Kokokiris,

Bruslé, Kentouri, & Fostier, 1999), simultaneous hermaphroditism (Alonso-Fernández et al., 2011), rudimentary hermaphroditism (Hughes, Stewart, Kendall, & Gray, 2008) and gonochorism (Francis & Pankhurst, 1988) and this diverse array of reproductive strategies caught the attention of reproductive biologists many decades ago (Buxton & Garratt, 1990).

According to Buxton (1992), identification of sex change is important since sex change has serious implications for their management and survival. Most of the commercially exploited sea breams are reported to change sex during their life cycle (Buxton, 1989) and there is evidence of significant changes in sex ratios brought about by selective exploitation. High fishing pressures on protandrous or protogynous fish have an undesirable effect such as removal of larger males and females respectively from a population (Buxton, 1993). This has resulted in considerable debate on the possibility that fish with such reproductive styles require special management and some valuable research has been undertaken in this direction (Punt, Garratt, & Govender, 1993).

Sparids are important candidates for aquaculture (Ingram, McKinnon, & Gooley, 2002) and they also make a significant contribution to recreational and commercial fisheries (Smallwood & Sumner, 2007). But the sex change in the Sparidae family is considered to be the most complex than in any other family of fish (Garratt, 1993a). The structural morphology of sparid gonads makes it difficult to determine sex change in sparid fish. Though sex change is well documented in Sparidae by Buxton and Garratt (1990), a systematic study on reproductive biology of many sparid fish is still lacking. The need for detailed descriptions of sex differentiation, gonad development and spawning behaviour in this family has been identified by a number of workers in this field (Atz, 1964; Buxton & Garratt, 1990; Garratt, 1993b; Hesp & Potter, 2003). Even within the same species of Sparids, different sexual expression can occur at different geographical locations (Alonso-Fernández et al., 2011; Hesp & Potter, 2003).

The Picnic seabream, *Acanthopagrus berda* (Forskkal, 1775) is a fairly small, estuary-dependent (Begg, 1978; Van der Elst, 1988) seabream with a wide distribution throughout the tropical Indo-West Pacific region (Iwatsuki & Heemstra, 2010). *A. berda*, commonly known as the gold-silk seabream is native to the Indian Ocean and is distributed along the estuarine and shallow coastal waters of India. The flesh of *A. berda* is excellent and therefore they are locally exploited by artisanal fisheries both in cast net and hook and line along the Indian coasts (FAO, 1984) and are sold fresh in markets (Shilta et al., 2018). This species is considered as an important commercial sparid fish (Kasahara, 1957) because of its recreational value, excellent meat quality, high economic value, ability to tolerate wide variations in salinity and temperature, easy adaptation to captivity and fast growth rate (Anonymous, 2012; Battaglene & Fielder, 1997; James, Mann, Beckely, & Govender, 2003; Rahim, Abbas, Ferrando, Gallus, & Ghaffar, 2017; Sadek, Osman, & Mansour, 2004; Samuel & Mathews, 1987; Thorogood & Blackshaw, 1992). This species in tropical Indian waters has the potential to attract commercial interests in the near future.

*Acanthopagrus berda* has been identified as a priority species for mariculture in India (Suresh Babu, Shilta, Asokan, & Vinod, 2017). Even though *A. berda* is one of the popular table fish in the country, reports on its reproductive biology are unavailable. The reproductive biology of each fish species is critical for the conservation and fish resource management (Tesfahun, 2019). It is reported that the breeding season of *A. berda* varies with geographic location. *A. berda* spawns between May and August in Africa (Kyle, 1986; Wallace, 1975); February and March in Hong Kong (Mok, 1985); June and September in Australia (Tobin, Sheaves, & Molony, 1997). Identifying the breeding season of fish species is important for their aquaculture development.

An understanding of the reproductive biology, especially detailed information on the changes in gonad during the reproductive cycle is a necessary component for species management in both wild and captive populations. Therefore the present study using histological methods was undertaken to describe the reproductive pattern and annual reproductive cycle of *A. berda* from Indian coast.

## 2 | MATERIALS AND METHODS

A total of 720 specimens of *A. berda* was obtained by random sampling from commercial cast net catches operated at a depth of 5 m from Korapuzha estuary from January to December 2016. The Korapuzha estuary (11°39.858N and 75°74.294E) is located about 10 km north of Calicut city, Kerala, India. The specimens were kept in wooden boxes and brought to the laboratory within 15 min. Fish were mopped with a filter paper before they were weighed to remove excess water from their body in order to ensure accuracy. Weight and length of each individual fish were measured using a sensitive digital weighing balance and a measuring board respectively. For each specimen, the total length (TL) was measured to the nearest mm, total fish weight (TW) to the nearest 0.1 g and the weight of the gonads (GW) was recorded to the nearest 0.01 g.

Sex and maturity stages were determined macroscopically. The gonads were examined macroscopically to determine whether they were active male, inactive male, active female, inactive female, transitional and undifferentiated. Examined male specimens were divided following the method of Grandcourt, Al Abdessalaam, Francis, and Al Shamsi (2004) into (I) Resting, (II) Maturing, (III) Mature, (IV) Running, (V) Spent and female specimens were divided following the method of Abou-Seedo et al. (2003) into (I) Virgin, (II) Developing virgin, (III) Developing, (1V) Maturing, (V) Mature, (VI) Running, (VII) Spent. Variation in the monthly composition of maturity stages was used to describe the reproductive cycle.

Gonad of five representative samples from each macroscopically determined different reproductively distinguished groups of ovotestes (active male, inactive male, active female, inactive female, transitional and undifferentiated) and five representative samples from each macroscopically determined maturity stages of both male (resting, maturing, mature, running, spent) and female (virgin, developing virgin, developing, maturing, mature, running,

**TABLE 1** Number of male and female *Acanthopagrus berda* per month and the results of the chi-square ($\chi^2$)

| Month | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Number of males | 28 | 22 | 8 | 20 | 10 | 20 | 8 | 30 | 24 | 58 | 22 | 26 |
| Number of females | 36 | 20 | 10 | 22 | 16 | 38 | 26 | 42 | 28 | 60 | 16 | 20 |
| Male:Female ratio | 1:1.29 | 1:0.91 | 1:1.25 | 1:1.0 | 1:1.6 | 1:1.9 | 1:3.2 | 1:1.4 | 1:1.17 | 1:1.03 | 1:0.73 | 1:0.77 |
| Male: Female significance | No | No | No | No | No | No | No | No | No | No | No | No |
| Different from 1:1 (P) | <0.05 | <0.05 | <0.05 | <0.05 | <0.05 | <0.05 | <0.05 | <0.05 | <0.05 | <0.05 | <0.05 | <0.05 |
| Chi-square ($\chi^2$) | 0.86 | 0.82 | 0.56 | 0.81 | 0.64 | 0.81 | 0.56 | 0.87 | 0.84 | 0.93 | 0.82 | 0.85 |

spent) were fixed in 10% neutral buffered formalin (NBF). Three sub-samples were taken from the anterior, middle and posterior portion of both the gonadal lobes and subsequently processed for histology. All the tissues were then washed in tap water for 6–8 hr and loaded in an automatic tissue processor (Leica, TP 1020) and dehydrated in different gradient solutions of isopropyl alcohol, xylene and finally embedded in paraffin wax. The embedded tissues were moulded into blocks and were trimmed and transverse section of 3–5 μm were obtained using microtome. The sections were stained with Harris haematoxylin and counterstained with eosin in compliance with the accepted procedures (Gabe, 1976). The slides were observed under a Zeiss Axio Lab A1 light microscope at magnifications of ×10 to confirm whether *A. berda* gonads were active male, inactive male, active female, inactive female, transitional or undifferentiated. The histological observation of different maturity stages of gonads was measured using Zeiss Axio Lab A1 light microscope at magnifications of ×40.

To quantify the changes in gonad weight during the annual sexual cycle and to determine the spawning season, monthly gonadosomatic index ($I_G$) (De Vlaming, Grossman, & Chapman, 1981) was calculated using the formula:

$$I_G = \frac{\text{Gonad weight (g)}}{\text{Body weight (g)}} \times 100$$

## 2.1 | Statistical analysis

Statistical differences in monthly $I_G$ were tested using analysis of variance (ANOVA), while Tukey's test was performed at a significance level of 0.05 (Zar, 2010). Monthly sex ratio, expressed as male: female, was analysed. Deviations from 1:1 null hypothesis were statistically tested using $\chi^2$–test.

# 3 | RESULTS

## 3.1 | Sex ratio

It was found that of the 720 specimens measured, 334 were females (46.39%) and 276 (38.33%) were males, 40 (5.56%) were transitional and 70 (9.72%) were undifferentiated. But the gonads of 152 males (active males) had only testicular tissue while the gonads of 124 males (inactive males about 1.72% in all specimens) had partly developed ovaries together with testes. On the basis of Koc, Cakir, and Aka (2002) study, these individuals were considered as males. Smaller length class (below 250 mm TL) were dominated by male (46.3%) followed by female (28.1%), undifferentiated (17.5%) and transitional (8.1%). Larger length class (above 250 mm TL) were dominated by female (69.0%) followed by male (28.5%) and transitional (2.5%). The overall male: female ratio (1:1.2) was similar with expected 1:1 ratio ($\chi^2$ = 9.39, $p$ > 0.05). Male: female ratio and corresponding chi-square ($\chi^2$) values for each month are presented in Table 1.

## 3.2 | Types of ovotestes in *A. berda*

The gonad of *A. berda* is classified into following ovotestes types based on the morphological and histological studies.

### 3.2.1 | Active males

Active males on slight abdominal pressure release semen from the testicular region. The morphological observation revealed that this type of ovotestes possesses dominant active white testicular lobes and small inactive ovarian lobes, lying within the grooves in the dorsomedial surface of the testis. The ovarian lobes are invisible in the case of completely ripe male specimens since the testicular tissue completely encircles the ovarian lobes (Figure 1a). The transverse section of active males showed extended lobules in which spermatogonial cells were distributed in crypts; tubule space and interior lumen dominated with more advanced gametogenic stages namely spermatocytes, spermatids and spermatozoa. Spermatogonia were absent in ovotestes of active males. Small ovarian lobes with oocytes in chromatin nucleolar and perinucleolar stages were observed, but no active oogenesis had taken place (Figure 2a). The active males were observed in individuals of 14.1–34.6 cm TL weighing 70–859 g (Figure 3a) from August to February (Figure 3b).

### 3.2.2 | Inactive males

In the case of inactive males, no free running of semen from the testicular region was observed. The morphological observation

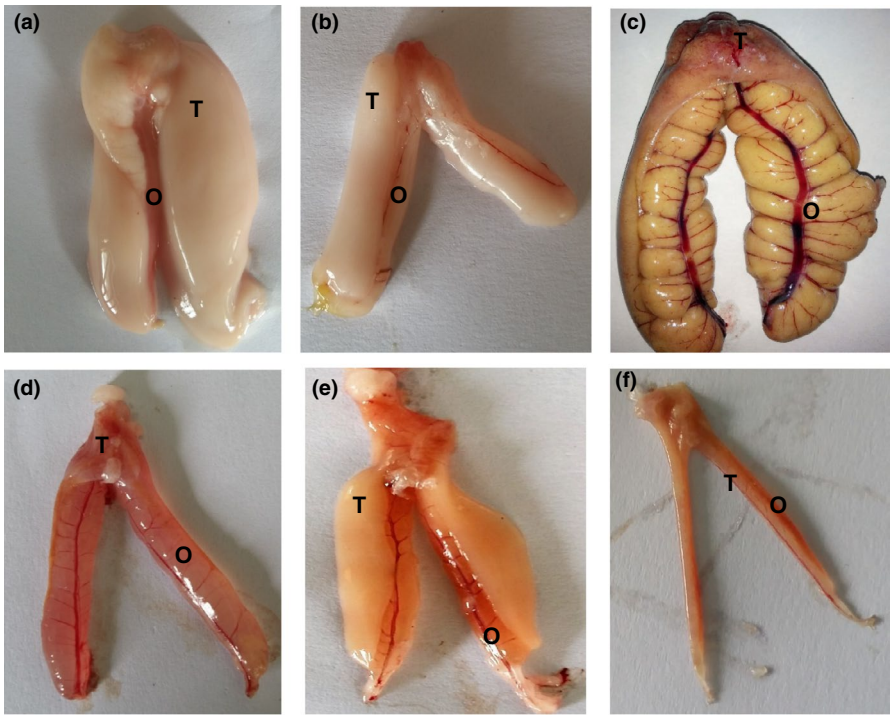



**FIGURE 1** Classification of ovotestes of *Acanthopagrus berda* based on morphological observation (a) active male (b) inactive male (c) active female (d) inactive female (e) transitional (f) undifferentiated ovotestes (O, ovary; T, testis)

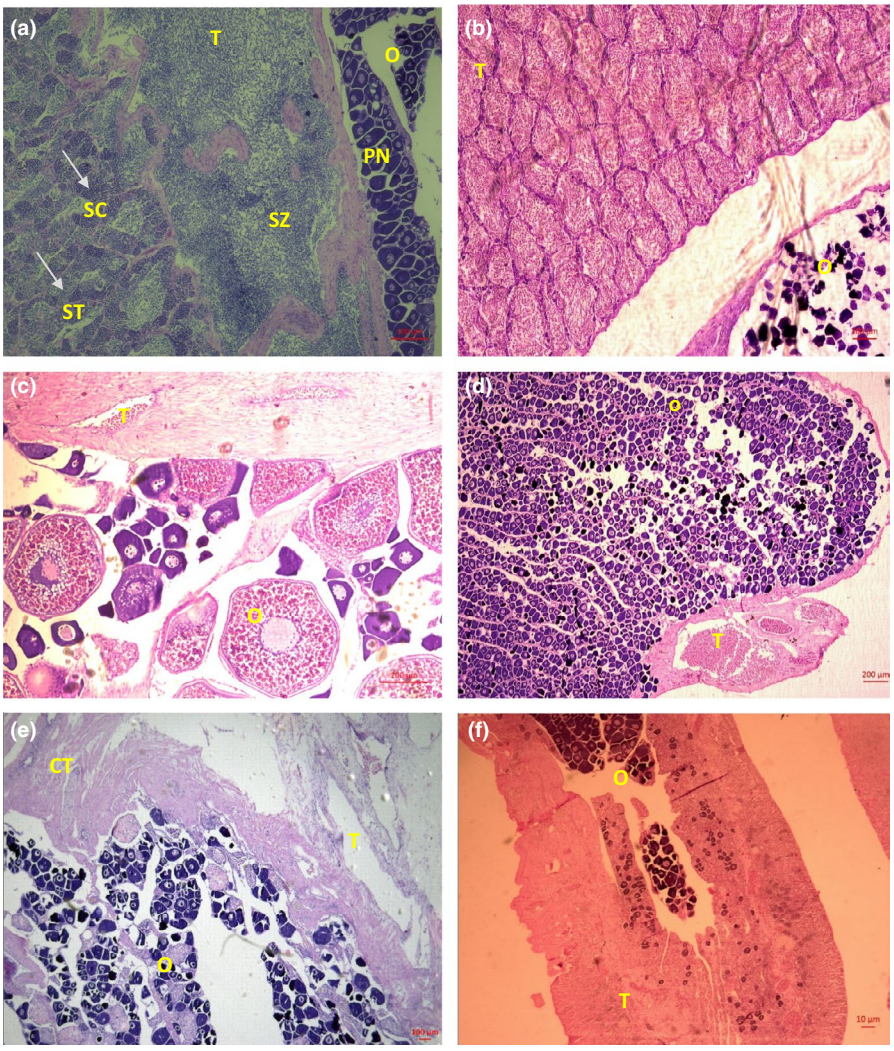



**FIGURE 2** Classification of ovotestes of *Acanthopagrus berda* based on histological observation (a) active male (b) inactive male (c) active female (d) inactive female (e) transitional (f) undifferentiated ovotestes (CT, connective tissue; O, ovary; PO, Perineuclear oocyte; SC, spermatocytes; ST, spermatids; SZ, spermatozoa; T, testis)

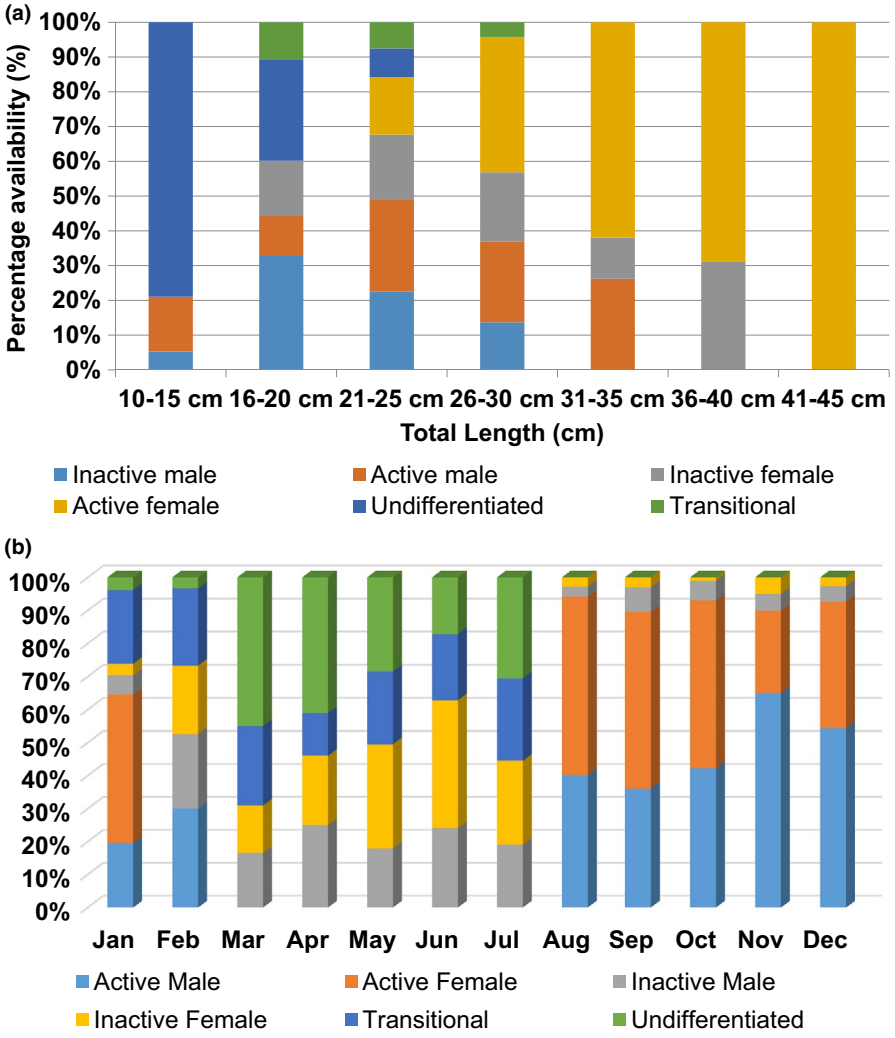



**FIGURE 3** Availability of different reproductively distinguished groups of *Acanthopagrus berda* (a) at different length classes (b) at different months

revealed that this type of ovotestes possesses dominant testicular lobes and inactive small or similar size ovarian lobes, lying within the grooves on the dorsal surface of the testis (Figure 1b). The histological studies revealed that testis of inactive males contain both ovarian and testicular portions. The testicular portion is characterized by spermatogonia with lesser spermatogenic activity. The ovarian portion contains oocytes of chromatin nucleolar and perinucleolar stage with further developments arrested (Figure 2b). Inactive males were observed in individuals of 14.0–28.7 cm TL (50.5–458.5 g) (Figure 3a) dominant from January to July (Figure 3b).

### 3.2.3 | Active females

The gonad of active females was cylindrical in shape, characterized by light to dark orange colour. The morphological observation revealed that the ovotestes were mostly dominated by ovarian lobes, whereas the reduced inactive testicular lobes appeared as a very thin band of tissue along the ventrolateral surface of the ovary (Figure 1c). The transverse section of active female ovotestes showed advanced stages of oogenesis (a large number of vitellogenic oocytes with some previtellogenic oocytes). No spermatogenic cells were observed in the remnant testis (Figure 2c). The active females were observed in individuals of 21.2–43.2 cm TL (109–1,753 g) (Figure 3a) from August to January (Figure 3b).

### 3.2.4 | Inactive females

The ovotestes of inactive females was dominated by ovarian lobes whereas testicular lobes appeared as a thin band of tissue along the ventrolateral surface of the ovarian lobes (Figure 1d). Histological sections of inactive female ovotestes showed numerous well developed ovarian lamellae with oocytes of chromatin nucleolar and perinucleolar oocytes. Remnants of testis appeared with no spermatogenic activity (Figure 2d). Inactive females were observed in individuals of 16–37.7 cm TL (100.4–1,250 g) (Figure 3a) dominant from January to July after the spawning period (Figure 3b).

### 3.2.5 | Transitional ovotestes

The transitional gonads were characterized by testicular and ovarian lobes of similar size or testicular lobe, reduced in size compared

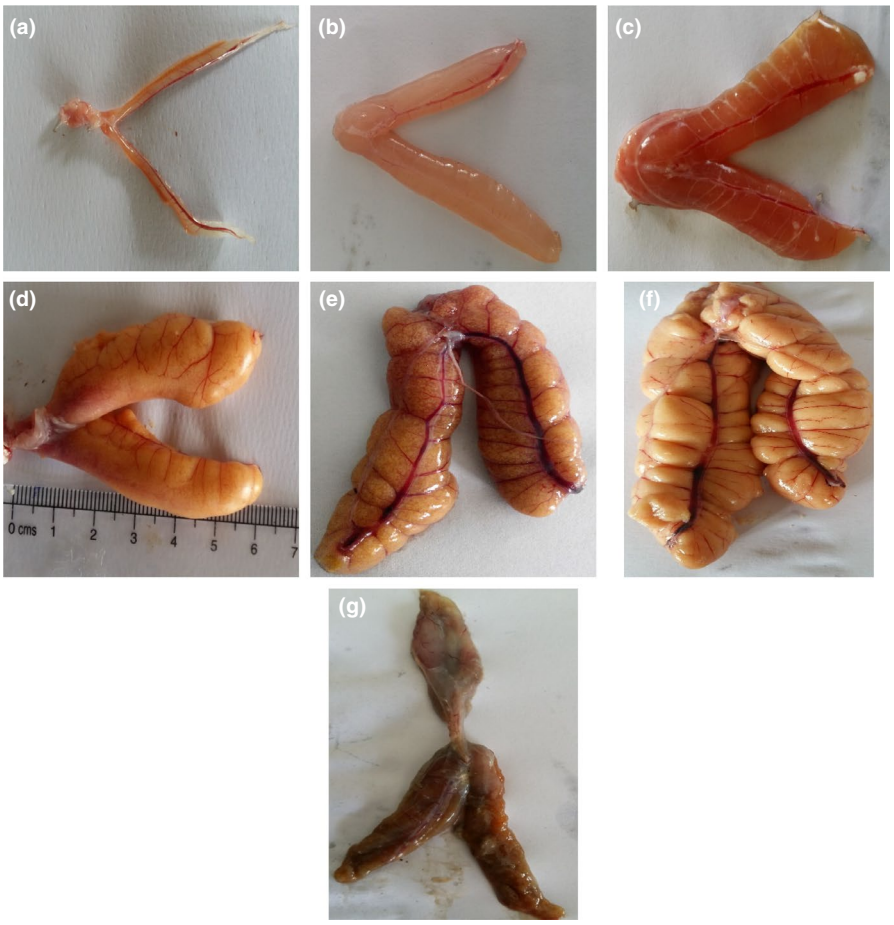



**FIGURE 4** Different maturity stages of *Acanthopagrus berda* ovary based on morphological observations (a) virgin (b) developing virgin (c) developing (d) maturing (e) mature (f) running (g) spent

with ovarian lobe (Figure 1e). Microscopical observation showed signs of degeneration in the testicular lobe, proliferation of connective tissue and empty sperm ducts. The ovarian lobes were characterized by oocytes of chromatin nucleolar and perinucleolar stages (Figure 2e). The transitional gonads were observed in individuals of 18.7–27.1 cm TL (Figure 3a) from January to July after the spawning (Figure 3b).

### 3.2.6 | Undifferentiated ovotestes

In this group, morphological observation of ovotestes was difficult to classify either as male or female. These ovotestes were thread-like structures containing an equal portion of testis and ovary (Figure 1f). Histological observations revealed testicular lobe containing spermatogenic cells and ovarian lobes with inactive oocytes of the chromatin nucleolar and perinucleolar stages. (Figure 2f). There was a simultaneous proliferation of gonial cells in both male and female elements, but further development was more rapid in the male element. A few previtellogenic oocytes were evident amongst proliferating gonia in the female element, but development in the male element included all stages of spermatogenesis, including the production of sperm. Undifferentiated gonads were observed in individuals of 15–25.4 cm TL (Figure 3a) from January to July (Figure 3b).

## 3.3 | Morphology of ovary of *A. berda*

The ovary of *A. berda* is a paired organ suspended by a thin mesorchium from the dorsal side of the peritoneal cavity. The ovarian lobes were fused posteriorly to form a short oviduct but are free anteriorly. The ovaries were cylindrical in shape with the right lobe larger than the left. The immature ovary was with smooth contours (Figure 4a–c), while the ripe ovary exhibited undulations with a heavy network of dilated blood vessels to meet the increased need for blood circulation (Figure 4e). Since *A. berda* is a protandrous hermaphrodite, remnants of testis lobe appeared as thin bands of tissue lying on the ventrolateral surface of ripe ovaries (Figure 4f).

## 3.4 | Maturity stages of the ovary

About seven maturity stages of the ovary were identified and the stages observed were virgin, developing virgin, developing, maturing, mature, running and spent.

### 3.4.1 | Stage I – Virgin

The macroscopic observation of ovary stage I revealed a small thread-like structure, translucent with slight brownish colouration (Figure 4a). Both ovarian and testicular tissues were present and

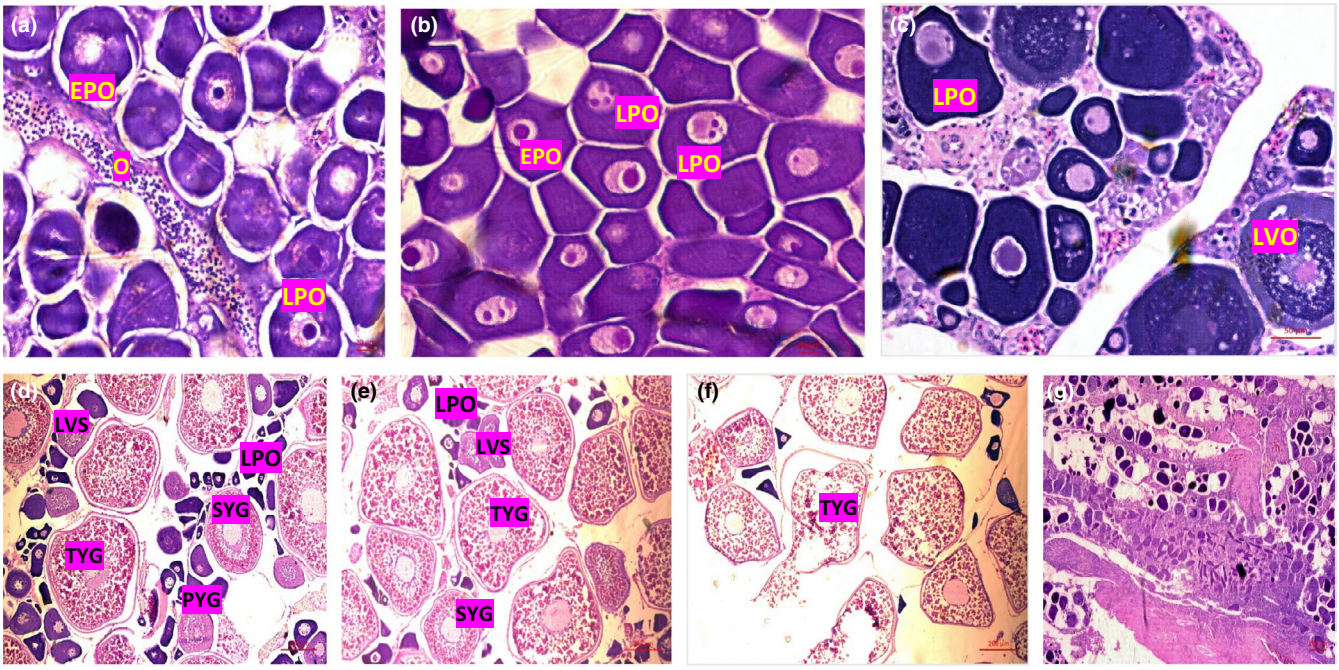



**FIGURE 5** Gonad transverse sections showing different maturity stages of *Acanthopagrus berda* ovaries (a) virgin (b) developing virgin (c) developing (d) maturing (e) mature (f) running (g) spent (EPO, early perinucleolar oocyte; LPO, late perinucleolar oocyte; PYG, primary yolk granule; SYG, secondary yolk granule; TYG, tertiary yolk granule; LVS, lipid vesicle stage)

it occupied about 10% of the peritoneal cavity. The microscopic examination of virgin ovary revealed the presence of oogonia, early perinucleolar oocytes and few late perinucleolar oocytes (Figure 5a). Virgin females were observed from March to August with peak availability during the month of June (monsoon season) (Figure 6a).

### 3.4.2 | Stage II – Developing virgin

Stage II ovary occupied about 20%–25% of the peritoneal cavity. The developing virgin ovary is cylindrical in shape with light orange-brown colouration (Figure 4b). Few blood capillaries were visible around the ovary. Microscopically, large-size late perinuclear oocytes (Figure 5b) were found dominant in this stage. The developing virgin was observed from February to July with peak availability during June (monsoon season) (Figure 6a).

### 3.4.3 | Stage III – Developing

At this stage blood capillaries were visible around the ovary and the ovary was cylindrical in shape, orange in colour and occupied about 40% of the peritoneal cavity (Figure 4c). In the histological sections of developing ovary, lipid vesicle stage oocytes made their appearance in addition to perinucleus oocytes (Figure 5c). The developing females were observed from May to September with peak availability during July (monsoon season) (Figure 6a).

### 3.4.4 | Stage IV – Maturing

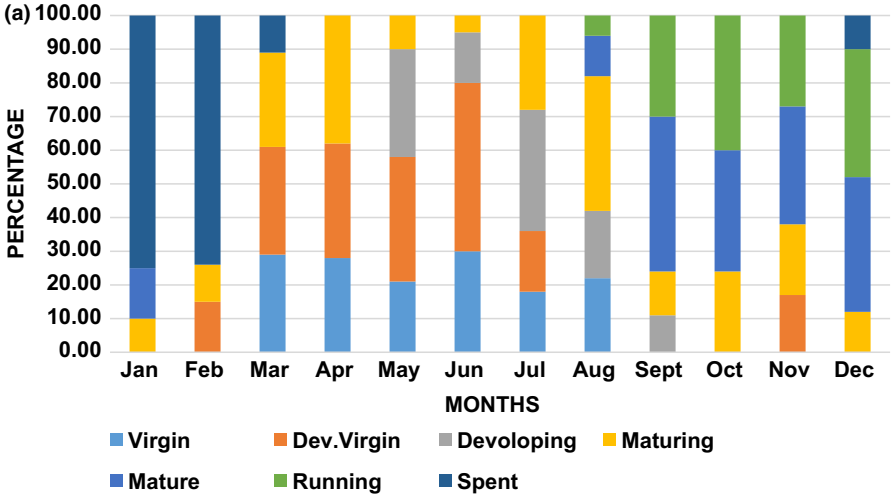
The ovary was yellowish orange to reddish-orange in colour at this stage (Figure 4d) and occupied about 50%–60% of the peritoneal cavity. The ovaries showed undulations and oocytes were with a slightly granular appearance. Microscopically, oocytes with lipid vesicles and yolk granule were found dominant at this stage with few oocytes in perinuclear stages (Figure 5d). Such females occurred from January to December with peak availability during August (monsoon) (Figure 6a).

### 3.4.5 | Stage V – Mature

The ovary of a mature females appeared swollen, pale orange to red in colour with a heavy network of blood vessels surrounding the organ, occupying about 70% of the peritoneal cavity (Figure 4e). The ovaries showed greater undulations with large vitellogenic oocytes clearly visible through the ovarian wall. Histological observations revealed numerous large, advanced vitellogenic oocytes with few early and late perinuclear oocytes and large lipid vesicle oocytes (Figure 5e). Mature females occurred from August to January (monsoon and post monsoon) with peak availability during September (Figure 6a).

### 3.4.6 | Stage VI – Running

The ovary occupied about 80%–95% of the peritoneal cavity, dark yellowish-brown in colour, with an extensive network of blood vessels surrounding it. Large-size vitellogenic oocytes were clearly



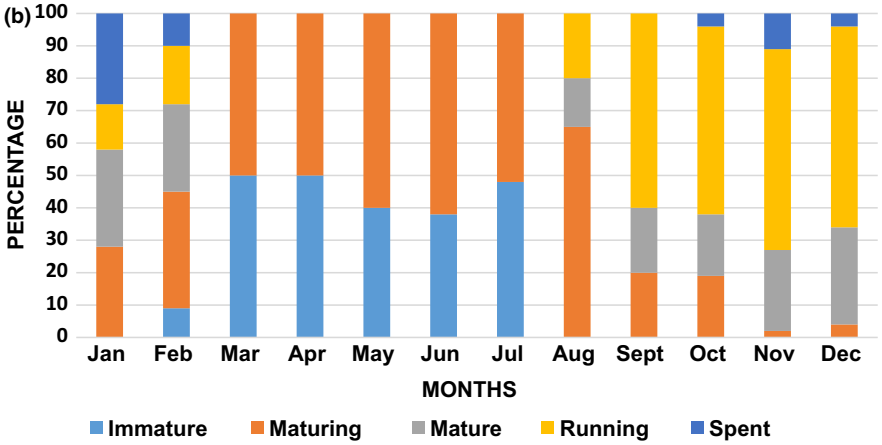




**FIGURE 6** Monthly distribution of maturity stages in *Acanthopagrus berda* throughout the period from January to December 2016 (a) male (b) female

visible beneath the transparent ovarian wall (Figure 4f). Microscopic observation revealed the presence of very large-size vitellogenic oocytes with coarse yolk granules in the cytoplasm (Figure 5f). Running females were observed from August to December (monsoon and post monsoon) with peak availability during October (Figure 6a).

### 3.4.7 | Stage VII – Spent

The spent ovary was observed as flabby, purplish-brown in colour with a sudden decrease in size with few translucent oocytes remaining in the ovary (Figure 4g). Histological sections revealed ovigerous folds containing a large number of ruptured, postovulatory follicles and atretic follicles (Figure 5g). These females occurred in December to March samples (post monsoon) (Figure 6a).

## 3.5 | Maturity stages of testis of *A. berda*

About five maturity stages of the testis were identified and the stages observed were resting, maturing, mature, running and spent.

### 3.5.1 | Stage I – Resting (Immature)

The macroscopic observation of testis stage I revealed it as thin, creamy white colour (Figure 7a), occupying about 10% of the peritoneal cavity. The microscopic examination of resting testis revealed the presence of nests of spermatogonia, each spermatogonium with a spherical nucleus (Figure 8a) small lobules, many with no lumens. The resting males were observed from February to July with peak availability from March to April months (pre-monsoon) (Figure 6b).

### 3.5.2 | Stage II – Maturing

The testis occupied about 20%–40% of the peritoneal cavity at this stage. The morphology of maturing testis is cylindrical, white coloured with no milt (Figure 7b). Active spermatogenesis begins at this stage. Histology revealed the presence of continuous germinal epithelium throughout the testis with all stages of spermatogenesis (Figure 8b). The seminiferous tubules of the testes were filled with spermatozoa. The maturing testis was observed from January to December with peak availability during the month of August (monsoon) (Figure 6b).

### 3.5.3 | Stage III – Mature

The testis appeared swollen and white with milt, but not free running and occupying about 50%–60% of the peritoneal cavity (Figure 7c). Histological observations revealed continuous

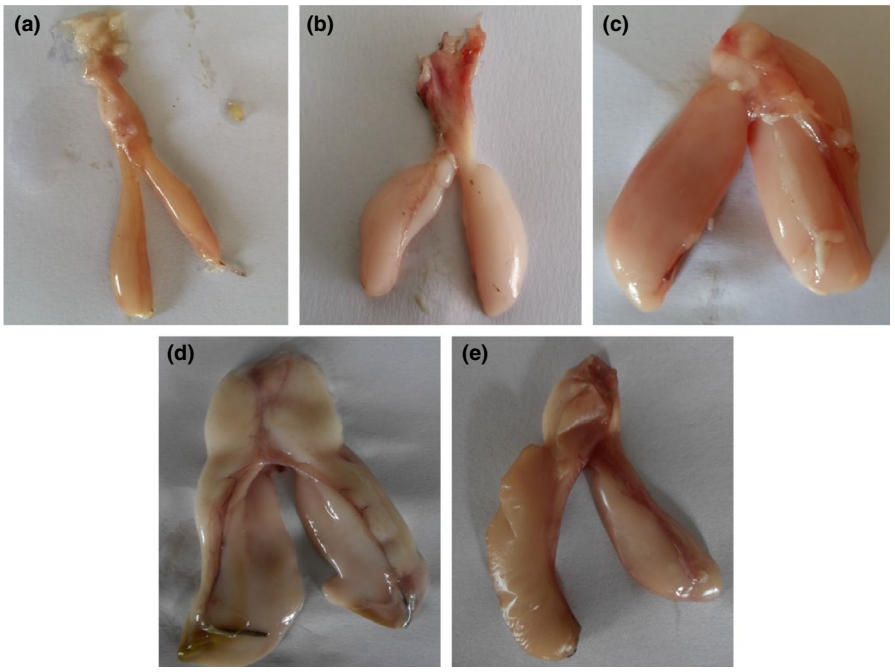



**FIGURE 7** Different maturity stages of *Acanthopagrus berda* testis based on morphological observations (a) resting (b) maturing (c) mature (d) running (e) spent

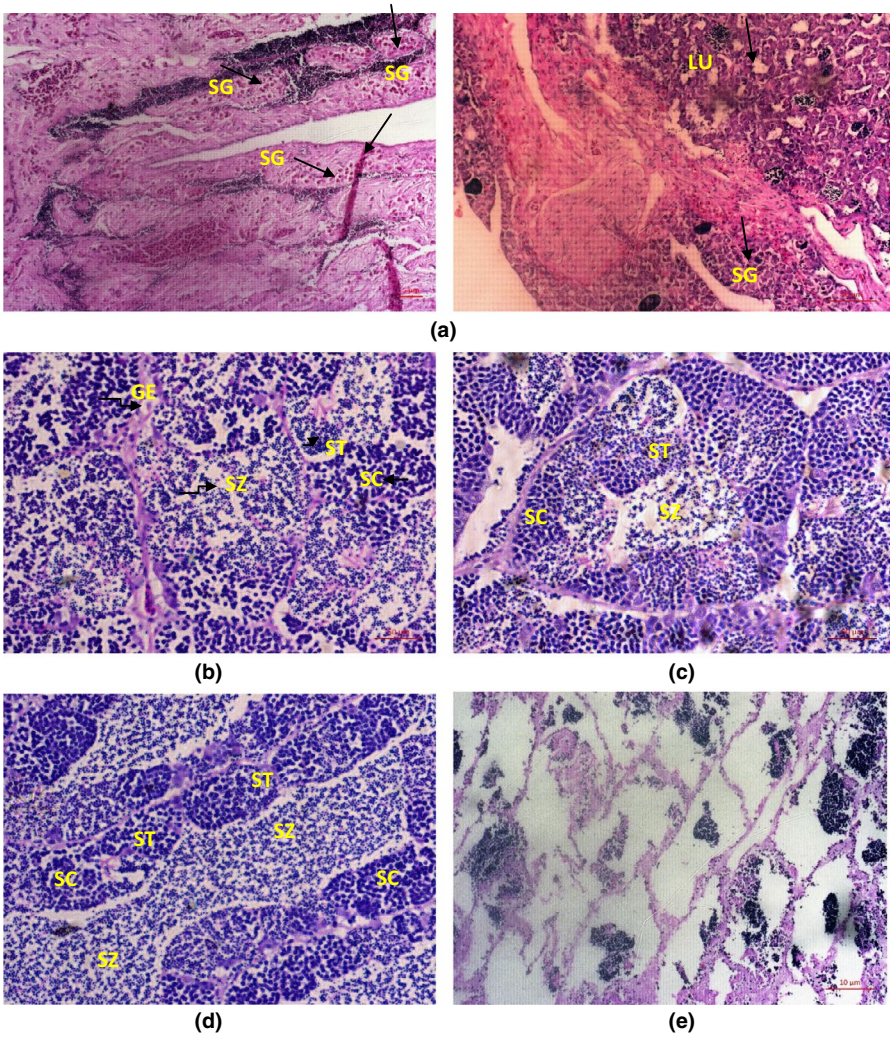



**FIGURE 8** Gonad transverse sections showing different maturity stages of *Acanthopagrus berda* testis (a) resting (immature) (b) maturing (c) mature (d) running (e) spent (GE, germinal epithelium; SC, spermatocytes; SG, spermatogonium; ST, spermatids; SZ, spermatozoa)

germinal epithelium throughout the testis with all stages of spermatogenesis. The seminiferous tubules had expanded with a copious amount of spermatozoa in lumen and ducts (Figure 8c). Mature males occurred from August to February (monsoon and post monsoon) with peak availability during December (post monsoon) (Figure 6b).

### 3.5.4 | Stage IV – Running

At this stage, the testis occupied about 75%–80% of the peritoneal cavity and milky white, with milt freely flowing when cut (Figure 7d). Histological observations revealed distended seminiferous tubules filled with numerous mature spermatozoa in lumen and ducts (Figure 8d). Running males occurred from August to February with peak availability from August to December (monsoon and post monsoon) (Figure 6b).

### 3.5.5 | Stage V – Spent

The spent testis had a brown bruised appearance with a very small amount of residual milt (Figure 7e). Histological sections revealed that the seminiferous tubules were no longer distended with only a few spermatozoa present in the lumen of the primary sperm duct. (Figure 8e). Spent males occurred from October to February samples with peak availability in January (post monsoon) (Figure 6b).

### 3.6 | Gonado-somatic index ($I_G$)

Monthly evaluation of $I_G$ of male and female of *A. berda* showed an increasing trend from August to December with the maximum $I_G$ during October. From January to July there was a sharp drop in the $I_G$ (Figure 9). Intersex individuals were observed from January to July with maximum $I_G$ observed during February (Figure 9). A highly significant ($p < 0.05$) increase was recorded in October corresponding to vitellogenesis when a mean value of 3.9 was reached. $I_G$ was generally lower in individuals with predominantly testicular tissue. A significant increase occurred in August (maturing stage) when active spermatogenesis was recovered, followed by a rapid, highly significant increase (the maximum value of 1.68) in October, during spawning.

Thus the results of the present study indicate that the reproductive cycle of *A. berda* collected from the wild consisted of the following phases: resting phase lasting from February to July (dominance of immature male; virgin and developing female gonads); pre-spawning phase occurring from March to August (dominance of maturing gonads) and a spawning phase from August to December (dominance of running gonads). Reproductively active males and females (running) were observed between August and January (monsoon and post monsoon), with the highest percentage of spawning activity during October (post monsoon), coinciding with the highest values of $I_G$ (Figure 9). Atretic oocytes were observed from December to March; their incidence increased during January (post-monsoon), towards the end of the reproductive season, indicating the end of spawning activity.

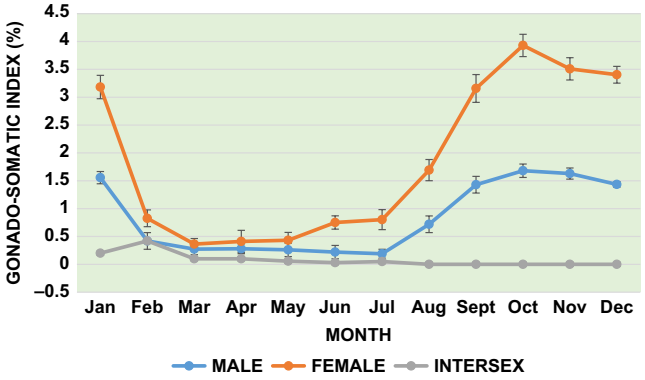



**FIGURE 9** Monthly variation in Gonado-somatic Index ($I_G$) of *Acanthopagrus berda* collected from Korapuzha from January to December 2016

## 4 | DISCUSSION

The present study focuses on the annual reproductive cycle of wild-caught *A. berda* from Korapuzha estuary, Calicut, India from January to December 2016. In our previous report, we reported the occurrence of different reproductively distinguished groups of *A. berda* (active male, active female and transitional stages) at a particular season (December and January months) (Shilta et al., 2018). In the present study, the occurrence and prevalence of these sex variants throughout the annual reproductive cycle with emphasis on the various developmental stages in the testis and ovary were evaluated.

The microscopic and macroscopic investigation of the gonad structure through observations of complete annual reproductive cycle showed that the gonad of *A. berda* possesses "ovotestes", where the testis and ovary are simultaneously present within the gonad separated by a connective tissue similar to the gonadal structure observed in other Sparids such as *Acanthopagrus latus* (Abou-Seedo, Dadzie, Al-Kanaan, & Jalaja, 2003); *Rhabdosargus sarba* (Hughes et al., 2008); *Coris julis*, *Serranus scriba*, *Diplodus annularis* (Alonso-Fernandez et al., 2011) and *Chrysophrys auratus* (Saunders, Fowler, & Gillanders, 2012). The morphological and the histological observations of different sections of the gonads of *A. berda* revealed the presence of active male, inactive male, active female, inactive female, undifferentiated and transitional individuals. The ovotestes of active males were dominated by testicular lobes almost completely encircling the inactive small ovarian lobes, whereas, in case of active females, ovotestes are mostly dominated by ovarian lobes, whereas the reduced inactive testicular lobes appear as a very thin band of tissue along the ventrolateral surface of the ovary. A similar type of ovotestes have been described for many other protandrous and protogynous sparid fishes (Buxton & Clarke, 1989; Chang & Yueh, 1990). One sexual area (either testis or ovary) predominated over the other throughout the annual cycle, a characteristic which is common among the sparids (Buxton & Garratt, 1990), has also been reported for *A. berda* from other areas (Tobin et al., 1997). Buxton and Garratt

(1990) reported that the presence of ovotestes in Sparidae family is a pre-adaptation for sex change in which reproductive success is size related.

The ovotestes obtained from few individuals of 15–25 cm TL are classified as 'Undifferentiated' where the morphological observation of these ovotestes was difficult to classify them as either male or female. Histological examination of undifferentiated gonad revealed that the gonad is differentiated into juvenile ovotestes with separate male and female elements indicating the possibility of juvenile hermaphroditism in developing ovotestes of *A. berda*. Histological evidence presented in this study suggests that *A. berda* in Indian waters follow similar patterns of gonadal development of this species in the African waters (Garratt, 1993a). In both the studies, it was found that undifferentiated (immature) gonads are composed of roughly equal volumes of male and female tissue and there was a simultaneous proliferation of gonial cells in both male and female elements with further development more rapid in the male element. Garratt (1993a) also observed that all gonads towards the end of the first year of life or early in the second year (length class of 100–149 mm) in *A. berda* were bisexual (ie, differentiation of male and female germinal tissues), further, the reduction division is initially in the male direction and all fish appear to mature first as males. Thereafter, the proportion of females increases rapidly with a proportional decrease in males. Similar developments were reported in other sparids *Mylio macrocephalus* (Okada, 1965) and *Boops boops* (Michele & Lafaurie, 1974).

In our study, oocytes in the female ovotestes of inactive males and active males were arrested in the early perinucleolar stage throughout all seasons. Similarly, in the ovotestes of other protandrous sparids of *Acanthopagrus* genus namely, *Acanthopagrus schlegeli* (Kinoshita, 1936), *M. macrocephalus* (Okada, 1965), *A. latus* and *A. cuvieri* (Abu-Hakima, 1984), the oocyte development never passed the previtellogenic stage until sex separation was almost complete and the testis had completely regressed.

According to our data, the inactive and active males (140–250 mm TL) were observed dominant in smaller length classes whereas inactive and active females (251–450 mm TL) were observed dominant in larger length classes. These results were in accordance with those of Abu-Hakima (1984), Abol-Munafi and Umeda (1994), Abou-Seedo et al. (2003) and Hesp, Potter, and Hall (2004) in other *Acathopagrus* species. These observations indicated that in *A. berda*, the juvenile ovotestes appeared to mature as a male in most of the individuals, although a few primary females were observed in smaller length classes (below 250 mm TL) and a few primary males were observed in larger length classes (above 250 mm TL). Similarly, Vahabnezhad, Kaymaram, Taghavi Motlagh, Valinassab, and Fatemi (2016) reported few primary males amongst the larger size class in *A. latus*. Further, Hesp et al., (2004) reported that in *A. latus*, after the spawning period, the testicular tissue will regress markedly and will become a gonad that is predominantly characterized either by a testicular zone containing spermatids or an ovarian zone containing oocytes. The fish will remain as a female throughout the rest of its life once the fish becomes a functional female (Vahabnezhad et al., 2016).

Further, histological observation of transitional gonads in the current study showed signs of degeneration in the testicular lobe, the proliferation of connective tissue and empty sperm ducts which further confirms the protandrous sex change in *A. berda* collected from tropical Indian waters. The protandrous hermaphroditism in *A. berda* has been reported earlier in the African (Garratt, 1993a; James et al., 2003) and Australian waters (Tobin et al., 1997). Sadovy and Shapiro (1987) stated that the gonads of fish undergoing sex change may be expected to show degeneration of the germinal tissue of the primary sex accompanied by the proliferation of the tissue of the opposite sex. Most of the *Acanthopagrus* sp namely *A. latus* (Abou-Seedo et al., 2003), *A. australis* (Pollock, 1985), *A. schlegelii* (Lee et al., 2001), *A. bifasciatus* (Etessami, 1983) are reported as protandrous hermaphrodites.

The size advantage model by Ghiselin (1969) explains that sequential hermaphroditism occurs when an individual reproduces most efficiently as a member of one sex when small or young, but as a member of the other sex when it gets older or larger; it predicts protogyny where there is sexual selection for larger males and protandry where the young stages must hunt for a suitable environment. In accordance with the above statement, the juvenile phase of *A. berda* is spent in unstable and often harsh estuarine environments (sudden fluctuations in temperature and salinity) (James, 2001) and therefore the evolution of a mating system has overcome the necessity to move out into the marine environment to spawn, may have led to strong selection pressure favouring protandry in this species (Garratt, 1993a). In order to survive harsh environments in estuaries it may be essential to direct most of the metabolic energy into somatic growth and in such circumstances it would be better to be male first and change to female only when and if a large size is attained or remains as male if stressed (Garratt, 1993a; Warner, 1988). Therefore in the present study, *A. berda* which mature as males from the juvenile ovotestes, function first as males and then change sex to female, but few continue to function as either males or females throughout their lifespan indicating digynous protandrous hermaphroditism. A similar reproductive style has been reported in *Acanthopagrus australis* (Pollock, 1985); *Diplodus sargus* (Micale & Perdichizzi, 1994) and *Salpa salpa* (van der Walt & Mann, 1998).

The overall sex ratio obtained in the present study was 1:1.2 (M:F). Tobin (1998) also observed 1.01:1 (M:F) unbiased sex ratio for *A. berda* collected from the site Deluge Inlet of Australian waters whereas all the other sites namely, Mendel creek (1.25:1), Cocoa creek (2.92:1), Blacksoil creek (3.4:1), Cattle creek (5.52:1), Alligator creek (6.14:1), Meunga creek (6.58:1) of Australian waters showed male-biased sex ratio. Garratt (1993a) reported male-biased sex ratio for *A. berda* from South Africa (8.8:1). Earlier studies by Sadovy and Shapiro (1987) and Garratt (1993a) confirmed that bimodal size-frequency distributions and sex ratios which differ from unity are evident in many hermaphrodite species, but these are not reliable indicators of sex change. Therefore, sex ratio is certainly not a reliable tool to conclude the sex change pattern in *A. berda*.

The gonadal developmental stages of male *A. berda* conforms similar to most other teleosts (Abou Shabana, Abd El Rahman, Al Absawey, & Assem, 2012; Al-Absawy, 2010) with slight modification as resting, maturing, mature, running and spent. The stages of maturity of the ovary were observed as seven, similar to the observations of Abu-hakima, Al-Abdl Elah, and El- Zahr, (1980) and Abou-Seedo et al. (2003) in other *Acanthopagrus* species. One of the interesting observations made during this study is that even though, *A. berda* is a protandrous hermaphrodite, all the specimens dissected during the spawning period (August–December) showed clear structural dimorphism and no transitional gonads were observed during the spawning period. Tobin (1998) also reported a similar observation in *A. berda* collected from Australian waters.

Different factors determine the season of fish breeding. Many fish species have one peak breeding period in a year, while others have two peaks (Dadebo, 2000). Both monthly gonado-somatic indices and macroscopically determined ovarian stages strongly indicate that spawning of *A. berda* in tropical Indian waters starts during monsoon season (August) and continues till post monsoon (December), with one peak spawning during October (post monsoon). The spawning season of *A. berda* in the present study coincided with the monsoon season of the South west coast of India (June–August). Environmental factors are key determinants of spawning season in the natural aquatic environment and in tropical countries, rainfall associated factors such as fluctuations in water level and seasonal flooding play a significant role in the timing of intensive breeding of fish (Admassu, Abera, & Tadesse, 2015). Further, Kolding, Tirasin, and Karenge (1992) and Dadebo (2000) reported that the peak spawning of fish takes place during the rainy season when there is a rich source of food supplied by a flood of terrestrial origin.

Contradictory to our results, Wallace (1975) and Kyle (1986) reported that *A. berda* spawns between May and August, with peak spawning in May and June in St. Lucia Estuary, Republic of South Africa; Mok (1985) reported that the peak spawning period of *A. berda* in Hong Kong lasts only for few weeks between February and March whereas Tobin et al. (1997) reported that the spawning of *A. berda* in Australian waters was observed from June to September. The change of spawning season of *A. berda* across various countries may be due to change in the environmental parameters such as sea surface temperature and the photoperiod since the duration of spawning season is negatively correlated with these environmental parameters (Tesfahun, 2019).

Earlier reports indicate that the spawning season of Sparids vary with species, season and geographic locations. *Sparodon durbanensis* has a restricted breeding season between August and January, during spring and summer (Buxton & Clarke, 1991); spawning season of *Chrysoblephus puniceus* in South Africa extends from July to November with peak spawning occurring in August-September (Garratt, Govender, & Punt, 1993);*Sparus auratus* spawn in autumn from November to January (Cowden, 1995); *Diplodus puntazzo* (Sharpsnout sea bream) spawn from September to October (Micale, Perdichizzi, & Basciano, 1996). The spawning season of yellowfin bream, *A. australis* from Townsville (Australia) was found to extend for a period of at least 10 weeks, from mid-June to early September (Cowden, 1995) whereas from Moreton Bay (Australia) this species has a short spawning season from April to August, with a peak period between July and August (Pollock, 1982). Crossland (1981) observed that *Pagrus auratus* spawn between October and January in Hauraki Gulf in New Zealand when the water temperature is between 16 and 21°C whereas Cowden (1995) observed that the spawning season is in spring, from mid-April to early June when water temperatures range between 12 and 25°C.

The sex change in Sparid fish is most likely to occur in the months immediately following spawning (Cody & Bortone, 1992; Micale & Perdichizzi, 1994; Pollock, 1985). Similarly, in the present study, the presence of transitional ovotestes during the post spawning season (January–July) indicates the possibility of sex change after the spawning in *A. berda*. Sex reversal, in *S. aurata* takes place at the end of the spawning season from May to September (Moretti, Fernandez-Criado, Cittolin, & Guidastri, 1999), whereas sex reversal begins in the transitional of *A. latus* from July to August, after spawning in functional males, at 14.9–20.2 cm standard length (Abou-Seedo et al., 2003).The studies conducted by Tobin et al. (1997), also stated that *A. berda* in Australian waters reproduce between June and September and transitional individuals are observed during the post spawning period (October onwards).

From the present study, it can be concluded that *A. berda* collected from the wild in the Indian waters exhibits digynous protandrous hermaphroditism and their reproductive cycle consist of resting phase, lasting from February to July; pre-spawning phase, occurring from March to August and spawning phase from August to December. The simultaneous availability of running males and females of *A. berda* from August to December indicates the opportunity for the development of captive breeding, seed production and hatchery technology for this important commercial food fish during this season. At present, India is looking for potential native food fish for mariculture development and *A. berda* is considered as one of the priority species due to its high market demand. Understanding the reproductive strategies of *A. berda* is important in developing standardized protocol for their brood-stock development and the biological information derived from the present study will be a benchmark for developing commercial mariculture activities of *A. berda*.

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## CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

## ETHICAL APPROVAL

All applicable international, national and/or institutional guidelines for the care and use of animals were followed by the authors

## DATA ACCESSIBILITY

The data that support the findings of this study are openly available in BOOK OF ABSTRACTS BRAQCON 2019 at http://braqcon.org/downloads/

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