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POSTOVULATORY FOLLICLE DEGENERATION AND ATRESIA IN HORSE MACKEREL *Trachurus trachurus* FROM THE EAST COAST OF ALGERIA

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ABSTRACT

The present study focuses on the detailed description of postovulatory follicles (POFs) resorption and atresia in horse mackerel from Algerian waters. From February 2013 to February 2014, 155 female horse mackerel were randomly collected. Histological sections of ovaries were analyzed. Few POFs (7.28% of early POFs and 2.91% of old POFs of the total observed oocytes) were detected. Morphological changes of POF resorption were discussed in the current study. No particular shape was observed. Four types of atretic oocytes were determined: α = 34.38%, β = 5.28%, δ = 2.37% and γ = 0.94%, which was reported for the first time in horse mackerel. The incidence of α atresia was higher in the yolked (21.48%) than in the unyolked oocytes (12.89%). α atretic oocytes can be classified into two main types: non-bursting (capsulated, lipoidal and cystic atresia) and bursting (multiple bursts, single bursts, phagocytic bursts and liquified bursts). Further studies are required to better understand the reproductive strategies of fish in relation to postovulatory follicle resorption and atresia.

How to Cite

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INTRODUCTION

Horse mackerel *Trachurus trachurus* is a species known for its economic value (Abaunza et al., 2008; El Mghazli et al., 2022). It is widely distributed in all oceanic waters in tropical and moderate subtropical seas. It is also present in the northeast Atlantic from the Bay of Biscay to Mauritania, the Black Sea and especially in the Mediterranean (Campbell, 2005; Bektas and Osman, 2009; Basilone et al., 2023).

Histological studies primarily focused on the description of different stages according to the development of sexual cells (Fontana, 1969; Wallace and Selman, 1981; Carrasson and Bau, 2003; Saeed et al., 2010). In this respect, maturity stages, POF degeneration and atresia stages are precisely determined according to the oocyte development state and its morphological characteristics (Hunter and Macewicz, 1985; Haslob et al., 2012).

The study of POF degeneration is important in fishery analysis because it permits the assignment of spawning of females to daily classes to provide estimates of the daily fraction of spawning fish in the population (Hunter and Goldberg, 1980). In addition, atresia plays a significant role in fish reproductive strategies, as it is a fine-tuning mechanism by which a species regulates fecundity (Brown-Petersen et al., 2011).

Many works have been conducted on horse mackerel in relation to gonads histological assessment in different regions including the North Sea and English Channel (Macer, 1974), Saronikos Gulf (Karlou-Riga and Economidis, 1996), Portuguese coast (Costa, 2001, 2004, 2009) and northeast Atlantic and the Mediterranean (Gordo et al., 2008). The aims of these reports focused on the determination of *T. trachurus* fecundity, measurement of oocyte diameters, comparison of maturity stages derived from macroscopic and microscopic examination, determining atresia stages and atretic states.

Reports on *T. trachurus* of Mediterranean waters, especially in Algeria are very scarce mainly concerning reproductive physiology which remains poorly understood. In the present study, morphological changes in POF degeneration process and types of atresia were discussed for the first time in *T. trachurus*. In addition, the present investigation provides information about the prevalence and intensity of atresia and POF degeneration within the population studied. This type of research is crucial for understanding reproductive processes in fish species and can have implications for fisheries management and conservation efforts.

MATERIALS AND METHODS

Study area and fish sampling

The present study was carried out from February 2013 to February 2014, with the scientific vessel "GRINE BELKACEM" throughout the "ALDEM 2013" survey. 155 female specimens of horse mackerel were randomly collected at different sites on the Algerian east coast (Fig. 1). Each specimen was measured for total length and weight. The ovaries were weighed and evaluated macroscopically and microscopically, based on different criteria (gonad color, consistency, vascularization, their proportion in relation to the abdominal cavity and oocyte development).

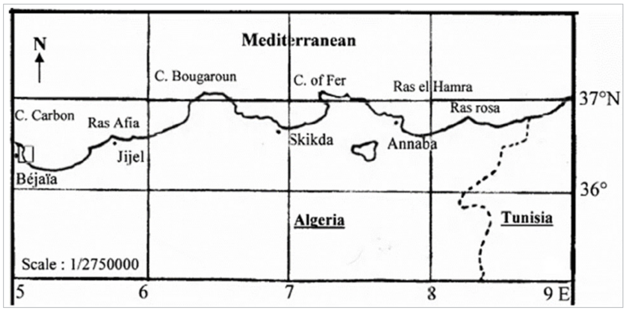


Fig 1. Map of the study area, eastern coast of Algeria (Ramdane et al., 2007)

Histological study

Histological sections were performed according to Martoja and Martoja-Pierson (1967) as follows: gonads were fixed in 10% neutralized formalin and divided into equal pieces of transverse portions of 5 mm thickness. These portions were then dehydrated through increasing ethanol concentrations (70-95%), cleared in xylene and embedded in paraffin. Histological sections of 3-µm thickness were then performed using a Leica RM2025 rotary microtome. Sections were mounted on glass microscope slides, rehydrated, stained with Mayer's haemalun-eosin and mounted with Canada balsam. Samples were then examined by light microscopy and photographed using a digital camera.

POF and atresia stage identification

Morphological changes of follicles (POFs and atretic), the incidence of early and old postovulatory follicles and atresia stages were estimated according to the works of Hunter and Macewicz (1985) and Ganias et al. (2003, 2007).

Oocyte number estimates

The number, the mean number and the rate of oocytes and POFs per ovary were determined from each histological section comprising 16 microscopic fields. The oocytes and follicles counted are the following: the normal unyolked oocytes, the normal oocytes with advanced yolk formation, the hydrated oocytes, the unyolked oocytes, the yolked oocytes with the α atresia stage, the yolked oocytes with the β atresia stage, the yolked oocytes with the γ atresia stage, the yolked oocytes with the δ atresia stage, the early postovulatory follicles and the old postovulatory follicles.

RESULTS

Biometric analysis

The total length for the whole sample ranged from 12.5 to 26.2 cm, while the body weight ranged from 13.6 to 164.9 g. The weights of ovaries ranged from 0.01 to 14.12 g. Six macroscopic and microscopic stages were determined for sexual maturity, including immature, early maturation, late maturation, mature, spawning and post-spawning.

Morphological characteristics of postovulatory follicles

In this study, we noted a few ovaries (n = 3) with empty follicles and a lack of postovulatory follicles. The degeneration process generally occurs in March and December. At the beginning of this process, we noticed the occurrence of an empty folded structure with no clear degeneration (Fig. 2a). This structure is formed by a convoluted granulosa cell layer with a large lumen. The early POF diameter ranged from 196.8 to 539.3 µm. The granulosa cells have prominent healthy nuclei arranged linearly in the granulosa cell layer. The thecal cell layer was clearly defined and appeared closely attached to the granulosa cell layer. However, old POFs showed pronounced signs of degeneration; the lumen became very narrow and disappeared after a while. The granulosa cells degenerated thereafter and displayed a few intact cell membranes, numerous vacuoles and pyknotic nuclei. The linear arrangement of granulosa cell nuclei became less distinct (Fig. 2b). The old POFs had the smallest size; they occupied approximately the space of a primary oocyte. They appeared as a compact structure with many vacuoles and few granulosa cells with pycnotic nuclei (Fig. 2c).

Morphological characteristics of atresia

Four atresia stages of development were observed in the oocytes of *T. trachurus* (Fig. 3 and 4), which are: alpha (α), beta (β), gamma (γ) and delta (δ).

The alpha stage (α) (Fig. 3) is the initial phase of atresia and is characterized by striking hypertrophy and hyperplasia in the granulosa cells which are disorganized and invade the oocyte vitellus. This invasion is followed by the absorption of vitellus through phagocytotic activities in parallel with the disintegration of zona radiata. On the basis of morphological differences between the unyolked and yolked oocytes, alpha atretic follicles were mainly of two types: bursting and non-bursting. Non-bursting atresia is defined by the non-ruptured follicle layers. It is very common in the early oocyte stages. Three types can be assessed:

1. Capsulated atresia: the oocyte appeared as a dark stain mass (Fig. 3a),
2. Cystic atresia: the oocyte lost its normal identity and was reduced in size, leaving a wide clear perivitelline space between the ooplasm and the oocyte membrane (Fig. 3b),
3. Lipoidal atresia: the ooplasm was invaded by vacuoles and formed a lipoid material surrounded by a crumpled and thick follicular layer (Fig. 3c).

Bursting atresia, defined as ruptured follicular layers, is observed in the late stage of oocyte development where the oocyte is large. On the basis of histological characteristics, this type can be classified into four types:

1. Multiple bursts: atretic follicle showed several ruptured sites (Fig. 3d,e),

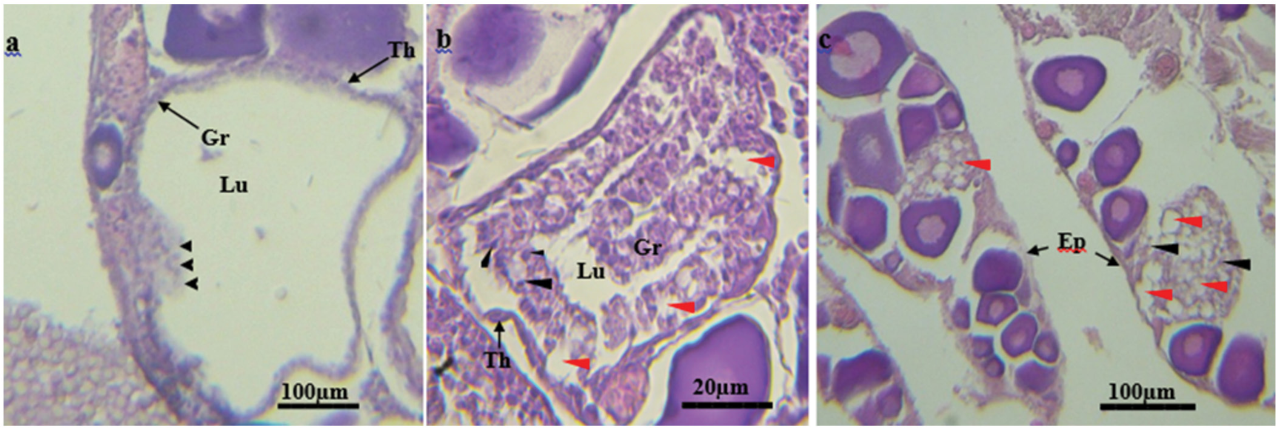


Fig 2. Microphotographs of a postovulatory follicle (POF) at consecutive phases of deterioration in *T. trachurus*, showing the degeneration of POF size and shape, and the state of the granulosa. **a:** New POF with large lumen, ovulation site (black arrowhead), and healthy granulosa cell layer attached to the theca; **b:** Old POF showing a narrow lumen, a thick granulosa cell layer with pyknotic nuclei (black arrowhead) and numerous vacuoles (red arrowhead); **c:** Degenerated POF with few granulosa cells with pycnotic nuclei (black arrowhead) and many vacuoles (red arrowhead). Lu: Lumen; Gr: Granulosa; Th: Theca; Ep: Epithelium of an ovarian lamella.

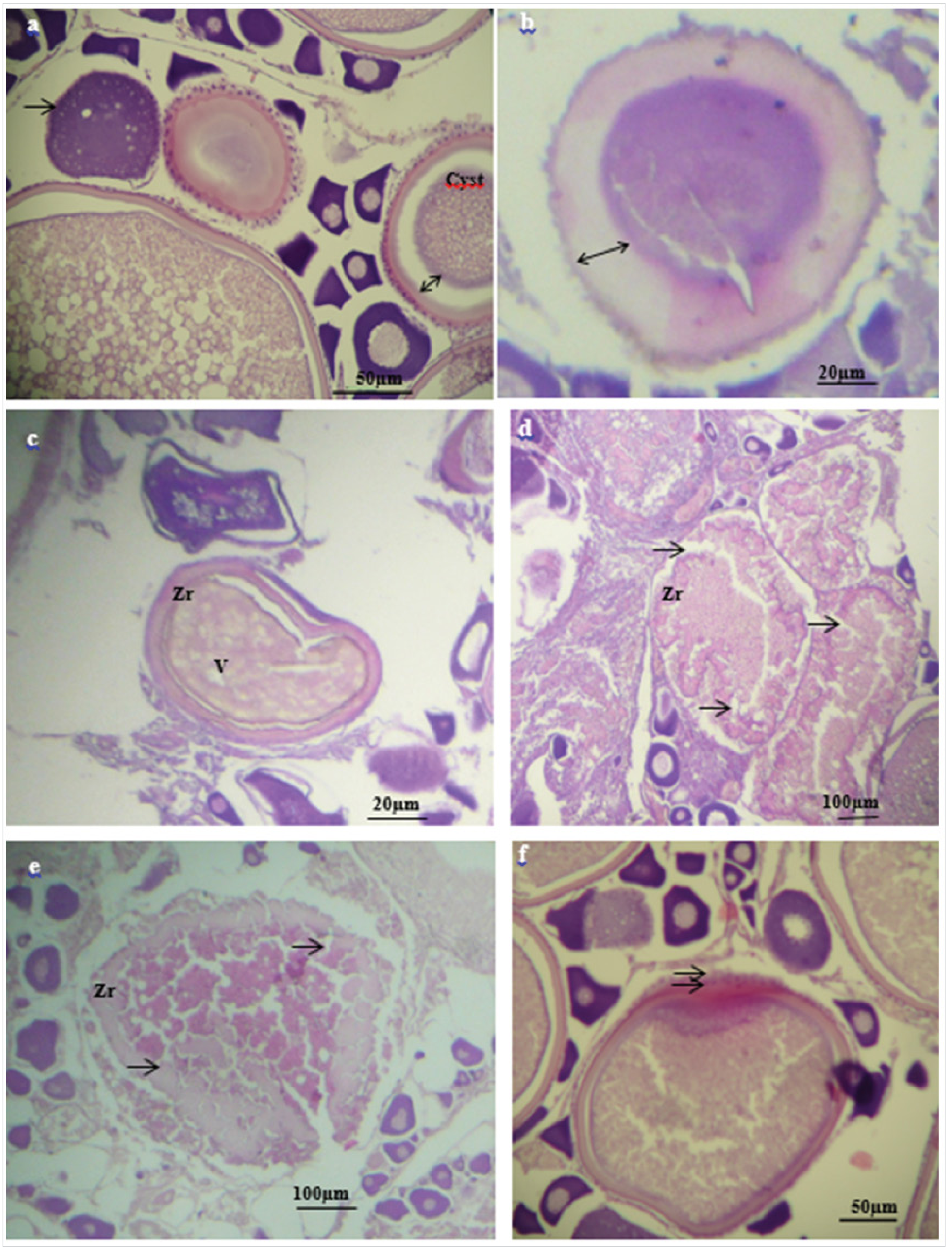
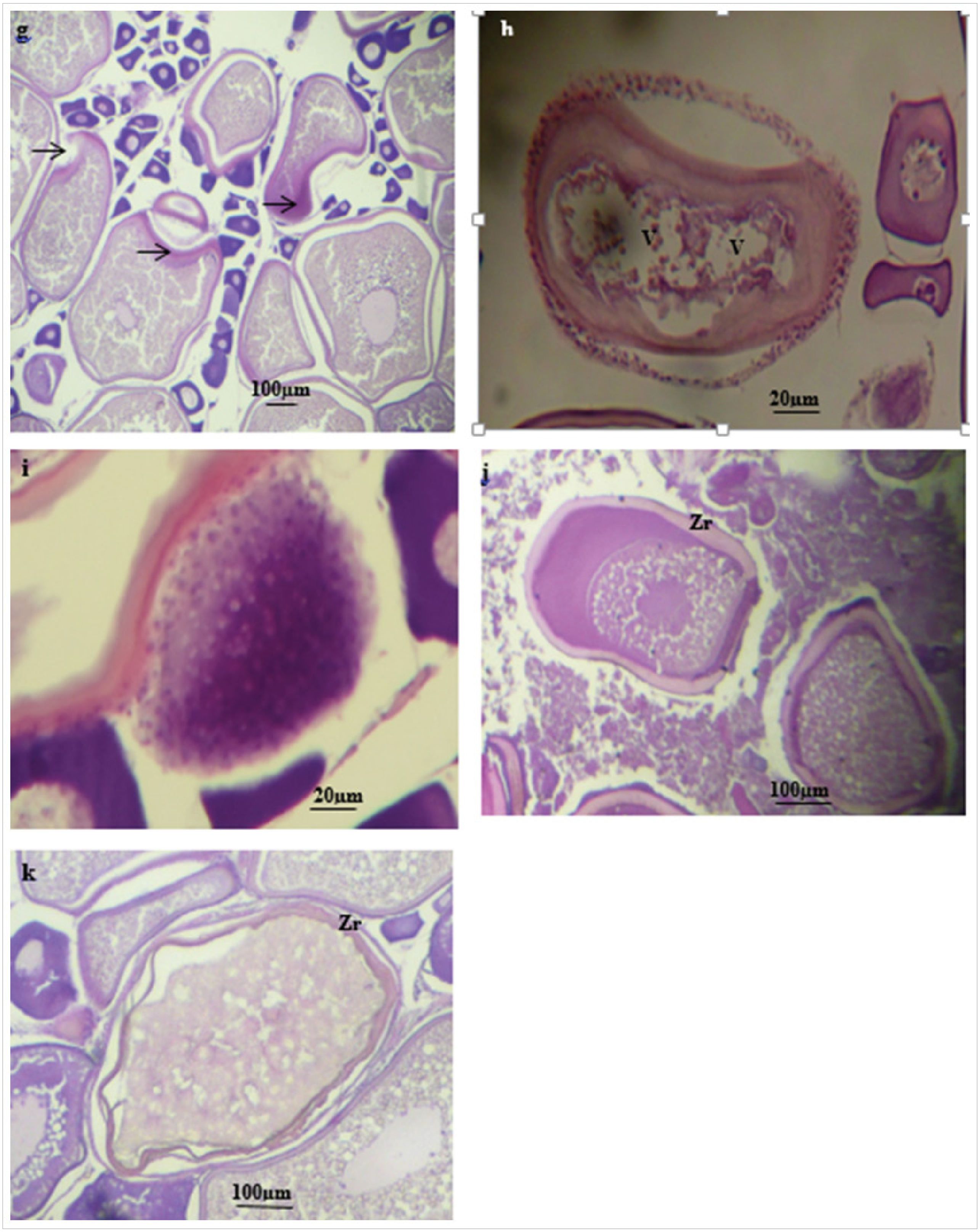


Fig 3. Light microphotographs of oocytes at the α atresia stage with different types

a: Non-bursting atresia (capsulate atresia showed by the arrow); **b:** Non-bursting atresia (cystic atresia showing a wide clear perivitelline space between the ooplasm and the oocyte membrane (double arrow); **c:** Non-bursting atresia (lipoidal atresia); **d, e:** Bursting atresia (multiple bursts showing numerous ruptures (arrows) in zona radiata); **f:** Bursting atresia (single burst showed by arrows). Zn: Zona radiata; Gr: Granulosa; Thc: Thecal cells; V: Vacuoles; prvs: perivitelline space; Cyst: Cystic atresia; Bc: Blood cells.



Continued. Fig 3. Light microphotographs of oocytes at the α atresia stage with different types

g: Bursting atresia (single burst shown by arrows); **h, i:** Bursting atresia (phagocytic atresia); **j:** Bursting atresia (liquefied burst, early stage); **k:** Bursting atresia (liquefied burst, advanced stage with wrinkled follicular layer). Zn: Zona radiata; Gr: Granulosa; Thc: Thecal cells; V: Vacuoles; Cyst: Cystic atresia; Bc: Blood cells.

2. Single bursts: atretic follicle showed one ruptured site (Fig. 3f,g),
3. Phagocytic bursts: the follicle cells transformed into phagocytic cells invading the ooplasm through the ruptured parts of the follicular wall (Fig. 3h,i),
4. Liquefied bursts: atretic follicles contained large vacuoles in the ooplasm and the follicular layer was thick and wrinkled in the late stages (Fig. 3j,k).

Beta atretic follicle (β) (Fig. 4a) is a compact structure composed of several vacuoles in the cytoplasm and numerous disorganized granulosa cells surrounded by a thin thecal layer. In the late beta stage, vacuoles are filled with a yellow substance produced by phagocytes which solidifies to form small globules in the ooplasm (Fig. 4b). Beta-stage atretic follicles may easily be confused with late postovulatory follicles. However, POFs are distinguished from all types of atresia because atretic follicles constitute enclosed cellular structures which are separated from the epithelium of the lamellae (Fig. 3 and Fig. 4a), whereas POFs always maintain an opening towards the ovarian lumen and remain on the epithelium until full resorption (Fig. 2a, b and c).

In the gamma stage (γ) (Fig. 4c), the remaining oocyte appears small, irregular in shape, colored yellow-brown with H-E staining and surrounded by the thecal cells. The incidence of this stage is very low (0.94%). The delta stage (δ) (Fig. 4d) is characterized by the presence of a few granulosa cells with a dark yellow-brown, granular pigment and blood cells.

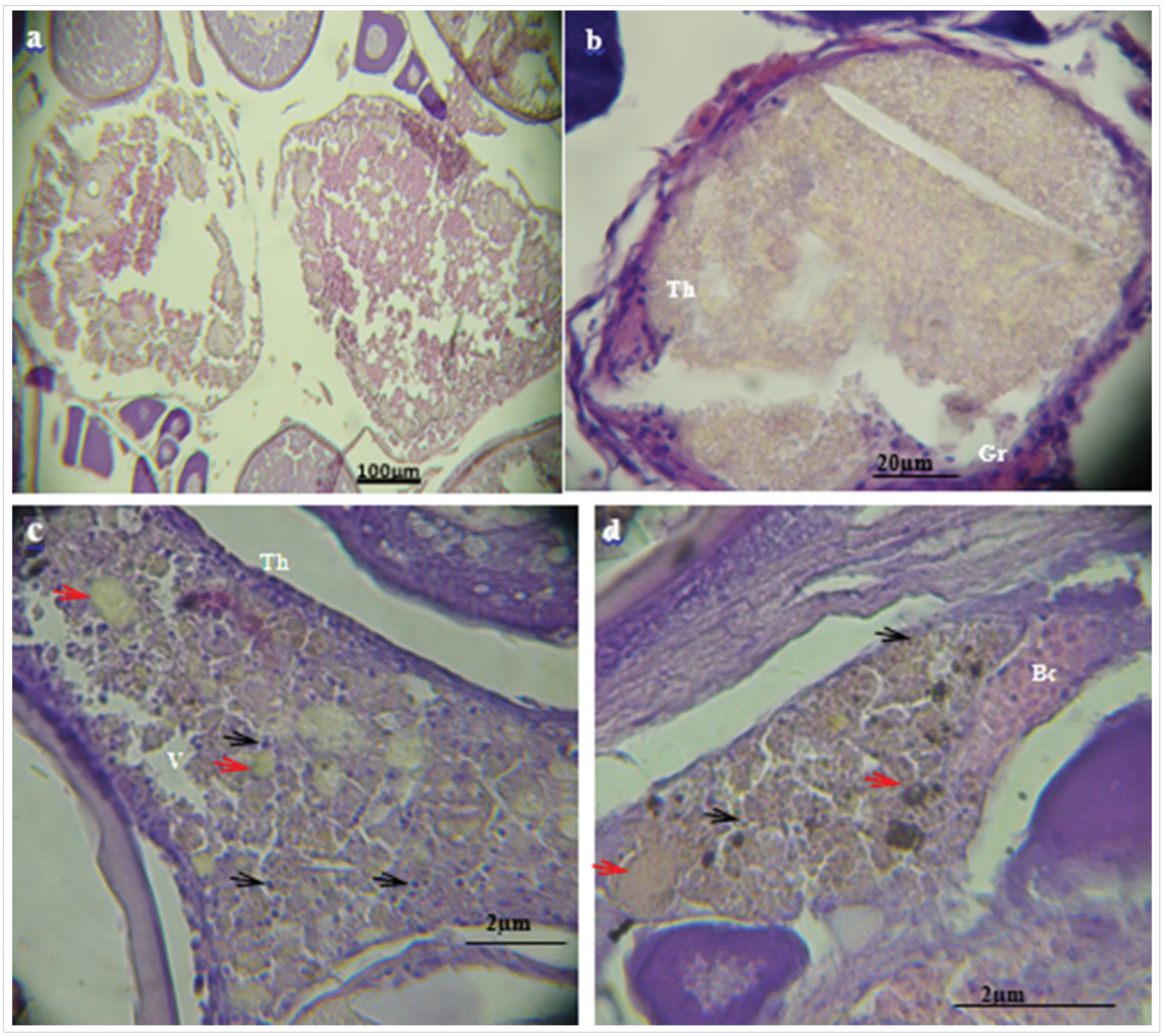


Fig 4. : Light microphotographs of oocytes at β, γ and δ atresia stages (**a:** early β atresia stage, **b:** late β atresia stage, **c:** γ atresia stage showing disorganized granulosa cells with pycnotic nuclei (black arrows) and filled vacuoles with yellow substance (red arrows), **d:** δ atresia stage showing few granulosa cells (black arrows) and vacuoles with dark yellow-brown pigment (red arrows)). Zn: Zona radiata; Gr: Granulosa; Thc: Thecal cells; V: Vacuoles; Cyst: Cystic atresia; Bc: Blood cells.

Table 1. Mean number and percentage of oocytes, POFs and different stages of atresia (N.U.O: Normal unyolked oocyte; N.Y.O: Normal yolked oocyte; H.O: Hydrated oocyte; α.U.O: α unyolked oocyte; α.Y.O: α yolked oocyte; β.At: β atresia; γ.At.: γ atresia; δ.At: δ atresia; E.POFs : Early postovulatory follicles; L.POFs: Late postovulatory follicles)

	N.U.O	N.Y.O	H.O	α.U.O	α.Y.O	β.At.	γ.At.	δ.At.	E.POFs	L.POFs
Mean number	54	99	1	42	71	17	3	8	24	10
Percentage (%)	16.54	30.07	0.24	12.89	21.48	5.28	0.94	2.37	7.28	2.91

Incidence of atresia

Table 1 reveals that the percentages of normal unyolked oocytes (16.54%) and normal yolked oocytes (30.07%) are higher than those of α unyolked oocytes (12.89%) and α yolked oocytes (21.48%), respectively. The incidence of the α stage (34.38%) is higher than the other stages. The lower rate of atresia is observed in the γ stage (0.94%). The present results show a few numbers of POFs (mean number = 33 follicles).

DISCUSSION

The present study described POF degeneration and atretic stages in *T. trachurus* from Algerian waters. The postovulatory follicle (POF) consists of the follicular layers that remain in the ovary after the release of the mature oocyte during spawning (Saidapur, 1982; Lowerre-Barbieri et al., 2011 & Charitonidou et al., 2020). In this study, we noted a few ovaries with empty follicles and a lack of postovulatory follicles. This result appears to be common in other *Trachurus* species. Macer (1974), Andrianov (1985) and Marshall et al. (1993) reported similar results for *T. murphyi*, *T. trachurus*, and *T. declivis*, respectively. According to Ganias et al. (2007), fast resorption of POFs is essential for an indeterminate spawner as the aggregation of old POFs would restrict the space available for the development of new oocytes. On the other hand, postovulatory follicles almost disappear from the ovary within 24 h of spawning in marine fish that lay pelagic eggs (Hunter and Macewicz, 1985). For Marshall et al. (1993), the absence of postovulatory follicles is possibly due to rapid reabsorption. We support this hypothesis for *Trachurus* species as these species are indeterminate spawners. In addition, according to Yamaguchi et al. (2023), the presence of POFs in the ovaries of many individuals is a sign that fish have already spawned and that a female spawns multiple times during a spawning season.

In fish, many species show similar features in postovulatory follicle degeneration (Hunter and Macewicz, 1985). Histological changes follow the same pattern of degeneration described for several fish species in different locations: Pacific sardine *Sardinops sagax* (Goldberg et al., 1984); Japanese sardine *Sardinops melanostictus* (Murayama et al., 1994); Atlantic menhaden *Brevoortia tyrannus* (Fitzhugh and Hettler, 1995); South African sardine *S. sagax* (Akkers et al., 1996); Mediterranean sardine *S. pilchardus* (Ganias et al., 2003); Chinese *Hemiculter leucisculus* (Wang et al., 2014). In the current study, the degenerative process of POFs revealed the same features described above. However, no particular shape was observed in POF disappearance as reported in the Iberian sardine *Sardina pilchardus* and *Engraulis encrasicolus* where the evolution in the shape of POFs went consecutively from an irregular to a semi-rectangular, and finally a triangular shape (Ganias et al., 2007 and Ferreri et al., 2021).

Follicular atresia is an involution process widespread in the ovaries of fishes and other vertebrates, and observed in all stages of the reproductive cycle, although most frequently during post-spawning period (Wootton and Smith, 2015). Atresia presents marked morphological changes in both oocyte and follicular layers. According to the succession of these changes, four stages of atresia were observed (α, β, γ and δ) in the current study. The presence of α, β and δ is in accordance with that reported for the same species (*T. trachurus*) in Saronikos Gulf by Karlou-Riga and Economidis (1996). However, the γ stage was not reported by these authors. According to Hunter and Macewicz (1985), the absence of the γ stage is due to its short duration or to the fact that the follicle passes directly from the β to the δ stage without passing through the intervening γ stage. This hypothesis could explain the lowest rate of the γ stage (0.94%), revealed for the first time in our results. Atretic stages showed similar characteristics to those described by different authors (Hunter and Macewicz, 1985 and Karlou-Riga and Economidis, 1996 for *Engraulis mordax* and *T. trachurus*, respectively). However, different types of the α stage were discussed for the first time in *T. trachurus* in the present study. On the basis of morphological differences between and within unyolked and yolked oocytes, alpha atretic follicles were mainly of two types: bursting and non-bursting. These results were similar to those reported by Rastogi (1968), Ramadan and El-Halfawy (2007), and Azab et al. (2019). In the present study, the mean number of oocytes with the α atresia stage (113 oocytes) was higher than those for β (17 oocytes), γ (3 oocytes) and δ (8 oocytes) stages. Moreover, atresia was most common in yolked oocytes. These results were similar to those reported for *T. trachurus* of the North Sea and English Channel (Macer, 1974; Eltink, 1991), of Saronikos Gulf (Karlou-Riga and Economidis, 1996), of the northeast Atlantic (Gordo et al., 2008) and for *Trachurus declivis* (Marshallet al., 1993). The high incidence and the level of atresia seem to be influenced by several factors such as temperature (Linares-Casenave et al., 2002), stress (Guraya, 1986), pollution (Domínguez-Petit and Saborido-Rey, 2005), parasites (Clarke et al., 2006; Ichalal et al., 2019) and can have serious consequences for fish populations as non-spawned vitellogenic oocytes can reduce the reproductive potential due to a decrease in the number of viable offspring (Miranda et al., 1999 & Santos et al., 2005).

CONCLUSION

The present results reported the first detailed description of postovulatory follicle resorption and atresia in horse mackerel *T. trachurus*. The evolution of this resorption was described and showed no particular shape compared to other work reported for many fish species. Different types of atresia were exclusively observed in the α atresia stage. Further studies are required to deeply understand fish reproductive strategies in relation to postovulatory follicle resorption and atresia.

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POSTOVULACIJSKA DEGENERACIJA FOLIKULA I ATREZIJA U ŠARUNA (*Trachurus trachurus*) S ISTOČNE OBALE ALŽIRA

SAŽETAK

U ovom radu prikazan je detaljan opis resorpcije i atrezije postovulatornih folikula (POF) u šaruna iz alžirskih voda. Od veljače 2013. do veljače 2014. godine nasumično je prikupljeno 155 jedinki ženki šaruna. Analizirani su histološki isječci jajnika. Otkriveno je nekoliko POF-ova (7,28% ranih POF-ova i 2,91% starih POF-ova od ukupnog broja promatranih oocita). U ovoj studiji analizirane su morfološke promjene resorpcije POF-a. Nije uočen specifičan oblik. Utvrđena su četiri tipa atretičnih oocita: α = 34,38%, β = 5,28%, δ = 2,37% i γ = 0,94%, što je prvi put zabilježeno kod šaruna. Učestalost α atrezije bila je veća u oocitima s žumanjkom (21,48%), nego u oocitima bez žumanjka (12,89%). α atretične jajne stanice mogu se klasificirati u dvije glavne vrste: one koje ne pucaju (kapsulirana, lipoidna i cistična atrezija) i pucajuće (višestruke eksplozije, pojedinačne eksplozije, fagocitne eksplozije i ukapljene eksplozije). Potrebna su daljnja istraživanja kako bi se dublje razumjele reproduktivne strategije riba u odnosu na resorpciju i atreziju postovulatornih folikula.

Ključne riječi: šarun, *Trachurus trachurus*, postovulatorni folikuli, atrezija, alžirska obala

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