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OVARIAN ATRESIA IN CEPHALOPODS

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Ovarian atresia is described for the first time in cephalopods. Detailed histological examination of ovaries of *Loligo vulgaris reynaudii* in various stages of maturity revealed atresia in primary, previtellogenic and vitellogenic oocytes. These were analysed separately. Previtellogenic and vitellogenic oocytes could be subdivided into five clear stages, whereas primary atretic oocytes are given a general description. Follicular atresia lowers the number of maturing and mature eggs in the ovary, so previous fecundity estimates for cephalopods may have been too high. To correct potential fecundity estimates for losses arising from atresia, it is necessary to estimate the duration of each atresia stage in relation to the total spawning period.

Determination of fecundity in cephalopods can be particularly difficult, because many species are not truly semelparous and may exhibit a more flexible pattern of reproduction, for example, the possibility of an alternative 1- or 2-year lifespan suggested by Mesnil (1977). For the chokka squid *Loligo vulgaris reynaudii* it is now clear that spawning takes place over a protracted period, both sexes moving between spawning sites (Melo and Sauer in prep.). This fact in itself can complicate the determination of fecundity. However, detailed histological examination of the ovary reveals another complicating factor, that of ovarian atresia (oocyte degeneration and resorption). Not only does atresia occur in fully mature individuals, but it happens across the whole maturity range.

Atresia has been described in many species, including *Carassius auratus* (Beach 1959, Khoo 1975), *Scomber scomber* (Bara 1960), *Pleuronectes platessa* (Barr 1963), *Poecilia reticulata* (Lambert and Van Oordt 1965) and *Sebastodes paucispinis* (Moser 1967). Knowledge of its extent is particularly important when evaluating reproductive success. The lifetime reproductive output of females containing atretic oocytes is reduced both directly and indirectly. Not only has a spawning opportunity been missed, but the energy expended to produce the unspawned oocyte could have been diverted to the development of somatic tissue (Bagenal 1967). An atretic mass of oocytes may also limit lifetime reproductive capacity by suppressing subsequent development of oocytes (Trippel and Harvey 1990). It may also cause a significant decrease in fecundity in species with long spawning periods (Sakun and Svirskiy 1993).

To the authors' knowledge, oocyte atresia has not yet been described in cephalopods. However, Laptikhovsky and Nigmatullin (1993) and Nigmatullin and Laptikhovsky (1994) reported the presence of both protoplasmic and vitellogenic atretic oocytes in the ovaries of spent female *Illex argentinus*. The aim of the present study was to describe and analyse atretic oocytes at different stages of degeneration, and to attempt to elucidate the role of this process in the life cycle of a loliginid squid.

MATERIAL AND METHODS

An average of 50 ovaries per month was collected throughout the year (except February) and throughout the distributional range of *L. v. reynaudii.* Squid were caught by trawl from the Sea Fisheries Research Institute's F.R.S. *Africana*, and by hand-jigging. No samples were available for the month of February. After measuring the dorsal mantle length of each specimen, ovaries were immediately removed and preserved in Bouins solution for 24 h, dehydrated in a graded alcohol series, cleared with toluene and embedded in paraplast. Histological sections of 6–7μ were cut and stained with Harris' haematoxylin and eosin. Atresia stages were classified on the basis of the degree of hypertrophy of the granulosa and thecal layers, the breakdown of the zona radiata, phagocytosis of the yolk granule (in vitellogenic oocytes) and the quantity of connective tissue in the atretic follicle.

In order to assess losses through atresia in mature individuals, a count of vitellogenic oocytes was made on five ovaries of females of different maturity stages, but of similar size. The various ovarian stages were classified histologically.

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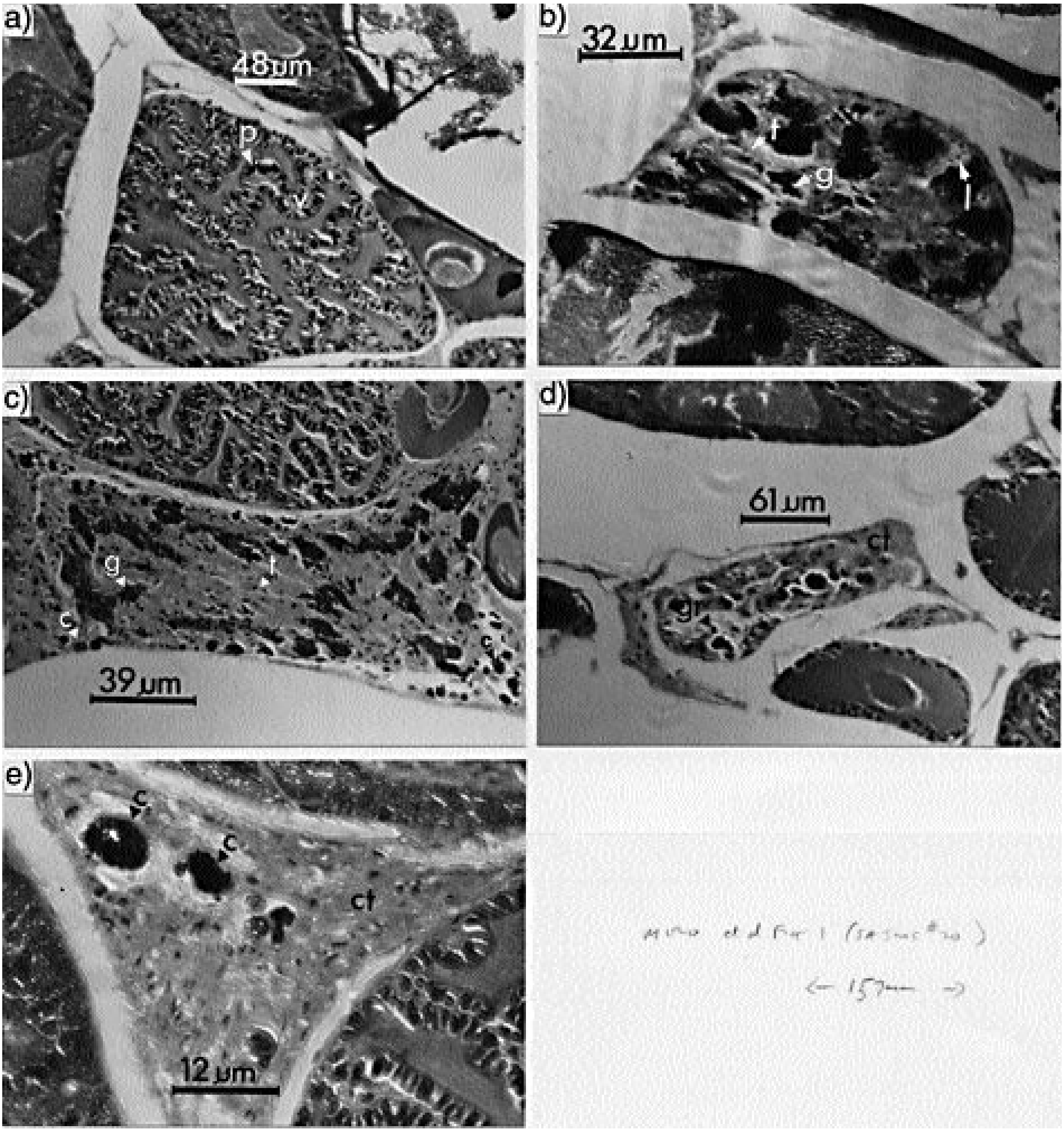

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Fig. 1: Previtellogenic atretic oocyte. (a) Stage 1, showing vacuolated granulosa cells (v) and pycnotic nuclei (p); (b) Stage 2, showing irregular patches of granulosa cells (g) and strands of thecal (t) connective tissue and lymphoid cells (l); (c) Stage 3, showing hyperplasia of the thecal layer (t) accompanied by marked degeneration of granulosa cells (g) – small cysts of phagocytic follicular cells are visible (c); (d) Stage 4, showing connective tissue fibres (ct) and granulocytes (gr); (e) Stage 5, showing cysts of phagocytic follicular cells (c) and invading connective tissue (ct)

RESULTS

Histogenesis of atretic oocytes

Atresia was recognized by changes in the cytoplasm and in the granulosa and thecal cells of the oocytes. In *L. v. reynaudii*, it was found in all stages of oocyte development. Primary, previtellogenic and vitellogenic atretic oocytes were analysed separately. Previtellogenic and vitellogenic atretic oocytes could be subdivided into five stages, whereas primary atretic oocytes could be given only a general description.

ATRESIA OF PREVITELLOGENIC OOCYTES

Stage 1 (Fig. 1a) – This stage is characterized by a total disorganization of the granulosa layer. The granulosa cells are arranged randomly, have lost their string-like organization, and the walls and cells are no longer well defined. The cytoplasm of the granulosa cells tends to stain basophilically, so that chromatin contrast between nucleus and cytoplasm is not sharp. The nuclei of the granulosa cells become elongated. Sometimes, pycnotic nuclei and vacuoles can be seen in the granulosa layer. Cells of the thecal layer penetrate the atretic oocyte. Small portions of the remnant cytoplasm of the oocyte are present.

Stage 2 (Fig. 1b) – The cavity of the atretic follicle is filled with large granulosa cells of irregular shape, with distinct vacuolated cytoplasm and indistinct cell boundaries. The cytoplasm stains acidophilically, and in many instances the nuclei are no longer visible. In some sections of the follicle the granulosa cells form cumulus or islands, which tend to fuse into short and long strips, giving a syncytial appearance. The nuclei of these cells are large and round, with a prominent nuclear membrane, and are strongly basophilic. Adjacent to the irregular patches of granulosa cells are small cells with basophilic cytoplasm and small nuclei, which may be lymphoid cells. The thecal layer has thickened, and in numerous places strands of thecal connective tissue and blood capillaries have penetrated into the granulosa. Remnants of the oocyte can be seen in some cases.

Stage 3 (Fig. 1c) – The atretic follicles are smaller. The entire body of the follicle is surrounded by a thick layer of flattened fusiform cells, possibly thecal in origin. A small area of fibrous tissue, associated with the invading connective tissue cells, is present in the centre of the follicle. The nature of the granulosa cells alters considerably. The nuclei become pycnotic, the cytoplasm is reduced and becomes denser, and the cells become atrophic and noticeably decrease in number. Small pockets or cysts of cells are present around the periphery of the follicle, internal to the theca. Because the appearance of the nuclei and the cytoplasm of these cells is similar to that of the follicular epithelium, it is probable that the follicular cells become phagocytic and remove the debris of the atretic follicle. There are large intercellular cavities.

Stage 4 (Fig. 1d) – The atretic follicle is small and there is a thin irregular, reticular network of fine connective tissue fibres. Pigment granules are frequently observed and occasional granulocytes are present in the thecal stroma. A few cysts of cells similar to those described in Stage 3 are still present.

Stage 5 (Fig. 1e) – The reduction of the atretic follicle continues and there is complete resorption of the granulosa cells. The entire follicle becomes invaded by connective tissue and is reduced to a small scar in the ovarian stroma.

ATRESIA OF VITELLOGENIC OOCYTES

Stage 1 (Fig. 2a) – The granulosa layer is hypertrophic and surrounds the oocyte, which exhibits signs of degeneration, including vacuolation and disintegration of the zona radiata. During the early phase of this event, the granulosa remains in a single layer, but after a short interval, it becomes transformed into a wall two or three cells deep and thickens substantially. The granulosa contains large cells of irregular shape containing vacuolated cytoplasm and elongated nuclei with a prominent nuclear membrane. The zona radiata also undergoes some changes. Its radial striations disappear, it thickens in some places and in other places it becomes thin, with fissures or crevices. The theca is still thin and contains blood vessels.

Stage 2 (Fig. 2b) – This stage is marked by obvious hypertrophy of the granulosa that becomes very thick. No divisions among these cells were found, but their number and size increase considerably. The cells of the granulosa are relatively large and their elongated nuclei become rounded or spherical, placed mostly in the peripheral cytoplasm. Some nuclei become pycnotic when stained with haematoxylin. The cytoplasm of the granulosa is filled with vacuoles of various sizes. Cell limits are not well defined. As resorption proceeds the zona radiata breaks down and the granulosa cells enter the yolk and begin to phagocytose the yolk granules, which gradually disappear. The cytoplasm of the atretic follicle forms a cortical layer around the cell periphery. In some places in Stages VII and VIII oocytes (Melo and Sauer in prep.), the follicular cells perforate deep in the form of cords, engulfing the yolk granules. The zona radiata contracts, partly loses its contact with the granulosa layer, and breaks into segments. The yolk

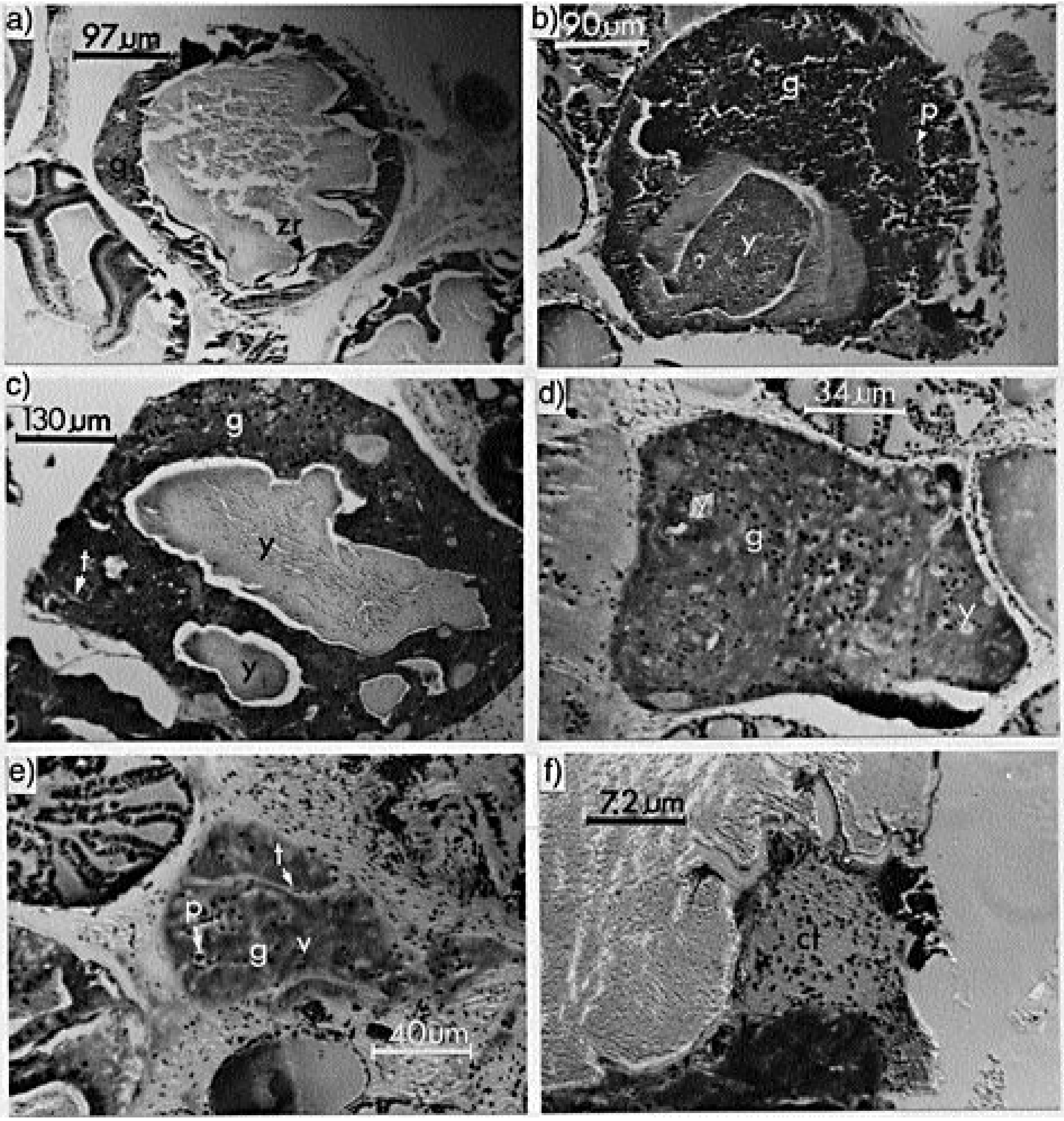

Fig. 2: Vitellogenic atretic oocyte. (a) Stage 1, showing hypertrophic granulosa cells (g) and the dissolving zona radiata (zr); (b) Stage 2, showing multilayered zona granulosa (g), pycnotic nuclei (p) and eroded yolk granules (y); (c) Stage 2, showing the granulosa layer (g) engulfing the homogenized yolk (y) - note the thecal layer (t) penetrating the granulosa; (d) Stage 3, showing the central cavity completely filled by the granulosa cell (g) mass – remnants of yolk (y) remain among the invasive phagocytosed granulosa cells; (e) Stage 4, showing appreciable degeneration of the granulosa cells (g) – a few pycnotic nuclei (p) are visible, the theca has thickened and the thecal cells (t) are penetrating inwards; (f) Stage 5, showing invasion of the oocyte by connective tissue (ct)

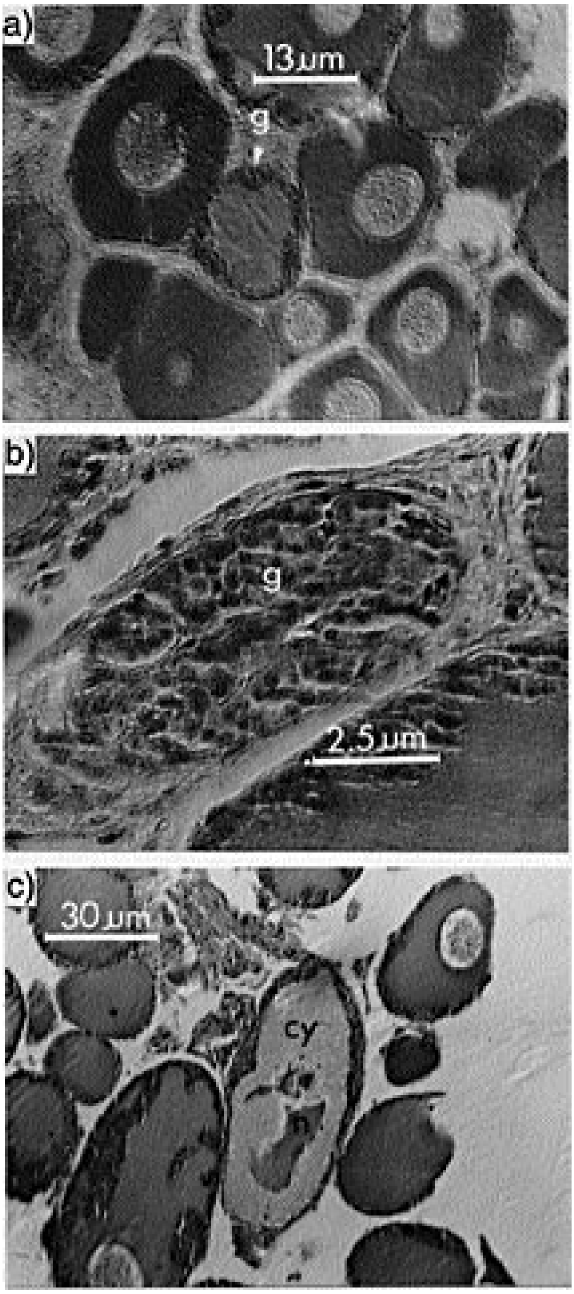

Fig. 3: (a) Primary oocyte undergoing atresia – note enlargement of granulosa layer (g) and disintegration of the nucleus; (b) late stage of atresia of a primary oocyte showing proliferation of granulosa cells (g); (c) primary atretic advanced oocyte, showing floculent cytoplasm (cy) and disintegration of the nucleus (n)

granules liquefy and fill the spaces created by the broken layer of the zona radiata. The thecal layer occasionally penetrates into the granulosa (Fig. 2c).

Stage 3 (Fig. 2d) – This stage is characterized by folding and collapse of the follicular wall, with both thecal and granulosa layers now in the antrum previously occupied by the oocyte. The number of pycnotic nuclei increases further and the vacuolated cytoplasm contains a few yolk granules. The theca thickens and penetrates into the granulosa. The atretic oocytes are now very much smaller.

Stage 4 (Fig. 2e) – The granulosa cell alters considerably. The nuclei become pycnotic, their cytoplasm becoming flocculent with fusiform nuclei. Discerning whether the cells are fused into a syncytium or retain their individuality is not possible. The most conspicuous feature is the marked hyperplasia of the theca, that undergoes a three- to fourfold increase in thickness. The follicles decrease in size.

Stage 5 (Fig. 2f) – Once the yolk is completely phagocytosed, the atretic follicle collapses and there is progressive resorption of the granulosa cells. The latter are degenerating, the nuclei are pycnotic and there is no appreciable cytoplasm. The atretic follicle then follows a similar pattern to that of Stage 5 previtellogenic oocytes, i.e. it is invaded by fibroblasts associated with the penetrating connective tissue.

PRIMARY OOCYTES (Fig. 3)

In primary oocytes the resorption process is similar to that described by Hunter and Macewicz (1985). The nucleus disintegrates and the granulosa cells regress and phagocytose the unyolked oocyte. In more-advanced oocytes, the cytoplasm changes from its usually hyaline basophilia to a flocculated, dusty blue or greyish lavender hue (Fig. 3c).

Seasonal cycle and the occurrence of atretic stages

The monthly mean percentage of ovary atresia from squid collected on their spawning grounds is shown in Figure 4. Atretic oocytes were present in the ovaries throughout the year. During the peak spawning season of the species (September–December), the percentage of atretic oocytes ranged from a low of 1.8% in September to 16.7% in December. The highest percentages of atretic oocytes were found in January (52.2%) and March (63.2%).

Few primary atretic oocytes were present in immature and developing ovaries during January, May or September. Most of the atretic stages of previtellogenic oocytes were found throughout the year in developing, maturing and partially spent ovaries, but they were

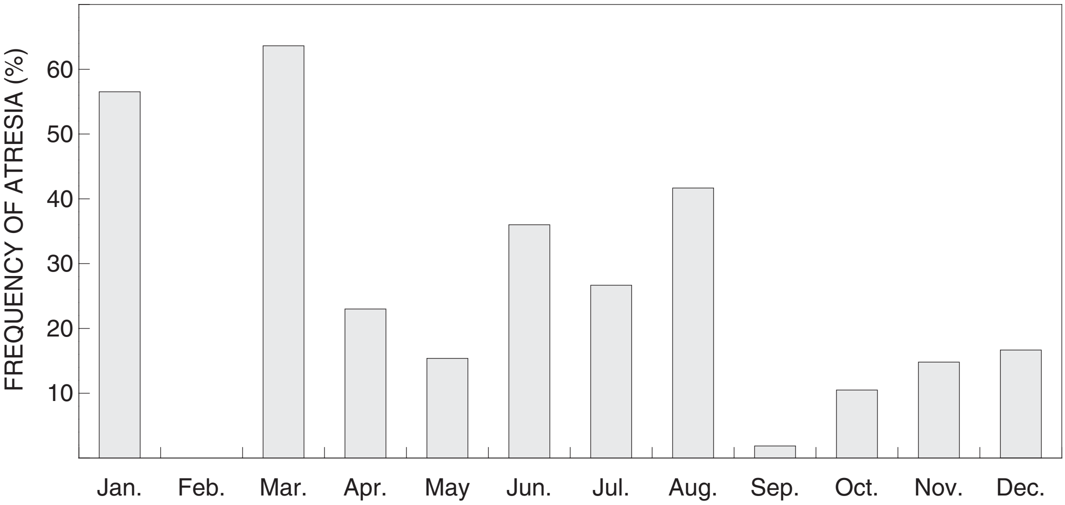

Fig. 4: Monthly percentage of ovary atresia in *L. v. reynaudii* (no data for February)

most abundant in partially spent individuals (Fig. 5a). There was a high percentage of atretic vitellogenic oocytes in December and April (Fig. 5b), and they were particularly prevalent in totally spent ovaries (>80% of oocytes being atretic).

Effects of oocyte atresia on fecundity

Table I shows that evidence of atresia of vitellogenic oocytes first appears in maturing ovaries and increases in partially spent individuals. In totally spent animals, a high percentage of vitellogenic oocytes were atretic, but the actual number of oocytes present was small. Assuming that oocytes with advanced yolk formation constitute a discrete batch, the implication is that 7.6% of the first batch of oocytes is reabsorbed. This will obviously affect estimation of fecundity, because a correction factor would have to be introduced should all oocytes be counted as viable. In ripe ovaries the incidence of atresia was variable, with a mean value of 5.9% (*SD* 7.1). Of course, such variability may be simply a consequence of sampling ovaries from which different numbers of oocyte batches had already been released.

Table I: Mean number of oocytes with advanced yolk formation per histological section for various maturity stages in the chokka squid

Maturity stage	Mean number of oocytes			
	Normal	Atretic	% atretic	*SD*
Maturing	325.2	24.8	7.6	±2.2
Ripe	248.0	15.4	5.9	±7.1
Partially spent	130.0	50.0	38.5	±4.2
Spent	10.3	80.0	88.6	±5.5

DISCUSSION

Atresia is frequently observed in many species of fish (Pickford and Atz 1957, Ball 1960, Hoar 1969, Khoo 1975). It has now also been shown to be an integral part of the reproductive strategy of at least one species of squid, with the histological atretic states providing a useful index of the reproductive capability of the population.

Although there is atresia during all stages of oocyte development in *L. v. reynaudii,* it was most frequent in the later part of the life cycle, in late previtellogenic and vitellogenic oocytes. The low percentages of atresia in mature individuals early in the spawning season might be an indication of the end of one of several spawning bouts. During the spawning season, squid return to a particular spawning site over a number of days (Sauer *et al.* 1997) and move between sites over a period of weeks (Sauer *et al.* in prep.). Therefore, it can be assumed that *L. v. reynaudii* undergoes more than one cycle of oocyte maturation, spawning and, presumably, atresia.

The high percentage of atresia found late in the spawning season (>50% of advanced vitellogenic

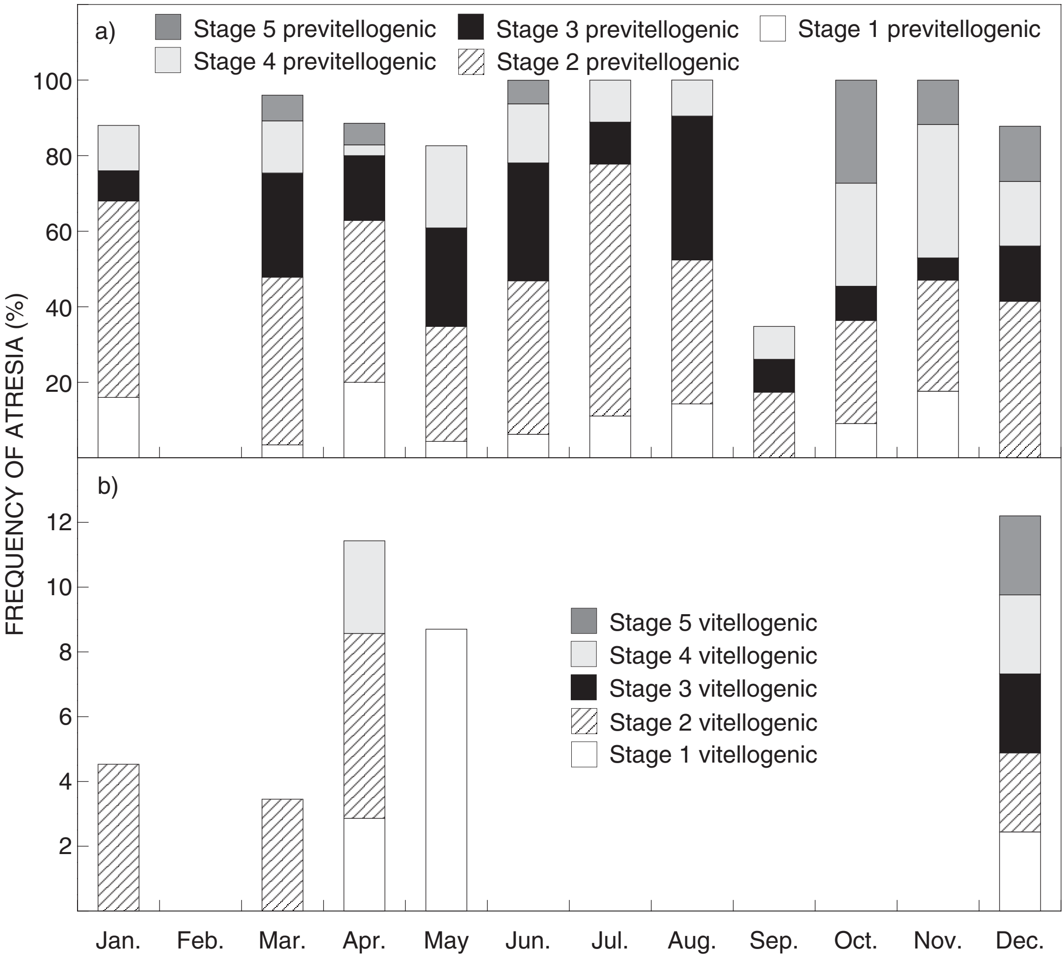

Fig. 5: Monthly percentage occurrence of (a) different previtellogenic atretic stages, (b) different vitellogenic atretic stages

oocytes) reflects mature animals that have spawned, indeed probably the end of spawning for that spawning population. This statement is supported by the conclusion of Hunter and Macewicz (1985), who state that highly atretic ovaries are indicative of animals that have ended their reproductive season, and therefore should be considered "spent" or post-spawning.

As already mentioned, the presence of both protoplasmic and vitellogenic atretic oocytes has also been reported by Laptikhovsky and Nigmatullin (1993) and Nigmatullin and Laptikhovsky (1994) in ovaries of spent *Illex argentinus* females. In fish that spawn over several seasons, the function of the atretic follicles in spent ovaries is obviously resorption of the vitellogenic oocytes which were not spawned (Beach 1959). For what is postulated to be an annual species, the explanation is not so simple. *L. v. reynaudii* on the inshore spawning grounds are in poorer condition than those offshore (Sauer 1991). Therefore, it is possible that a portion of the stock of remaining vitellogenic oocytes late in the season may provide an additional energy reserve for the final spawning bouts prior to death.

Why should there be pre-ovulatory degeneration of oocytes? Several factors have been advanced as reasons for ovary atresia in fish, including overcrowding (Swingle 1956), environmental condition such as temperature and day length (De Vlaming *et al*. 1982), food restriction (Tyler and Dunn 1976) and body size

(Lam *et al.* 1978). It also appears that atresia is controlled by the endocrine gland (Lambert and Van Oordt 1965, Hoar 1969, Khoo 1975). Ovarian atresia may also depend upon the level of energy reserves (Hunter and Macewicz 1985). A possible explanation for atresia in *L. v. reynaudii,* given that atretic oocytes are present in all stages of gonadal recrudescence, may be that atresia plays a role in the removal of surplus oocytes for which there are inadequate energy reserves to proceed with oocyte maturation. Oogenesis is expensive energetically, particularly in short-lived species, in which a substantial quantity of vitellus is accumulated by the ripe ovary. Therefore, it seems likely that, after a certain minimum fecundity has been achieved, under some conditions of food availability, part of the energy resources may be redirected to growth during maturation. In general, atresia may be of adaptive significance in avoiding a superfluous energy budget. However, additional information on the dynamics of oocyte maturation and gonad growth is necessary to provide support for such a hypothesis.

The mechanism of resorption of atretic oocytes has been the subject of many studies. Beach (1959), Ball (1960) and Khoo (1975) suggested that follicular cells are responsible for the removal of atretic oocytes by phagocytosis, whereas Barfurth (1886) inferred that oocyte resorption may be attributed to the activity of the follicular cells, cells of connective tissue origin, and the phagocytic activity derived from the vascular system. Wallace (1903) concluded that oocyte resorption is a result of an interaction of both leucocytes and follicular cells. The evidence provided in this study confirms the role of the follicular cells. This is particularly noticeable in the case of atretic vitellogenic oocytes, which are invaded by numerous cells of follicular origin. During the terminal phase of the resorptive process, cells of fibroblast origin were implicated in the lytic removal of the oocyte remnants, i.e. they were either invading fibroblasts (as seen in the younger oocyte stages) or modified fibroblasts serving as follicular cells in the case of older oocytes. The role performed by leucocytes was confined to the terminal re-establishment of stromal tissue.

Ignoring atresia may have significant consequences for accurate determination of fecundity in cephalopods. In describing the dynamics of cephalopod populations, several estimates of fecundity have been made (e.g. Mangold-Wirz 1963, Brunetti *et al.* 1991). They have been based on the number of eggs in the oviducts and total counts of vitelline oocytes, both in the ovary and oviducts (Durward *et al.* 1979, Coelho *et al.* 1982, Rodhouse and Hatfield 1990). None of these studies reported atretic oocytes. Certainly, follicular atresia lowers the number of maturing eggs in the ovary and, therefore, the fecundity values reported previously may be overestimates. However, correction of potential fecundity estimates for losses arising from atresia is problematic. It is necessary to estimate the duration of each atresia stage in relation to the total spawning period (Witthames and Greer-Walker 1991). For example, although it has been shown by Melo and Sauer (in prep.) that chokka squid are serial spawners, it has not been possible to determine how many batches are spawned from a particular ovary, or the number of eggs released per batch. Analysis of squid collected regularly over a complete spawning season may provide the answers to some of these intriguing questions.

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