

Caveat observator: the many faces of pre-spawning atresia in marine bivalve reproductive cycles

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Abstract Of the hundreds of publications on bivalve reproductive cycles, only a handful reports the presence of pre-spawning oocyte autolysis, or atresia. This is at variance with the author's practical experience, in which pre-spawning oocyte atresia has been found in every bivalve reproductive cycle investigated. Failure to identify pre-spawning atresia will lead to over-estimations of fecundity, reproductive effort, and anticipated larval density and recruitment. On the intuition that the phenomenon is under-reported due to unfamiliarity with the histological characteristics of atresia, it is presented here within the context of the study of bivalve reproductive cycles, the reported incidence of pre-spawning atresia, and the histological profiles of this phenomenon in several commercially important bivalve families. Despite superficial variability, the assembled data allow the presentation of underlying common characteristics. It is postulated that pre-spawning oocyte atresia is a widespread, yet seldom-identified phenomenon in marine bivalves, which probably affects previous and current data on fecundity and reproductive effort, both in wild and cultured populations. The information presented here is intended to both increase awareness of this process, and lead to more realistic interpretations of bivalve reproductive cycles, fecundity, and reproductive effort.

Introduction: the study of bivalve reproduction

There are only two indigenous sources of increase in any population: somatic growth (increase in biomass) and reproduction (increase in numbers). The proper management of animal populations, wild or cultured, obviously requires detailed knowledge of their reproductive biology. To this end, marine bivalve reproduction, and particularly the reproductive cycles, has been intensively studied since the 1930s (see reviews by Andrews 1979; Sastry 1979; Mackie 1984; Gosling 2015). To avoid confusion, it should be noted that the term 'reproductive cycle' includes all events from gametogenesis to gamete release and resorption of residual gametes, whereas the term 'gametogenic cycle' refers only to events of gametogenesis.

In addition to fundamental understanding of this component of population increase, on a zootechnological level, adequate knowledge of bivalve reproductive cycles allows more effective timing for critical activities such as spat collector placement, elucidation of stock-recruitment relations (Sause et al. 1987), more efficient conditioning (Martínez et al. 2000; Chávez-Villalba et al. 2002a, b; Martínez and Pérez 2003; González-Araya et al. 2013; Barber and Blake 2016; Gómez-Robles and Saucedo 2009), and also provides an indication of reproductive effort (Lucas 1982; Bayne et al. 1983; Thompson 1984; Castagna 2001; Dutertre et al. 2009). Particular emphasis is placed on the female gametes, which are much easier to monitor and study than the male gametes; ultimately, estimations or indicators of fecundity are one of the most useful pieces of information in fisheries and aquaculture (Jennings et al. 2001).

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Available techniques

Reproduction impacts many aspects of organism and population biology, so it is not surprising that many techniques are used to study or account for it, from numerous standpoints. The presence of the shell, the small size of bivalve oocytes (30–100 μm , depending on species), as well as the indistinctness of the gonad in most families, preclude techniques often used in fish biology, such as manual expression of gametes, mass determinations, and visual counts of oocytes. Not surprisingly, the simplest techniques, such as dry tissue weights, condition indices, and gonad smears, also supply the most succinct, even rudimentary information—which may, however, be adequate for some purposes (e.g. Wiborg 1963; Beninger 1984; Beninger and Lucas 1984; Rogan et al. 1991; Sawusdee et al. 2015). The much more complex and time-consuming technique of gonad histological examination nevertheless constitutes a mainstay of the study of bivalve reproductive cycles, due to the amount of information which may be obtained (Beninger 1987; Gómez-Robles and Saucedo 2009; Barber and Blake 2016).

Interpretation of histological preparations requires more than a passing familiarity with the processes being studied, the effects of various stains on different cell types and components, possible confounding variables, and the characteristics of each tissue and cell type. It is thus not surprising that much histology remains squarely in the qualitative domain. Early attempts to quantify reproductive cycle histological data using ‘staging’ (Chipperfield 1953; Lubet 1959; Reddiath 1962; Lucas 1965) have been carried through to the present day (Duprat-Bertazzi and García-Domínguez 2005; Marroquin-Mora and Rice 2008; Yurimoto et al. 2008; Castaños et al. 2009; Thompson et al. 2014; and review by Gosling 2015), despite serious and persistent drawbacks. These include a high degree of subjectivity, the multiplicity of scaling schemes, and data which are both semi-quantitative and discontinuous, rendering statistical analysis inappropriate and invalid (Beninger 1987).

Improved quantitative histological techniques such as stereology and cell or tissue diameter or area calculation have been progressively developed since the 1960’s (Weibel et al. 1966; Elias et al. 1971; Briarty 1975; Hefferman and Walker 1989; Lango-Reynoso et al. 2000; Mayhew 2000; Beninger et al. 2001, 2010a, b; Cáceres-Puig et al. 2009; Thompson et al. 2014), and when applied to the study of bivalve reproductive cycles beginning in the 1970s, they have allowed a much more detailed, objective, and precise evaluation (Bayne et al. 1978; Newell and Bayne 1980; Lowe et al. 1982; Newell et al. 1982; Sundet and Lee 1984; Kennedy and Van Huekelem 1985; Pipe 1985; MacDonald and Thompson 1986; Beninger

1987; Morales-Alamo and Mann 1989; Pazos et al. 1996; Dutertre et al. 2009, 2010; Gómez-Robles and Saucedo 2009; Thompson et al. 2014). Unfortunately, these techniques require further expertise and time commitments, at the end of a very long process of sample preparation, and this may explain why comparatively few studies have made use of these powerful tools.

The cell types associated with the gonad and with gametogenesis have been identified over the course of the preceding decades of investigation, and form the basis for both the staging and the quantitative techniques (Chipperfield 1953; Lubet 1959; Reddiath 1962; Lucas 1965; Bayne et al. 1978; Newell and Bayne 1980; Lowe et al. 1982; Newell et al. 1982; Sundet and Lee 1984; Kennedy and Van Huekelem 1985; Pipe 1985; MacDonald and Thompson 1986; Beninger 1987; Morales-Alamo and Mann 1989; Pazos et al. 1996; Dutertre et al. 2009, 2010; Vaschenko et al. 2013).

Awareness of oocyte atresia

There are many variations on the spawning theme; some species have one or two massive spawns during the reproductive period, while others release small numbers of gametes almost continually throughout this period (‘dribble spawners’); many others show a stronger or weaker tendency toward one or the other of these extremes (see reviews by Seed 1976; Sastry 1979; Mackie 1984; Gosling 2015). Regardless of the spawning schedule, it has long been known that bivalves cannot spawn all of their oocytes prior to the end of the reproductive period. The remaining gametes are called ‘residual’ or ‘relict’ oocytes (ova), and it is well-known that they degenerate within the gonad, and are resorbed by macrophages (Le Pennec et al. 1991). Although some authors simply designate the process as ‘lysis’, ‘autolysis’, ‘resorption’ or ‘degeneration’, the term ‘atresia’ has progressively emerged in the literature to designate this type of oocyte degeneration, which manifests as the autolysis of structurally normal oocytes.

The term ‘atresia’ is (perhaps hastily) borrowed from the vertebrate reproductive literature, where it refers to the programmed apoptotic reduction in number of ovarian follicles and their oocytes (Hsueh et al. 1995; Kaipia and Hsueh 1997; Miranda et al. 1999; Rideout et al. 2000; Hardardotti et al. 2001; Jennings et al. 2001; Linares-Casenave et al. 2002; Skjæraasen et al. 2013). In the invertebrate biological literature, its meaning has shifted to designate oocyte degeneration in all types of gametogenic structures (including acini, tubules, trabeculae, etc. although an apoptotic mechanism has not yet been demonstrated (or investigated).

How common is pre-spawning oocyte atresia?

The destruction and resorption of residual oocytes is not a surprising phenomenon; however, the same process prior to spawning is far more intriguing. Compared to the hundreds of published studies on bivalve reproductive cycles (Web of Science® lists 376 titles containing the key words ‘bivalve and reproductive cycle’), very few have identified pre-spawning oocyte atresia, first described by Tang (1941), and followed by sparse reports in the intervening years (Christiansen and Olivier 1971; Ozanai 1975; Albertini 1985; Lowe and Pipe 1985, 1986, 1987; Lubet et al. 1986; Pipe 1987; Lowe 1988; Paulet et al. 1992; Dorange and Le Pennec 1989; De Gaulejac et al. 1995; Steele and Mulcahy 1999; Cantillanez et al. 2005a, b; Fearman et al. 2009; Camacho-Mondragón et al. 2012, 2015a, b; Vaschenko et al. 2013).

Everything appears rare if it is only rarely identified. It is obviously impossible to know whether, or how often, pre-spawning oocyte atresia has been overlooked by researchers studying bivalve reproductive cycles. However, most of these researchers will admit that they are not accomplished bivalve histologists, and hence are susceptible to overlooking the symptoms of pre-spawning atresia (indeed, many are probably unaware of the existence of the phenomenon).

In contrast to the extremely rare reports of pre-spawning oocyte atresia in the published literature, every bivalve reproductive cycle examined by the author has manifested some level of pre-spawning atresia: (1) *Placopecten magellanicus* in the Bay of Fundy, Canada (Beninger 1987, revisited in the present work), (2) *Pecten maximus* in the Bay of St Brieuc, France (present work), (3) two populations of *Crassostrea gigas* in the Bay of Bourgneuf, France (Dutertre et al. 2010), and (4) three populations of *Tapes philippinarum* on the French Atlantic coast (ongoing work). For the record, the only marine gastropod examined in detail,

Crepidula fornicata, has also shown major pre-spawning oocyte atresia (Beninger et al. 2010a, b; Valdizan et al. 2011).

It is important to note that while all atresic oocytes degenerate and lyse, to the untrained eye, the fine histological profile of the process of oocyte atresia appears to be highly variable depending on the bivalve families examined (see below). This apparent variability of profiles could be a contributing factor to the dearth of identification, and subsequent reports, in the literature.

This paper presents a review of the structural characteristics and consequences of bivalve oocyte atresia as they are known to this point, with an emphasis on pre-spawning atresia. The ultimate goal is to heighten the awareness of those who work on bivalve reproductive cycles, so that they might more easily identify and understand the implications of oocyte atresia.

Characteristics of oocyte atresia

Despite the superficial variability in histological profiles, it will be seen that bivalve pre-spawning oocyte atresia actually presents a common underlying set of characteristics. These will be reviewed in the most commercially important bivalve families.

Mytilidae

The presence of oocyte atresia has been stereologically quantified in the mussels *Mytilus edulis* and *M. galloprovincialis*, although without supporting descriptions or micrographs (Lowe and Pipe 1985, 1986; Fearman et al. 2009). Recent photomicrographs are available in Suárez et al. (2005, and Fig. 1) and in Beesley et al. (2008). Healthy mature oocytes are somewhat polygonal, despite

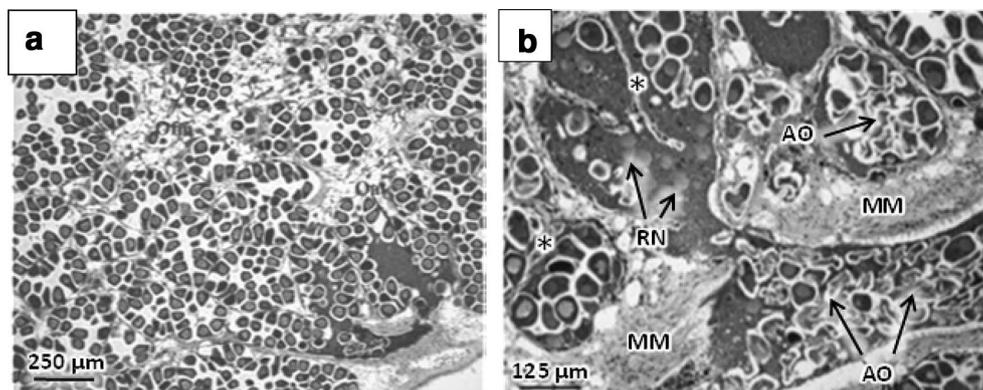


Fig. 1 Oocyte atresia in *Mytilus galloprovincialis* (Mytilidae). **a** Low-power micrograph showing general aspect of mature gonad. **b** Female gonad showing pre-spawning atresia. AO atresic oocytes, MM

macrophage matrix, RN residual nuclei after cell membrane degeneration, Asterisk cytoplasmic retraction in early stages of atresia. Re-interpreted from Suárez et al. (2005)

ample available space in the acini (Fig. 1a). Atresic oocytes are either found within a macrophage matrix, becoming increasingly shrunken and fading into the matrix, or they appear to shrink and autolyze, eventually assuming highly irregular membranous shapes, containing very little cytoplasm (Fig. 1b).

At the ultrastructural level, the cytoplasm becomes vacuolated, the perivitelline space increases, precipitating the detachment of microvilli, and the cell membrane eventually ruptures and degenerates completely, releasing the cytoplasm (Pipe 1987).

Pinnidae

Photomicrographs showing normal and atresic oocytes in the high-value pinnid species *Atrina maura* are available in Camacho-Mondragón et al. (2012, 2015a, b) and Fig. 2). Atresic oocytes reacted poorly with the histological stains, and were much more irregular in shape compared to normal oocytes. The acini showed accumulations of debris, and the inter-acinal tissue was hypertrophied, probably from the presence of macrophages.

At the ultrastructural level, De Gaulejac et al. (1995) and Camacho-Mondragón et al. (2015a, b) report that oocyte atresia in *Pinna nobilis* and *Atrina maura* proceeds with

cytoplasmic vacuolation, degenerating mitochondria, distended endoplasmic reticulum and nuclear envelope, the appearance of electron-dense inclusions in the nucleus, the agglomeration of lipid and lipoprotein granules in the cytoplasm, the degeneration of the vitelline envelope, and detachment of microvilli.

Pectinidae

Both histological and ultrastructural studies have documented oocyte atresia in the Pectinidae (Tang 1941; Christiansen and Olivier 1971; Ozanai 1975; Paulet et al. 1992; Dorange and Le Penec 1989; Avendaño and Le Penec 1997; Cantillanez et al. 2005a, b; Beninger and Le Penec 2016). Histologically, oocyte atresia unfolds as follows (Fig. 3): (1) the cytoplasm withdraws slightly from the cell membrane, (2) the cell assumes an irregular, jagged shape, with further cytoplasmic withdrawal; the normally spherical nucleus becomes irregular, (3) the cell membranes collapse, the cytoplasm and nucleus disappear, and the remnant cell membranes assume typical whorl shapes, chaotically packed upon each other. The haemolymph sinus around the intestine (which passes through the gonad in pectinids) is massively invaded by macrophage cells, which then stream off toward the degenerating acini and oocytes

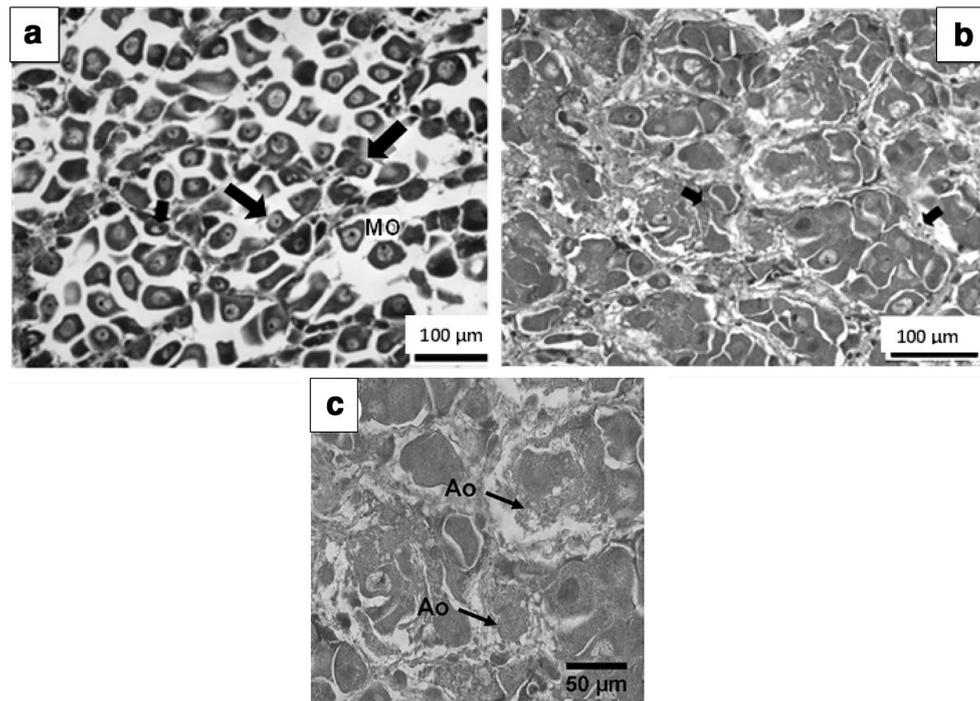


Fig. 2 Oocyte atresia in *Atrina maura* (Pinnidae). **a** Normal gonad; arrows show pre-vitellogenic oocytes; MO mature oocytes. **b** Atresic gonad; all oocytes are in some stage of atresia (arrows). From Camacho-Mondragón et al. (2012). **c** Pre-spawning atresic gonad, all

oocytes in some stage of atresia; Ao late-stage atresia, oocyte membranes disintegrated, cytoplasm spilling into acinal lumen. From Camacho-Mondragón et al. (2015a, b)

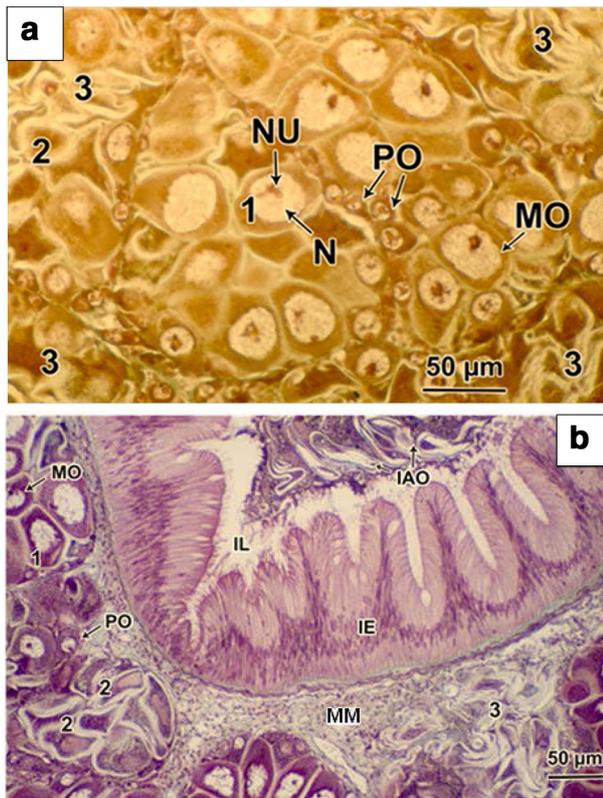


Fig. 3 **a** *Placopecten magellanicus* and **b** *Pecten maximus*. Stages in oocyte atresia. 1 Cytoplasmic retraction, and chromatin clumping around nucleoli. 2 Cell membrane folding, oocyte assumes pronounced irregular shape, nucleus becomes elongated and irregular, chromatin strands not visible. 3 Cells assume extremely irregular shape, cytoplasm emptied, nucleus and nucleolus missing. IAO ingested atresic oocytes, IL intestinal lumen, MM macrophage matrix; MO mature oocyte; N nucleus, Nu nucleolus, PO pedunculated (immature) oocytes. Original micrographs

(Fig. 3b). At the ultrastructural level, the principal atresic events are the dilation of the endoplasmic reticulum, cytoplasmic vacuolation, mitochondrial deformation, nuclear expansion, lobulation, and rupture, an increase in perivitelline space, microvillar detachment, and cell membrane rupture (Dorange and Le Pennec 1989; Beninger and Le Pennec 2016).

Although post-spawning atresia in pectinids proceeds to complete resorption of the residual oocytes, atresic oocytes may be voided during spawning, and even ingested upon emission (Fig. 3b, and Le Pennec et al. 1991).

Ostreidae

Pre-spawning atresia has been reported in two temperate *Crassostrea* species: *C. gigas* (Steele and Mulcahy 1999; Dutertre et al. 2010) and *C. angulata* (Vaschenko et al. 2013), and probably overlooked in other studies of *C. gigas* (Chávez-Villalba et al. 2002a, b, Chávez-Villalba et al.

2003). ‘Rare occurrence of atretic (sic) oocytes’, with no further description, was reported for *C. gigas* at the onset of gametogenesis in North-Western Mexico (Chávez-Villalba et al. 2007).

Healthy mature oyster oocytes are normally polygonal, due to close packing in the acinal lumen. The nucleus is spherical, and the cytoplasm fills the oocyte completely (Fig. 4 a). Atresia is characterized by both cytological changes and unusual effects of fixation. The oocytes become variably lobular, and eventually shrunken, both in cell size, and in the empty space they leave upon retraction (Fig. 4c, d). Cytoplasmic staining becomes extremely pronounced (probably due to increased membrane permeability; Steele and Mulcahy (1999) refer to a ‘granular’ cytoplasm), rendering observation of the nuclei and nucleoli problematic in some cells. However, nuclei and nucleoli are observed in many late-stage atresic oocytes. In the final stages, atresic oocytes are surrounded by a dense matrix of macrophage-type cells, indicative of intense phagocytic activity. Since this matrix does not constitute a true tissue, it exhibits tears upon histological sectioning (Fig. 4d). Within the shrunken oocytes, some cytoplasmic retraction is evident. The normally well-dispersed euchromatin becomes clumped within the nucleus (Fig. 4c).

Atresia has been reported in the tropical oyster *Crassostrea corteziensis*; however, it was judged to be post-spawning (although the micrograph shows a full acinus), and very little description was given. Irregular cell nuclear shape was evident, however, and the chromatin appeared to have lost all structure (Rodríguez-Jaramillo et al. 2008). No atresia of any type was reported for *Crassostrea virginica* reared in tropical lagoons (Aranda et al. 2014); this may be due to a failure to identify the phenomenon.

Pteriidae

Prespawning oocyte atresia in *Pinctada mazatlanica* is evident in the photomicrographs of Saucedo et al. (2001). The process shows close similarities with that of the Ostreidae. The normally polygonal mature oocytes shrink and become irregularly lobular, the cytoplasm shows altered staining and retraction, the nuclear envelope becomes irregular, the nucleolus shrinks and eventually disappears, and the chromatin becomes much clumped. Peduncular (previtellogenetic) atresic oocytes are slightly more lobular than normal peduncular oocytes, and show the same staining alterations and chromatin clumping described above (Fig. 5).

Veneridae

Based on recent work (P. Beninger, in preparation), atresic oocytes of *Tapes philippinarum* show fewer obvious signs of atresia compared to the other species

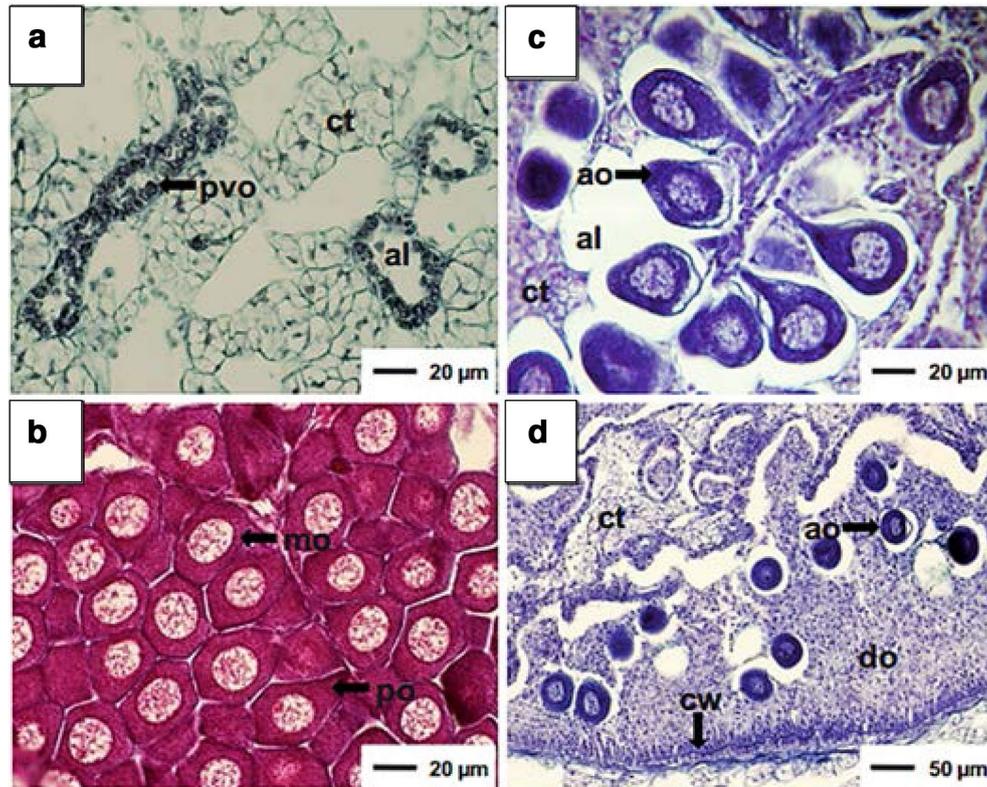


Fig. 4 Oocyte atresia in *Crassostrea gigas*. **a** Normal pre-vitellogenic oocytes at beginning of oogenesis cycle; **b** normal mature oocytes; note polygonal shape, clear, spherical nucleus, well-dispersed chromatin of mature and late-stage pedunculated oocytes. **c** Immature atresic oocytes in acinal lumen; note darkly staining, irregular nucleus and cytoplasm, cytoplasmic retraction, abundant macrophages surrounding oocytes. **d** Mature atresic oocytes, acinal structure lost. Note shrunken cytoplasm, dark nucleus and cyto-

plasm, irregular nuclear shape, spherical oocyte shape, abundant macrophage cells surrounding oocytes; empty spaces of completely resorbed oocytes in macrophage matrix. *al* acinal lumen, *ao* atresic oocyte, *ct*: connective tissue, *cw* ciliated wall of evacuating duct, *mm* macrophage matrix, *mo* mature oocyte, *po* pedunculated oocyte, *pvo* pre-vitellogenic oocyte. From Dutertre et al. (2009), re-interpreted and re-labelled

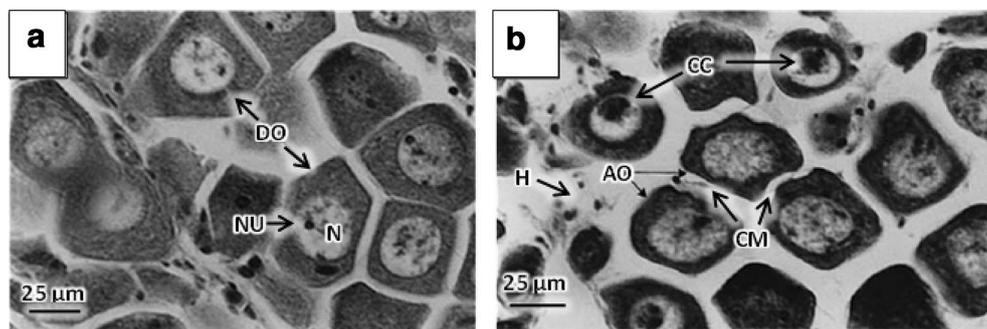


Fig. 5 Oocyte atresia in *Pinctada mazatlanica* (Pteriidae). **a** Normal oogenesis; *DO* developing oocytes, *N* nucleus, *NU* nucleolus. Note well-dispersed chromatin. **b** Pre-spawning atresia; *AO* atresic oocytes, *CC* clumped chromatin. Note darker-staining cytoplasm, shrunken,

irregular oocyte shape, with retraction from cell membrane (*CM*), irregular nuclear envelopes, and lack of small, distinct nucleoli. From Saucedo et al. (2001), re-interpreted and re-labelled

described above. The most prominent features are the alteration of their cytoplasmic and nuclear staining properties, the enlargement and subsequent disappearance of the nucleolus, the modification of the nuclear envelope,

and chromatin clumping. The oocytes appear much darker than the neighbouring healthy oocytes (Fig. 6). As atresia unfolds, the cytoplasm of the slightly irregular, spherical cell (Fig. 6a) exhibits more pronounced,

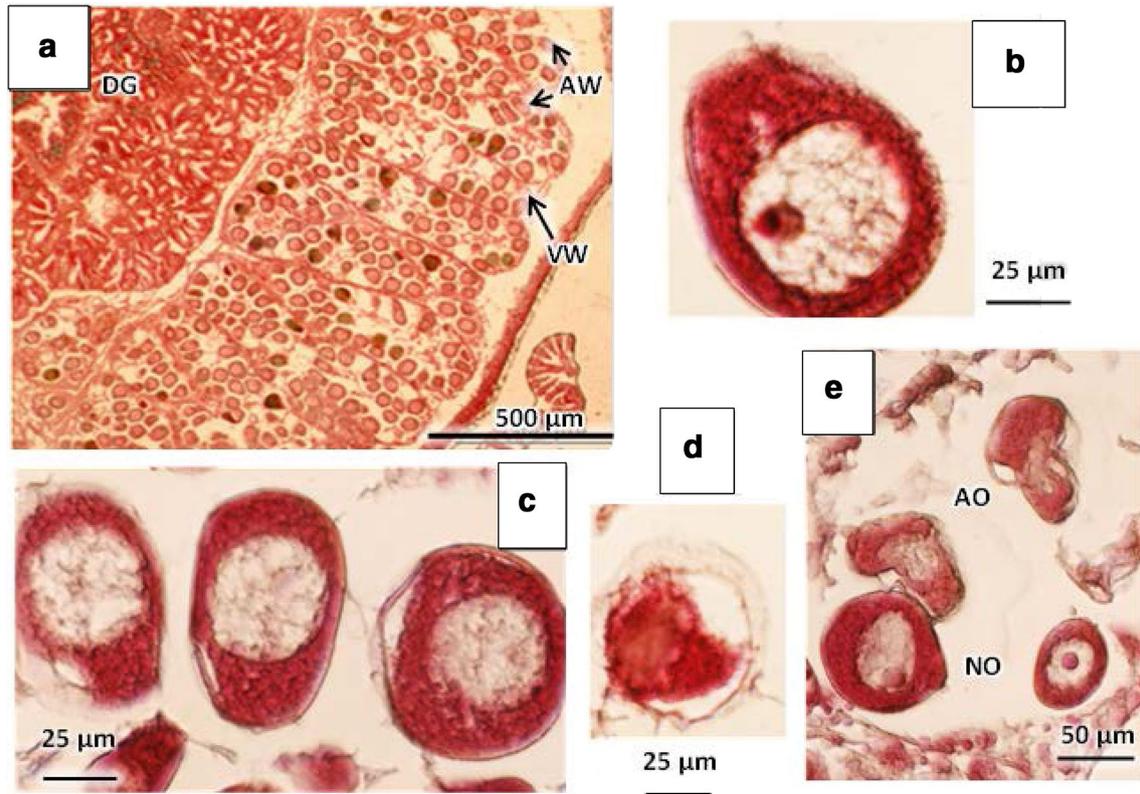


Fig. 6 Oocyte atresia in *Tapes philippinarum* (Veneridae). **a** General view of gonad acini containing healthy and atresic (discoloured) oocytes. **b** Early stage atresia: note darkly staining cytoplasm, heterogeneous nucleolus, slight euchromatin clumping. **c** Early stage atresia showing cytoplasmic retraction, nucleoli absent. **d** Late stage

atresia, showing pronounced cytoplasmic retraction, nuclear degeneration, cell membrane separation. **e** Late stage atresia, two atresic oocytes adjacent to and touching two normal oocytes. Atresic oocytes shrunken and misshapen, nuclei misshapen and degenerate, cell membranes loose and folded. Original photomicrographs

even polychromatic, staining, while the nucleus becomes darker due to condensation of euchromatin, and the nucleoli disappear (Fig. 6b). In the final stages, the nucleus itself disappears, and the oocyte appears as a variably coloured, irregular ellipsoid (Fig. 6c). In atresic oocytes observed during active gametogenesis, no further degeneration or residual membranes are observed, so it is assumed that they are emitted along with the

normal oocytes. In contrast to the pectinid and mytilid typologies, atresic oocytes can be surrounded by healthy oocytes (Fig. 6a); the phenomenon does not appear to be propagated within the acini.

Post-gametogenic (i.e. end of reproductive season) females present acini in which residual, atresic oocytes as well as residual membranes may be observed, indicating that these structures are resorbed.

Table 1 Oocyte histological symptoms of pre-spawning atresia (reported or *post-facto* interpreted) in various bivalve families

Family	Altered Cell shape	Cytoplasmic retraction	Altered staining	Irregular nuclear envelope/shape	Chromatin clumping/destructuring	Nucleolar hypertrophy/absence	Nuclear degeneration/absence	Cell lysis, empty
Mytilidae	I	I	NA	I	NA	NA	NA	I
Ostreidae	I	I	I	I	I	/	/	NA
Pectinidae	I	I	I	I	I	I	I	I
Pinnidae	I	I	I	I	/	I	I	I
Pteriidae	I	I	I	I	I	I	NA	NA
Veneridae	I	I	I	I	I	I	I	I

I feature present, NA no information available, / feature absent

Common cytological processes

Despite the somewhat variable histological features of oocyte atresia, familiarity with the histological profiles reveals several basic, common features which are differentially expressed in the various bivalve families examined. As summarized in Table 1, atresic oocytes in all of the families examined to date show some degree of altered shape and staining properties (the latter with the exception of the Mytilidae, for which no information is available), as well as cytoplasmic retraction, at some point in the process. With the exception of the Veneridae, all families studied also show alteration of nuclear shape, and most present nucleolar and chromatin anomalies, usually preceding complete nuclear degeneration.

Although atresia of residual oocytes always terminates in cell lysis and the emptying of cell contents, pre-spawning atresic oocytes may simply be spawned before this terminal phase occurs, as observed in the Ostreidae, Pectinidae, and Veneridae.

Magnitude of error

Obviously, if pre-spawning atresic oocytes are either not quantified, or worse, not even identified, the interpretation of the relevant bivalve reproductive cycles will be compromised. If quantification is a goal, e.g. for relative fecundity estimates (volume fractions of mature oocytes), this will produce intrinsically biased, erroneous data. The prevalence of oocyte atresia (i.e. percent of individuals affected in a population) has been shown to vary geographically and seasonally, attaining values as high as 75–80% in a population of the mussel *Mytilus galloprovincialis* (Ortiz-Zarragoitia and Cajaville 2010). Stereology is currently the only way to estimate the extent of potential error if atresic oocytes are mis-identified as normal oocytes. A comparison of stereological counts was recently performed, in which *Tapes philippinarum* atresic oocytes were assigned to their own category vs assigning them to normal oocyte categories (P. Beninger, in preparation). Over 3 gametogenic cycles spanning a 24-month period, the over-estimation of healthy oocytes was ~30%; this value increased to 40% for months in which pre-spawning atresia was particularly prevalent. The histological profiles of this species suggests that atresic propagation is limited; however, the profiles in the Pectinidae, Ostreidae, and Mytilidae show that atresic propagation is widespread, such that all oocytes in each affected acinus are compromised. The magnitude of error is thus likely to be far greater in these commercially important families when atresia is prevalent in the population, leading to a gross over-estimation of fecundity. This

may be a contributing factor to the observed weak mean spat yield from oocytes [less than 1%—Slater (2005)].

Pre-spawning oocyte atresia: a purpose?

Keeping in mind the human penchant for teleology, it has been argued that in animals in general, atresia (in the case of bivalves, pre-spawning atresia) may serve to remove oocytes carrying deleterious mutations in their mitochondria (Krakauer and Mira 1999). While this argument may be reasonable for species which retain their oocytes over their entire life span, it seems tenuous for species such as nearshore bivalves which retain their oocytes for a few weeks at most (no long-term oocyte storage has been documented; most species spawn, totally or partially, within days or weeks of oocyte maturity).

In their treatise on bivalve reproduction, Motavkine and Varaksine (1983) proposed three functionally distinct types of oocyte atresia in marine invertebrates:

- Residual—in every species examined to date, spawning does not empty the gonad entirely. The residual oocytes degenerate within the gonad, and the debris is cleared by macrophage haemocytes.
- Ecological—this type of atresia is a response to unfavourable environmental conditions. In the economically important family Pectinidae, pre-spawning atresia is the unmistakable symptom of an impending aborted spawn (Paulet et al. 1992). This type of atresia may be relatively common, since it has been reported in the clam *Corbicula japonica*, in the suspensivorous gastropod *Crepidula fornicata*, and in the oyster *Crasostrea gigas* (Baba et al. 1999; Dutertre et al. 2009; Beninger et al. 2010a, b; Vaschenko et al. 2013). As such, it conveys a very important piece of information: despite the presence of mature oocytes and a hypertrophied gonad, the impending spawn of an atresic individual will be severely compromised. Failure to identify atresic oocytes will, therefore, not only underestimate the reproductive effort, it may also result in an interpretation (e.g. an impending successful spawn) that is the exact opposite of reality (an unsuccessful or totally aborted spawn).
- Physiological—this type of atresia functions as a physiological regulatory mechanism governing the number of oocytes to be spawned. Supernumerary oocytes undergo degeneration without affecting the oocytes which are destined for spawning. This obviously assumes a complex regulatory mechanism which is as yet unknown, but which promises to be an exciting field for further research.

Soon after the recognition of atresia in the scallop (*Pecten maximus*) reproductive cycle, a link was established between pre-spawning atresia and water temperature: at temperatures below the optimum for larval development, atresia was particularly prevalent (Paulet et al. 1992). A similar link was observed for *Corbicula japonica* (Baba et al. 1999) and for the oyster *Crassostrea gigas* (Dutertre et al. 2009). The limited available data thus point to a link between atresia and cooler water temperatures in these temperate species. On the other hand, pre-spawning atresia appeared to be related to water temperatures >25 °C in the warmer-water pen shell *Atrina maura* (Camacho-Mondragón et al. 2015a, b). Taken together, these studies suggest that pre-spawning atresia allows bivalves to abort spawns for which the temperature conditions would compromise larval development or exotrophy.

The potential role of salinity in triggering pre-spawning atresia has scarcely been investigated, probably because of the relatively stable salinity conditions of most marine bivalves. Salinity extremes have been implicated, however, in the initiation of pre-spawning atresia in the brackish-water *Corbicula japonica* (Baba et al. 1999).

Some of the autolysing gametes will recycle metabolites and energy, which could be re-directed to more pressing physiological tasks, such as constitution of reserves for winter survival (Le Pennec et al. 1991).

A similar line of reasoning may be followed concerning trophic adequacy during gametogenesis. Mussels (*Mytilus galloprovincialis*) fed with the unicellular alga *Pavlova lutheri* alone produced a greater proportion of animals with atresic oocytes, associated with a lower proportion of hatched larvae, compared to mussels fed with a mixed diet of *P. lutheri* and *Chaetoceros calcitrans* (Fearman et al. 2009). It thus appears that mussels with poor-quality diets react as scallops do under unfavourable temperature conditions, resulting in a compromised spawn. Whether these processes are simple consequences of unfavourable gametogenic conditions, or whether they constitute an adaptive process, contributing to the optimization of reproductive effort, is not known—nor is it germane to the reality of reduced recruitment.

To date, very sparse data are available concerning the effects of other environmental conditions on pre-spawning atresia. Studies concerning hydrocarbon and other pollutant inputs generally point to increased atresia with exposure (Lowe and Pipe 1985, 1986, 1987; Lowe 1988; Vaschenko et al. 1997; Steele and Mulcahy 1999; Ortiz-Zarragoitia and Cajaville 2010). On the other hand, heavy levels of systemic *Perkinsus* sp. infection do not appear to affect the degree of oocyte atresia in the clam *Ruditapes decussatus* (Casas and Villalba 2012). Similarly, no pre-spawning oocyte atresia was observed in *Mytilus edulis* exposed to CO₂-acidified seawater (Beesley et al. 2008). Apparently,

not all unfavourable environmental conditions precipitate or aggravate pre-spawning oocyte atresia.

Conclusion

The prejudice caused by non-recognition of oocyte atresia goes far beyond the serious over-estimation of reproductive effort. Non-recognition of oocyte atresia, which may occur at several points in a reproductive cycle, may invalidate the interpretation of the entire cycle. Conversely, a seemingly incomprehensible cycle may suddenly become clear once atresia is recognized and accounted for (Dutertre et al. 2009; Beninger et al. 2010a, b).

From the foregoing, it is clear that the recognition and quantification of oocyte atresia is essential to the proper interpretation of reproductive processes in marine bivalves. Failure to do so may lead to biased estimates/indicators of fecundity, reproductive effort, and recruitment, as well as misunderstood signals for timing and significance of spawning [a possible case in point being the absence of a significant correlation between gonad size and spatfall (Slater 2005; Andersen et al. 2011)]. It is hoped that awareness of oocyte atresia and its consequences will be reflected in future publications concerning bivalve reproductive cycles.

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Compliance with ethical standards

Conflict of interest The author is unaware of any conflict of interest regarding this manuscript. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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