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Cloaked bivalve oocytes: lessons in evolution, ecology, and scientific awareness

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We have recently observed a gelatinous coat surrounding the oocytes of *Cerastoderma edule* within which the development of early larval stages takes place (Fig. 1). Although variously coated oocytes are common in the wider marine world, and among other molluscs, most bivalve researchers have never encountered such a thing. And when they do, many simply ignore it, while others mislabel it as a "perivitelline space" (Gustafson and Reid 1986, Kandeel et al. 2013). Of course, the immediate question is: Why should we care? We should care first because of the ecological and evolutionary lessons and perspectives this feature holds. And we should care because it tells us something very important about how the process of science funding can shape our view of the natural world.

First of all, what is this cloak? Of the few authors who have actually reported its existence, most simply designate it as a "gelatinous covering" (Creek 1960), "jelly coat" (Hodgson and Burke 1988, Gros et al. 1997), or "adhesive gelatinous egg capsule" (Gustafson and Lutz 1992). Unpublished data indicate that in *Codakia orbicularis*, the coat is composed of glycoproteins and proteoglycans (cited in Gros et al. 1997); this is consistent with the staining we recently obtained using Alcian blue, and the lack of any periodic acid–Schiff staining in the common cockle, *Cerastoderma edule* (Fig. 1B). Although some bivalve species deposit gelatinous egg masses on the substratum, these are functionally and morphologically different structures, characteristic of species with entirely benthic development (Ockelman 1958, Collin and Giribet 2010).

The next question is, obviously: What makes it? Because the bivalve germinal epithelium has no secretory cells, and no auxiliary cells have been observed constructing such a feature around developing oocytes, the most likely origin is the oocyte itself—and this has also been reported in unpublished work (cited in Gros et al. 1997). Histological sections show a thin cloak around young oocytes (not shown), and a very thick one around mature oocytes (Fig. 1B).

With respect to evolutionary lessons, coated oocytes have been observed in species from four of the six subclasses of the Bivalvia. There appears to be no taxonomic or evolutionary pattern in their occurrence; they are found both in the primitive Cryptodonta and in the much later Heterodonta and Anomalodesmata (Table 1). In each of these subclasses, there are also many species without coated oocytes, even within the same family (e.g., Pectinidae and Veneridae). The possibility that this is the result of multiple convergent evolutions of an identical character seems so remote as to be highly improbable. Conversely, if all bivalves possess the genetic and metabolomic equipment to produce such coats (i.e., this is a pleisiomorphic character), why have so few such examples been observed? Assuming that it is a differentially expressed pleisiomorphic character, why is there no phylogenetic or taxonomic footprint?

If there is no phylogenetic relationship for the expression of this character, we might ask if there is an ecological one. There is no indication that any ecological parameter can switch this character on or off. All *Cerastoderma edule*, as well as its sister species *Cerastoderma glaucum*, present this character. Table 1 recapitulates some of the most important ecological parameters for marine bivalves: water temperature, depth, and habitat. Again, no pattern is evident; coated oocytes are found in bivalves living at all temperatures, at all depths to the edge of the continental shelf, and in both epibenthic and endobenthic habitats. The endobenthic preponderance of the 14 coated species is easily explained by the fact that the vast majority of all bivalve species are endobenthic; similarly, the preponderance of reports from shallow depths probably represents material constraints: easily accessible bivalves are sampled more often than those which require shipboard procedures.

Having ascertained that the presence of coated bivalve oocytes is not related to the major abiotic characteristics of the marine habitat, we naturally proceed to question what selective advantage such a character might present. We may set aside the possibility that the sheath contributes to the energy reserves necessary for the first developmental stages, because it does not decrease in

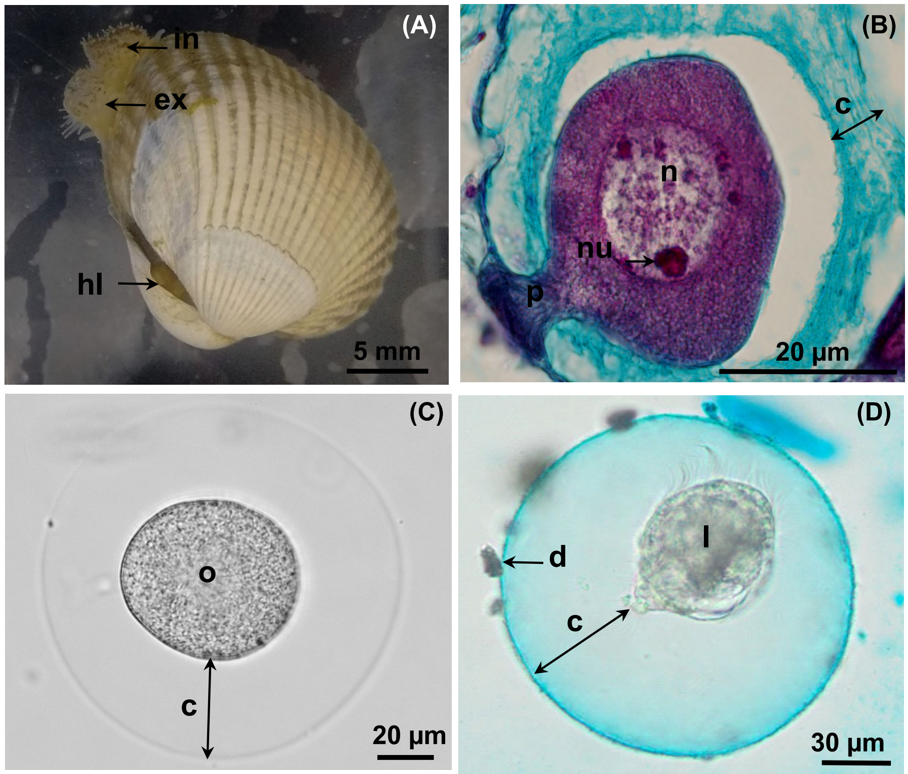

FIG. 1. *Cerastoderma edule.* (A) External view, showing both inhalant (in) and exhalant (ex) siphons. (B) Histological section of pedunculated (i.e., young) oocyte. Nucleus (n), nucleolus (nu), peduncle (p) and jelly coat (c) stained with Alcian blue, indicating acid mucopolysaccharides (AMPS). (C) Unstained, spawned oocyte surrounded by jelly coat (c). (D) Young veliger larva (l, approximately 24 h in laboratory) developing within Alcian blue–stained jelly coat (c). Note adhering detritus particles (d).

size over the course of larval development (Fig. 1C, D). Four alternative possibilities come to mind:

1) Mechanical protection. Especially in the shallow coastal habitats, currents can bring planktonic larvae into abrasive contact with topographic features. The sticky oocyte coat rapidly accumulates detrital particles (Fig. 1D), giving it a layer of nonliving protection, supported by a shock-absorbing mucus layer.
2) Predator protection. The 50-µm oocyte becomes a 200-µm spawned oocyte/larva once the mucus coat is fully hydrated (Fig. 1C, D), removing it from the prey size range of many copepods, which are the most numerous and voracious planktonic predators. Larger predators are fewer in number, further reducing predation pressure. In addition, the jelly coat itself, as well as the accumulated seston particles, may be unappealing or poorly recognized visually or olfactorily, resembling detritus or inorganic particulate matter rather than living food.
3) Postpredation protection. Many invertebrate oocytes are swallowed whole during spawns, for example, by fish (Fuiman et al. 2015). The acid mucopolysaccharide (AMPS) oocyte coat is undoubtedly resistant to digestion conditions (the intestine and stomach are themselves protected by a coating of AMPS), such that even if swallowed, a fertilized oocyte or larva may survive passage through the gut, as has been observed for copepod eggs (Flinkman et al. 1994).
4) Microbial protection—AMPS is well-known as both a physical and a chemical barrier to opportunistic microorganisms (Romo et al. 2016), and the marine environment is a veritable soup of hungry microorganisms. And finally, for spermatozoa which already function at low Reynolds numbers (i.e., even swimming in water is like swimming in honey for us), this thick, viscous coat will impose severe challenges to successful fertilization, opening the possibility of sperm competition and sperm selection.

The advantages provided by the jelly coat appear to be substantial, but all biologists know that they must have a cost. Among the angles that could be investigated, fecundity immediately comes to mind. The oocyte coat occupies a very significant amount of space in the gonad

TABLE 1. Occurrence of gelatinous oocyte coat among bivalve taxa, arranged from most primitive to most recent.

Subclass	Family	Genus and species	Habitat						Endo	References
			Cold	Temp	Warm	Shallow	Shelf	Epi		
Protobranchia	Solemyidae	*Solemya reidi*	×			×			×	Gustafson and Reid (1986)
		S. velum		×		×			×	Gustafson and Lutz (1992)
Pteriomorphia	Pectinidae	*Chlamys hastata*	×				×	×		Hodgson and Burke (1988)
Paleoheterodonta	NR									
Heterodonta	Astartidae	*Astarte sulcata*	×	×		×	×		×	Saleuddin (1965)†
	Cardiidae	*Cerastoderma glaucum*			×	×			×	Kingston (1974), Kandeel et al. (2013)†
		C. edule	×	×		×			×	Creek (1960), present study
	Donacidae	*Dona× vittatus*		×		×			×	Frenkiel and Mouëza (1979)
	Lucinidae	*Lucinoma aequizonata*			×	×			×	Gros et al. (1999)
		Codakia orbicularis			×	×			×	Alatalo et al. (1984); Gros et al. (1997)
	Thyasiridae	*Thysasira gouldi*	×			×	×	×	×	Blacknell and Ansell (1974)
	Semelidae	*Scrobicularia plana*		×		×			×	Frenkiel and Mouëza (1979)
	Veneridae	*Mercenaria mercenaria*	×	×	×	×			×	Loosanoff and Davis (1950)
		M. camechiensis			×	×			×	Loosanoff and Davis (1963)
		Venus striatula	×	×	×	×			×	Ansell (1961)
	Arcticidae	*Arctica islandica*	×				×		×	Lutz et al. (1982)
Anomalodesmata	Laternulidae	*Laternula elliptica*	×				×		×	Ansell and Harvey (1997); Peck et al. (2007)
	Pandoridae	*Pandora inaequivalvis*	×	×		×		×	×	Allen (1961)

Note: Epi, epibenthic; Endo, endobenthic; NR, none reported to date; Temp, temperate; Shelf, found over the depth range of the continental shelf.
† Not reporzted, but visible in drawings/micrographs.

acinus, which could otherwise be occupied by more oocytes. Do species with coated oocytes produce fewer oocytes annually than species with uncoated oocytes, or do they compensate for fewer oocytes by having longer spawning periods? Larval survival is another obvious research tack. Does the oocyte coat reduce larval mortality, especially in the early, essentially endotrophic stages? Energetics is also an interesting angle—How much of the total reproductive production budget does oocyte coating represent? And finally, one is left with a sense of awe that a feature such as this could be either switched on or off, species by species, in so many distantly and closely related taxa.

Perhaps the most interesting lesson provided by bivalve coated oocytes is in what they tell us about the way we conduct science itself. Just as it is obvious that nobody works for free (not counting the overtime scientists put in!), it is obvious that it is usually the species for which a budget has been allocated that will be studied. A quick check of published papers on bivalve biology will show that an overwhelming majority concern the few species that support major fishery and/or aquaculture industries. As it happens, none of them have been reported to have coated oocytes. A lack of major commercial importance is typical of the 17 species in which individually coated oocytes (as opposed to benthic egg masses) have been observed to date (Table 1). The result is that most bivalve biologists, working on the high-profile (and comparatively well-funded) major commercial species, have no idea that coated bivalve oocytes exist. The specialists have a blinkered view of their subject.

There may be many more bivalve species with coated oocytes out there. As long as marine bivalve researchers focus preponderantly on the high-profile commercial species, we will simply continue not to assimilate this basic fact into our scientific consciousness. Ignoring the existence of these oocytes not only ignores the phenomenon, but also closes to scientific inquiry all of the fascinating questions it raises. It is likely that many similar situations exist with respect to orphan taxa, and, more generally, orphan scientific questions.

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