

MECHANICAL FORCES IMPOSED ON ECHINOID EGGS DURING SPAWNING: MITIGATION OF FORCES BY FIBROUS NETWORKS WITHIN EGG EXTRACELLULAR LAYERS

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Summary

Many echinoderms spawn large numbers of eggs in rapid spawning bouts directly into the water column. During spawning, the eggs pass from the gonad along a narrow oviduct and through a rigid gonopore before reaching the water. As the eggs traverse this pathway, they are exposed to shear stress induced by the development of a velocity gradient within the fluid formed by the eggs. In some species, the diameter of the eggs is larger than the diameter of the gonopore. In these cases, the eggs also experience strain resulting from compression of the egg as it passes through the relatively small gonopore. The magnitude of shear stress experienced by eggs differs among species depending upon the viscosity of the eggs. The degree of strain experienced by eggs differs among species depending upon the relative sizes of the egg and gonopore and also changes within species as they grow. Recent evidence suggests that these forces have the propensity to damage eggs, thereby reducing their fertilizability, or to destroy them. Experimental evidence shows that the jelly coat around the eggs can protect them from shear stresses and reduce the strain imposed on them under a compressive force. Echinoderm eggs are surrounded by a jelly coat that has a composite structure of irregularly arranged fibrous networks embedded in a

jelly matrix. These fibrous networks have characteristics that are similar to those of engineered and biological materials that are known to reduce the transmission of mechanical forces to other structures. Given this similarity to other materials, three possible mechanisms for the action of the jelly coat may be identified. First, the apparent viscosity of the eggs of echinoids declines as the rate at which they are sheared during spawning increases. This reduction in viscosity with increasing shear rate (shear-thinning) may, in part, be due to the structure of the jelly coat and its resultant non-Newtonian nature. Second, experimental evidence indicates that the jelly coat preferentially deforms under a compressive load, reducing the transmission of that load to the egg. Third, the jelly (but not the fibers in the coating) may deform in a nearly viscous manner. In this case, the fibers may serve to provide an elastic 'backbone' to the layer and remain in place to stiffen the outer layer of the egg. The composite structure of the jelly coat and the morphology of the fibrous network are likely to be critical to all these mechanisms.

Key words: echinoid, gamete properties, spawning, gamete evolution, fertilization, fibre-reinforced material.

Introduction

Many echinoderms spawn eggs freely into the water column (free spawning), where fertilization occurs. Because of this life history strategy, they release large numbers of eggs in rapid spawning bouts. Therefore, a large amount of fluid (formed by the eggs) is released from the gonad, travels along an oviduct, through a gonopore and into the water surrounding a spawning female. As the eggs traverse this pathway from gonad to sea water, they are exposed to flow-induced shear stresses (force per unit area) within the oviduct and gonopore (Thomas and Bolton, 1999). In cases where the eggs are larger than the gonopore, they also experience strain. Flow-induced shear stresses are the result of shear imposed on the eggs within a

velocity gradient in the fluid as it passes through the oviduct/gonopore complex. Strain results from the compression of the eggs as they are squeezed through a gonopore, the diameter of which, in many species, is smaller than that of the egg itself. Evidence from echinoids indicates that shear stress can damage and decrease the fertilizability of eggs (Mead and Denny, 1995; Thomas et al., 1999). Thus, there is potential for selection of properties that may decrease damage caused by shear stress and strain experienced by echinoderm eggs during spawning. There are two potential scenarios for egg properties to reduce damage caused by physical forces: (i) they may reduce the forces imposed on the

egg or (ii) they may protect eggs from the forces they experience during spawning.

One of the major factors contributing to the magnitude of the shear stress experienced by eggs in the oviduct is the viscosity of the spawned material. The higher the viscosity of the material, the greater is the shear stress experienced by the eggs. Thomas (1994) and Thomas and Bolton (1999) have determined that the viscosity of the gametes of four species of sea urchin declines with increasing shear rate (i.e. shear-thinning). This decline in viscosity with increasing shear rate reduces the estimated shear stress experienced by eggs during their passage along the oviduct (Thomas and Bolton, 1999). Therefore, shear-thinning of echinoderm eggs has the potential to reduce the incidence of gamete damage caused by the high shear stress the eggs experience as they pass through the oviduct/gonopore complex.

At least one property of echinoderm eggs, the extracellular layers (referred to here as the jelly coat), can protect them from damage induced by shear stress (Thomas et al., 1999; Thomas and Bolton, 1999). These jelly coats potentially play multiple roles in echinoderm reproduction. In addition to protecting eggs from shear stress, they play important roles in the fertilization processes (e.g. Hagström, 1956; Vaquier and Moy, 1977; Tilney et al., 1978; SeGall and Lennarz, 1979; Garbers and Kopf, 1980; Nomura and Isaka, 1985; Miller and Ax, 1990). These coats are composed of polysaccharides and glycoproteins (Kidd, 1978; SeGall and Lennarz, 1979; Crawford and Abed, 1986) arranged in concentric layers of complex fibrous networks within a polysaccharide matrix (Kidd, 1978; Holland, 1980; Crawford and Abed, 1986; Sousa et al., 1993; Bonnell et al., 1993, 1994). Fibrous structures embedded in materials often provide mechanical strength to the material (e.g. Sastry et al., 1998), and this fibrous network may be responsible for the protective properties of the jelly coat. Here, we examine the forces that act upon eggs during spawning and the role of the fibrous network within the jelly coat in reducing the effects of these forces.

Forces acting on echinoderm eggs during spawning

During spawning, echinoderm eggs pass along the oviduct (Fig. 1), where they experience shear stress (Thomas and Bolton, 1999). After passage along the oviduct, the eggs are released through a rigid gonopore. The forces that eggs experience as they pass through this pore depend on the

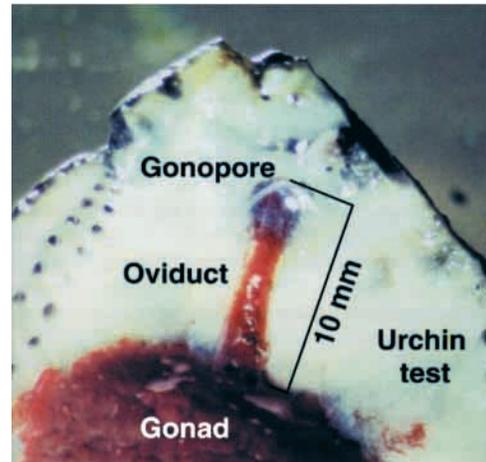


Fig. 1. A single gonad, oviduct and gonopore complex of a female *Arbacia punctulata*.

relative sizes of the egg and the gonopore. In many echinoid species, the diameter of the gonopore is smaller than that of the egg. In these cases, the eggs experience strain in conjunction with shear stress as they are compressed through a relatively narrow gonopore. The magnitude of strain can be estimated by subtracting the gonopore diameter from the egg diameter and dividing by the original diameter of the egg (Table 1). The larger this ratio, the higher the strain imposed on the egg as it passes through the gonopore. This estimate of strain does not include the effect of shearing of the egg surface; it characterizes only the relative strain to which the eggs of various species are subjected during spawning.

Three possible loading conditions can be delineated for echinoderm eggs on the basis of the range of egg and gonopore diameters observed in some echinoid species (Table 1). In the first case, the diameter of the egg is smaller than that of the gonopore, but the diameter of the egg plus jelly coat is larger. Evidence suggests that the jelly coat deforms more readily than the egg (see below). Thus, the coat is preferentially compressed and sheared as it passes through the gonopore (Fig. 2A), preventing the compression of the egg (see below). In the second case, the diameter of the egg is larger than that of the gonopore (Fig. 2B). In this case, the egg itself is compressed and sheared as it passes through the gonopore. In the third case, the diameter of the egg and the jelly coat that surrounds it together are smaller than that of the gonopore (Fig. 2C). Forces acting on the eggs in this case are a result of flow-induced shear

Fig. 2. Possible scenarios for egg/jelly coat compression during passage through the gonopore. (A) When the egg is of smaller diameter than the gonopore, the jelly layer preferentially compresses, reducing the transmission of force to the egg. (B) When the egg is of larger diameter than the gonopore, both the egg and the jelly coat are compressed and sheared. (C) When the egg and jelly coat together are of smaller diameter than the gonopore, the egg is not compressed and experiences only flow-induced shear stress.

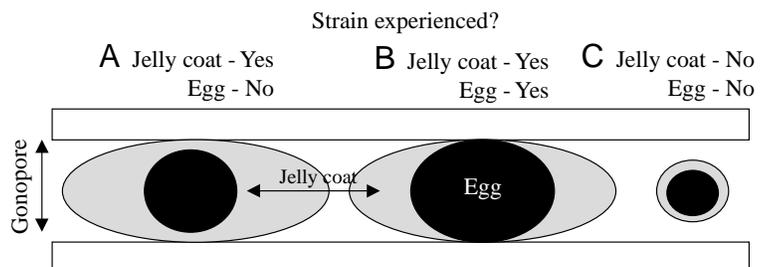


Table 1. Range of gonopore and test diameters and egg diameters for echinoids with both lecithotrophic (L) and planktotrophic (P) development

Family/species	Development mode	Gonopore diameter range (μm)*	Urchin test diameter range (mm)*	Egg diameter (μm)‡	Strain range	Egg/gonopore diameter range
Echinothuroidea						
<i>Aresoma fenestratum</i>	L	200–2400	30–130	1250	0.84–NS	6.25–0.52
Diadematoida						
<i>Diadema antillarum</i>	P	30–1330	10–90	73	0.59–NS	2.43–0.05
Cidaroida						
<i>Phyllacanthus parvispinus</i>	L	50–1570	20–70	500	0.90–NS	10.00–0.32
<i>Phyllacanthus imperialis</i>	L	120–1480	20–60	500	0.76–NS	4.2–0.33
<i>Euclidaris metularia</i>	P	70–480	10–30	90	0.22–NS	1.29–0.19
<i>Euclidaris thouarsi</i>	P	50–950	7–70	86	0.42–NS	1.72–0.09
<i>Prionocidaris baculosa</i>	P	120–670	20–41	150	0.20–NS	1.25–0.22
Echinometridae						
<i>Heliocidaris erythrogramma</i>	L	20–1310	20–100	400	0.95–NS	20.00–0.30
<i>Heliocidaris tuberculata</i>	P	80–1070	20–80	95	0.16–NS	1.19–0.09
<i>Echinometra lucunter</i>	P	30–670	40–50	82	0.63–NS	2.73–0.12
Temnopleuridae						
<i>Holopneustes inflatus</i>	L	40–700	10–40	500	0.92–NS	12.50–0.71
<i>Mespilia globulus</i>	P	40–630	4–40	80	0.50–NS	2.00–0.12
Strongylocentrotidae						
<i>Strongylocentrotus franciscanus</i>	P	160–1880	40–90	130	NS–NS	0.81–0.07
<i>Strongylocentrotus purpuratus</i>	P	110–1850	10–90	80	NS–NS	0.73–0.04

Strain experienced by eggs as they pass through the gonopore is estimated as (egg diameter minus gonopore diameter)/egg diameter. When the eggs are smaller than the gonopore, there is no strain (NS).

Egg/gonopore diameters are calculated as egg diameter/the range of gonopore diameters.

*Data from Emlet, 1989; ‡data from Emlet et al., 1987.

stresses only. These flow-induced shear stresses in the oviduct alone, however, can reach 10–40 Pa (Thomas and Bolton, 1999). These shear stresses will be even higher as the eggs pass through the gonopore, where the channel diameter is at a minimum, but these relatively small eggs will not experience the high shear contact forces that the larger eggs will encounter.

In echinoids, egg size is correlated to developmental type. Species with lecithotrophic development have larger eggs than do those with planktotrophic development (e.g. Emlet et al., 1987). The diameter of the gonopore, however, does not differ to the same extent between these developmental modes (Emlet, 1989). Therefore, it might be expected that lecithotrophic eggs would experience different forces from planktotrophic eggs. Table 1 lists the egg and gonopore dimensions and strain for a number of echinoderm species. Also listed is the ratio of egg to gonopore diameter. This ratio provides an index of the potential for compression of the eggs as they pass through the gonopore. The larger the ratio, the more the egg is compressed and the greater the strain experienced by the eggs during spawning. Comparison of the mean ratios of egg to gonopore diameters for lecithotrophic and planktotrophic species indicates that lecithotrophic eggs experience greater strain than do planktotrophic eggs (mean of the ratio of egg to gonopore

diameter for lecithotrophs 0.44 ± 0.18 to 10.59 ± 6.17 , for planktotrophs 0.11 ± 0.06 to 1.57 ± 0.70 ; means \pm s.d., $N=6$ and 9 , respectively). Further, within some species, the strain experienced by eggs changes as an individual grows. The diameter of the gonopores of echinoids increases linearly as they grow (Emlet, 1989); however, there is no apparent relationship between body size and egg size in echinoids (S. George, unpublished data). Because echinoids become reproductive at a small size (Emlet, 1989), their eggs are exposed to different strain regimes over the course of their development. Assuming that echinoids become reproductive at the time that their gonopores open, it is apparent that the eggs of most of the species examined here are exposed to strain induced by passage through the gonopore during spawning at some stages of their development (Table 1). It is also apparent that the magnitude of this strain differs among species.

Extracellular layers

There has been considerable interest in the roles of jelly coats in echinoderm biology; however, the idea that the jelly coat protects the eggs from shear stress in the oviduct is new (Thomas et al., 1999; Thomas and Bolton, 1999). The jelly coat of at least one echinoid, *Arbacia punctulata*, makes up 3–11 %

(mean 7%) of the total energy provided to the combined egg and jelly coat (Bolton and Thomas, 2000). Within the context of current life history theory (e.g. Emlet et al., 1987; McEdward, 1997), the partitioning of such substantial amounts of finite maternal energy reserves to jelly coats may involve a trade-off in fecundity and/or in the amount of energy partitioned to each egg. Thus, it is likely that there is a significant advantage to reproduction that results from the presence of these complex structures surrounding echinoid eggs.

The jelly coats of echinoderm eggs have been hypothesized to have a number of potential roles in the fertilization process including: (i) reduction of the incidence of polyspermy and cross-fertilization (Hagström, 1956); (ii) induction of the acrosomal reaction (Tilney et al., 1978; SeGall and Lennarz, 1979); (iii) induction of egg-sperm binding (Vaquier and Moy, 1977); (iv) activation and chemotaxis of sperm (Garbers and Kopf, 1980; Nomura and Isaka, 1985); (v) species-specific egg-sperm recognition (Miller and Ax, 1990); and (vi) enlargement of the effective size of the egg thereby, increasing the likelihood of a sperm-egg collision (Epel, 1991; Levitan, 1996).

While jelly coats clearly have important roles in fertilization, they have a very complex structure that is not likely to be important to any of these hypothesized roles. Thus, they may serve an additional role in resisting damage due to forces from shear stress and strain. The complex structure of the jelly coats may be critical to protecting eggs from these forces. The jelly coat surrounding echinoderm eggs is composed of two layers: an outer transparent glycoprotein jelly coat, and an inner vitelline membrane that abuts the plasma membrane of the egg (Kanatani and Nagahama, 1983). The jelly coat is produced prior to spawning and varies in thickness among species (Kanatani and Nagahama, 1983; e.g. 1.5 μm in *Pisaster ochraceus*, 45 μm in *Ctenopleura fisheri*; Chia and Koss, 1994). The jelly coat consists of several concentric layers of complex fibrous networks (Kidd, 1978; Holland, 1980; Crawford and Abed, 1986; Sousa et al., 1993; Bonnell et al., 1993, 1994). The inner layer consists of a dense network of fibers (Kidd, 1978; Bonnell et al., 1994) that are resistant to mechanical and chemical disruption in some species (Kidd, 1978). The middle layer is composed of a network of thicker fibers and is surrounded by a dense outer layer (Kidd, 1978; Crawford and Abed, 1986; Bonnell et al., 1994). These layers are reminiscent of networks that provide mechanical strength to numerous engineering materials (e.g. Sastry et al., 1998).

Fibrous networks and resistance to forces

Fiber-reinforced composites have properties that enable them to withstand and absorb physical stresses better than monolithic materials (e.g. Sastry et al., 1998). Natural structures, such as those found in the echinoderm jelly coat, and cost-effective manufactured systems share an inherent variability in construction. This variability in construction has

important implications for the way in which the fibrous networks within the jelly coat may function. Determining whether the morphology of the jelly coat provides the characteristics required for mechanical stiffness and strength can best be accomplished by comparing the morphology of the jelly coat with that of materials known to provide mechanical reinforcement. Further, statistical simulations that incorporate specific characteristics of reinforcing networks can be compared with the network found within jelly coats.

Comparison of the structure of materials that are known to provide mechanical strength to materials with the structure of the jelly coat provides evidence that the fibrous network within the jelly coat functions to provide mechanical stiffness and strength. First, the general morphology of the fibrous network within the jelly coat is one of fibers (reinforcing phase) that are stiffer than the 'matrix' or continuum phase (jelly), and this network retains its structural integrity under loads that disintegrate the jelly. The repeated washing and centrifuging necessary to separate the components of the jelly coat (Bonnell et al., 1993; A. M. Sastry, personal observation) demonstrates this integrity. Second, the fibrous network within the jelly layer shows considerable connectivity (degree of connections within the fiber network; see figures in Bonnell et al., 1993, 1994). For a reinforcing material appreciably to affect the mechanical properties of a composite, there must be sufficient quantities of the reinforcing phase to allow full connection. Distributed, but unconnected, particles or fibers within a soft material do not provide substantial reinforcement.

The identification of the point at which a particular phase of a composite is present in sufficient quantities to form a network (the percolation point) in a material has been studied extensively and is known as percolation theory. Electronic and thermal conductivity have been used to determine or verify the so-called 'percolation point' in porous materials (Kirkpatrick, 1973; McLachlan, 1988; Ostoja-Starzewski et al., 1994, 1996). The percolation point can be defined as the volume fraction of (conductive or reinforcing) particles within a domain of given size at which a continuous network that spans the domain is likely to arise. Below the percolation point, a conductive or load-bearing phase distributed in a 'matrix' phase will provide very low conductivity or reinforcement for the composite. Above the percolation point, distributed particles that are bonded to one another (as in the cross-linked materials in the jelly coat) provide non-negligible electrical conductivity.

Determination of the conductivity of a network allows its connectivity to be assessed; if the conductivity is non-negligible, it can be deduced that percolation has been achieved. Thus, the conduction studies cited above have provided excellent insight into the percolation statistics of a large class of stochastic fibrous media such as that observed in the echinoid egg jelly coat. The calculation of conductivity in such a network is different from that for mechanical properties (e.g. Cheng et al., 2000; Wang et al., 2000). Calculation of the conductivity, however, provides direct insight into connectivity which, in turn, allows some insight into the mechanical properties even though the mechanical

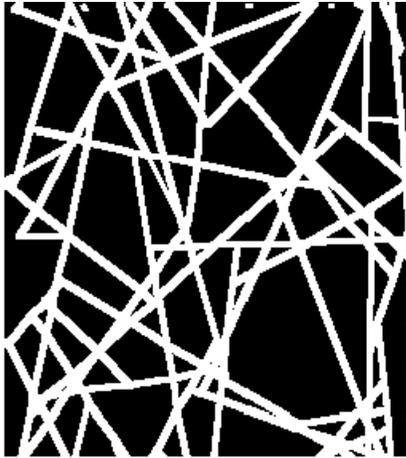


Fig. 3. An example of a simulated fibrous network within a compliant matrix. Note the degree of connectivity and volume fraction of fibers within the matrix. In this simulated network, the volume fraction of the network is 20%, the average fiber length/unit volume is 1.5 and the length:diameter ratio of the fibers is 100.

properties are somewhat more difficult to calculate for these stochastic fibrous materials.

Because of the complexity of irregular arrays, determining the degree of connectivity required for mechanical reinforcement requires the use of micro- or nano-mechanical assumptions (Wang et al., 2000; Wang and Sastry, 2000). In a regular array, the stresses at intersections of phases and the maximum stresses in the array can be calculated exactly and deterministically. Stochastic or statistically defined microstructures, such as those found in the echinoderm jelly coat, must be simulated to determine what the likely range of behaviors will be. Recently, Sastry and co-workers (Sastry et al., 1998; Cheng and Sastry, 1999; Cheng et al., 2000; Wang et al., 2000; Wang and Sastry, 2000) have undertaken a series of statistical investigations on the mechanics of stochastic networks similar to those found in echinoid jelly coats. The fibers in these materials (including substrates for electrochemical applications, human peripheral nerves and reinforcements for polymeric composites) have been modeled using stochastic simulation. Fig. 3 is the result of a statistical simulation of a reinforced composite that has sufficient connectivity to exceed the percolation point (and thus can provide significant mechanical reinforcement). Comparison of this simulation with the structure of the fibrous network within the jelly coat of echinoids (Bonnell et al., 1993, 1994) lends support to the contention that the fibrous network within the jelly coat has sufficient quantities of fibers and enough connectivity to be a reinforcing material.

The jelly coat surrounding echinoid eggs may both reduce the transmission of forces to the egg and protect the egg from the forces to which they are exposed by three possible mechanisms. First, the apparent viscosity of the eggs of echinoids declines as the rate at which they are sheared during spawning increases (Thomas, 1994; Thomas and Bolton,

1999). This reduction in apparent viscosity with increasing shear rate (shear-thinning) may, in part, be due to the structure of the jelly coat because similar materials are known to have a non-Newtonian nature (Fung, 1990). This reduction in viscosity with increasing shear rate, in turn, reduces the shear stress transmitted to the egg during spawning. Second, experimental evidence indicates that the jelly coat preferentially deforms under a compressive load. In an experiment, eggs of the echinoid *Echinometra vanbrunti* were pressed between a mica plate attached to a fine glass rod and a stationary glass plate (see Davidson et al., 1999, for example). As force was applied to the egg with an intact jelly coat the egg experienced little strain until the jelly coat had been compressed 30 μm . At this point the egg began to experience some strain but the jelly coat continued to compress preferentially up to a compression of 60 μm . When the combined egg and jelly coat were compressed 30 μm between the glass plates, the mean deformation of the egg and jelly coat combined was $25.5 \pm 12.2 \mu\text{m}$ (mean \pm s.d., $N=7$). The deformation of the egg within the jelly coat, however, had a mean deformation of $5.7 \pm 4.3 \mu\text{m}$ ($N=7$). Therefore, deformation of the jelly coat accounts for most of the deformation of the egg and jelly coat combined, indicating that the jelly coat preferentially deforms reducing the transmission of the applied force to the egg. Third, the jelly (but not the fibers in the coating) may deform in a nearly viscous manner. In this case, the fibers may serve to provide an elastic 'backbone' to the layer and remain in place to stiffen the outer layer of the egg. The fibers, then, could be assumed to play an important role: their presence serves as a substratum and reinforcement for the jelly coat, which might, in the absence of these fibers, be entirely removed or permanently deformed in the presence of moderate shear forces. This function is the purpose of stiff and viscous or viscoelastic (compliant) material combinations in engineered composites, the mechanical advantages of which are well understood.

Evidence that jelly coats protect eggs

Recent studies indicate that the jelly coat surrounding the eggs of echinoids protects them from the effects of shear stress. Experiments in which the eggs of the echinoid *Lytichinus variegatus*, both with and without a jelly coat, were exposed to shear stresses ranging from 0.3 to 2 Pa show that eggs with jelly coats remained intact and fertilizable at greater shear stresses than those with their coat removed (Thomas et al., 1999). Similarly, when eggs of *Arbacia punctulata* with a jelly coat were exposed to shear stresses up to 2 Pa, 100% of the eggs survived. However, when eggs without a jelly coat were exposed to the same shear stresses, a significant proportion (29%) of the eggs was destroyed (Thomas and Bolton, 1999).

There is also evidence that jelly coats decrease the strain on eggs caused by an external force and increase survival of eggs exposed to such a force. Eggs of the echinoid *Stronglylocentrotus franciscanus* were pressed between a mica plate attached to a fine glass rod and a stationary glass plate

(see Davidson et al., 1999). The rod was calibrated for force applied, and strain on the eggs was measured from captured video images. Strain was calculated for eggs as the initial diameter of the egg (ignoring the jelly coat) minus its final diameter divided by its initial diameter. The strain measured for eggs within jelly coats was significantly (ANOVA, $F=18.46$, $P=0.002$) smaller (0.05 ± 0.04 , mean \pm s.d., $N=7$) than that of eggs without jelly coats (0.14 ± 0.04 , mean \pm s.d., $N=9$). Furthermore, 100% of the eggs with a jelly coat survived compression, whereas approximately 50% of the eggs without a jelly coat were destroyed when subjected to the same force. These results strongly suggest that the jelly coat surrounding echinoid eggs can protect them both from shear stresses resulting from flow-induced shear during spawning and from strain resulting from the compressive forces experienced when large eggs pass through a small gonopore.

Concluding remarks

When echinoderm eggs are spawned, they are exposed to shear stress in the oviduct and gonopore and may be exposed to strain depending on the relative size of the egg and gonopore (Table 1). These forces differ among species because of the relative dimensions of the eggs and the gonopores and because egg viscosity differs among species (Thomas, 1994; Thomas and Bolton, 1999). The forces experienced by eggs within a species also change as the size of the gonopore changes with growth. The shear stresses estimated for eggs within the oviduct are higher than those shown to cause damage to eggs that have had their jelly coat experimentally removed (Thomas et al., 1999; Thomas and Bolton, 1999). This potential for egg damage may be an important selective pressure for traits that may reduce damage to eggs passing through the oviduct/gonopore complex. Evidence suggests that the jelly coats play a role in protecting eggs from shear forces (Thomas et al., 1999; Thomas and Bolton, 1999) and strain imposed by compression as they pass through the gonopore. Given the range of shear and compressive forces experienced by echinoderm eggs, it is possible that the characteristics of jelly coats may vary among species in ways that correlate with forces experienced by eggs during spawning.

For example, shear-thinning (a decrease in viscosity with increasing shear rate) of the eggs decreases the shear stress experienced in the oviduct of echinoderms during spawning (Thomas, 1994; Thomas and Bolton, 1999). In the absence of shear-thinning, the shear stress experienced by eggs can be 10^3 – 10^5 times higher than that experienced when eggs shear-thin. The mechanisms responsible for shear-thinning of echinoderm eggs are not known. A comparative analysis may indicate that the characteristics of the jelly coat correlate with viscosity and with the resultant shear stresses and compressive forces experienced by eggs during spawning.

The structure of the jelly coat has been characterized for some species (Bonnell et al., 1993, 1994); however, specific characteristics of the fiber network that could explain the functional role of the network in protecting eggs have not been

recorded. Characteristics of interest include the size, angles of attachment and density of fibers within the jelly matrix, all of which affect the distribution of forces within fiber-reinforced materials (e.g. Sastry et al., 1993). Also, specific characteristics of the attachment between the egg and the jelly coat could prove interesting with regard to the distribution and transmission of shear and compressive forces. An engineering analysis within a comparative biological approach could provide supporting evidence for the hypothesis that the fiber network within jelly coats functions to reduce the forces experienced by eggs during spawning.

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