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A review of the effects of environmental stress on embryonic development within intertidal gastropod egg masses

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Abstract

Gastropod egg masses are often deposited in the intertidal zone, where they are exposed to variable and often stressful environmental conditions that may affect the encapsulated embryonic development and survival of offspring. The present paper reviews data on developmental variation in gastropod egg masses owing to temperature, salinity, ultraviolet radiation (UVR) and oxygen availability. In general, increases in temperature or oxygen availability accelerate development, whereas UVR or extremes of salinity and temperature slow development and/or increase embryonic mortality. The relationships among these factors are discussed, as are their interactions with biotic factors, such as fouling, embryonic position within the egg mass and predation. One purpose of the present review is to raise awareness of these interactions so they become a focus for future research. Protective mechanisms of egg masses against environmental stresses are also reviewed.

Additional keywords: mollusc, oxygen availability, reproduction, salinity, temperature, ultraviolet radiation.

Introduction

Intertidal organisms face a variety of selective challenges while reproducing. They must protect their offspring against the environmental extremes of the intertidal zone, as well as against risks of predation and infection. Many gastropods have adapted to these challenges by laying their eggs in benthic masses. Although gastropod egg masses include a striking array of varied structures, they can be divided into two general categories: capsular and gelatinous, as defined below (see Figs 1,2).

Benthic egg masses are believed to provide protection to the developing embryos from environmental stresses and predation (Thorson 1950; Pechenik 1979; Strathmann 1985). Nevertheless, environmental factors still affect embryonic development, sometimes deleteriously. Gastropod intracapsular embryonic development and mortality may be influenced by temperature, salinity, ultraviolet radiation (UVR), oxygen availability, water flow, fouling, embryonic position, predation and parental history. These factors do not usually operate independently (Fig. 3) and, consequently, confounding relationships should be considered when studying embryonic development within gastropod egg masses. Once it is known how embryos react to certain environmental factors, it may be possible to predict their response to the associated local and global environmental events, such as thermal fluctuations and the thinning ozone layer.

Previous reviews have been written about gastropod egg masses, but discussion relating to benthic egg masses is typically ancillary to theoretical discussion of general reproductive patterns (e.g. Thorson 1950; Gallardo and Perron 1982). Other reviews cover potential protective mechanisms of egg masses, but they do not focus on the effects of environmental stresses on the embryos within (e.g. Pechenik 1979; Eyster 1986; Rawlings 1999). Still other reviews on gastropod egg masses are confined to one geographic region (e.g.

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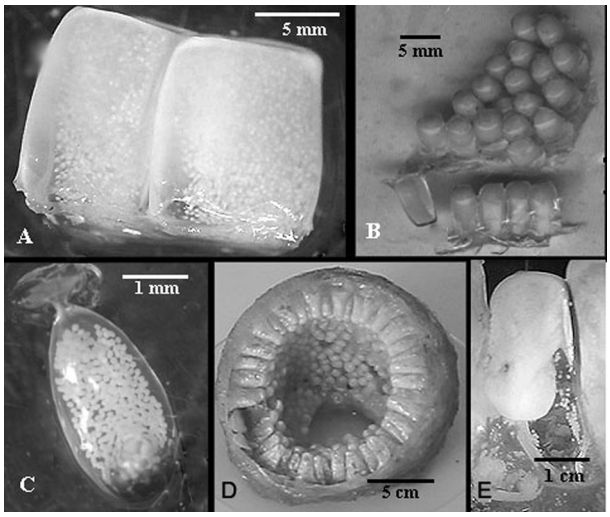

Fig. 1. Morphological variation in capsular caenogastropod egg masses collected along the Illawarra coastline, NSW. (*a*) *Dicathais orbita* capsules with swimming veligers. (*b*) Part of *Ranella australasia* egg mass. (*c*) *Mitra carbonaria* capsule containing trocophores. (*d*) Intact *Cabestena spenglerii* egg mass consisting of numerous capsules removed from brooding adult. (*e*) *C. spenglerii* capsule with only a few discrete eggs. The rest of the eggs have degenerated into a solid mass near the top of the capsule following exposure to sunlight.

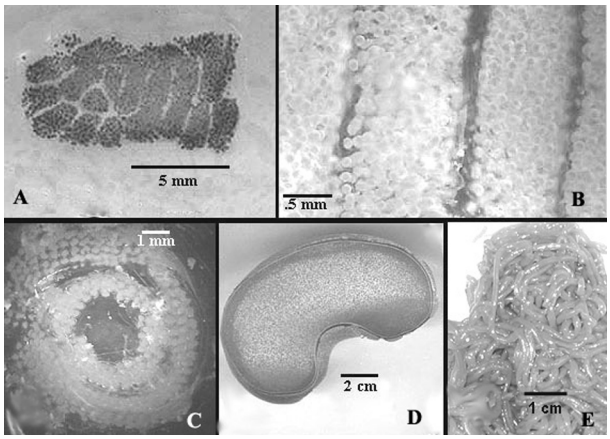

Fig. 2. Gelatinous egg masses collected along the Illawarra coastline, NSW. (*a*) *Bembicium nanum* egg mass with varying embryonic development. Peripheral embryos are more developed than central embryos as evidenced by their darker more developed shells. (*b*) *Dolabrifera brazieri* egg mass with veligers. (*c*) *Rostanga arbutus* egg mass with undeveloped eggs. (*d*) *Polinices (Conuber)* spp. egg mass. (*e*) *Dolabella auricularia* egg mass.

Strathmann 1987). Upon examination of the literature, very few studies were found that considered more than one environmental factor at a time (Table 1). Thus, there is a fundamental gap in our understanding of how confounding or interdependent environmental factors influence embryonic development in gastropod egg masses. The primary purpose of the present review is to consolidate available research about abiotic effects on gastropod egg mass development and to examine the complex relationships between abiotic factors, embryonic development and biotic factors, such as predation, fouling and embryonic position. It is hoped that this will help promote and guide future multifactorial research on embryonic development and mortality.

Egg mass structure and phylogeny

Because the structure and composition of egg masses are related to their phylogeny, it is necessary to clarify the taxonomic stance adopted in the present paper. In this review, gastropod classification will follow Beesley *et al*. (1998) (Table 2). Capsular egg masses are found among the Neritopsina and some Caenogastropoda (Fig. 1; Table 2). Gelatinous

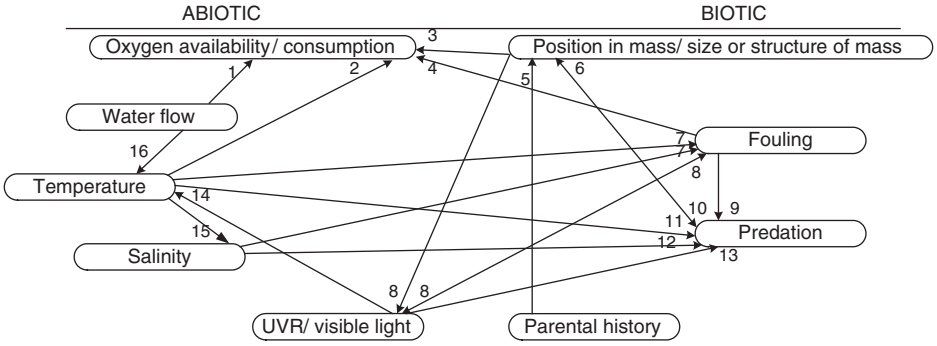

Fig. 3. Interactions of abiotic and biotic variables that can affect embryonic development within gastropod egg masses. The relationships illustrated are by no means ubiquitous or exhaustive. Rather, each arrow represents a potential relationship that has been identified in at least one study: 1, Kranenbarg *et al*. (2001); 2, Woods (1999); 3, Chaffee and Strathmann (1984); 4, Cohen and Strathmann (1996); Clark and Goetzfried (1978); 5, personal observation; 7, Lee and Kim (2002); 8, Biermann *et al*. 1992; 9, Laudien and Wahl (1999); 10, Rawlings (1990); 11, Sanford (1999); 12, McClanahan (1992); 13, Williamson *et al*. (1999); 14, Wissmann (2003); 15, personal observation; 16, Sabo *et al*. (1999). A single arrow indicates a relationship in which one variable affects the other. A double arrow indicates a relationship in which both variables affect each other.

masses are found among the Heterobranchia (Fig. 2*b*–*d*) and among some Caenogastropoda (Fig. 2*a*,*d*; Table 2). Some vetigastropods encase their eggs in jelly masses, although these often lack the organisation of heterobranch egg masses (Hickman 1992).

Capsular egg masses of many caenogastropods consist of multiple distinct capsules often connected to one another by a common basal layer (Fig. 1*b*,*d*). The often tough leathery capsule wall characteristic of neogastropods is composed of several structurally and chemically distinct layers (Tamarin and Carriker 1967; LeBoeuf 1971), sometimes sealed with an apical plug (Sullivan and Bonar 1985). Eggs and embryos are located inside the capsule walls, where they develop within intracapsular fluid (Bayne 1968). Some species use non-viable eggs called nurse eggs to nourish developing embryos (Gallardo and Perron 1982; Hoagland 1986). Neritid capsules have a calcareous apical capsule wall made with particles from a specialised crystal sac (D'Asaro 1986) and, thus, differ from caenogastropod egg capsules. Despite the fact that *Nerita atramentosa* is one of the most common snails on the rocky shore of south-eastern Australia, there is no published research to date examining the effects of environmental stresses on embryos of neritid egg capsules. Regrettably, they will not be discussed any further in the present review other than to note that such research would be interesting because neritid capsules are often deposited high on the shore (R. Przeslawski, personal observations).

Gelatinous egg masses consist of a jelly matrix in which many eggs are embedded (Fig. 2). A microscopic vitelline capsule surrounds each egg or small group of eggs (Eyster 1986; Klussmann-Kolb and Wägele 2001; Fig. 2). Some species lay egg masses that are a variation on the typical gelatinous egg mass structure. Naticid sand collars, for example, comprise adherent sand grains in addition to a gelatinous matrix in which microscopic capsules and embryos are embedded (Giglioli 1955). Other taxa, such as some Amphibolids, also incorporate relatively large amounts of sand into their egg masses (Benkendorff 1999; Pechenik *et al*. 2003). Unlike capsular masses, gelatinous masses ensure that embryos are isolated from other embryos within a mass by their surrounding

Table 1. Experiments on the developmental effects of various factors on encapsulated marine gastropod development

Reference	*n*	Abiotic					Biotic		
		Temperature	Salinity	UV	O_2/flow	Position	Foul	Parental history	Predation
Ganaros (1958)	1	x							
Thompson (1958)	1	x							
Scheltema (1965)	1		x						
Scheltema (1967)	1	x							
Hagerman (1970)	1								
Spight (1975)	1	x							
Switzer-Dunlap and Hadfield (1977)	4	x							
Pechenik (1978)	2				x				
Dehnel and Kong (1979)	1	x							
Pechenik (1982)	3		x						
Pechenik (1983)	1		x						
Chaffee and Strathmann (1984)	2								
Rose (1986)	1	x	x						
Roller and Stickle (1989)	1	x	x						
Rawlings (1990)	1								x
Rodriguez *et al.* (1991)	1	x							
Biermann *et al.* (1992)	1			x		x	x		
Palmer (1994)	1	x							
Booth (1995)	1				x	x			
Strathmann and Strathmann (1995)	3				x	x			
Cohen and Strathmann (1996)	2			x	x	x	x		
Rawlings (1996)	1			x					
Richmond and Woodin (1996)	1		x						
Woods and DeSilets (1997)	1		x						
Carefoot *et al.* (1998)	1			x					
Podolsky *et al.* (1998)	1	x							
Cancino *et al.* (2000)	1				x				
Podolsky (2000)	1	x							
Pechenik *et al.* (2003)	1	x	x		x				
Przeslawski *et al.* 2004	23			x					

n, Number of mollusc species studied; position, embryonic position; foul, algal or microfaunal fouling; history, parental history. An 'x' denotes a variable examined in the listed study.

Table 2. Orthogastropod classification system and corresponding egg mass type that occurs in at least some species within each group (Beesley *et al.* 1998)
First tier of classification is superorder followed by order/superfamily and family. Species listed are representative of some egg masses commonly found in south-east Australia (Benkendorff 1999; R. Przeslawski, personal observations)

Taxa	Egg mass type	SE NSW representative species
Vetigastropoda		
Trochoidea	Gelatinous, capsules[1]	
Neritopsina		
Neritoidea	Capsule	*Nerita atramentosa*
Caenogastropoda		
Sorbeoconchia		
Campaniloidea	Gelatinous	
Cerithioidea	Gelatinous, capsules[2]	
Hypogastropoda		
Littorinimorpha	Gelatinous, capsule	*Bembicium nanum*, *Cabestana spengleri*
Neogastropoda	Capsule	*Dicathais orbita*, *Mitra carbonaria*
Heterobranchia		
Architectonicoidea	Gelatinous	
Pyramidelloidea	Gelatinous	
Rissoelloidea	Capsule	
Cephalaspidea	Gelatinous	*Bullina lineata*, *Hydatina physis*
Sacoglossa	Gelatinous	*Oxynoe viridis*, *Elysia australis*
Anaspidea	Gelatinous	*Aplysia* sp., *Bursatella leachii*
Notaspidea	Gelatinous	*Pleurobranchus* sp., *Berthellina citrina*
Thecosomata	Gelatinous	
Gymnosomata	Gelatinous	
Nudibranchia	Gelatinous	
Doridina	Gelatinous	*Dendrodoris nigra*, *Rostanga arbutus*
Dendronotina	Gelatinous	*Melibe australis*
Arminina	Gelatinous	
Aeolidina	Gelatinous	*Austraeolis ornata*, *Spurilla macleayi*
Basommatophora	Gelatinous	*Siphonaria* sp., *Salinator* sp.

[1]Trochoideans have various modes of reproduction; only a few species lay benthic egg masses (Hickman 1992).
[2]Some species of Cerithioidea are viviparous.

vitelline capsule. It is likely that many embryos receive their nutrition from intracapsular fluid (Moran 1999), whereas others receive nutrition from yolk granules or sacs associated with the egg mass (Clark and Goetzfried 1978; Williams 1980; Boucher 1983).

Among gastropod egg masses, considerable variation can occur in the number of eggs per capsule (Grant 1983; Strathmann 1985), egg and embryo size (Strathmann 1977; Christiansen and Fenchel 1979) and colour (D'Asaro 1966; Switzer-Dunlap and Hadfield 1977), as well as the shape and size of the egg mass (Hurst 1967; Chambers and McQuaid 1994). Although at least some of this variation occurs among individuals of the same species (Eyster 1979), there are only a very few studies that examine how much of this variation is due to environmental effects (e.g. Thompson 1958; Hagerman 1970; Cheung 1997). Thus, it can be difficult to determine the difference between intrinsic variation and environmental effects on gastropod egg masses. The present review considers variation in embryonic development.

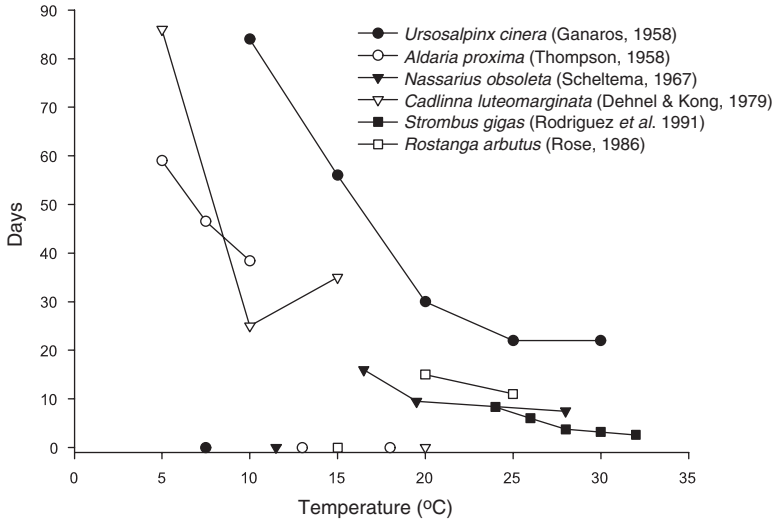

Fig. 4. The effects of temperature on developmental rate in benthic gastropod egg masses according to available literature. Unconnected symbols resting on the *x*-axis represent egg masses that did not hatch at the specified temperature. At 10°C, *Urosalpinx cinera* took longer than the experimental period of 84 days to hatch. The values for *Strombus gigas* were obtained using calculations performed by Rodriguez *et al*. (1991) as they did not present raw data.

Terminology

For clarity and consistency, 'egg' will refer to anything before the blastomere stage, including unfertilised eggs. Developing young will be referred to as 'embryos' until they leave the capsule (Giese and Pearse 1974). As accepted in most previous research, 'capsule' will describe both the rigid layered wall in capsular masses, as well as the vitelline membrane surrounding embryos in gelatinous egg masses. 'Egg mass' will refer to the entire discrete gelatinous mass or capsule group in one site. In the case of species that lay among spawning aggregations (e.g. many *Aplysia* or neogastropods), this definition could include ribbons or capsules from several individuals deposited in the same mass. 'Dead' and 'dying embryos' will include seriously deformed immobile embryos and embryos showing tissue damage or loose debris within an internal capsule (Woods and DeSilets 1997; Fig. 1*e*).

Temperature

Within tolerable temperature ranges for each species, the encapsulation period generally decreases as temperature increases for many invertebrates (Rothlisberg 1979; Boucher 1983; Rumrill 1990), including molluscs (Kress 1975; O'Dor *et al*. 1982; Palmer 1994; Caveriviere *et al*. 1999; Fig. 4). For gastropod embryos within capsular egg masses, it has even been suggested that hatching time can be estimated knowing only the taxon and the temperature (Spight 1975; Palmer 1994). This, however, assumes that all other variables discussed in the present paper are static or do not significantly affect the embryonic developmental rate. In addition, predicting hatching time based solely on taxon and temperature may be problematic owing to potential geographic or temporal variation in temperature compensation. This has been observed, for example, in the muricid *Nucella*

emarginata (Deshayes, 1839), with Alaskan populations hatching in significantly less time at temperatures 10°C lower than British Columbian populations (Palmer 1994).

Embryos become stressed and often die if exposed to extreme temperatures relative to their natural environment (Fig. 4) and seem more vulnerable to temperature extremes than adults. Thompson (1958), for example, found that the adult nudibranch *Adalaria proxima* (Alder & Hancock, 1854) spawned and remained healthy at a relatively high 13°C, but this temperature was lethal to eggs. Despite vulnerability to both high and low temperature extremes (Fig. 4), gastropod embryos may be more tolerant of lower temperatures within their range than higher temperatures. Struhsaker and Costlow (1969) found that planktotrophic larvae of *Littorina picta* had a high survival rate at temperatures lower than their established optimal developmental temperatures, but the larvae had lower survival rates at temperatures higher than optimal conditions. Similar observations have been made on encapsulated gastropod embryos. For example, Dehnel and Kong (1979) examined the effects of temperature on the egg masses of the nudibranch *Cadlinna luteomarginata* (MacFarland, 1966) along the coast of British Columbia and found the hatching time was fourfold faster at 15°C than at 5°C, although there was no difference in overall hatching success. However, at 20°C, the average summer temperature, embryos degenerated by the fourth cleavage stage (Fig. 4). Thus, the embryos of this species seemed much more tolerant of lower temperatures than higher temperatures within their natural thermal range, but because the egg masses used in the study were collected in winter, it is possible that they were better adapted to cold than those laid in the summer. Indeed, Dehnel and Kong (1979) do not specify whether this population even lays in the summer months or whether the egg masses persist into the spring and summer. Nevertheless, my own preliminary observations on south-eastern Australian gastropods are consistent with the suggestion that embryos of both gelatinous and capsular egg masses are more tolerant of low than high temperature extremes.

Although there is a lethal low and high temperature for gastropod embryos (Fig. 4), some embryos are able to protect against high temperatures to a certain extent. Recent research has revealed the presence of heat shock proteins inside the gelatinous egg masses of the cephalaspid *Melanochlamys diomedea* (Bergh, 1894) (Podolsky and Hoffmann 1998; Podolsky 2000). These proteins allow embryos to withstand high temperatures, such as those reached during low tide on a summer day, by preventing the degradation of proteins during heat stress and facilitating the refolding of proteins. These thermally protective proteins develop as the embryos mature (Podolsky and Hoffmann 1998). Thus, undeveloped embryos are especially vulnerable to high temperatures and they become less vulnerable to temperature extremes as they develop (Thorson 1950). It is presently unknown whether egg masses of other species contain thermally protective proteins.

Low temperatures can affect embryonic development by prolonging or halting it. Scheltema (1967) found that the embryonic development of the neogastropod *Ilyanassa obsoleta* (Say, 1822) slowed significantly as the temperature dropped (Fig. 4). The embryos ceased development at the lower threshold of the species' temperature range. However, these embryos remained viable for up to 9 weeks of exposure and continued development when returned to their normal temperature. Similarly, Ganaros (1958) found that embryos of the muricid *Urosalpinx cinerea* (Say, 1822) remained viable after being subjected to sub-freezing temperatures and, if only exposed for a short period, they recovered and developed fully. However, the embryonic mortality rate increased as exposure time to cold water increased. No similar studies have been conducted on embryos of gelatinous egg masses.

Strathmann and Chaffee (1984) point out that lower temperatures decrease embryonic metabolic rates, thus resulting in slower development. In addition, they suggest that lower temperatures could decrease intracapsular fluid viscosity and diffusion rates, thereby decreasing oxygen availability to the embryos (Fig. 3). However, as metabolic rate slows, the demand for oxygen will also decrease; thus, the effects of less oxygen availability may be negligible in light of lower embryonic metabolism. Further research is needed to determine causes and effects of changes in oxygen availability, temperature, metabolic rates and developmental rates, because these are likely to be interdependent factors.

The available literature presents dissenting views about whether temperature is the primary developmental regulator in certain gastropod populations. It has been suggested that although temperature often influences the speed of development, oxygen availability is the primary factor controlling the encapsulated development of embryos (Cancino *et al*. 2003). Furthermore, Clarke (1982) notes that many Antarctic marine invertebrates have very slow embryonic development, but suggests that this is not necessarily due to the extreme low temperatures. Rather, molluscs that have evolved in the Antarctic show temperature compensation and should not be subject to slow embryonic developmental rates due to low temperatures. Clarke (1982) suggests that, instead, it is the large egg size that results in the slow development of Antarctic invertebrate embryos. However, it is difficult to examine separately the effects of low temperature and large egg size in the field in polar regions because they often occur concurrently. In contrast, other studies suggest that temperature is the primary variable that controls the embryonic developmental rate (Spight 1975; Hoegh-Guldberg and Pearse 1995). It is unlikely that the relationship between temperature and egg size will be resolved until comparative experimental research is conducted, preferably on a species capable of producing eggs of different sizes (e.g. Jones *et al*. 1996) or a broad range of species with the same larval hatching type that produce eggs of different sizes (Clark and Goetzfried 1978).

Despite the obvious effect of temperature on gastropod developmental rate, some researchers fail to present adequate temperature data when reporting hatching times of egg masses (e.g. Govindan and Natarajan 1974; Pilkington 1974; Creese 1980). If the temperature is unknown, the developmental rate data are essentially useless. Therefore, it is imperative that all researchers reporting hatching times of gastropod egg masses monitor or control the temperature (e.g. Hurst 1967; Rose 1985; Chung *et al*. 2002).

Temperature is bound to several other abiotic and biotic factors that affect gastropod embryonic development (Fig. 3). First, the seawater temperature of intertidal pools or other still water is higher in sunlight than in shade. Therefore, it can become difficult to separate the effects of UVR and temperature in the field. The effects of UVR and sunlight on temperature are easily controlled in an artificial seawater system where temperature can be kept independent of light. Furthermore, UVR and temperature significantly interact to cause coral zooxanthellae expulsion (Wissmann 2003), as well as to affect the growth of intertidal algae (Hoffmann *et al*. 2003). No such studies examining the potentially synergistic effects of temperature and UVR have been conducted on gastropod egg masses.

The position of embryos within a mass may also influence their reaction to temperature stress. Embryos in the centre of a large mass are better protected from short-term environmental changes than embryos located peripherally (Strathmann and Hess 1999). In addition, temperature may directly affect predation (Sanford 1999) and microalgal fouling (Lee and Kim 2002). Furthermore, embryonic tolerance to temperature may be linked to salinity (Pechenik *et al*. 2003). Rose (1986) found that embryos of the nudibranch *Rostanga arbutus* (Angas, 1864) show the widest temperature tolerance at an intermediate salinity of

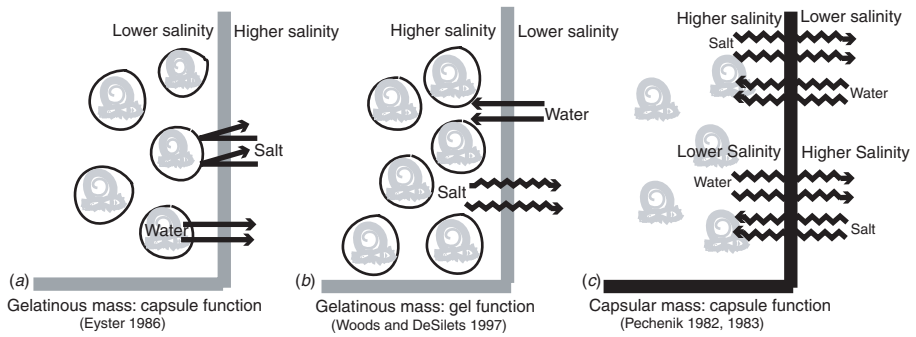

Fig. 5. The embryonic protection afforded by capsular and gelatinous egg mass structures to changes in salinty. A zig-zag line means the rate of movement is decreased, but the overall magnitude of change is slight. Mechanisms illustrated are based on research from listed references. (*a*) Function of vitelline capsules within gelatinous egg masses. (*b*) Function of gelatinous matrix. (*c*) Function of capsule walls in neogastropod egg masses.

34 p.p.t. Finally, higher temperatures have been associated with increased oxygen availability and consumption within egg masses (Roller and Stickle 1989; Woods 1999). All these factors should be considered when examining the effects of temperature on gastropod embryonic development.

Salinity

As with temperature, salinity extremes can affect embryonic mortality in egg masses. As salinity deviates from that within a species' normal habitat, the mortality of gastropod embryos increases (Struhsaker and Costlow 1969; Pechenik 1982; Woods and DeSilets 1997). However, as embryos develop they seem to become more tolerant to a wider range of salinities (Struhsaker and Costlow 1969; Pechenik 1983; Richmond and Woodin 1996). Thus, developing embryos vulnerable to salinity changes may require the protection of the egg capsule or associated gel matrix. Scheltema (1965) did not notice any significant differences between the levels of salinity that proved lethal to adults and hatched veligers of *Ilyanassa obsoleta*. It is possible that embryos of some species, particularly those in estuarine habitats, like *I. obsoleta*, use the protection of an egg capsule against salinity changes only during early development. Unfortunately, there is no comparable research among gelatinous egg masses and further research comparing the response of embryos, juveniles and adults is needed for both capsular and gelatinous egg masses.

Embryos within gelatinous egg masses do seem to be protected to some degree against salinity changes by both their vitelline capsules and the gelatinous matrix. In a detailed study of nudibranch capsules, Eyster (1986) examined the vitelline capsule structure in relation to salinity. She found that the capsule walls inhibit the passage of large molecules, including salts (Fig. 5*a*). She also noted that the capsules retain full structural integrity for the duration of encapsulation. However, embryos within the capsules were still vulnerable to high salinities owing to water efflux (Fig. 5*a*). Woods and DeSilets (1997) conducted similar experiments on the gelatinous matrix of *Melanochlamys diomedea* egg masses collected in areas subjected to periodic freshwater influx. They separated some embryonic capsules from the surrounding gel and exposed these to various test salinities. The gel improved survival only in very low salinity conditions by slowing the rate of salt efflux (Fig. 5*b*). The embryos themselves were equally tolerant to high salinities, regardless of the

presence of surrounding gel. Pechenik *et al*. (2003) similarly found that the embryos of the estuarine pulmonate *Amphibola crenata* (Gmelin 1791) were tolerant to extremely low salinities. The gelatinous egg collar itself showed no protective function to salinity changes, but tolerance was a property of the surrounding egg capsule or the embryos themselves. Further research examining both vitelline capsules and gelatinous matrices would likely reveal a combined protection of embryos against salinity changes that varied among species. These studies would be worthwhile on species that lay their egg masses in small intertidal pools, where salinity can reach high levels during low tide. Egg masses of such species may provide more effective protection against high salinities rather than low salinities. Indeed, a study comparing species that spawn in potentially high-salinity environments with estuarine species may reveal interesting adaptive differences to the extremes of low and high salinity.

In contrast with vitelline capsules within gelatinous masses, the much larger leathery capsules of some neogastropods are permeable to both NaCl and water, although this permeability may vary among species within a genus (Pechenik 1982; Fig. 5*c*). Despite this apparent lack of protection against salinity changes, encapsulated embryos were found to have a significantly higher tolerance to salinity changes than embryos removed prematurely from the egg capsule (Pechenik 1983). Thus, the higher tolerance of encapsulated embryos to salinity stress is likely a result of capsule wall function. The capsules probably reduce the rate of salinity change, despite not protecting against the magnitude of change (Pechenik 1982, 1983). So far, these studies have been restricted to the genus *Nucella* (Table 2). Research on different species would provide a more general understanding of the role of neogastropod egg capsules in providing protection from salinity fluctuations. Furthermore, the potential function of intracapsular fluid and other capsular contents in protection against changes in salinity remains unexplored.

In addition to embryonic mortality, salinity may also affect developmental rate. Rose (1986) observed that *Rostanga arbutus* embryos reared in 40 p.p.t. seawater developed more slowly than embryos reared in 34 p.p.t. seawater at the same temperature. Low salinities have also been shown to prolong embryonic development in other opisthobranchs, the sacoglossan *Elysia viridis* (Montagu, 1804) (Hagerman 1970) and three species of *Doto* (Kress 1975). Reasons for this are unknown, but may be due to the association between salinity and embryonic oxygen consumption rates, although this has only been documented on capsular egg masses (Roller and Stickle 1989).

Salinity is directly affected by temperature, with higher temperatures often leading to increased salinity through evapouration in small intertidal pools (R. Przeslawski, personal observations). Salinity itself affects some biotic factors that can influence gastropod embryonic development (Fig. 3). Salinity can influence the abundance and diversity of predators. As salinity deviates from normal conditions in a particular environment, the number of predators can decrease (McClanahan 1992). Similarly, salinity can affect the abundance and diversity of potential fouling microorganisms (Kocak and Kucuksezgin 2000; Lee and Kim 2002). Moreover, temperature may influence the effect of salinity changes on embryos. For example, Pechenik *et al*. (2003) found a significant interaction between salinity and temperature on the developmental rate and hatching success of *Amphibola crenata*.

Ultraviolet radiation

Ultraviolet radiation, especially UV-B, is deleterious to many organisms (Karanas *et al*. 1981; Wood 1987; Bothwell *et al*. 1994). Among gastropod egg masses, exposure to UVR

can stunt development, produce deformities and cause death (Biermann *et al*. 1992; Rawlings 1996; Carefoot *et al*. 1998). The severity of the effects of UVR may depend upon the age of the embryos. Biermann *et al*. (1992) exposed fresh and mature egg masses of the nudibranch *Archidoris montereyensis* (MacFarland, 1966) to sunlight and found the rates of embryonic mortality and deformity were significantly less in the mature egg ribbons. However, the previous history of the mature egg masses was unknown. It is therefore possible other variables contributed to the mortality difference among fresh and mature egg masses. Although the developmental risk is probably greatest during cleavage and early embryo development, UVR still poses a serious risk to embryos for the duration of their encapsulation.

The most logical protection against UVR exposure is for the adults to lay egg masses under boulders or in other areas shielded from sunlight. Spawning under boulders may also protect egg masses against desiccation, predation and high temperatures. Benkendorff and Davis (2002) have found that over half the molluscs depositing egg masses on intertidal reefs around Wollongong (NSW, Australia) exclusively attached them to the undersides of boulders. Other taxa occasionally lay in areas exposed to UVR, such as *Aplysia* species (Przeslawski *et al*. 2004). Indeed, certain molluscs, such as some *Siphonaria* species, lay exclusively in habitats exposed to full sunlight (Creese 1980; Benkendorff and Davis 2002). The vulnerability to and protection against UVR of certain amphibians is species specific (Blaustein *et al*. 1994), and even population specific (Belden and Blaustein 2002). Recent work among gastropod egg masses has also revealed species-specific UVR vulnerability. Przeslawski *et al*. (2004) have found that egg masses of species that lay exclusively in shaded habitats are very vulnerable to the harmful effects of UVR, whereas those that lay consistently in UVR-exposed habitats are not.

It has been suggested that species that regularly lay in UVR-exposed environments possess structural or chemical protection against UVR (Biermann *et al*. 1992). One possibility is that the egg masses are biochemically protected through UV-absorbing compounds. Ultraviolet-radiation-absorbing compounds, such as mycosporine-like amino acids (MAAs), have been identified recently in many marine organisms (reviewed by Shick and Dunlap 2002), including pelagic invertebrate eggs (Epel *et al*. 1999). It is generally accepted that marine animals obtain these MAAs from their diet or symbiosis with algae because animals lack the biochemical pathway to synthesise MAAs (Stochaj *et al*. 1994; Mason *et al*. 1998; Shick *et al*. 1999). With only a few exceptions discussed below, it is unknown whether gastropod egg masses contain UV-absorbing compounds.

To date, no MAAs or other UV-absorbing compounds have been found in capsular egg masses, although only those of the neogastoprods *Trophon* cf. *geversianus* (Pallas, 1774) and *Nucella emarginata* have been examined (Karentz *et al*. 1991; Rawlings 1996). Karentz *et al*. (1991) surveyed a broad range of marine Antarctic organisms, including a capsular egg mass from the neogastropod *Trophon* cf. *geversianus* and a gelatinous egg ribbon from the vetigastropod *Margarella antarctica* (Lamy, 1905), and found that 90% of all organisms contained MAAs. Whereas most organisms contained a substantial concentration of a variety of MAAs, the two gastropod egg masses examined showed little or no sign of MAAs, despite their presence in the adults. Unfortunately, the authors do not specify whether the egg masses were collected from shaded or sunny habitats. Rawlings (1996) attempted to extract MAAs from capsules of the neogastropod *Nucella emarginata*, but without success. However, only the capsule walls were tested for MAAs, not the intracapsular fluid or embryos. Rawlings (1996) did, however, conclusively show that the

outer capsule wall absorbed UVR, particularly UV-B. Thus, embryos within the leathery capsule may have no need for the additional protection of MAAs.

In contrast with the experiments mentioned above, Carefoot *et al*. (1998) found that the gelatinous egg masses of *Aplysia dactylomela* (Rang, 1828) were rich in MAAs, but adult diet determined their presence. *Aplysia* species lay their egg masses both under boulders and in areas exposed to sunlight, so the presence of MAAs may be an evolved protective mechanism rather than a coincidental dietary benefit. It would be worthwhile to conduct similar experiments on gastropods with different laying habitats, particularly those that lay exclusively in environments exposed to UVR, to determine whether the presence of MAA in egg masses is an evolved protection (Cockell and Knowland 1999).

The effects of UVR on gastropod egg masses are potentially confounded with several other factors (Fig. 3), such as the placement of embryos within the egg mass. In gelatinous egg masses, where the embryos have a fixed position, the surrounding gel and embryos near the top can act as a shield for the inner embryos (Biermann *et al*. 1992). In addition, the water depth at which the egg masses occur could influence UVR penetration. Significant amounts of UV-B can be transmitted through 5–10 m water, whereas biologically harmful UVR can penetrate more than 20 m below the surface (Karentz and Lutze 1990; Booth and Morrow 1997). The penetration of UVR in seawater also depends on water clarity and, thus, UVR and the transmission of visible light can vary among regions at a similar depths depending on the amount of sediment, phytoplankton and dissolved solutes (Shooter *et al*. 1998). Exposure to UVR can also be affected by surface fouling on the egg mass. Algal fouling is greater in sunlight and it has been suggested that such a covering over the egg mass could significantly shield the embryos within from UVR (Biermann *et al*. 1992). Like salinity and temperature, UVR and associated visible light directly affect microalgal fouling (Biermann *et al*. 1992) and predation (Williamson *et al*. 1999). As mentioned previously, UVR can also interact significantly with temperature (Hoffmann *et al*. 2003; Wissmann 2003) and the effects of this potential relationship need to be investigated on gastropod egg masses.

Oxygen availability

Oxygen availability can dramatically influence the development of embryos within egg masses. In a series of experiments, Strathmann and Strathmann (1995) demonstrated that oxygen limited embryonic development within gelatinous opisthobranch egg masses. They found that embryos of three species showed arrested development during hypoxia until they were returned to a normal oxygen level. Furthermore, lower oxygen availability throughout the development period reduced shell length at hatching. These observations have recently been supported in the capsular egg masses of *Chorus giganteus* (Lesson, 1829) (Cancino *et al*. 2003).

The direct effects of oxygen availability on gastropod embryo development are usually not studied independently but, rather, are used to explain the effects of other environmental factors. Oxygen availability within egg masses is inextricably linked to water flow, embryonic position within the egg mass and fouling (Fig. 3).

Among gelatinous egg masses, flowing water accelerates the rate of embryonic development by decreasing hatching time and increasing embryo activity (Eyster 1986) because it most likely increases the overall oxygen supply to the mass through diffusion (Strathmann and Hess 1999). Chaffee and Strathmann (1984) found that flowing water decreases asynchronous development within a spherical gelatinous mass, whereas still water promotes relatively high developmental variation. The same study found no effect of

still water on development among elongated gelatinous ribbons. Biermann *et al*. (1992) also found a significant interaction between water flow and egg mass thickness. There was no difference in embryonic developmental rates between egg ribbons maintained in still water and those exposed to a strong current; but, when the thin ribbons of the egg masses were layered, forming a thicker structure, there was a noticeable developmental retardation in still water. Therefore, it is likely that the shape of the egg mass determines, in part, the developmental effects of oxygen availability as controlled by water flow (Kranenbarg *et al*. 2001). There has been no similar research into the combined effects of oxygen availability, water flow and egg mass structure on the development of embryos within capsular egg masses.

The effects of desiccation on embryonic oxygen availability have not yet been studied in detail. Many intertidal gastropod egg masses can tolerate brief periods of desiccation (Strathmann 1987) and some species are desiccated daily in the intertidal zone during low tides (D'Asaro 1970; Benkendorff 1999; R. Przeslawski, personal observations). However, if the egg masses are allowed to dry out for more than several hours, the embryos within will die (Creese 1980; Spight 1977). The intertidal capsules of *Ilyanassa obsoleta* were no more effective protecting against desiccation than the capsules of a subtidal nassariid (Pechenik 1978). It is not known why certain egg masses are laid consistently in areas regularly subject to desiccation. Pechenik *et al*. (2003) found that pulmonate embryos in a sandy gelatinous egg mass hatched faster if they were exposed to air for a few hours a day and suggested that this reflected the greater oxygen availability in the air-exposed egg masses, although this has yet to be tested. If air exposure does, indeed, decrease the encapsulation period, then this may outweigh the potential risks associated with desiccation.

The placement of the embryos within the egg mass also influences embryonic oxygen availability. Many neogastropods deposit their egg capsules in a clump and the capsules near the periphery will generally develop faster than the central capsules (R. Przeslawski, personal observations). This trend is even more accentuated in gelatinous masses (Fig. 2*a*). Because embryos in a capsular mass are free to move within a relatively large chamber (D'Asaro 1986; Fig. 1), their position within the capsule changes constantly and oxygen supply is relatively uniform for most embryos within a capsule (Strathmann and Chaffee 1984). However, eggs and embryos of gelatinous masses are fixed in one location within the whole mass (Hurst 1967; Switzer-Dunlap and Hadfield 1977; Fig. 2). Embryos located within the central region of a gelatinous egg mass frequently show arrested or retarded development compared with embryos located peripherally (Chaffee and Strathmann 1984; Biermann *et al*. 1992; Lee and Strathmann 1998; Fig. 2*a*), which is associated with lower oxygen availability (Strathmann and Strathmann 1995). The egg masses of several species are normally hypoxic in central locations (Cohen and Strathmann 1996; Woods 1999). As a result, central embryos can be more developmentally dependent on environmental factors like water flow and algal fouling, whereas those at the periphery are more vulnerable to other environmental conditions, such as desiccation and extremes in temperature and salinity.

Although many selective pressures exist to reduce the period of encapsulation (Havenhand 1993), the benefits of the delayed development of centrally located embryos may outweigh the risks of slower development. A large egg mass with varying developmental rates can contribute to populations by releasing viable embryos from the mass over a period of days and even weeks (Gibson and Fu-Shiang 1994). With this bet-hedging strategy, veligers within one mass are exposed to a variety of conditions at

hatching. Chances for optimal conditions for at least some veligers are maximised. An extreme example of centrally retarded development is the naticid mud snail *Conuber sordidus* (Swainson, 1821), which lays its eggs in a large sausage-shaped jelly (Smith *et al*. 1989; Fig. 2*d*). Although the majority of the eggs are embedded near the outer surface, a large number of eggs exist throughout the entire mass. Because the egg mass is so large, the centrally located eggs are exposed to severe hypoxia and their development is arrested (Booth 1995). However, as the numerous peripheral embryos hatch, the gel surrounding them degrades and the oxygen available to the central region increases, enabling continued development of the internal embryos. Thus, a single egg mass can release viable veligers over a period of weeks depending on temperature (Booth 1995; R. Przeslawski, personal observations).

In addition to embryonic position, algal and microfaunal fouling can also have an effect on embryonic development by modifying oxygen availability. Algae alter the internal oxygen concentration of egg masses by producing oxygen in daylight and consuming oxygen at night (Strathmann 2000). By regulating the oxygen availability within egg masses, algal photosynthesis and metabolism may stabilise oxygen conditions in the egg mass, thereby controlling embryonic developmental rates (Cohen and Strathmann 1996). A study of amphibian eggs found that egg masses contained a green algae specific to amphibian eggs that increased oxygen availability to the embryos (Pinder and Friet 1994). No similar studies on potential symbiotic associations between algae and gastropod egg masses have been conducted.

Despite potential benefits to gastropod embryonic development, algae also promote protist and bacterial growth (Fogg 1983). Unlike algae, these organisms do not produce oxygen; in fact, they deplete available oxygen through respiration (Cohen and Strathmann 1996). Bacteria and fungi have been shown to be deleterious to gastropod larval development (Struhsaker and Costlow 1969, Biermann *et al*. 1992), although later developmental stages may be less susceptible (Struhsaker and Costlow 1969). It is not known whether the deleterious effects observed were due to hypoxia or to a byproduct of the fouling organisms. A more conclusive study was undertaken by Cancino *et al*. (2000), in which the oxygen availability to embryos of the muricid *Chorus giganteus* was reduced by sessile protozoa that fouled some egg capsules. The protozoa decreased oxygen tension and the embryos within fouled capsules not only had a much longer hatching time, but they also showed marked impairment of shell growth.

Certain egg masses are not vulnerable to heavy algal fouling owing to the laying behaviour of the adult. Because sunlight is necessary for algae to flourish, the risk of fouling is low when an egg mass is laid under boulders. Moreover, some egg masses hatch in a few days and are not heavily fouled owing to this short development period. It is not known whether gastropod egg masses contain any biochemical protection against algal fouling.

Similarly, gastropod egg masses may also provide protection against bacterial fouling and infection. Benkendorff *et al*. (2001) have reported antimicrobial properties in both capsular and gelatinous egg masses of 39 species of molluscs. In contrast, Pechenik *et al*. (1984) did not find any antibiotic properties in the intracapsular fluid of *Nucella lapillus* (Linnaeus, 1758) capsules, although this result should be interpreted cautiously because there were limitations in the methods used to test for antimicrobial activity (Benkendorff *et al*. 2000*a*). In addition, Pechenik *et al*. (1984) do not indicate the age of the capsules examined. Because chemical ripening has recently been found to occur in related species (Benkendorff *et al*. 2000*b*), active compounds may have decomposed in mature or stressed egg capsules.

Oxygen availability and consumption may also be interdependent with several abiotic factors (Fig. 3). Although oxygen availability is affected by temperature (Green and Carrit 1967), Cancino *et al*. (2003) found no significant interaction between temperature and oxygen availability on the encapsulated development of *Chorus giganteus.* Further research on capsular and gelatinous egg masses examining the potential relationship between oxygen availability and temperature would help clarify any interactions. Another study revealed a significant interaction between temperature and salinity on embryonic oxygen consumption (Roller and Stickle 1989). Temperature and salinity most likely affect oxygen consumption by affecting the health and metabolism of the embryos, as well as influencing the rates of oxygen diffusion.

Discussion

Gastropod egg masses are often exposed to a wide variety of environmental conditions in the intertidal regions in which they are commonly laid. These environmental factors affect embryonic development and mortality, but they are not themselves independent of each other. The present paper has reviewed abiotic factors affecting gastropod embryonic development and mortality: temperature, salinity, oxygen availability and UVR. In addition, relationships among these factors and their interactions with biotic factors were explored (Fig. 1).

Despite recent advances in our understanding of gastropod egg mass structure and development, there are still large gaps in our knowledge. First and foremost, fundamental structural and developmental data are still needed for the egg masses of many gastropods. Although North American and European species have been studied relatively frequently (e.g. Strathmann 1987) and several comprehensive studies have examined the egg mass structure of some Australasian taxa (Pilkington 1974; Rose 1985), details about the egg masses and embryos of many species remain unknown. In addition, possible egg mass or capsule changes over time have not been examined for most species. Without basic structural and developmental knowledge, there is no foundation for comparisons of the effects of environmental effects on egg mass development.

The majority of studies pertaining to environmental effects on gastropod egg mass development examine only one variable at a time (Table 1). There is, of course, nothing wrong with this approach and it can provide valuable information as long as other potential factors influencing development are controlled or are negligible. However, a multifactorial approach can reveal the relationships among factors that control embryonic development and mortality. This can be accomplished using various treatment combinations of two or more factors (e.g. Pechenik *et al*. 2003). Whenever possible, researchers should couple laboratory based experiments with field measurements of the factors examined and *in situ* developmental data of encapsulated gastropod embryos. This will ensure the relevance of laboratory studies and allow researchers to better interpret findings in the field.

Understanding the complex relationships among some of these factors will further our understanding of gastropod development in their natural environment. The present review has only discussed the potential effects of biotic variables on gastropod embryonic development in relation to their interactions with abiotic variables. There are still relatively few studies on the direct effects of biotic variables on gastropod egg mass development (Table 1), and future research should aim to clarify the interactions between abiotic and biotic factors that affect gastropod embryonic development (Fig. 3).

Comparisons of the developmental effects of various environmental factors on capsular and gelatinous masses are needed to better understand the differences among taxa regarding

vulnerability and possible protection of egg masses against harmful environmental factors (e.g. Przeslawski *et al*. 2004). Such studies could have interesting implications for evolutionary divergences of certain groups of gastropods through comparative examinations of structural adaptations of egg masses. Within the context of the present review, capsular egg masses were represented exclusively by caenogastropods, whereas gelatinous egg masses, with one exception (Booth 1995), were heterobranchs. Although egg mass structure and phylogeny are closely related, there are enough exceptions (see Table 2) so that future research should attempt to distinguish the effects of phylogeny from egg mass structure. Further comparative research on the effects of environmental stresses on gelatinous caenogastropod, capsular caenogastropod, and heterobranch egg masses may help separate the effects of environmental stresses based on phylogeny or structure.

Finally, further research on a range of species is necessary in order to determine possible relationships among various gastropod groups and populations. Struhsaker and Costlow (1969) state that the tolerance of embryos to changes in conditions like salinity may be contingent on the stability of the environment in which the adults are normally found. Thus, larvae in a subtidal tropical region with stable conditions would be expected to be less tolerant of environmental changes compared with larvae in an intertidal temperate region experiencing abrupt salinity and temperature changes. This hypothesis remains largely untested because researchers have yet to study empirically the effects of environmental stability on egg mass tolerance to environmental stresses. Such studies could provide valuable developmental information on a broad geographical range of species while identifying the vulnerabilities and tolerances of gastropod embryos.

Tolerance to environmental stress by encapsulated gastropod embryos may also depend on the zone of the shore in which they occur. Rawlings (1999) has suggested that intertidal egg masses may be no more effective in protecting against environmental stresses than subtidal egg masses, but this has yet to be tested. Studies comparing the developmental effects of environmental stresses between intertidal and subtidal egg masses may reveal habitat-specific adaptations important to intertidal ecological research. Regardless of the results, such studies would lead to examination of an evolutionary basis for intertidal spawning. For example, Spight (1977) found that *Thais lamellosa* showed no preference for intertidal spawning habitats, such as tidepools with reduced physical stresses, and that they often deposited their egg capsules in habitats where embryonic mortality was relatively high. Spight (1977) suggested that this may be due to higher site quality for other life stages, which outweighed the embryonic costs. Although several studies have explored the adaptations of egg masses to intertidal environmental stresses (reviewed by Pechenik 1978; Rawlings 1999), there is a severe lack of knowledge pertaining to the evolutionary advantages associated with egg mass deposition in this habitat. Species may deposit egg masses in the intertidal zone to minimise encapsulation period, reduce predation or fouling, or vary larval dispersal; however, this remains speculative. Survival advantages must exist to counteract the risks associated with spawning in such a physiologically hostile environment, but these are not necessarily the same for all taxa. With proper multifactorial experiments on a range of gastropod species, we can further understand the complex effects of intertidal environmental stresses on encapsulated gastropod development.

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