ROLE OF ENCAPSULATION IN INVERTEBRATE LIFE HISTORIES

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Many marine invertebrates encapsulate their embryos. Encapsulation is particularly common among polychaetes and gastropods and may take the form of gelatinous egg masses or firm, leathery egg capsules (Thorson 1946). Such structures are generally considered to be “protective” (e.g., Carriker 1955; Davis 1974; Gibbs 1968; Hunt 1966; Jägersten 1972; Mileikovsky 1971; Shuto 1974; Sverdrup et al. 1942), but what they protect against is uncertain. Individuals that emerge from capsules and egg masses as crawling juveniles clearly avoid predation in the plankton and the mortality potentially associated with dispersal away from favorable areas during development (Hendler and Franz 1971). Sverdrup et al. (1942, p. 317) suggested that egg masses and “protective” capsules function to decrease “loss from excessive dispersal and other hazards of a floating existence during the period of incubation.” The egg masses of the polychaete Scoloplos armiger and the gastropod Retusa canaliculata are thought to function by retaining embryos in an environment favorable to their continued development (Chapman 1965; Gibbs 1968; Wells and Wells 1962).

However, many invertebrate species emerge from their egg capsules or egg masses as swimming larvae which subsequently spend many weeks feeding and growing in the plankton before metamorphosing to the benthos (Thorson 1946, 1950). The veligers of at least some tropical gastropods may spend many months in the plankton after escaping from their egg capsules, long enough, in fact, to be dispersed across the Atlantic Ocean (Scheltema 1971). I refer to such a reproductive pattern as “mixed” development, since it incorporates aspects of both direct and pelagic developments (Mileikovsky 1971), but is ecologically distinct from either of these two developmental categories.

Gastropod egg capsules and egg masses, in particular, are structurally and chemically complex (Bayne 1968; Flower et al. 1969; Fretter 1941; Gibson et al. 1970; Hunt 1966, 1971; Tamarin and Carriker 1967), and formation of gastropod egg capsules has required especially great morphological, physiological, and often behavioral specializations in adults (Fretter 1941; Fretter and Graham 1962; Giglioli 1955). The energy expenditure associated with encapsulation appears high

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<table>
<thead>
<tr>
<th>Group</th>
<th>Location Studied</th>
<th>No. Species Considered</th>
<th>Percent with Mixed Development</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gastropoda</td>
<td>Denmark</td>
<td>54</td>
<td>63</td>
<td>Thorson 1946</td>
</tr>
<tr>
<td>Gastropoda</td>
<td>England</td>
<td>97</td>
<td>45</td>
<td>Fretter and Graham 1962</td>
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<td>Gastropoda</td>
<td>Hawaii</td>
<td>31</td>
<td>97</td>
<td>Ostergaard 1950</td>
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<tr>
<td>Prosobranch gastropods</td>
<td>South Florida,</td>
<td>18</td>
<td>50</td>
<td>D'Asaro 1970</td>
</tr>
<tr>
<td></td>
<td>Bahamas</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Opisthobranch gastropods</td>
<td>Washington</td>
<td>30</td>
<td>100</td>
<td>Hurst 1967</td>
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<tr>
<td>Mesogastropoda</td>
<td>Caribbean</td>
<td>24</td>
<td>71</td>
<td>Bandel 1975</td>
</tr>
<tr>
<td>Prosobranch gastropods</td>
<td>New Zealand</td>
<td>25</td>
<td>60</td>
<td>Pilkington 1974</td>
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</tbody>
</table>
as well (Stickle 1973), which further suggests that encapsulation must have substantial survival value even in mixed life histories.

The primary function of egg capsules and jelly masses in mixed life histories can not be to limit dispersal of developmental stages, nor does encapsulation protect against other dangers of planktonic development. This paper will consider the survival advantages associated with the short period of encapsulation in mixed developments. Many of the arguments given here also apply to life histories in which a long-swimming larval stage follows a period of brooding by the adult.

MIXED DEVELOPMENT

Mixed development occurs primarily in four phyla of invertebrates. Among the molluscs, mixed development is prominent in the Gastropoda. Table 1 summarizes data from some of the major surveys of gastropod reproduction, all of which included at least 15 species whose developments were determined with certainty. This type of life history is especially prominent in opisthobranchs. Within the Prosobranchia, mixed development is most common among mesogastropods, but is also encountered within the Archaeogastropoda (e.g., *Neritina layardi*, Govindan and Natarajan 1972) and Neogastropoda (e.g., *Nassarius obsoletus*, Scheltema 1962).

Within the Polychaeta, mixed development is characteristic of the Spionidae (Blake 1969; Hannerz 1956), and is found sporadically in other polychaete families including the Polynoidae (Thorson 1946), Phyllodocidae (Thorson 1946), Orbiniidae (Gibbs 1968), Capitellidae (Gibbs 1968), Dorvelleidae (Åkesson 1973), Onuphidae (Costello and Henley 1971) and Nereidae (Read 1974).

Finally, the embryos of most nemerteans and some turbellarians initiate development within gelatinous egg masses and subsequently exhibit a freeswimming larval stage of long duration (Hyman 1959; Thorson 1946).

By definition, members of a species with mixed development spend only a portion of their prejuvenile period encapsulated. In some species this period of encapsulation represents less than 10% of the total prejuvenile development (table 2). Most larvae of benthic marine invertebrates are capable of delaying their metamorphosis in the absence of an appropriate substrate (Crisp 1974), thus prolonging their stay in the plankton and further decreasing the relative time spent encapsulated.

*Survival Advantages of Mixed Development*

Most encapsulated embryos can be raised successfully after their artificial removal from the incubating structure (Costello and Henley 1971), demonstrating that encapsulation is usually not obligate. Although the capsules of some species may serve to confine the developing embryos with an external food source in the form of nurse eggs, many encapsulated species lack nurse eggs (Fretter and Graham 1962; Thorson 1946, 1950).

Boekhout and Horn (1949) suggested that the egg-mass jelly of the polychaete *Axiotella mucosa* may serve as a culture medium for diatoms which can then be used as a food source by developing embryos, but "there is no evidence that the
<table>
<thead>
<tr>
<th>Species</th>
<th>Prehatch Development (days)</th>
<th>Planktonic Development (days)</th>
<th>Percent Planktonic</th>
<th>Reference</th>
</tr>
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<tr>
<td><em>Polydora ciliata</em> (P)</td>
<td>5</td>
<td>14–28</td>
<td>74–85</td>
<td>Hannerz 1956; Wilson 1928; Darr and Polk 1973</td>
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<td><em>Nassarius obsoletus</em> (G)</td>
<td>10</td>
<td>21</td>
<td>67</td>
<td>Scheltema 1967</td>
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<tr>
<td><em>Aeolidiella glauca</em></td>
<td>11</td>
<td>36</td>
<td>77</td>
<td>Hadfield 1963</td>
</tr>
<tr>
<td><em>Hydrobia ulvae</em> (G)</td>
<td>10</td>
<td>28</td>
<td>74</td>
<td>Pilkington 1971; Fish &amp; Fish 1977</td>
</tr>
<tr>
<td><em>Polinices variegata</em> (G)</td>
<td>8–10</td>
<td>25–64</td>
<td>71–89</td>
<td>Dacey 1965; Hanks 1960; Scheltema 1971</td>
</tr>
<tr>
<td><em>Charonia variegata</em> (G)</td>
<td>42–56*</td>
<td>219</td>
<td>80–84</td>
<td>Scheltema 1971</td>
</tr>
</tbody>
</table>

**Note.**—Data are based on laboratory observations. The duration of planktonic existence listed in the table does not include the period during which larvae can delay metamorphosis. P = Polychaeta, G = Gastropoda.
* Data from congeneric species, *C. tritonis* (Berg 1971).
laying of eggs in cocoons confers any nutritive advantage' (Chapman 1965, p. 195). Egg-mass jelly itself appears to be of little nutritional value to developing embryos (Chapman 1965; Gibbs 1968). Thorson (1950) suggested that egg capsules may protect embryos against bacterial and protozoan attack. This suggestion has never been tested directly, although some evidence against this hypothesis is presented below.

Some authors have suggested that intertidal egg capsules and egg masses protect embryos against desiccation (e.g., Fretter and Graham 1962; Houbrick 1973), but the limited evidence available indicates that encapsulation does not prevent substantial desiccation-induced mortality of gastropods developing in the intertidal zone (Pechenik 1978; Spight 1977). Thorson (1946) and Skoog (1973) surmised that egg masses might protect embryos from salinity changes. However, Gibbs (1968) has shown that egg masses of the polychaete *Scoloplos armiger* do not protect the enclosed embryos from osmotic fluctuations in the surrounding medium. Similarly, egg capsules of marine gastropods are believed to be permeable to both water and salts (Fretter and Graham 1962).

Gibbs (1968) suggested that the egg masses of *S. armiger* protect against predation. Carricker (1955) suggested a similar function for oyster drill egg capsules (*Urosalpinx cinerea*), and Gravier (1923) suggested this as the general function of all polychaete egg masses. However, the jelly masses of the polychaetes *Diopatra cuprea*, *Arenicola marina*, and *Axiothella mucosa* fail to protect embryos from predation by the gastropod *Nassarius vibex* (Hurst 1965), and egg capsules of the gastropod *Anachis avara* have been recovered from the guts of the ophiuroid *Ophioderma brevispinum* (G. Hendler, Smithsonian Oceanographic Sorting Center, personal communication). MacKenzie (1961) notes that 19%–42% of all *Eupleura caudata* egg capsules found in the field have been torn open by predators. The contents of egg capsules of *Thais lamellosa* and *Colus stimponi* are also accessible to predators (Spight 1975; West 1973), and the gastropod *Calliotoma annulatum* has been observed ingesting nudibranch egg masses (Perron 1975). Egg masses of the sea hare *Tethys Californicus* are preyed upon by starfish (MacGinitie 1934). Egg capsules of prosobranch mollusks in general are subject to predation by fish, crustaceans, polychaetes, and other prosobranch gastropods (D'Asaro 1970; MacKenzie 1961).

Other possible sources of the presumed survival advantage associated with encapsulation in mixed developments are suggested by a simple probability argument. Let \( P(D) \) be the probability of death on any given day in the plankton and let \( P(S) \) represent the probability of daily survival, so that \( P(S) + P(D) = 1 \). Assume that \( N \) days must pass between the time of egg laying and the entrance of juveniles into the benthos. The probability of mortality during \( N \) days of planktonic development is \( P(M) \), and

\[
P(M) = P(D) + P(S)P(D) + [P(S)]^2P(D) + \cdots + [P(S)]^{N-1}P(D).
\]

Now suppose that the embryos are enclosed in a capsule for a period of \( X \) days, during which time the probability of mortality is assumed to be negligible. If \( P(D) \) is unchanged,

\[
P(M') = P(D) + P(S)P(D) + [P(S)]^2P(D) + \cdots + [P(S)]^{N-X-1}P(D).
\]
Fig. 1.—Theoretical relationship between daily mortality rate and the survival advantage associated with 7 days of encapsulation \((X = 7)\) in a mixed development. Number adjacent to each point is total probability of death, \(P(M)\), during a free-swimming development of \(N\) days. Solid circle represents \(P(D) = .01\); open circle represents \(P(D) = .05\); solid triangle represents \(P(D) = .10\); open triangle represents \(P(D) = .25\).

The percent change in mortality accruing from \(X\) days of encapsulation is: 
\[
\frac{[P(M) - P(M')]}{P(M)} \times 100\%.
\]

For \(P(D) = 0.50\), \(P(M)\) and \(P(M')\) are nearly identical for most values of \(N\) and \(X\). If \(N\) is 21 days and \(X\) is 7 days of encapsulation, for instance, \(P(M') = 0.99999956\) and \(P(M) = 0.999999963\). The change in mortality is 0.000044%. Whether or not such small differences in mortality are biologically meaningful cannot be assessed. However, the benefits of encapsulation increase greatly as the daily probability of death, \(P(D)\), is allowed to decrease (fig. 1). For example, the "model" indicates that if \(P(D) = 0.05\), the total probability of death during 35 days in the plankton is 93.4%. Mortality is reduced by about 8% if the species spends the first 7 days of its development within an egg capsule or egg mass. The survival advantage conferred by a 7-day period of encapsulation declines slowly as the total developmental period becomes longer, but is still substantial when \(N = 100\) days if daily mortality rates are sufficiently low (fig. 1). Thus, if daily planktonic mortality rates for larvae are not too high, encapsulation can be shown to have substantial survival value even in a mixed life cycle.

The above argument assumes negligible prehatching mortality. As discussed earlier, this assumption may not be valid, especially for intertidal capsules. For such capsules, a particular great survival advantage must be associated with mixed development to offset the costs associated with exposure to intertidal stresses.
The argument also assumes that $P(D)$ is constant throughout development to the free-living benthic juvenile stage. If, however, $P(D)$ decreases with time (i.e., if the probability of survival in the plankton is greater for larvae than for embryos), short-term enclosure of the embryos further increases the probability of successful development to settlement. In comparison with embryos, larvae might be less susceptible to planktonic mortality if larvae display (1) reduced susceptibility to bacterial and protozoan attack, (2) greater tolerance of environmental fluctuations, and/or (3) reduced susceptibility to predation. These possibilities will be considered in order.

Present evidence indicates no decrease in susceptibility to microbial attack with increasing age for crustaceans and bivalve mollusks (e.g., Atkins 1954; Davis et al. 1954; Guillard 1959; Johnson 1960; Tubiash et al. 1970). Moreover, the egg capsules of the gastropod _U. cinerea_ are ineffective in preventing fungal attack upon the enclosed embryos (Ganaras 1957). Nudibranch jelly masses also fail to prevent bacterial and protozoan infestation (Hadfield 1963), as do the egg masses of the Cerithiiidae (Houbrick 1973), _Polydora_ spp. (Blake 1969), and _Limacina helicina_ (Paranjape 1968).

If early developmental stages are more traumatized by environmental stresses than are later stages, encapsulation could have an obvious survival advantage. Encapsulation would retain embryos in the parental habitat until they were better able to cope with conditions potentially encountered after being swept away. A substantial literature exists on salinity and temperature tolerances of marine invertebrates and their developmental stages, but few workers separate embryonic tolerances from those of the larvae; many fail to investigate prelarval tolerances at all. However, whereas the larvae of _Crassostrea virginica_ are more tolerant of pH changes and lowered salinities than are the embryos (Calabrese and Davis 1970; Davis and Calabrese 1964), early _Crassostrea virginica_ embryos tolerate a wider range of temperatures than do the larvae (Davis and Calabrese 1964). Although the embryonic stage of _Mercenaria mercenaria_ shows greater sensitivity to no. 2 fuel oil than does the larval stage during a 48-h test period (Byrne and Calder 1977), embryos of _N. obsoletus_ are more tolerant of no. 2 fuel oil than are the larvae (Pechenk, unpublished). No generalizations can be made. Yet, even if tolerances to environmental fluctuations generally improve during development, it is unlikely that the environmental changes that might be experienced by free-living embryos of _N. obsoletus_, for example, would be more drastic than the environmental stresses they are potentially exposed to by being encapsulated in the intertidal zone (Pechenk 1978).

There is no firm support for the first two mechanisms potentially leading to reduced developmental mortality. However, arguments can be advanced to support the hypothesis of differential predation pressure on planktonic embryos and larvae. Passive embryos might be exposed to higher predation pressure than active larvae of the same species simply because of their smaller size and possibly greater vulnerability to planktonic predators. Data on developmental mortality rates in the plankton must be accumulated before this possibility can be evaluated.

A second argument can be made for differential predation pressure on free-living embryos and larvae by considering the relative safety of the planktonic and
benthic habitats. Invertebrate eggs and embryos are generally incapable of keeping themselves off the bottom; there are few reports of positively-buoyant marine invertebrate zygotes. Free-living prelarval stages are therefore potentially exposed to an entire set of predators that larvae easily avoid during their planktonic existence.

Although planktonic predation is most certainly high, "'enemies on the bottom are generally more abundant'" (Carriker 1961, p. 234). Thorson (1966) called attention to a tremendous array of small benthic predators. Among the major meiofaunal predators upon settling developmental stages, he listed turbellarians, harpacticoid copepods, and foraminifera. In addition, he considered deposit feeders such as Echinocardium and omnivores such as Cancer and Pagurus to be important sources of benthic mortality. Activities of filter feeders have been widely cited as potential sources of larval mortality (e.g., Carriker 1951, 1961; Thorson 1966). Indeed, the photopositive swimming behavior exhibited by larvae of many invertebrate species after hatching may be an adaptation for quickly removing larvae from the "vicinity of benthic filter feeders which might engulf them" (Crisp 1974, p. 186).

Although the impact of the benthos on mortality rates of free-living developmental stages has never been quantified, the potential impact is great. Sellmer (1967) reported 79% mortality of juvenile Gemma gemma during the first month after their liberation into the benthos. Thorson's data (1966) indicate a mortality of at least 98.4% of all settled spat before they have attained a size sufficient to be collected by a 2 mm sieve, and Ayers (1956) suggested a 99% mortality of postlarval Mya arenaria before the attainment of sexual competency. MacGinitie (1934) suggested that predation by the benthos at settlement accounts for most of the mortality occurring during the development of species with free-swimming larvae.

The possibility of differential predation by the benthos on freeliving larval and prelarval stages thus provides another possible explanation for the widespread occurrence of mixed development among marine invertebrates. Limited periods of brooding and encapsulation may increase the probability of survival during development simply by retaining developmental stages until they are capable of actively staying away from the bottom. The production of planktonic egg capsules by species of the gastropod genus Littorina is consistent with this hypothesis. Most pelagic egg capsules produced by Littorina spp. contain only one or a few eggs each (Borkowski 1971; Fretter and Graham 1962; Thorson 1946), minimizing capsule sinking rates (Linke 1933 cited by Lebour 1937). The egg capsule of Littorina littorea appears particularly well designed for maintaining embryos in surface waters (Lebour 1937; Thorson 1946). The ridges present on the fertilization membrane produced by the echinoderm Comanthus japonica are believed to serve this same function (Holland 1977).

The hypothesis of differential vulnerability to benthic predation is viable only if free-living developmental stages are safer in the plankton than they would be if in contact with the benthos. Much additional information on embryonic, larval, and juvenile mortality rates of benthic marine invertebrates and on the sources of developmental mortality needs to be accumulated before the benefits of encapsulation in mixed developments can be fully understood.
ROLE OF ENCAPSULATION

SUMMARY

Many benthic marine invertebrate species have mixed life histories, in which larvae emerge into the plankton to continue their development after a relatively short period of encapsulation. In such cases, the benefits of encapsulation are not obvious and are considered here. A simple probability argument is constructed which suggests that even a short period of encapsulation can significantly reduce mortality during mixed development if daily mortality rates in the plankton are below some critical level. Survival benefits of even short periods of encapsulation would be augmented further if free-living larvae were less susceptible to mortality than were free-living embryos. Encapsulation may reduce developmental mortality in mixed life cycles simply by retaining developmental stages until they are better able to avoid planktonic and benthic predation.

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LITERATURE CITED


