

DETACHMENT OF EGG MASSES OF A POLYCHAETE: ENVIRONMENTAL RISKS OF BENTHIC PROTECTIVE DEVELOPMENT¹

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Abstract. Females of the maldanid polychaete *Axiiothella mucosa* attach gelatinous egg masses to the surface openings of their vertical tubes. This study assessed the risks to the embryos due to environmental stresses. In Florida, embryonic development takes 7–8 d, after which the embryos crawl free from the egg mass and assume a benthic existence. Contrary to earlier suggestions, diatoms growing within and on the egg masses do not contribute significantly to embryonic nutrition. By marking cohorts of egg masses, it was shown that most egg masses become detached from the parental tube before natural release of the juveniles. A caging experiment established that water currents, rather than predators or other biological disturbances, are the cause of detachment. Detached egg masses often become abraded, resulting in the early release of embryos; prematurely released embryos showed significant reductions in survivorship relative to late-stage embryos released artificially. On average, detached egg masses produced less than half the number of juveniles released from egg masses that developed entirely in the laboratory in the absence of environmental stresses and from egg masses that remained attached in the field to the parental tubes. Thus, physical factors that cause detachment impose a significant reduction in the number of juveniles released. Encapsulation of embryos does not guarantee high survivorship of those offspring.

Key words: *Axiiothella*; *benthos*; *egg mass*; *Florida*; *life history theory*; *polychaete*; *reproductive tactics*.

INTRODUCTION

Many marine benthic invertebrates sequester their embryos for some or all of embryonic development in egg capsules or other encapsulating structures. Encapsulation is posited to be advantageous in protecting eggs or embryos from planktonic predation (Vance 1973a, b, Pechenik 1979), preventing dispersal from favorable habitats (Chapman 1965, Gibbs 1968), and protecting eggs and embryos from environmental stresses (Krishnamoorthi 1951, 1963). The advantages of encapsulation are mitigated by the energetic costs of producing the encapsulating structures (Perron 1981), energy which could otherwise be shunted into increased fecundity. In addition, there is a suite of risks that affect the success of benthic protective development. Egg capsules are subject to predation from a variety of invertebrates (MacKenzie 1961, Haydock 1964, Glynn 1965, Emlen 1966, Phillips 1969, Spight 1977), although all of the reported data deal with the leathery capsules of prosobranch gastropods. A second class of risks, which has received considerably less attention, concerns the potential damage to protective capsules from environmental factors such as desiccation (Feare 1970, Spight 1977). As will be argued, such risks are potentially important and need to be quantified in order to understand the adaptive bases of reproductive patterns of marine invertebrates (Pechenik 1979). This paper presents quantitative assessment of

environmental risks for the egg masses of a non-prosobranch, the polychaete *Axiiothella mucosa*.

STUDY ORGANISM AND SITE

Axiiothella mucosa (Andrews) is a common maldanid polychaete ranging from North Carolina to Florida (Day 1973). The worms attain lengths of 50 mm and are oriented head downwards in sediment tubes on sandy bottoms in intertidal and very shallow subtidal habitats (Andrews 1891, Hartman 1945, Day 1973, Young and Young 1977, 1978).

The reproduction of *A. mucosa* has been described by Bookhout and Horn (1949). Females produce a gelatinous mass in which are embedded 500–1000 eggs, each 250–260 μm in diameter. The egg mass, ovoidal in shape and 50 mm in the longest dimension, is attached to an auxiliary arm of the female's vertical tube. The egg masses provide a suitable substrate for *Nitzschia* sp. and other benthic diatoms; these diatoms were observed in the guts of developing embryos. In North Carolina, juveniles leave the egg mass after 11–14 d at 20°C, at which time they have ≈ 14 segments and are 1 mm long (Bookhout and Horn 1949). In the warmer waters of Florida, development is similar but more rapid; juveniles 1 mm in length emerge from the egg masses after only 7 or 8 d. The juveniles assume a benthic existence when they crawl from the egg mass. Although juveniles may be wafted into the water column by water currents, they do not actively maintain themselves in the plankton. Following the terminology of Giese and Pearse (1974), prehatching, developmental stages within the egg masses are referred to here

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as embryos, and the hatching stages as juveniles. There is no larval stage.

A population of *A. mucosa* was investigated in a small lagoon near Sebastian Inlet, Florida (27°47.5' N, 80°26.6' W). Sebastian Inlet is the northernmost of three inlets of the Indian River lagoon, a bar-built estuary along the southeast coast of Florida (see Young and Young 1977 for a map of the Indian River). The study site is characterized by a well-sorted sand sediment and is located at the -0.1 m tide level. A large bed of the marine angiosperm *Halodule wrightii* is located seaward of the *A. mucosa* population.

Hurst (1965) showed that the neogastropod *Nassarius vibex* is a predator of the eggs of *A. mucosa*. However, during the course of my study, only two *N. vibex* were observed on the flat and neither was preying on *A. mucosa* eggs.

Observations revealed that a large number of the egg masses of *A. mucosa* had been detached from the female tubes. Some egg masses were stranded in the wrack line at the high tide level, and others had obviously been abraded and torn as they were wafted across the flat by the rising and falling tides. The present study determined the percentage of egg masses which become detached before natural release of the juveniles, and examined the consequences of such detachment on the number of viable juveniles that are released.

MATERIALS AND METHODS

To quantify the incidence of detachment of egg masses, a survivorship analysis of egg masses was conducted in July-August, 1983. Nine 1-m² quadrats (three quadrats in three different parts of the flat, but equidistant from the mouth of the inlet) were marked with wooden dowels on the sand flat. Each day, newly "born" egg masses were marked by inserting a color-coded wooden skewer into the sediment adjacent to the egg mass. Egg mass "death" was recorded when it was observed that the egg mass had become detached. Survivorship data for 15 cohorts of egg masses were obtained in this fashion. The positions of egg masses were mapped daily except when neap tides and onshore winds prevented accurate censusing of the quadrats. Natural release of juveniles is indicated by collapsed egg masses, which deteriorate entirely in 2 or 3 d (W. H. Wilson, Jr., *personal observation*). To test for possible differences among days and areas of the flat for the number of egg masses appearing at each census, a two-way ANOVA was performed. The three different areas of the flat where the quadrats were established served as one factor, with sampling date as the second factor. Before analysis, Bartlett's test was used to confirm homogeneity of variances.

To determine the relative importance of physical factors (tidal currents, wind-driven currents) and biological factors (predation, biological disturbance) in detaching egg masses, a caging experiment was performed. The cages were constructed of chicken-wire

mesh (25 mm openings) attached to wooden stakes (15 × 15 mm). Three treatments were utilized: (1) full cage treatment with cages 30 × 30 × 18 cm high, (2) cage control treatment with three-sided cages (lacking roof and fourth side), and (3) control areas of natural, unmanipulated substrate. The cage control tested for possible alterations of the hydrodynamic regime by the cage structure, which might alter the detachment rate of egg masses. I used relatively large-mesh caging material to attempt to minimize cage-induced turbulence, which might in itself cause detachment of egg masses and hence confound the data. Nonetheless, 25-mm mesh is fine enough to exclude portunid crabs, flatfish, and rays, which appear to be the major biological disturbance agents in the area. Each treatment was replicated three times. The experiment was terminated 4 d later by recording the number of attached, marked egg masses in each area. With a finding of no significant difference between the cage control and control treatments with respect to the percentage of egg masses remaining attached, a significant difference between the full cage and control treatments would implicate biological disturbance/predation as the major source of detachment (specifically, those organisms large enough to be excluded by the 25-mm mesh would be implicated); finding no difference between the full cage and control treatments would implicate physical factors as the causal agent. The significance of differences in the percentages of egg masses remaining attached was tested by a one-way ANOVA, after transformation of the data with the arcsine \sqrt{x} transformation.

To document possible effects of detachment of egg masses on the number of viable juveniles released, detached egg masses were collected from the field. It was impossible to know for how long a given egg mass had been attached before detachment. Therefore, I collected a large number of detached egg masses in an effort to approximate the typical distribution of detachment duration in the field. These egg masses were brought into the laboratory and maintained in individual fingerbowls of 10 cm diameter. Juveniles were counted and removed from the fingerbowls as they were released. Two controls were used for this set of observations. A large cohort of egg masses laid in September 1983 was marked. Seven days after the egg masses were laid, I collected those that were still attached, placed them in individual fingerbowls in the laboratory, and counted the juveniles that were released. A second control was established by collecting 12 egg masses from that large September cohort shortly after they were laid, bringing them to the laboratory, and allowing them to develop entirely in still water.

A final treatment, to test for the effects of egg mass desiccation on embryo survivorship, was conducted by bringing six freshly laid egg masses into the laboratory. Four times during the following week, the water in the fingerbowls was decanted and the egg masses were placed in the sun for 2 h. In the field, detached

TABLE 1. Survivorship data for 15 cohorts of egg masses. The number of egg masses remaining on every sampling day is given.

Cohort	Sampling day											Proportion attached for 7 d*
	0	1	2	3	4	5	6	7	8	9	10	
	Number of egg masses											
13 July	13	10	...	6	6	5	5	4	3	1	0	0.31
14 July	10	...	6	3	3	1	0					0.0
16 July	101	78	73	50	43	26	6	0				0.0
17 July	22	15	14	13	10	1	0					0.0
18 July	19	16	14	10	6	0						0.0
19 July	9	3	1	1	0							0.0
20 July	2	2	1	1	0							0.0
21 July	1	0										0.0
22 July	0											...
23 July	0											...
25 July	0											...
26 July	34	32	25	24	17	12	9	5	3	0.35
27 July	22	18	14	5	5	5	5	3	0	0.23
28 July	38	24	18	16	10	4	0			0.11
31 July	36	28	20	13	6	3	0					0.0
1 Aug	42	40	35	29	21	0						0.0
2 Aug	37	34	32	24	0							0.0
3 Aug	1	1	1	0								0.0
4 Aug	0											...
Total†	270	217	197	141	86	30	6					0.0

* The proportion of each cohort that remained attached to the female tube for 7 d, after which time embryonic development is nearly complete.

† Excludes those cohorts for which one or more daily censuses are missing.

egg masses that are stranded in the wrack line are exposed to direct sunlight for even longer periods of time. When all the egg masses in the four treatments had ceased to release juveniles, I calculated the total number of juveniles released from each egg mass. The data had heterogeneous variances and non-normal distributions, which could not be corrected by transformation. The data were analyzed with the nonparametric Kruskal-Wallis test, followed by pairwise median tests (Siegel 1956).

Many of the egg masses detached in the field had been abraded by being dragged over the sand bottom, resulting in the premature release of eggs or juveniles. To assess the effects of early release of embryos, egg masses of various ages were torn open. As a control for the handling procedure, embryos that would have emerged within 24 h were removed from old egg masses. All artificially released embryos were maintained in clean seawater in fingerbowls. Survivorship of embryos was determined after 48 h. The survivorship of young embryos (six or fewer setigers) was compared to that of older embryos (12 or more setigers) with a one-way ANOVA, after applying an arcsine \sqrt{x} transformation to the data to homogenize the variances (Bartlett's test, $P > .05$).

To assess the significance of the diatom flora within the egg masses in providing nutrition for the developing embryos, 1–2 d old egg masses were collected in March 1985. Nine egg masses were placed in individual fingerbowls and maintained in the culture room, where sunlight entered through full-length windows

spanning the northeast wall. Nine egg masses were placed in individual fingerbowls and maintained in a light-tight box. The egg masses were maintained at 20°C. The egg masses kept in darkness remained clear, indicating absence of diatoms. Juveniles were counted and removed from each fingerbowl during daily censuses. When the egg masses had ceased to release juveniles, the total number of embryos released by each egg mass was calculated. The significance of differences in the mean number of juveniles released in the two treatments was tested with Student's t test.

RESULTS

The *A. mucosa* population in the Sebastian Inlet flat is synchronous with respect to major egg-laying bouts. A two-way ANOVA indicated that there were no significant differences in the number of egg masses deposited in the three different parts of the flat ($F = 1.08$, $P > .05$). However, there was a strong temporal effect ($F = 3.42$, $P < .01$). The interaction was not significant ($F = 1.02$, $P < .05$). The synchronicity of egg laying was not correlated with lunar periodicity or the time of exposure during low tide.

It is apparent from the survivorship data for the 15 cohorts of egg masses (Table 1) that a large number of egg masses are detached before 7 or 8 d, when they naturally rupture to release the embryos. For 11 of the 15 cohorts, none of the egg masses remained attached until natural release of the embryos. The processes detaching the egg masses are temporally variable; the

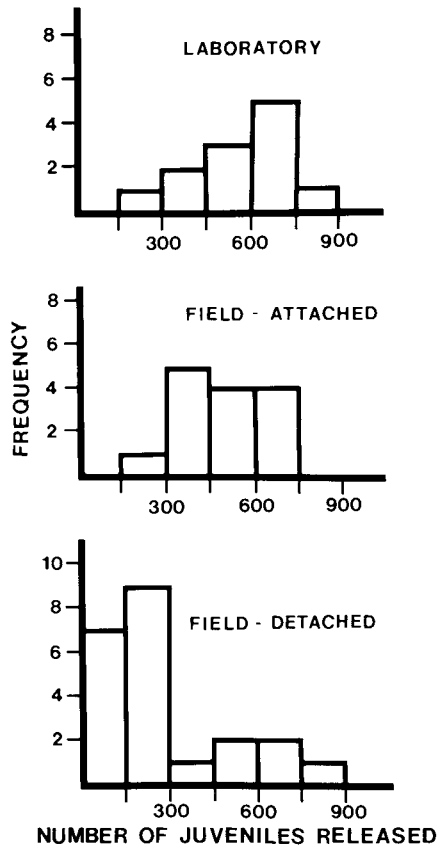


FIG. 1. Distributions of the number of juveniles released per egg mass from egg masses that developed in the laboratory (LABORATORY), egg masses that remained attached to the female tube for all of embryonic development (FIELD-ATTACHED), and egg masses that were detached from the female tube for unknown periods of time (FIELD-DETACHED).

cohorts of 13 July, 26 July, and 27 July showed relatively high survivorship.

In the caging experiment, the mean survivorships of egg masses were 0.34 for the control treatment, 0.26 for the partial cage (cage control) treatment, and 0.24 for the full cage treatment. A one-way ANOVA indicates that there were no significant differences among the three treatments ($F = 1.12$, $P > .10$). Since there was no significant difference in survivorship of egg masses between the cage control and control areas, no obvious cage-induced hydrodynamic artifact was present. Because there was no difference in survivorship of the egg masses in the predator exclusion treatment and the two treatments where predators had free access, physical processes are implicated as the primary agents causing detachment of egg masses. I consider less likely the alternative explanation that small organisms that were not excluded by the 25-mm mesh of the full cages were responsible for detachment of egg masses.

Some of the consequences of detachment of egg masses on the number of juveniles released can be seen in a comparison of the mean numbers released from

four experimental treatments. There was no significant difference between the two control treatments (median test, $P > .20$) in the number of juveniles released: egg masses that developed entirely in the laboratory (mean = 567.2 juveniles released) vs. egg masses that remained attached to the female tube for 7 d before they were brought into the laboratory (mean = 466.8 juveniles released). The number released in each of these treatments was significantly greater (median test, $P < .01$) than in the treatment in which detached egg masses were brought into the laboratory and allowed to release juveniles (mean = 271.0 juveniles). The egg masses in the desiccation treatment (mean = 62.3 juveniles released), in which the egg masses were subjected subaerially to direct sunlight for a total of 8 h, produced the fewest juveniles of all the treatments (median tests, $P < .01$ for all comparisons).

In the experiment in which young and old embryos were released artificially from egg masses, 0.95 of the late-stage (12-setiger) embryos survived whereas only 0.23 of the early-stage (6-setiger) embryos survived. These means are significantly different (one-way ANOVA, $F = 97.30$, $P < .01$).

The distributions of the number of juveniles released from each egg mass (Fig. 1) are normal for both the laboratory treatment and the field-attached treatment (d'Agostino's test, $P > .10$ for both cases), but the distribution for the detached treatment is decidedly nonnormal (d'Agostino's test, $P < .01$). As stated in Materials and Methods, it is not possible to know how long each of the detached egg masses in the control treatments had been detached and hence subject to desiccation and abrasion. It is clear from inspection of Fig. 1 that some of the detached egg masses produced

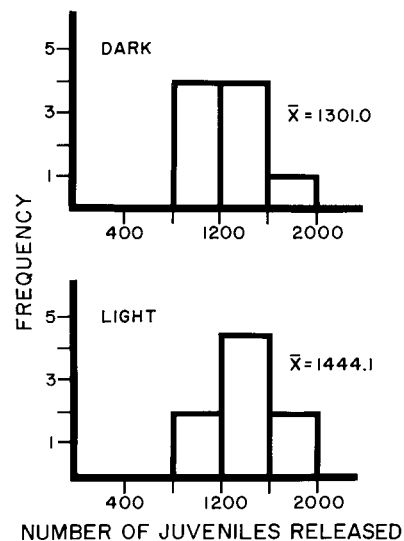


FIG. 2. Distributions of the number of juveniles released per egg mass from egg masses that developed in the laboratory under dark conditions (DARK) and under lighted conditions (LIGHT) where diatoms were able to grow.

as many juveniles as the egg masses in the control treatments, but most of them produced considerably fewer viable juveniles. I suggest that those egg masses from the detached treatment that produced large numbers of juveniles had only recently been detached, while those that produced few viable juveniles had been detached for longer periods of time.

There was no significant difference in the number of viable juveniles produced in the two treatments of the light/dark experiment ($t = 0.97$, $P > .30$; Fig. 2). Hence, diatoms are not necessary for the development and survival of embryos. It should be noted that the sizes of the emerging juveniles were not measured; it is conceivable that juveniles from egg masses with diatoms may have been larger when they crawled free of the egg masses. The reason for the increase in the number of juveniles produced from 1985 egg masses (Fig. 2) relative to 1983 egg masses (Fig. 1) is not known.

DISCUSSION

Recent theoretical considerations of the evolution of reproductive modes of marine benthic invertebrates (planktotrophy, lecithotrophy, benthic development) are based on the relative intensities of benthic and planktonic predation and the abundance of phytoplankton (Vance 1973a, b, Caswell 1981, Grant 1983). All of these models incorporate a benthic mortality term for encapsulated embryos. Although such a mortality term is mathematically similar to a term for environmental risks, there is no explicit term accommodating environmental risks in these models. In a model to explain the adaptive significance of encapsulation for a portion of embryonic development, Pechenik (1979) explicitly assumed that benthic mortality of encapsulated embryos was zero, noting that such an assumption may not be valid and that "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 . . . can be fully understood." The present data are significant in this regard. It is demonstrated that few of the egg masses of *A. mucosa* remain attached for all of embryonic development (Table 1); evidence from the caging experiment (see Results) shows that this detachment occurs primarily through the agency of water currents. Detached egg masses are sometimes stranded in the high intertidal zone, where desiccation lowers the number of released juveniles by an order of magnitude (see Results). Abrasion of detached egg masses causes early release of embryos, and survivorship of embryos released early was low in the laboratory (see Results).

Extrapolation from the quadrat data yields the conclusion that only a small percentage of the egg masses that must have been detached from the sand flat each day could be found on the flat. However, dispersal of

entire egg masses is not likely to have a selective basis. The distribution of *A. mucosa* is primarily intertidal, with some individuals occurring in shallow subtidal areas of <1 m depth (Andrews 1891, Hartman 1945, Day 1973, Young and Young 1977, 1978). Egg masses swept to deeper waters seem to have little chance of success. Additionally, egg masses carried to other intertidal areas would be abraded even more than the egg masses collected from the study site (Fig. 1). The parsimonious explanation for the present data is that the females are producing the best possible cement for attaching their egg masses to their tubes and that the significant reduction in the number of juveniles released due to the effects of physical processes is not sufficient to select against the evolutionary maintenance of egg mass production.

Bookhout and Horn (1949) claimed that the diatom flora, primarily *Nitzschia*, within the egg masses of *A. mucosa* are utilized by the embryos as food. No data on the relative abundances of *Nitzschia* in the egg masses and in the adjacent sediment were given. The data from the light/dark experiment (Fig. 2) indicate that egg masses without diatoms release as many juveniles as egg masses maintained in sunlight. Hence, photosynthesis by the diatom flora is not necessary for successful embryonic development, and the purpose of the gelatinous egg mass cannot be to serve as a diatom garden.

It is intriguing to consider the adaptive significance of such gelatinous encapsulating structures. Such ovoidal egg masses have arisen at least three times in metazoan evolution: in *A. mucosa*, in the orbinid polychaete *Scoloplos armiger* (Chapman 1965, Gibbs 1968), and in many cephalaspidean opisthobranchs (Chaffee and Strathmann 1984, Hadfield and Switzer-Dunlap 1984). Gibbs (1968) demonstrated that the encapsulated embryos of *S. armiger* are no better protected from desiccation stress than excapsulated embryos. No data on the ability of any of these egg masses to ameliorate salinity stress or prevent bacterial or protozoan attack have been gathered. Pechenik's (1979) suggestion that sequestering of embryos until they are better able to avoid planktonic and benthic predation by the acquisition of increased size or swimming abilities remains a compelling hypothesis (see Pennington and Chia 1984). Whatever the selective basis of the egg masses of *A. mucosa*, a set of environmental risks, acting to diminish the number of juveniles released, must be recognized to understand the evolutionary significance of such benthic protective development.

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