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SUBSTRATE DISCRIMINATION IN *PECTINATELLA MAGNIFICA* LEIDY (BRYOZOA)

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INTRODUCTION

The ability of larvae of normally benthic organisms to recognize substrates suitable for metamorphosis has been demonstrated by a number of investigators (Jägersten, 1940; Wilson, 1952; Silén, 1954; Scheltema, 1961). As often as not some organic factor has been shown to be critical in the choice of a favourable site. In most cases settling may be delayed in the absence of a metamorphosis-inducing factor demonstrable in the surrounding sediments. Larvae, provided with clean glass surfaces only, often delay metamorphosis until small amounts of suitable sediments are introduced.

Preliminary observations during the summer of 1968 suggested that larvae released from mature colonies of *Pectinatella magnifica* Leidy tended to settle on the glass surfaces or slate bottom exposed through the sediments in holding aquaria. If such larvae were transferred to clean glassware, they settled and metamorphosed readily on the bottom of the dish. Subsequent experiments convinced me that the larvae demonstrated a clear preference for large particles when offered a variety of substrates. This paper provides evidence that, in at least one group of invertebrates, particle size plays a dominant role in habitat selection. An intriguing question underlies this process. What constitutes a suitable attachment site?

METHODS AND MATERIALS

This work was carried out during the summer of 1969 at the F.T. Stone Laboratory, Put In Bay, Ohio. All experiments were conducted at 25° C. with incandescent illumination providing 14 hr. of light alternating with 10 hr. of darkness. The Lake Erie water used was filtered through several layers of cloth and then through two thicknesses of Whatman no. 1 filter paper. The larvae used in the experiments were harvested each evening from mature colonies of *Pectinatella magnifica* maintained in lake water aquaria. Experimental chambers were 3½ in. (100 c.c.) or 4½ in. (250 c.c.) Carolina Stacking Culture Dishes. All glassware was rinsed with distilled water after washing.

Natural sediments

Sediments were collected from a South Bass Island beach below the water level. These sediments were washed repeatedly to remove as much organic matter as possible. Subsequent microscopic examination verified the thoroughness of this step. The sediments were separated into size classes in U.S. Standard Sieves according to the scheme in Table 1. Following the practice of Eriksen (1963), the size fractions were selected in ϕ units (Inman, 1952). The substrate fractions were carefully distributed in each culture dish so that the material covered 50% of the bottom (180° segment). The general arrangement of substrate in culture dishes is illustrated in Fig. 1. As the experiments proceeded the larvae could settle on the clean glass portion, the substrate portion, or both. The only exception to this plan was the series involving the ϕ −4 pebble structure. In this case three pebbles were offered in each trial. The experimental dishes were arranged in the incubator so that the centre line (between clear and substrate surface) was parallel to the direction of the light source and thus evenly illuminated.

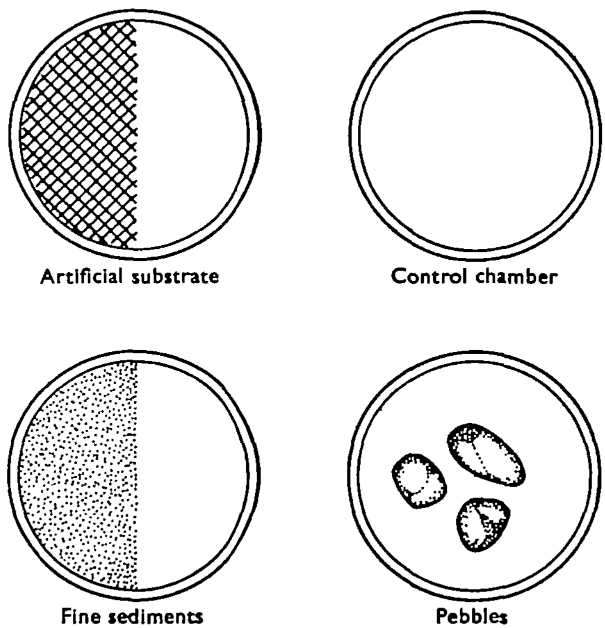

Fig. 1

Table 1. *Description of size fractions of substrates*

Substrate	ϕ scale*	Passed sieve	Retained by sieve	Size range (mm.)
Pebbles	−4	(hand picked)		16–32
		No.	No.	
Gravel	−1	5	10	2–4
Coarse Sand	1	18	20	0·84–1
Medium Sand	2	35	40	0·42–0·5
Fine Sand	3	60	120	0·125–0·25

* The ϕ scale expresses the size fractions in units suggested by Inman (1952).

Other substrates

Since aquatic ecologists are continually evaluating artificial or foreign surfaces as sampling devices, several materials were tested at this time. These materials were compared for attractiveness with several natural surfaces. The substrates tested in the portion of the study were: plastic window screen 18 × 16 mesh, aluminium window screen 18 × 16 mesh, 3M Conservation Web No. 200 (3M Company, St Paul, Minnesota), freshly crushed limestone from a terrestrial site, dead *Typha* stem from a submerged collection, water-logged wood from old dock piling. The freshly crushed limestone was selected in pieces in the ϕ −4 range of the pebbles used before. All of the other materials were cut to fit 180° segments of the bottom of each culture dish so as to provide settling opportunity similar to the sediments.

RESULTS

In these experiments larval settlement is reported as a percentage of total larvae because mortality was not significant. In all of the experiments conducted the mortality for a 24-hr. period was usually zero and never was more than 1%.

The experiments were begun in the evening utilizing broods of larvae usually released between 9.00 p.m. and midnight. Settlement was determined 24 hr. later.

Table 2. *Results of substrate selection by larvae of* Pectinatella magnifica *Leidy*

Substrate	No. of trials	Total larvae*	Settled on glass	Settled on substrate	Ratio	Percent on substrate
Control	11	310	310	(clean glass culture dish only)		
Pebble	27	588	84	504	0·17	86
Gravel	16	439	86	353	0·24	80
Coarse sand	6	180	137	43	3·19	24
Medium sand	19	345	322	23	14·00	7
Fine sand	19	390	379	11	34·46	3

* Mortality in any 24-hr. experiment never exceeded 1%.

Table 3. *Settlement of larvae of* Pectinatella magnifica *Leidy on selected substrates*

Substrate	Number of trials	Total larvae*	Settled on glass	Settled on substrate	Percent on substrate
3M Web no. 200	10	245	198	47	19
Crushed limestone	10	300	30	270	90
Typha stem	9	90	29	61	68
Wood (water-logged)	14	320	40	280	88
Aluminium screen	10	100	100	0	0
Plastic screen	10	100	82	18	18

* Mortality in any 24-hr. experiment never exceeded 1%.

Although the experimental design provided a 14-hr. period of illumination, observation disclosed that most larval settlement occurred during the period of darkness. The results of the sediment-preference experiments are readily apparent. These data are summarized in Table 2. When provided only with a clean glass surface (culture dish), the larvae will settle and metamorphose with no apparent difficulty. If clean pebbles are provided, the larvae will favour the stone over the glass surface. However, as the size of substrate particle is reduced, the selective favour is likewise reduced. If larvae encounter only sand-size particles, preference clearly returns to the glass surface.

The results of experiments in which larvae were offered various selected surfaces are summarized in Table 3. It is clear from these data that naturally occurring surfaces were favoured over manufactured materials.

DISCUSSION

The factors responsible for the induction of metamorphosis in the Phylactolaemata are poorly understood. The embryology including the developmental steps leading to metamorphosis has been summarized by Hyman (1959). The embryo develops into a ciliated oval larva of up to 2·0 mm. in length. Upon rupturing of the embryo sac of the parent polypide the larva swims freely for a period of a few minutes to 24 hr. At this time the primary polypides are already formed. The larva swims with the pole opposite the polypides forward; that is, it leads with its aboral surface. Upon contact with a suitable substrate the larva attaches with a glandular secretion, the polypides expand at once, and the young colony is formed.

The aboral pole contains a concentration of nerve cells which presumably function in larval orientation. If these cells are in fact sensory, the question remains: sensitive to what? If the major factor in larval settlement is light or colour of substrate, we might expect to uncover this bias experimentally. The data presented above, however. show no correlation between settling and substrate colour. Beyond that, routine observation disclosed that most of the larvae settled during the dark period. The phenomenon of large masses of bryozoa occurring in water pipes void of illumination is well known.

The question of the role of chemoreception with subsequent modification of settling behaviour must be considered. The larvae clearly rejected some artificial surfaces. Very few larvae settled on materials such as the 3M Web and window screen material, while at the same time clean glass and freshly quarried limestone were apparently favoured. The picture becomes a little clearer if we consider natural substrates. These data indicate that the larvae definitely preferred large firm objects to smaller particles. Direct microscopic observation of larval exploration suggests that the choice of site might be based upon some sort of leverage relationship. If the substrate itself moves under the force of initial contact (e.g. small grain compared to larva), the site is rejected and the larva moves on. Obviously this cannot be the whole story because of the rejection of some of the firm but artificial materials mentioned above.

Most of the work with settlement of marine larvae has pointed toward a positive requirement for an organic substance in the induction of metamorphosis. Wilson (1955) suggests the importance of microflora on the sediment grains contacted by *Ophelia* larvae. Determination of chemical factors or microflora were clearly beyond the scope of this preliminary investigation. These aspects must be accounted for before other conclusions may be accepted. If, however, these factors play a role in the settlement of *Pectinatella* it appears that they may provide negative control, since the total surface area increases as the substrate particles decrease in size. The work of Jonasson (1963) on Danish lakes has shown that bryozoa will colonize hostile environments if a firm substrate is provided. In this case mesh traps intended for aquatic insects were colonized when placed on barren mud bottom or areas exposed to wave action.

SUMMARY

1. This study is concerned with the role of particle size in habitat selection by the larvae of the colonial bryozoan *Pectinatella magnifica* Leidy.

2. All experiments were conducted at 25° C. with a 14/10 LD photoperiod.

3. When larvae are provided with a clean glass surface only, they settle and metamorphose with no apparent difficulty.

4. If natural pebbles are provided, the larvae will favour the stone over the glass surface.

5. As the size of substrate particle is reduced, the selective favour is likewise reduced.

6. If larvae encounter only sand-size particles, the preference will return to the glass surface.

7. In experiments in which larvae are offered various other surfaces, settling larvae clearly favoured naturally occurring surfaces over manufactured materials.

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