

Relations between encrusting bryozoans and substrate: an example from the Danian of Denmark

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In the Lower Danian bryozoan limestone mounds exposed in the coastal cliff of Karlby (Jylland), fragments of cyclostome and cheilostome bryozoan colonies constitute more than 90 wt% of preserved benthic fauna in the $>1/2$ mm fractions. Of the cheilostome bryozoans, encrusting colonies normally make up between 5 and 30 wt%. The encrusting fauna is found on skeletal remains of other benthic invertebrates, predominantly stems of erect, bushy bryozoans. The proportion of encrusted stems in the

fraction 1.19–1.41 mm is between five and ten times larger than in the fraction 0.500–0.595 mm. In the former fraction more than 50% of the fragments may be encrusted. Fragments of approximately identically sized stems belonging to different species are not used to equal extents as substrate. Fragments with an overall smooth, but in detail relatively coarse, surface are most often encrusted, whereas fragments are avoided that have as surface sculpture a network of ridges and hollows. Investigations of the growth site selection of six encrusting species show that specific attachment preferences according to both size and surface topography of the substrate were present, separating closely related and very similar species. This could have been anticipated from the high density and diversity of the bryozoan fauna.

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Substrate type and availability are amongst the most important environmental factors controlling the distribution of bryozoans, and numerous studies have shown that bryozoans commonly exhibit a strong preference for a particular type of substrate. Some species clearly select a flexible growth site such as algae, whereas others prefer a hard substrate, mainly rocks or shells. Within each of these two groups, furthermore, some sorts of substrate are apparently more suitable for settlement than others (Rogick & Croasdale 1949; Ryland 1959, 1962, 1970, 1973; Powell 1968; Powell & Crowell 1967; Cook 1968; Stebbing 1972, 1973; Hayward 1973, 1975; Moore 1973; Voigt 1973; Hayward & Harvey 1974; Harvey, Ryland & Hayward 1976). Most of these studies deal with the settlement of bryozoans on algae, and only a few workers have considered bryozoans encrusting other animals (e.g. Powell 1967; Ryland & Stebbing 1971; Stebbing 1971).

The purpose of the present paper is to examine the relations between the growth site selections of the encrusting cheilostome bryozoans and the amount and nature of the substrate in the Lower Danian bryozoan limestone mounds of

Denmark. The substrate available for settlement in the mounds consisted mainly of stems of erect, bushy bryozoans composed of a number of species having different morphologies. The substrate therefore showed a number of subtle differences with regards to diameter and to surface morphology, both of which appear to have influenced the larvae of the encrusting bryozoans in their choice of attachment surface.

The present analysis of substrate preferences combines a study of the composition of potential substrate, as well as the substrate actually used. It further considers the general environmental conditions since settling responses to substrate are likely to be influenced by other factors as well.

Material

The present analysis is based on thirty-nine samples collected in two separate sample traverses parallel to bedding in a single bryozoan biomicrite mound exposed in the coastal cliff at Karlby on the east coast of Jylland (fig. 1). Detailed descriptions of the locality, the sediment,

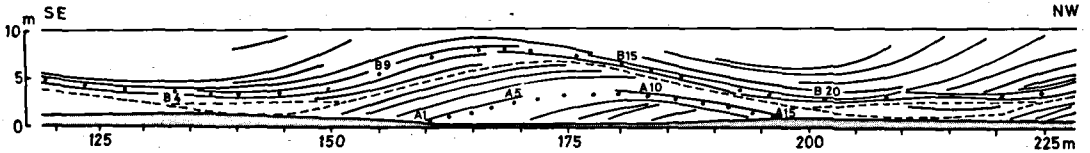


Fig. 1. Simplified sketch of a part of the coastal cliff at Kariby showing the structure of the investigated mound, and the location of the samples. The structure is picked out by flint layers. Note the assymetrical shape of the mound with higher dips on

the SE flank (10–25°) than on the NW flank (10–15°). Individual beds are also more or less assymetrical and, in general, they tend to be thinnest in the basins and thickest on the SE flank. For a full description see Thomsen (1976).

and the mode sampling are given by Thomsen (1976, and in prep.). The results form part of a study of the palaeoecology of the Danian cheilostome bryozoans, and the methods applied were to some extent guided by requirements imposed by parallel investigations of the non-encrusting part of the fauna. Each of the two sample series are considered to represent isochronous surfaces. The samples (300–400 g) were disintegrated and then separated into the following fractions: > 2 mm, 1–2 mm, ½–1 mm, 250–500 µm, 125–250 µm, and < 125 µm. The grain-size distribution of the sediment is shown in fig. 2. All samples consist of between 23 and 46% discrete skeletal fragments of marine invertebrates. The finer grained matrix (i.e. less than 125 µm), in addition to minute fragments of bryozoans, is characterized by remains of planktic forami-

fera and coccoliths. The benthic groups show only slight variations in relative abundance in the mound and bryozoans predominate throughout, making up more than 90% of the fauna by weight. Cyclostomes dominate among the bryozoans and constitute between 50 and 75% of this group. The only other benthic invertebrates recorded in all samples are echinoderms, brachiopods, and benthic foraminifera.

The present investigation concentrates on the ½–1 mm and 1–2 mm fractions since virtually all encrusted fragments are restricted to these fractions, and because the bryozoans in the finer and the coarser size fractions are less well preserved. Owing to the large number of bryozoan fragments in a fraction, the analyses were carried out on split fractions, containing between 1000 and 2500 identified fragments.

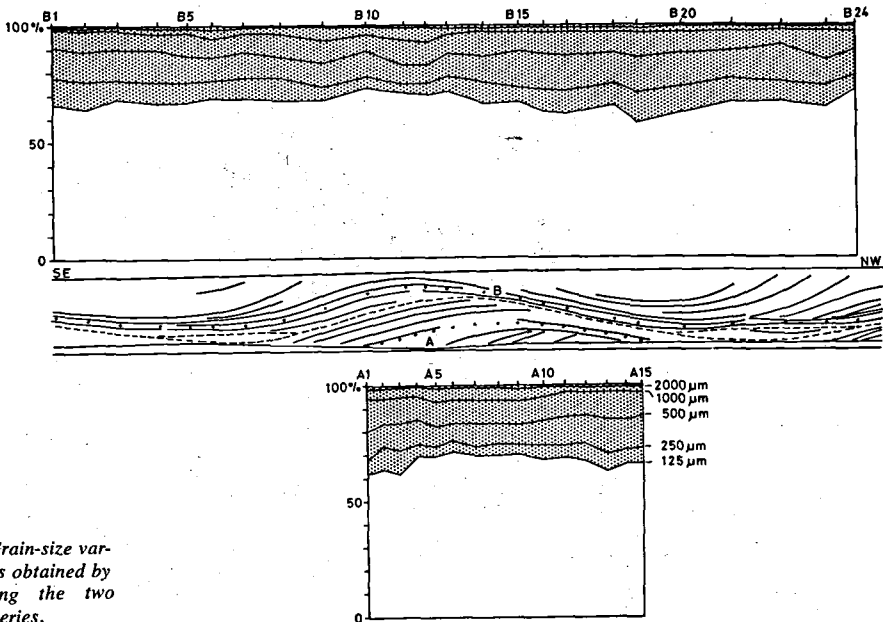


Fig. 2. Grain-size variations as obtained by wet-sieving the two sample series.

Palaeoenvironment

The distribution and morphology of the bryozoans in the mounds was mainly controlled by the movement of water over the mounds from the south-east (Thomsen 1976, and in prep.). This has been interpreted from sedimentological and biological evidence which consistently indicate higher water energy on the SE-flank and at the summit as compared with the NW-flank and the basins between adjacent mounds. The higher water velocities on the SE-flank are believed to have supplied these portions of the mounds with greater amounts of nutrients thereby permitting a dense cover of erect bushy bryozoans. In contrast, on the NW-flank and in the basins the density of the fauna was only about one third of the density on the SE-flank. Bryozoans colonies are never found in growth position in the mounds, but the fragments have not undergone significant transport (see fig. 4).

General substrate preferences

97 cheilostome species are recognized throughout the mound, and 63 of these have been found encrusting solid substrates. The encrusting colonies form only a minor part of the fauna (5-30 wt% of the cheilostome bryozoans). The majority of the bryozoan remains consist of stem-formed fragments, inferred to have formed parts of erect, bushy colonies (fig. 3). This study only considers encrusting colonies that are still adherent to a substrate, but it should be noted that fragments of 33 of the 62 encrusting species are also found as free unilamellar plates, indicating that these particular colonies had encrusted substrates that are not preserved. Finally, 13 species occur exclusively as now unattached plates.

Nearly all encrusting colonies still attached are found on fragments of colonies of erect bryozoans. A large proportion of the encrusting colo-

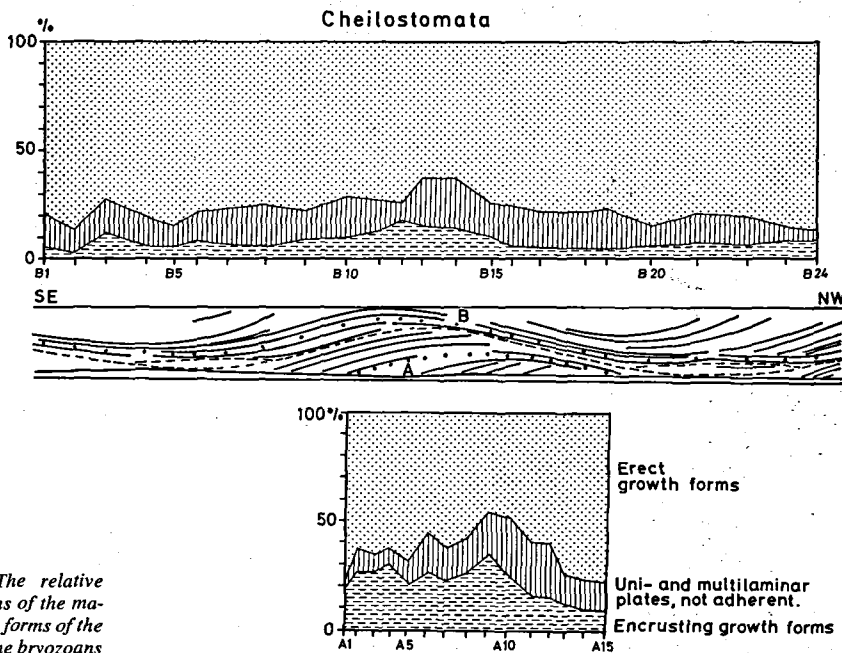


Fig. 3. The relative proportions of the major growth forms of the cheilostome bryozoans in the sample series.



Fig. 4. Fragmented colony of *Porina cylindrica* Voigt. The fragments are considered to have originated from a single colony which after death was overturned and fragmented by the weight of overburden. The individual fragments have not been transported and the cluster seems to reflect some morphological features of the original colony. Except for the lowermost part of the colony (situated centrally in the lower part

of the figure – the actual base is not preserved) which has a slightly thicker stem than the rest, there does not seem to be a significant trend in stem diameter between the proximal and the distal parts. Many erect cheilostome species seem to have had a mode of growth rather similar to *P. cylindrica* described here.

nies are continuous around the circumference of the stems, suggesting that most larvae settled on erect colonies still in growth position (see fig. 4). Fragments of dead colonies on the bottom were probably less favourable because of silting.

The effect of substrate size (stem diameter)

To demonstrate the role of the stem diameter on settlement of the bryozoan larvae six samples were selected from various parts of the mound. The stems in the 1–2 mm, ½–1 mm, and the ¼–½ mm fractions were subdivided into a number of more restricted size-classes by sieving (fig. 5). Measurements of stem diameters indicate that the distribution of the stems on the various sub-

fractions is largely independent of whether the stems are encrusted or not. The subfractions are therefore suitable for study of the relationship between the diameter of the stems and the proportion of stems encrusted. The exact diameters of the stems within each subfraction of one sample (A3) are shown in fig. 6. The distribution of the fragments in the various subfractions is controlled mainly by the diameters of the stems. However, owing to irregularities in the fragments the diameters within any one subfraction are normally smaller and have wider range than indicated by the boundaries of the subfractions. The absolute sizes of the subfractions (fig. 5) are therefore not important in themselves, but should

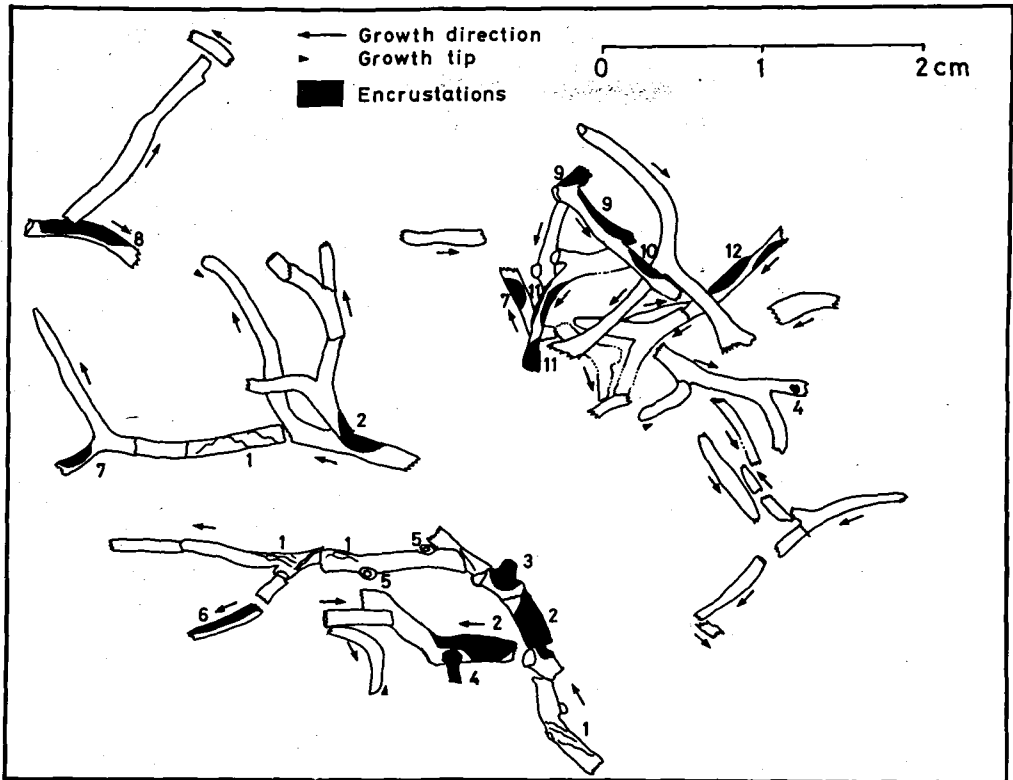


Fig. 4. In addition to *serpulids* (5), *indeterminable erect bryozoans* (3, 4), and *various encrusting cyclostomes* (1), the colony was used as substrate by eight encrusting cheilostomes: *Membraniporella squamulosa* (2), *Micropora hennigiana* (6), *Semeischariella complanata* (8), *Ellisina britannica* (9), *Floridina scutata*

(10), *Aechmella pindborgi* (11), *Tricephalopora subtriceps*, and an *unidentified species*. Since the specimen is seen from the lower side, the encrustations probably took place while the colony was still in growth position. The relief of the surface is 1 cm.

be considered in combination with the stem diameter distribution as shown in fig. 6.

Nevertheless, the proportion of encrusted stems in all samples shows a strong positive correlation with the diameter of the stems (fig. 5). The proportion in the 1.19–1.41 mm subfraction is between five and ten times higher than in the 0.500–0.595 mm subfraction. The largest difference in the proportion of encrustations between any two neighbouring subfraction is found between the 1.19–1.41 mm and 1.00–1.19 mm subfractions. The percentage of encrusted stems in the 1.00–1.19 mm subfraction is typically only a little more than half of the percentage in the 1.19–1.41 mm subfraction. Stems finer than 0.3–0.5 mm were rarely used as substrate.

The difference in the amount of encrustations

between the individual samples probably resulted from changes in the environmental conditions related to differences in the water movement between the various parts of the mound. The influence of the environment is more clearly demonstrated in fig. 7 which shows the relative proportion of fragments overgrown in the different parts of the mound. Within each of the two fractions 1–2 mm and ½–1 mm the proportion of encrusted stems is significantly higher on the SE-flank and the summit than on the NW-flank and in the basins. It further appears that cyclostome stems were, in general, preferred to cheilostome as substrate. The only exception is found in the 1–2 mm fraction on the upper part of the SE-flank. In this part of the mound this fraction is dominated by stems of the cheilostome

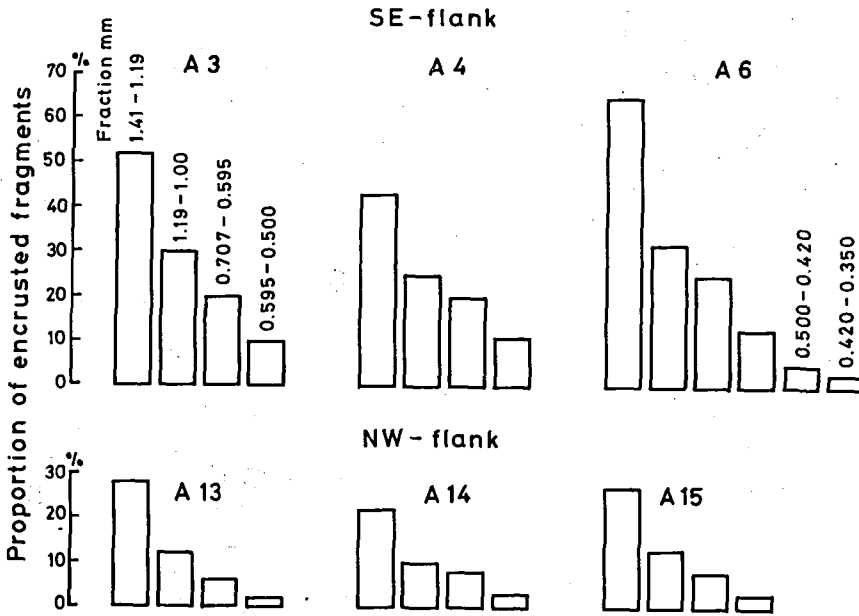


Fig. 5. Comparison of the proportion of fragments overgrown with encrusting bryozoans in sub-fractions of six samples from various parts of the mound. The actual diameter of the fragments within the individual sub-fractions of one sample (A3) are shown in fig. 6.

species *Porina salebrosa*, which seems to have provided the most favourable attachment site (see below).

The effect of substrate surface morphology
The influence of substrate morphology was investigated by determining the proportion of en-

crusted fragments of various erect taxa of approximately identical size. Six erect species were selected for this investigation, viz *Porina salebrosa* Marsson, *Floridina gothica* (d'Orbigny), *Columnotheca cribrosa* Marsson, *Onychocella columella* Berthelsen, *Membraniporidra declivis* (Marsson), and *Smittipora? prismatica* (d'Orbigny). Their external morphology is considered to adequately represent the total range of surface morphologies met with in the erect cheilostome fauna. Furthermore, in most samples they make up more than 75% of the erect cheilostomes available as substrate.

In all samples there is a striking proportional difference in the employment of the various species used as substrate (table 1). The significance of this difference is emphasized since it recurs in all samples, irrespective of the sample position in the mound and of the actual number of fragments overgrown. The species most favoured as a substrate is *P. salebrosa* (fig. 8A). Typically, fragments of this species are morphologically slightly compressed with generally overall smooth, though in detail coarse, surface. Deep hollows or pores are relatively scarce on most fragments, as the majority of the orifices are closed by calcareous lamellae. The only regular interruptions of the continuous surface are numerous scars of very small avicularia. Next to *P. sale-*

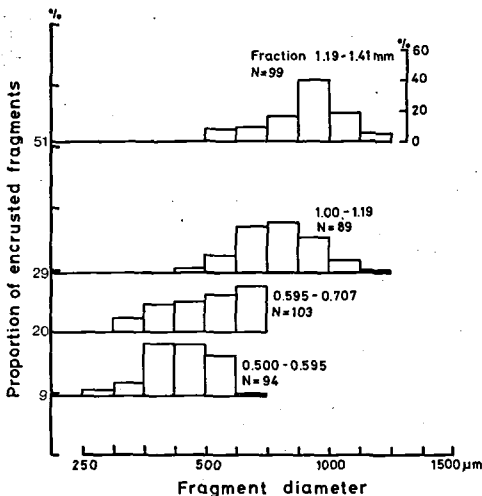


Fig. 6. The stem-diameters of the encrusted fragments within the four sub-fractions of sample A3. Measurements show that the stem-diameter distribution of the fragments without encrustations does not depart significantly from the pattern shown here.

Table 1. Proportion of fragments encrusted of various erect taxa in the 1-2 mm fraction (I), and the ½-1 mm fraction (II). Values in per cent. The proportion was not calculated if less than fifteen fragments of a particular species were observed. This is indicated by (+).

Sample number	Porina salebrosa		Columnotheca cribrosa		Floridina gothica		Onychocella columella		Smittipora? prismatica		Membraniporida declivis	
	I	II	I	II	I	II	I	II	I	II	I	II
A 1	49	8	22	0	20	3	9	+	+	0	10	0
A 2	41	10	18	4	16	4	20	0	+	+	8	+
A 3	57	9	31	2	28	2	11	0	0	0	4	+
A 4	54	14	15	2	16	5	10	0	0	0	+	+
A 5	50	11	23	6	18	1	12	7	11	7	12	0
A 6	68	12	24	4	13	9	21	5	3	4	8	+
A 7	46	13	0	0	25	3	20	0	+	0	7	+
A 8	39	4	25	+	+	0	4	+	+	0	+	+
A 9	29	10	3	+	+	0	4	0	+	0	0	+
A10	20	8	11	0	12	0	11	+	+	0	0	+
A11	26	12	10	0	5	2	0	0	0	0	0	+
A12	37	8	13	2	4	1	0	+	+	0	+	+
A13	11	4	15	0	3	1	+	+	+	+	0	+
A14	18	4	0	0	13	3	4	2	+	+	0	+
A15	30	8	0	0	8	1	0	0	0	0	0	0
B 1	17	0	0	0	0	1	0	+	+	0	0	0
B 2	10	4	0	0	0	+	0	+	+	+	+	+
B 3	16	5	12	0	+	3	0	+	0	+	0	+
B 4	13	3	0	0	0	0	+	+	+	0	+	+
B 5	17	4	8	0	0	0	+	+	0	0	+	+
B 6	15	10	8	0	0	0	0	+	0	+	+	+
B 7	16	7	3	0	0	0	7	+	0	0	+	0
B 8	19	3	3	0	0	+	8	0	0	0	+	0
B 9	27	9	0	9	7	8	0	+	0	0	11	+
B10	20	3	3	4	0	0	8	+	0	0	+	+
B11	37	7	19	0	8	0	5	0	+	2	9	+
B12	46	10	18	0	12	0	0	0	4	2	+	0
B13	26	4	17	0	16	5	13	0	+	5	+	0
B14	10	0	13	+	8	0	0	+	0	+	+	2
B15	23	4	11	0	0	0	9	+	+	+	+	+
B16	8	0	+	0	0	0	+	+	+	+	+	+
B17	18	3	4	0	4	0	+	+	+	+	0	+
B18	6	2	2	0	0	0	0	0	0	0	0	0
B19	9	0	0	0	0	0	0	0	0	0	0	0
B20	16	0	8	0	0	0	0	0	0	0	0	0
B21	10	2	6	0	8	1	0	0	0	0	0	0
B22	11	4	0	0	0	4	0	0	0	0	0	0
B23	11	2	8	2	7	2	0	0	0	0	0	0
B24	25	5	12	3	0	4	16	0	0	0	0	0

brosa, stems of *C. cribrosa* (fig. 8B) were preferred as substrate. Fragments of this species are cylindrical with peristomes arranged in discrete rings. The surface is smooth between the whorls, which are 0.4-0.6 mm apart, and only a few fragments have small pores.

The coilostegoid anascans *F. gothica* (fig. 8C), *O. columella* (fig. 8D) and *S? prismatica* (fig. 8E), on the other hand, were much less used as substrate than the ascophorans described above. In these species most of the frontal wall is formed by a more or less extensive, plane or concave cryptocyst. Owing to the apertures, gene-

rally larger than $0.2 \times 0.2 \text{ mm}^2$, the area of continuous surface, however, does not normally exceed 0.3×0.4^2 . On fragments of *M. declivis* (fig. 8F) plane and smooth surfaces are rarely present. The surface forms a network of convex ridges around large elliptical hollows. *M. declivis* was only rarely exploited as substrate.

Stems of the cyclostome group were preferred as substrate to stems of most cheilostome species (fig. 7). The surface of the cyclostome stems are as a whole characterized by numerous apertures which are, in general, less than 0.1 mm in diameter.

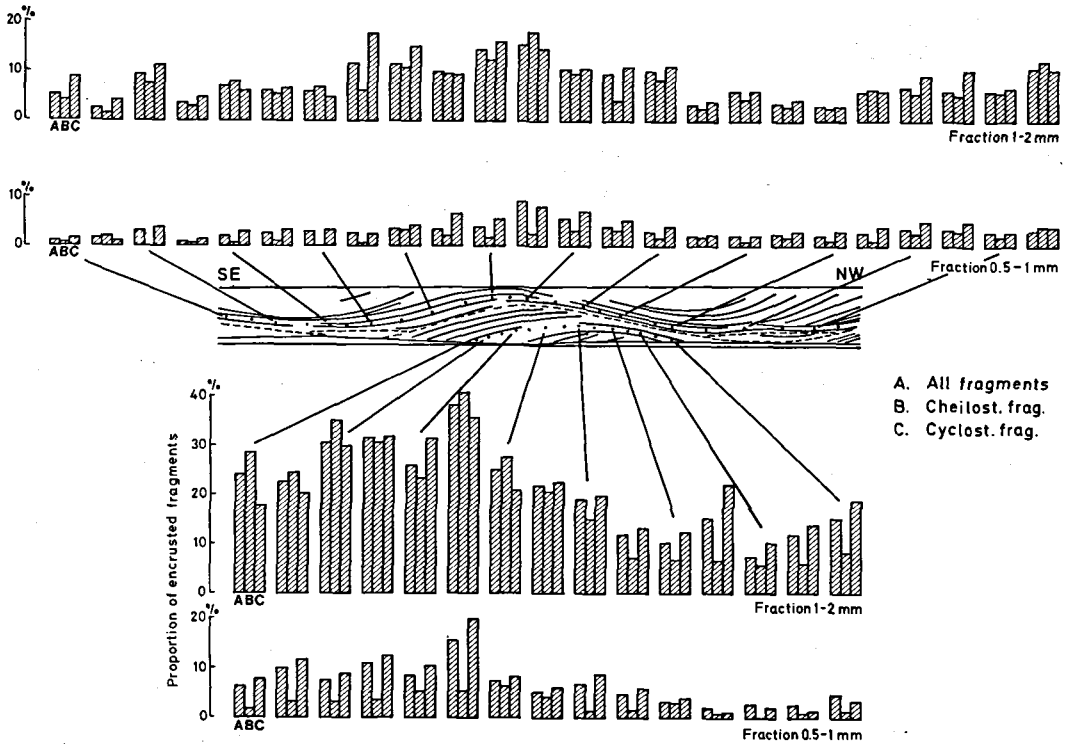


Fig. 7. Variation in the proportion of fragments in the 1-2 mm and 1/2-1 mm fractions encrusted with identified bryozoans.

Discussion

Diameter is obviously an important factor controlling the suitability of the stems as substrate. The minimum diameter of stems normally used for settlement in the bryozoan limestone is between 0.3 and 0.5 mm. Nevertheless, the choice of stems for settlement was to a large extent also influenced by their microtopography. The surface sculpture of *M. declivis*, *F. gothica*, and *S? prismatica*, and to a lesser degree also of *O. columella*, is a network of ridges separated by relatively large hollows. Stems of these species may have appeared to prospecting encrusting bryozoan larvae as a number of small grains, rather than as a large continuous surface. Uninterrupted planar surfaces of these species rarely exceed 0.1 mm². Conversely, the numerous small apertures, typically less than 0.1 mm in diameter, did not diminish the attraction of the cyclo-

stome stems to the encrusting larvae. The reason why *C. cribrosa* was not more heavily exploited may have been because of the very smooth convex surface of the stems. Apparently larvae of many modern species of encrusting bryozoans settle preferentially in concavities or grooves on the surfaces of algae and molluscs, whereas smooth convex surfaces characteristically are avoided (Ryland 1959, 1970; Hayward 1973; Hayward & Harvey 1974).

Hence it appears that stems with an overall smooth, but in detail coarse, surface were preferred as substrate. Intra-particle hollows less than 0.1 mm in diameter did not reduce the proportion of encrustations, whereas stems with hollows larger than 0.2 mm in diameter were unfavourable for settlement. Very smooth convex stems were also avoided.

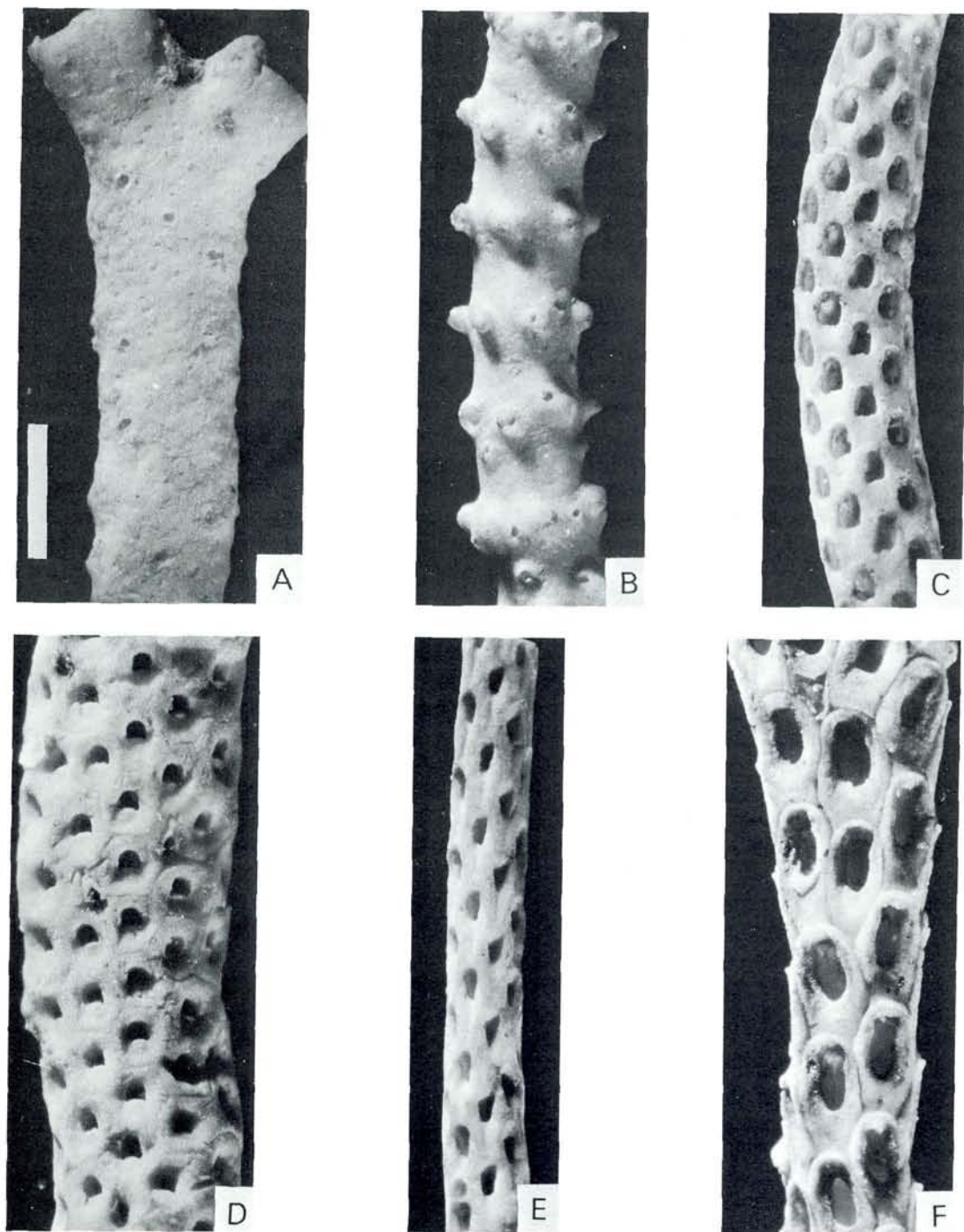


Fig. 8. Representative fragments of the six erect species analysed as substrate. A. *Porina salebrosa* Marsson, B. *Columnotheca cribrosa* Marsson, C. *Floridina gothica* (d'Orbigny), D. *Onychocella columella* Berthelsen, E. *Smittipora? prismatica* (d'Orbigny), and F. *Membraniporidra declivis* (Marsson). Bar scale 1 mm.

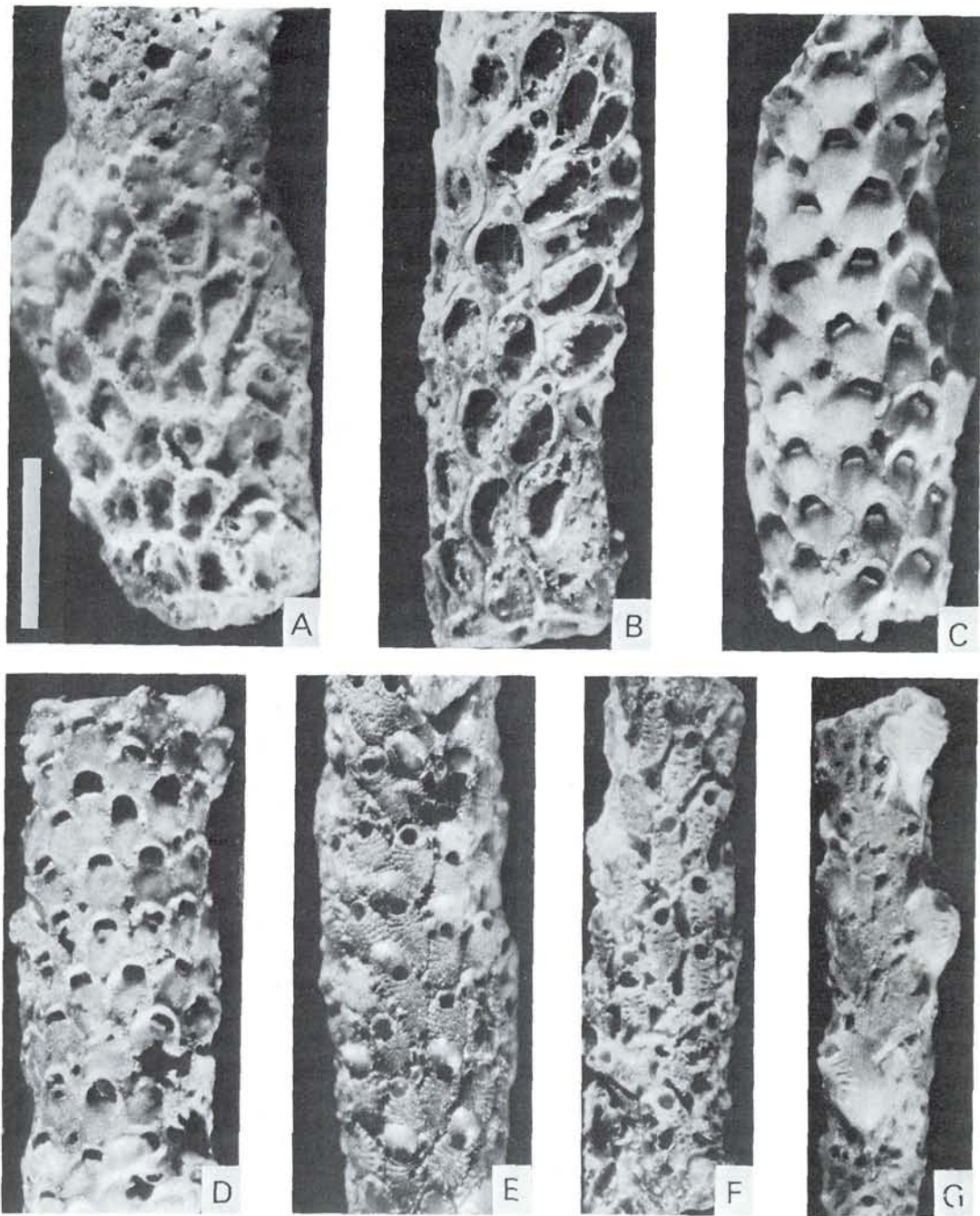


Fig. 9. A. *Ellisina humiliata* encrusting *Porina salebrosa*, B. *Ellisina britannica* encrusting *Porina salebrosa*, C. *Aechmella latistoma* encrusting a cyclostome fragment, D. *Aechmella pindborgi* encrusting *Porina salebrosa*, E. *Pliophloea* cf. *palea* encrusting a cyclostome fragment, F. *Pliophloea?* sp. encrusting a cyclostome fragment, and G. *Andriopora daniensis* Voigt encrusting a cyclostome fragment. Bar scale 1 mm.

Specific substrate preferences

During the investigation presented above it became evident that the encrusting species were not evenly distributed among the various sorts of substrate. Hence six of the most common encrusting cheilostome species were selected for further analysis of a possible specific nature of this substrate preference, viz. *Ellisina humiliata* (Brydone), *Ellisina britannica* (Brydone), *Aechmella latistoma* Berthelsen, *Aechmella pindborgi* Berthelsen, *Pliophloea* cf. *palea* Lang, and *Pliophloea?* sp. (see fig. 9). It should

be noted that *A. latistoma* also is common as unilamellar free plates.

In order to illustrate specific preferences related to surface morphology the available preserved substrates were divided into nine groups (fig. 10). One group comprises all the cyclostome fragments, six groups each include one of the most common erect cheilostome species, and two groups comprise the remaining cheilostomes and other constituents. This part of the study concentrates on the 1–2 mm fraction. Examination of a few samples showed that cyclostome fragments dominate as substrate in the fraction

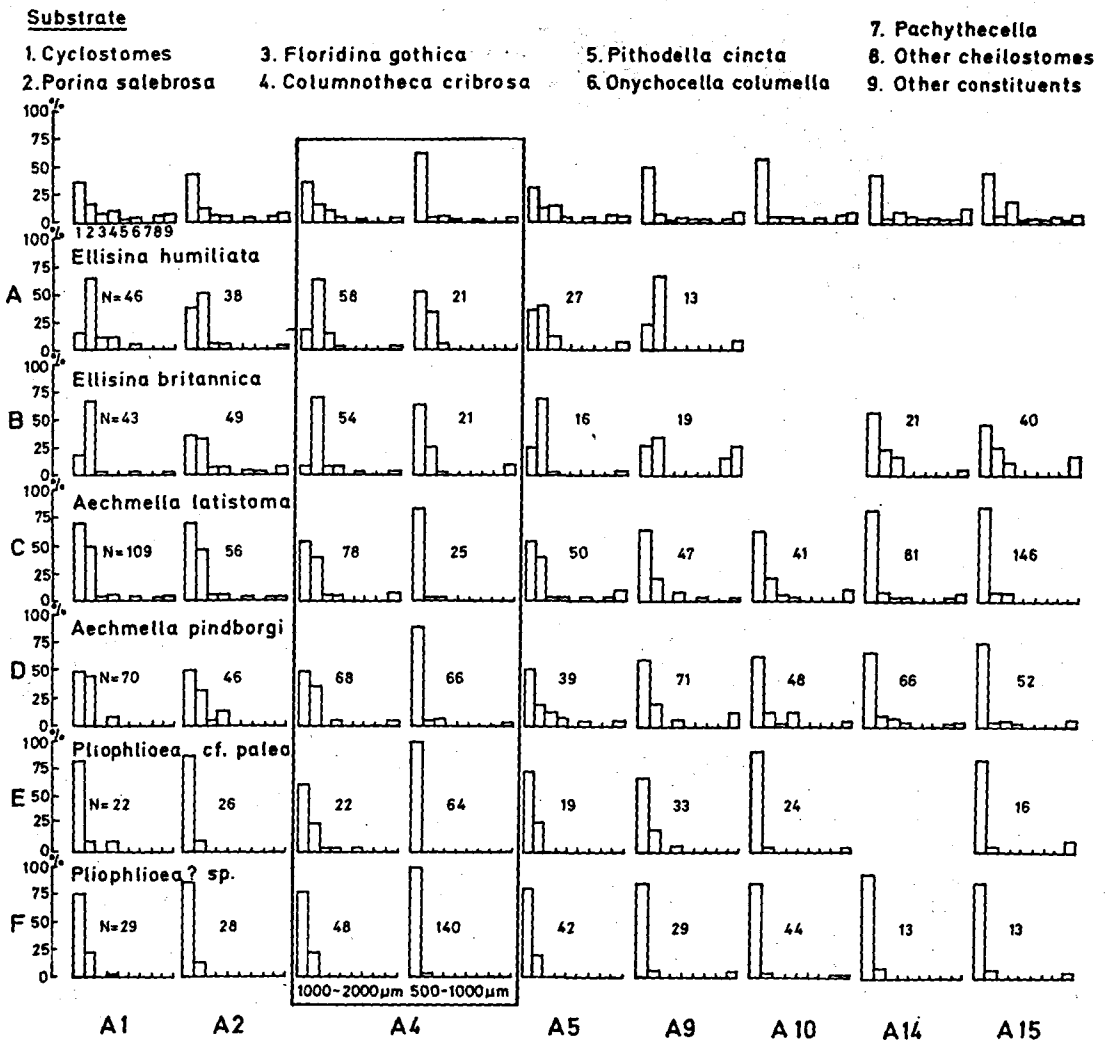


Fig. 10. Substrate choice of six selected encrusting cheilostome species in the 1–2 mm fraction in eight representative samples from various parts of the mound. The ½–1 mm frac-

tion was investigated only in one sample (A4). The uppermost row of diagrams shows the relative importance of the nine substrate groups.

$\frac{1}{2}$ –1 mm to such a degree that a complete analysis of this fraction would contribute little unless the cyclostome group were further subdivided (see sample A4, fig. 10).

The six encrusting species studied clearly show differences in their preference among the nine substrate groups (fig. 10): *E. humiliata* and *E. britannica* are found largely on stems of *P. salebrosa*, whereas *P. cf. palea* and *P?* sp. usually encrust cyclostome stems. In contrast, *A. latistoma* and *A. pindborgi* do not seem to have selected stems of one group in preference to another.

Specific preferences according to substrate size were elucidated by analysing the relative distribution of the encrusting species on each of the two subfractions 1–2 mm and $\frac{1}{2}$ –1 mm (fig. 11). *E. humiliata* and *E. britannica* are found more frequently on stems in the coarse fraction than in the fine, whereas *P. cf. palea* and *P?* sp. occur predominantly in the fine fraction. Furthermore, a distinct difference in the preferences of *A. latistoma* and *A. pindborgi* is apparent, in that the latter attains a higher proportion in the fine fraction than the coarse.

Obviously factors other than substrate size and morphology may have been of importance in the growth site choice of the encrusting bryozo-

ans. An example of larval selection that is not immediately explicable on the basis of substrate size and morphology is *Floridina scutata* (Levinson). Between 50 and 75% of the colonies of *F. scutata* encrust stems of *Floridina gothica* (fig. 8C), a species which otherwise is clearly avoided as substrate (see table 1 and fig. 10). This preference may possibly be related to influence of chemical factors.

Discussion and conclusion

Considering growth site preferences according to both substrate size and substrate morphology the six encrusting species seem to fall into three groups: *Ellisina humiliata* and *Ellisina britannica* settled preferentially on stems of *Porina salebrosa*. Hence the larvae of these species preferred thick stems provided with a smooth, though in detail coarse, surface. *Pliophloa cf. palea* and *Pliophloa?* sp. settled also on stems without marked irregularities, but in contrast to *E. humiliata* and *E. britannica*, these species selected stems with a small diameter. *Aechmella pindborgi* and *Aechmella latistoma* do not show the same distinct substrate preferences as the species mentioned above. The growth site selection of these two species seems to be relatively independent of substrate morphology, but it should be noted that *A. pindborgi* seems to prefer finer stems than *A. latistoma*.

Study of the growth site preferences of the six encrusting species indicates a relationship between the size and the surface morphology of the substrate, and the size of the zooids and the mode growth of the encrusting colony. The zooids of encrusting species *E. humiliata* and *E. britannica* are larger than the zooids of the other encrusting species under study. Moreover, the colonies of these two species closely follow the surface of substrate and even small irregularities in the substrate are reflected in the colony, either as irregularities in its growth pattern or as variations in the size and shape of the zooids. It was shown that *E. humiliata* and *E. britannica* preferred thick stems with a relative smooth surface. Conversely, thin stems seem not to have been unfavourable to species with small zooids, such as *P. cf. palea* and *P?* sp. The zooids of *A. latistoma* and *A. pindborgi* which are intermediate in size compared to the zooids of the two *Ellisina* species and the two *Pliophloa* species,

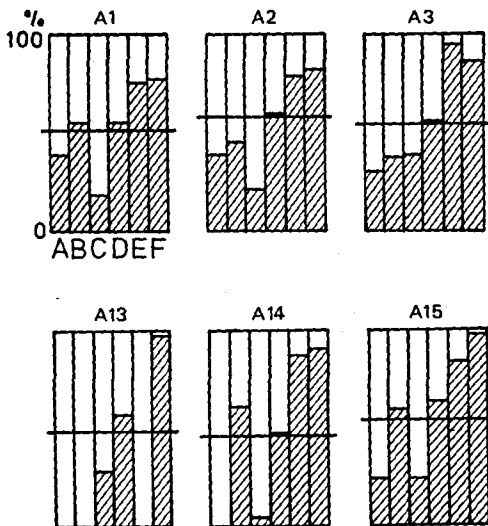


Fig. 11. The relative distribution between the fractions $\frac{1}{2}$ –1 mm (hatched) and 1–2 mm (white) of *Ellisina humiliata* (A), *Ellisina britannica* (B), *Aechmella latistoma* (C), *Aechmella pindborgi* (D), *Pliophloa cf. palea* (E), and *Pliophloa?* sp. (F).

do not always remain attached to the surface of the substrate, and the colony may even extend beyond the substrate. Small irregularities in the substrate are, in general, not clearly reflected in the colony. It is interesting to note that *Jsta. latistoma* and *A. pindborgi* in their growth site preferences seem less dependent on the surface morphology of the substrate than the other investigated species. It should also be mentioned that an increasing part of the encrusting fauna on stems finer than 0.5 mm consist of uniserial and pleuriserial colonies most commonly of the genera *Pyripora*, *Andriopora*, and *Aeolopora* (fig. 9G).

The specific substrate preference recurs in all samples, so it would seem that the differences in the substrate composition and other ecological conditions across the mound therefore have not influenced the settling responses of the larvae of the encrusting bryozoans.

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Dansk sammendrag

Cheilostome og cyclostome bryozoelementer udgør tilsammen mere end 90% af faunaa i Danian bryozoebankerne i Karlyb Klint. Mellem 5 og 30% af den cheilostome andel består af inkrusterende former, som i valget af substrat var fuldstændig afhængig af skeletraster af tidligere generationer af invertebrater; først og fremmest grene af opret voksende bryozoeolonier.

Bryozoegrenenes egnethed som substrat var imidlertid meget varierende, afhængig af deres størrelse og overflademorfologi. Således er andelen af overvoksede grenfragmenter i fraktionen 1.19–1.41 mm mellem fem og ti gange større end i fraktionen 0.500–0.595 mm. I den grove fraktion kan mere end 50% af grenfragmenterne være bevoxede. Sammenhængen mellem overfladens beskaffenhed og grenenes egnethed som substrat viser sig ved at grene med samme diameter, men med forskellige ydre morfologi, ikke har haft samme tiltrækningskraft på bryozoe-larverne. Grene med en jævn, men grovkornet overflade synes at have været mest velegnede som substrat, mens grene med store huller og andre større uregelmæssigheder blev undgået.

Undersøgelser af seks udvalgte inkrusterende arters substratvalg viser desuden at der har eksisteret betydelige forskelle mellem de enkelte arters krav til substratet. Nogle arter foretrak tilsyneladende tynde grene, mens andre forstinsvis slog sig ned på tykke. For andre arter igen synes valget mere at have været afhængigt af substratoverfladens morfologi.

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