

# Relation between currents and the growth of Palaeocene reef-mounds

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The Lower Palaeocene (Danian) reef-mounds of southern Scandinavia are asymmetrical with steep SE flanks and more gently sloping NW flanks. Fragments of mainly arborescent bryozoans make up between 23 and 45% by weight of the sediment. The asymmetrical development of the mounds is a result of differences in the accumulation rate of bryozoans which was controlled by the growth and density of the fauna. Density was relatively high on the SE flank and low on the NW flank. The morphology of individual bryozoan species also changes across the mound. Colonies living on the summit and the SE flank were more robust than colonies living on the NW flank and in the basins. The patterns of morphological and distributional changes are compared with the current regime of the mound reconstructed on the basis of model experiments in a flume. The experiments indicate that the current velocity was highest on the summit and lowest in the basins. Velocities on the flanks were intermediate but considerably higher on the upcurrent SE flank than on the downcurrent NW flank. The robustness of the colonies is positively correlated with the estimated current velocities, whereas the density of the fauna was highest in areas of relatively moderate velocities. The changes in density of the bryozoans, and consequently the asymmetrical growth of the mounds, were controlled by differences in food availability.

□ *Bryozoans, density variation, flume experiments, morphological variation, reef-mounds, water currents.*

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Relations between water movement and the growth and development of patch-reefs and reef-mounds have long attracted interest from both geologists and biologists. The asymmetrical shape and structure of many reefs and mounds indicate that the fauna controlling their development is often strongly influenced by water currents (Lowenstam 1950; Heckel 1974; Wilson 1975; Neuman, Kofoed & Keller 1977; James 1979; Brown & Dunne 1980; Mullins, Newton, Heath & VanBuren 1981; Braithwaite 1982).

In attempts to understand the process determining the shape and growth of these structures most studies have focused on spatial changes in the composition of their faunas. Little work has been attempted to document interpopulation morphologic variation and changes in population densities in a quantitative way. Together with insufficient knowledge of the hydrodynamic conditions, this has generally hampered detailed palaeoecological interpretations.

This study presents such a quantitative analysis on an asymmetrical Palaeocene reef-mound. The current regime is reconstructed and the flow pattern compared with the growth and distribution of the mound fauna. The reef-mounds selected for the study are the Lower Danian bryozoan

mounds exposed in the coastal cliff at Karlby, Denmark. The mounds lack a true framework structure, but there is no doubt that the abundant bryozoans were responsible for the mound-growth. Well-preserved fragments of bryozoans constitute more than 90% of the skeletal debris from the benthic fauna and about 30% of the sediment (Thomsen 1976). The bryozoans originally covered the mounds with a rich but spatially variable growth. There were significant differences in the density and composition of the fauna, and in the skeletal morphology of the individual species between the various parts of the mounds. The flow pattern of sea water to which these differences are related has been reconstructed on the basis of model experiments in a flume.

## Palaeogeography and description of the reef-mounds

The Lower Danian limestones of southern Scandinavia were deposited in an elongate sea which extended in a NW–SE direction across Denmark and southern Sweden (Fig. 1). The sea was bounded to the north by the Fennoscandian bor-

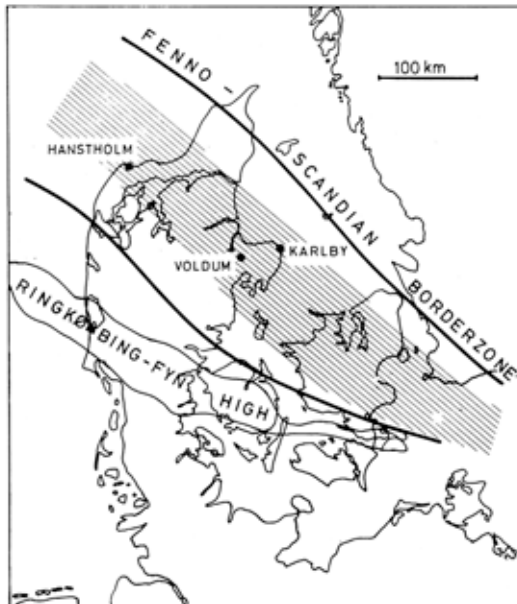


Fig. 1. Palaeogeographic reconstruction of the Lower Danian sea showing the distribution of the mound-forming bryozoan limestone (hatched) and the position of the localities. Map modified from Håkansson & Thomsen (1979).

der zone and to the south by the Ringkøbing-Fyn High (Håkansson & Thomsen 1979). The sea may have continued as a narrow strait across Poland and have been connected to the sea in which the Danian rocks of the Crimean Peninsula were deposited (Pożaryska 1965; Pożaryska & Szczuchura 1968). To the NW it may have had communication to the Atlantic and the Arctic

Oceans through a channel between Scotland and Norway (Thiede 1979).

The bryozoan limestone appears to have been deposited in a more or less central zone arranged lengthwise in the basin. The distribution of the bryozoans was apparently related to the depth and the current conditions of the sea (Håkansson & Thomsen 1979). Calcareous algae are entirely absent in the bryozoan limestone (E. B. Nielsen after Bromley 1979) and deposition probably occurred well below the photic zone (Bromley 1979). Thomsen (1976) suggested a depth range of 80–150 m for the formation of most of the bryozoan limestone.

Seen in two dimensions, as in the NW-SE section of Karlby Klint (Fig. 2), the mounds appear as up to 6 m high and 70 m long streamlined structures with the gradually tapering NW tails constituting more than 60% of the length of the structures. The mounds follow each other successively without intermound facies. They are composed of limestone beds which are thickest on the steep SE flanks and thinnest on the more gently sloping NW flanks and in the basins between adjacent mounds. In consequence of the asymmetrical accretion mound summits migrated progressively in a SE direction.

The three-dimensional shape of the mounds is not known in detail. Earlier field studies in Denmark and southern Sweden indicated that the shapes vary considerably from nearly circular discrete mounds to elongate ridge-like structures with the longest axis running perpendicular to the two-dimensional section shown in Fig. 2 (Brotzen 1959; Cheetham 1971; Håkansson

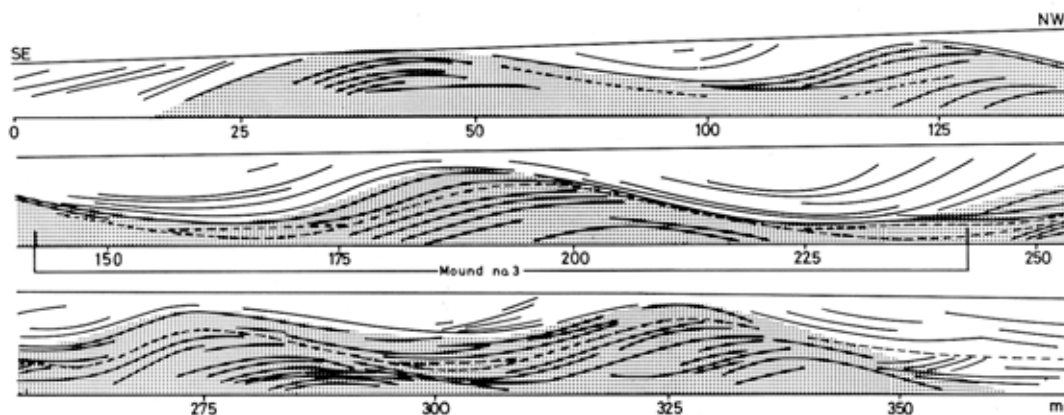


Fig. 2. Sketch of the southernmost 350 m of the coastal cliff at Karlby. The structure of the reef-mounds is outlined by flint layers (solid lines) and marly horizons (dashed lines). Dotted portion of the section shows the transverse shape of the model used in flume experiments (see Fig. 8).

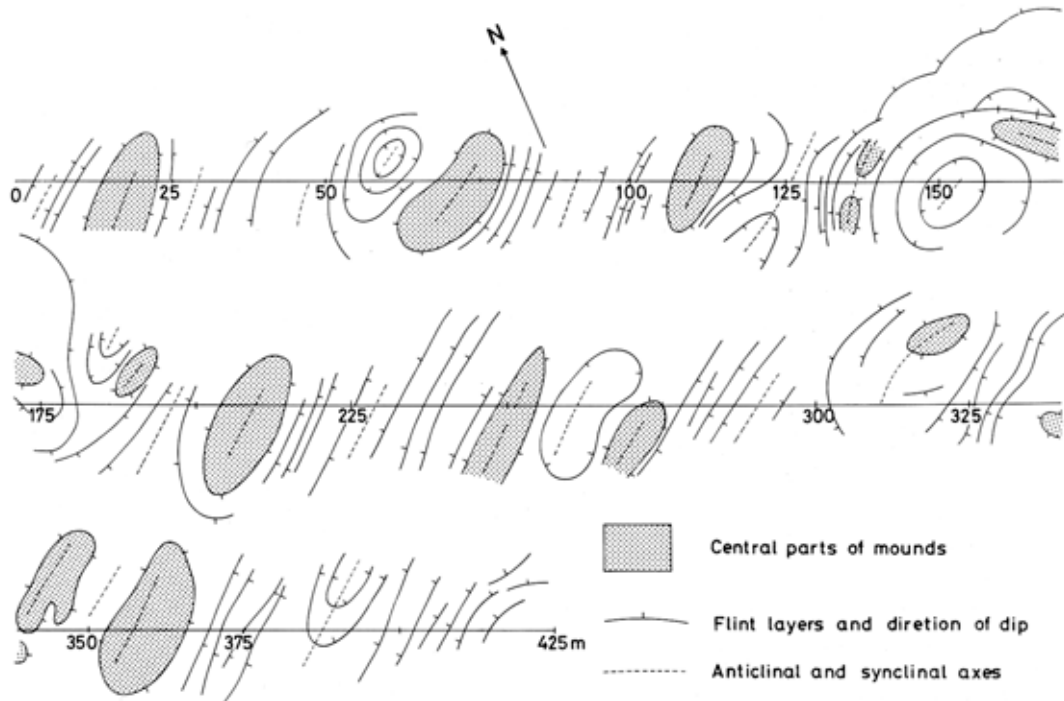


Fig. 3. Map of the coast east of Hanstholm (cf. Fig. 1) showing spatial distribution and shapes of bryozoan reef-mounds. The scale shows the approximate position of the coastline at mean tide level. Point 0 m on the scale is located 75 m east of Hamborg Landingssted.

1971; Thomsen 1976). An abrasion surface revealing horizontal sections of bryozoan mounds (Fig. 3) has recently been exposed on the North Sea coasts east of Hanstholm (Fig. 1). The limestone here is of Middle Danian age, but the mounds – although smaller – are similar in cross-section to those at Karlby. Most mounds at Hanstholm are discrete oval structures, with the longest axis running NE–SW. Some mounds are more elongate ridge-like structures, apparently with undulating crests. The spatial orientation of the mounds at Hanstholm is similar to the orientation estimated for the mounds at Karlby.

### Description of the biotic zones

Thirty-nine samples were collected along two transect lines across a single mound (Fig. 4). The two lines yielded essentially the same information and for brevity some of the results are presented only for one of the transects. Laboratory procedures have been described by Thomsen (1976).

The weakly lithified limestone is composed of 23–45% by weight of marine benthic invertebrates > 125  $\mu\text{m}$  in a finer-grained matrix composed mainly of coccoliths and planktic foraminiferans. Fragments of cheilostome and cyclostome bryozoans constitute more than 90% of the skeletal debris of the benthic fauna. The remaining macrofossils consist of echinoderms, brachiopods, molluscs, octocorals, and benthic foraminiferans. Aragonitic molluscs are not preserved. Spicules of sponges are rare, but abundant flint indicates that siliceous sponges were originally an important group. The preserved fossils show no indication of transportation (Thomsen 1976).

The present study, in general, concentrates on the cheilostome bryozoans which make up between 30 and 50% of the bryozoans. A total of 91 cheilostome species have been recognized. The important species are present in all parts of the mound but a large proportion of the species are rare and no more than 51 species were found in a single sample. Each sample consists of about 1000 cheilostome fragments. Arboresecent colonies which are dominant in terms of weight in-

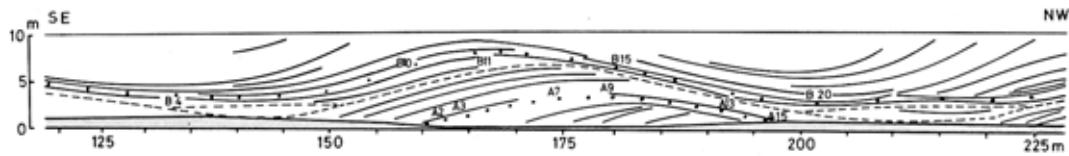


Fig. 4. Cross-section of the investigated reef-mound (no. 3 in Fig. 2) showing the position of the samples.

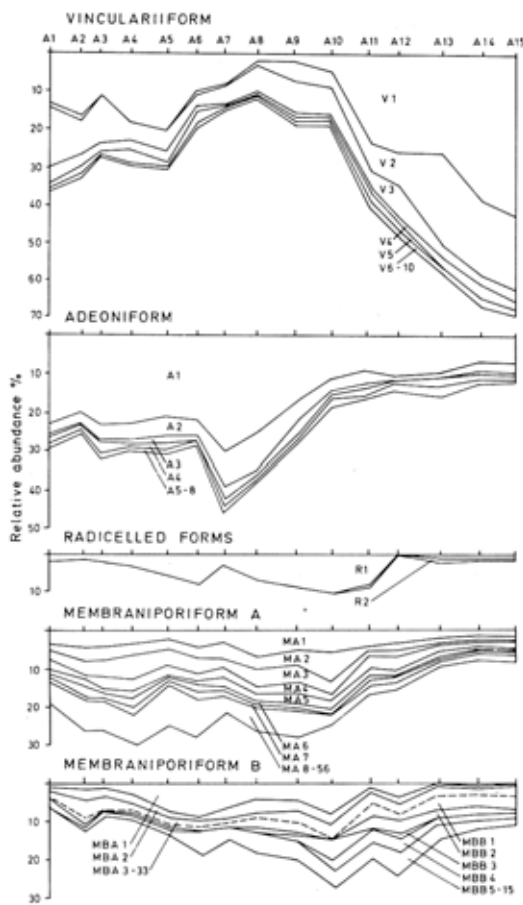


Fig. 5. Variation in abundance (weight equivalent percentages) of species of cheilostome bryozoans in the fraction < 0.5 mm of samples from the A samples series (cf. Fig. 4). The species are grouped according to their growth form and numbered as in Table 1.

clude 20 species. In contrast, the less important group of encrusting colonies is composed of 56 species. Fifteen species have other growth forms (see below).

There is no apparent difference in the diversity of species between samples from various parts of the mound, but differences are present in the

relative abundance of growth forms, in the relative abundance and morphology of individual species, and in the density of the fauna as a whole. For the sake of simplicity four habitats will be considered below: the summit, the steep SE flank, the more gently sloping NW flank, and the basins.

#### Relative abundance of growth forms

Rigidly arborescent colonies with branches that are circular in cross-section (vinculariiform habitus) characterize the flanks of the mound and are especially common on the gently sloping NW flank (Fig. 5, Table 1). In contrast, colonies in which the branches are compressed in cross-section (adeoniform habitus) dominate on the summit. Erect colonies connected to the substratum by flexible fibres (radicelled habitus) and encrusting colonies (membraniporiform A habitus) are most common on the steep SE flank and on the summit. Fragments included in the membraniporiform B group are unattached flat or curved plates. The group is apparently composed of two subgroups. Some plates belong to species that are also found encrusting solid substrates (termed MBA in Table 1 and Fig. 5). Others are found exclusively as unattached plates (termed MBB). Fragments in the first subgroup probably originate from colonies which were encrusting substrates that later disappeared. Their distributional pattern is similar to that of the encrusting colonies included in the membraniporiform A group. Fragments of the second subgroup probably belong to colonies that originally formed either unattached plates or large hollow tubes. This group is most common on the upper part of the NW flank (Fig. 5).

#### Variation in morphology of arborescent species

Variations in the morphology of the most common arborescent species have been treated in

detail by Thomsen (1977), and only a few important observations need to be discussed here.

Some species, like *Floridina gothica*, *Porina salebrosa*, and *Onychocella columella*, have branches in which the mean branch width changes significantly across the mound (Table 2). In other species, such as *Pachythecella lundgreni* and *Columnotheca cribrosa*, the branch width is constant (Table 2). Among the species in which the mean branch width varies significantly there seems to be a consistent pattern of higher means on the summit than on the steep SE flank, and of higher means on the SE flank than at the same horizontal level on the NW flank. The NW flank is, in general, not different from the basin. The populations from the four localities were examined further to test the significance of these differences. Multiple comparison of the means (the Student Newman Keul test, Sokal & Rohlf 1969:240) of each species shows that the differences between the summit, the SE flank, and the NW flank are, for the most part, significant (Table 3). Exceptions do occur but never between the same two localities in both sample transects. There is no significant difference between the NW flank and the basin.

#### Variation in relative abundance and density of arborescent species

The asymmetrical shape and structure of the mounds indicates that their development was controlled by variation in the density of the bryozoans. This variation can be quantified because it is possible to follow individual beds across the mound. Assuming that a bed is deposited within the same time interval throughout the mound, changes within the thickness of a bed are a result of variation in the rate of deposition. The relative accumulation rates of bryozoans can then be calculated by analysing the content of bryozoans in the limestone in the various parts of the mound. Such calculations give rates of accumulation of the SE flank, the summit and the NW flank in the proportions 10:5:3 (Fig. 6B). In order to convert these figures into absolute accumulation rate we have to know the absolute rate of deposition. Bromley (1979), taking account of hiatus within the sequence, suggests a minimum rate of deposition of about 20 cm/1000 years for the SE flanks on the basis of a calculated rock production rate of 10 cm/1000 years by Thomsen (1976). Using this figure the following absolute accumulation rates of bryozoans > 125 µm are

Table 1. List of the most important cheilostome bryozoans in the investigated mound. The species are arranged according to their growth form.

Vinculariiform	
V1	<i>Floridina gothica</i> (d'Orbigny)
V2	<i>Pachythecella lundgreni</i> (Pergens & Meunier)
V3	<i>Columnotheca cribrosa</i> Marsson
V5	' <i>Membranipora</i> ' <i>sparsispina</i> Voigt
V6	<i>Taeniopora articulata</i> Voigt
Adeoniform	
A1	<i>Porina salebrosa</i> Marsson
A2	<i>Onychocella columella</i> Berthelsen
A3	<i>Pithodella cincta</i> Marsson
A4	<i>Membraniporida declivis</i> (Marsson)
Radicelled forms	
R1	<i>Smittipora? prismatica</i> (v. Hagenow)
R2	<i>Stannocella pristis</i> (Levinsen)
Membraniporiform A	
MA1	<i>Achmella pindborgi</i> Berthelsen
MA2	<i>Pliophloea cf. palea</i> Lang
MA3	<i>Pliophloea</i> sp.
MA4	<i>Achmella latistoma</i> Berthelsen
MA5	<i>Membraniporella squamulosa</i> (v. Hagenow)
MA6	<i>Ellisina britannica</i> (Brydone)
MA7	<i>Ellisina reticulata</i> (Levinsen)
Membraniporiform B	
MBA1	<i>Semiescharinella complanata</i> d'Orbigny
MBA2	<i>Puncturiella sculpta</i> (d'Orbigny)
MBB1	<i>Callopora monocera</i> (Marsson)
MBB2	<i>Amphiblestrella elegans</i> (v. Hagenow)
MBB3	' <i>Membranipora</i> ' sp.
MBB4	<i>Thyracella</i> sp.

obtained; 95 g/m<sup>2</sup> per year on the steep SE flank, 50 g/m<sup>2</sup> per year on the summit, and 30 g/m<sup>2</sup> per year on the NW flank and in the basins. If all bryozoans are preserved the absolute accumulation rate is identical to the rate of production of skeletal material, which again is considered to be proportional to biomass and percent coverage of bryozoans.

Variations in the relative abundance of the five most important arborescent species are shown in Fig. 6C. The distributions are generalized from both the A (Fig. 5) and the B sample series. The investigated species are found in all parts of the mound, but in clearly different proportions. Species dominant on the summit are relatively rare in the basins and vice versa. There seems to be a relationship between the distributional pattern and the morphology and morphological plasticity of the various species. Species that are able to alter their branch width significantly (see Table 2) are, in general, more common and widespread than species which are not able to alter their

Table 2. Basic statistics and *F*-ratios for the branch width (in mm) of five cheilostome species from the summit, the SE flank, the NW flank, and the basin, each based on 40 measurements. *F*-ratios are calculated for each transect separately. Sample positions on the mound are shown in Fig. 4.

Species	Origin of samples										<i>F</i> -ratio	
	Summit		SE flank			NW flank			Basin			
	A7	A9	B11	A2	A3	B10	A13	A15	B15	B20		
<i>Porina salebrosa</i>	$\bar{x}$	0.89	0.88		0.86	0.83		0.68	0.69			26.07***
	sd	0.14	0.16		0.11	0.11		0.11	0.14			
<i>Porina salebrosa</i>	$\bar{x}$			0.95			0.86			0.79	0.79	11.41***
	sd			0.12			0.16			0.17	0.18	
<i>Floridina gothica</i>	$\bar{x}$	0.83	0.79		0.73	0.73		0.66	0.59			45.28***
	sd	0.11	0.11		0.10	0.08		0.07	0.07			
<i>Floridina gothica</i>	$\bar{x}$			0.81			0.66			0.54	0.59	92.59***
	sd			0.09			0.08			0.06	0.06	
<i>Onychoella columella</i>	$\bar{x}$	0.88	0.81		0.83	0.78		0.75	0.73			9.06***
	sd	0.12	0.13		0.11	0.09		0.11	0.10			
<i>Onychoella columella</i>	$\bar{x}$			0.89			0.79			0.76	0.72	6.84***
	sd			0.21			0.17			0.17	0.16	
<i>Columnotheca cribrosa</i>	$\bar{x}$	0.71	0.69		0.71	0.70		0.70	0.68			0.93 ns
	sd	0.06	0.08		0.07	0.08		0.08	0.07			
<i>Columnotheca cribrosa</i>	$\bar{x}$			0.73			0.72			0.71	0.72	0.60 ns
	sd			0.07			0.07			0.08	0.09	
<i>Pachythecella lundgreni</i>	$\bar{x}$	-	-		0.61	0.63		0.59	0.61			0.81 ns
	sd	-	-		0.07	0.08		0.09	0.08			
<i>Pachythecella lundgreni</i>	$\bar{x}$			-			0.62			0.57	0.57	0.69 ns
	sd			-			0.09			0.08	0.07	

\*\*\* significant,  $P < 0.001$ ; ns – not significant

Table 3. Multiple comparison among means of branch width of the species of *Porina salebrosa*, *Floridina gothica*, and *Onychoella columella*. Samples not considered significantly different are grouped in braces. Sample positions on the mound are shown in Fig. 4.

Species	Sample number					
<i>Porina salebrosa</i>	A7	A9	A2	A3	A13	A15
<i>Porina salebrosa</i>	B11	B10	B20	B15		
<i>Floridina gothica</i>	A7	A9	A2	A3	A13	A15
<i>Floridina gothica</i>	B11	B10	B20	B15		
<i>Onychoella columella</i>	A7	A2	A9	A3	A13	A15
<i>Onychoella columella</i>	B11	B10	B20	B15		

skeletal morphology. *Pachythecella lundgreni* and other delicate species that cannot change the branch width are abundant only on the lower part of the NW flank and in the basins. Fig. 6D presents estimates on the accumulation rate of the same five species. The estimates are based on the total accumulation rate of bryozoans (Fig. 6B) and the relative abundances of the species concerned (Fig. 6C). All arborescent species,

except for *Pachythecella lundgreni*, were more successful on the SE flank than in any other part of the mound. In fact the overall importance of the various species in the mound community differs considerably from that indicated by their relative abundances. For example, the average relative abundance integrated over all samples is 1.6 times higher for *Porina salebrosa* than for *Pachythecella lundgreni*. In terms of skeletal material, however, *Porina salebrosa* produces 3.2 times more than *Pachythecella lundgreni*, namely 2.3 g/m<sup>2</sup> per year as compared to 0.7 g/m<sup>2</sup> per year.

#### Variation in relative abundance and density of encrusting species

The distributional pattern of the dominant encrusting species is shown in Fig. 7B. The encrusting species are characterized by a relatively much more uniform distribution than the arborescent species. The six most common species occur in approximately equal proportions in all samples.

Nearly all encrusting species used dead branches of arborescent colonies as substrate.

Fig. 6. Variation in abundance across the reef-mound of the most important arborescent cheilostome bryozoans. □ A. Cross-sectional shape of the mound. □ B. Accumulation rate (in  $g/m^2$  per year) of all bryozoans. □ C. Relative abundances (in weight equivalent percentages) of the five most important species. Species are numbered as in Table 1. □ D. Accumulation rate (in  $g/m^2$  per year) of the same species as in C.

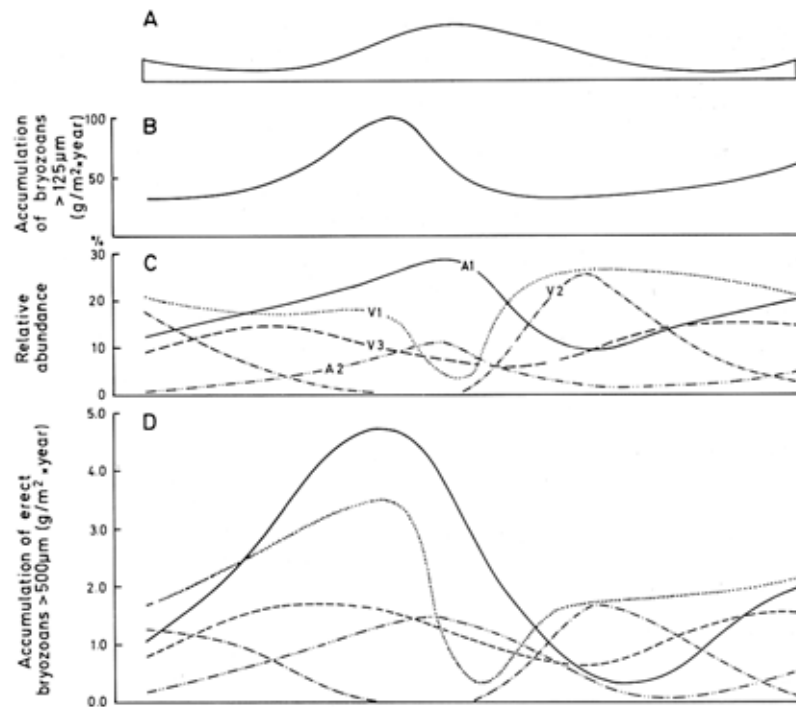
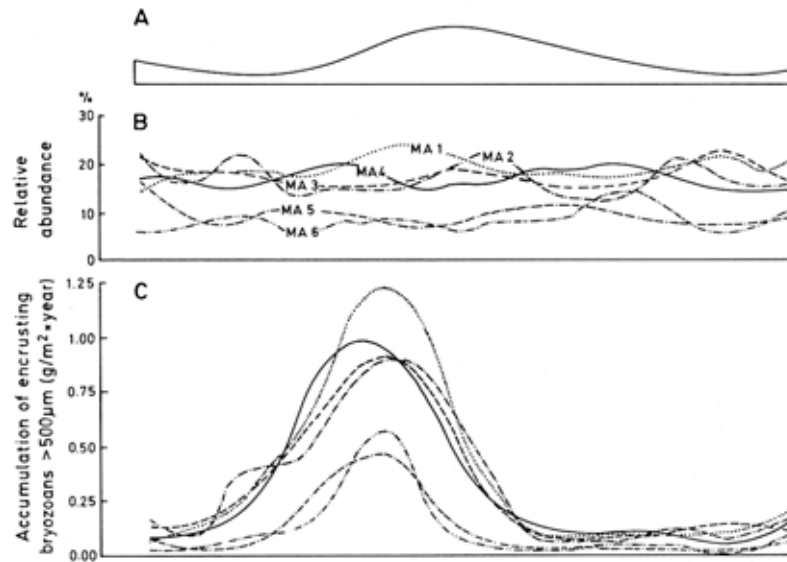


Fig. 7. Variation in abundance across the reef-mound of the most important encrusting cheilostome bryozoans. □ A. Cross-sectional shape of the mound. □ B. Relative abundances (in weight equivalent percentages) of the six most important species. Species are numbered as in Table 1. □ C. Accumulation rate (in  $g/m^2$  per year) of the same species as in B.



Comparison of samples from the SE flank and the NW flank taken at the same vertical level shows that the proportion of branches with an encrusting epifauna is always significantly higher on the SE flank (Table 4). The only pair of samples that are alike in the proportion of epi-

fauna are A8 and A9 from the summit of the mound. Less than 0.5 m below the summit the fraction of encrusted fragments on the NW flank is only half that on the SE flank. It is also of interest to note that the proportion of encrusted branches is significantly higher on the central and

Table 4. Comparison of the proportion of branches with an epifauna on the SE flank and the NW flank. Test from Sokal & Rohlf (1969:608). Sample positions on the mound are shown in Fig. 4.

Sample position on the mound		Vertical distance of samples from mound summit (m)	Proportion of branches ( $d > 0.5$ mm) with epifauna (%)		<i>t</i>
SE flank	NW flank		SE flank	NW flank	
A8	- A9	0.15	13 N = 1559	14 N = 2068	-0.87 ns
A7	- A10	0.40	16 N = 1866	8 N = 2056	5.38**
A6	- A11	0.70	23 N = 2089	6 N = 1759	15.62**
A5	- A12	1.00	16 N = 2272	7 N = 2037	9.42**
A4	- A13	1.40	18 N = 1907	4 N = 2028	14.85**
A3	- A14	1.80	16 N = 2019	5 N = 1271	10.39**
A2	- A15	2.20	15 N = 2080	6 N = 1920	15.64**
A1	- -	2.50	14 N = 2201	-	-

\*\* significant,  $P < 0.001$ ; ns - not significant.

Table 5. Differences in the proportion of branches with an epifauna between the summit (A8 + A9/2) and samples from the two flanks. Differences are tested according to Sokal & Rohlf (1969:608). Sample positions on the mound are shown in Fig. 4.

	SE flank						
	A7	A6	A5	A4	A3	A2	A1
Summit samples (A8 + A9)/2	2.5*	9.0**	2.5*	4.5**	2.5*	1.5ns	0.5ns
	NW flank						
	A10	A11	A12	A13	A14	A15	
Summit samples (A8 + A9)/2	-6.5**	-9.0**	-8.0**	-12.0**	-9.0**	-9.0**	

\*\* significant,  $P < 0.001$ ; \* significant,  $P < 0.02$ ; ns - not significant

upper part of the SE flank than on the actual summit (Table 5), which again has a higher proportion than the NW flank.

On an average the proportion of branches exploited as substrate by encrusting colonies is about three times higher on the SE flank than on

the NW flank. Since the density of arborescent colonies varied with a factor of about 3.3:1 between the same two habitats it follows that the difference in density among the encrusting colonies was in the order of 10:1 (Fig. 7C).

## Reconstruction of the current regime

In order to reconstruct the water movement over the mounds at Karlby, a physical model of the mounds was built in the scale 1:100 and tested in a flume. The model (Fig. 8) represents the south-easternmost 350 m of the section where five mounds are exposed (Fig. 2). The mounds were modelled to be geometrically similar to the originals with the assumption, however, that they are elongate ridge-like structures. This simplification is necessary since the exact shape of the mounds at Karlby is not known. The experiments are described in detail in the appendix. Only the conclusions are presented here, some of which have already been used in an earlier publication (Thomsen 1977).

The asymmetrical shape of the mounds and the asymmetrical distribution of the benthic fauna show that the current direction was parallel to



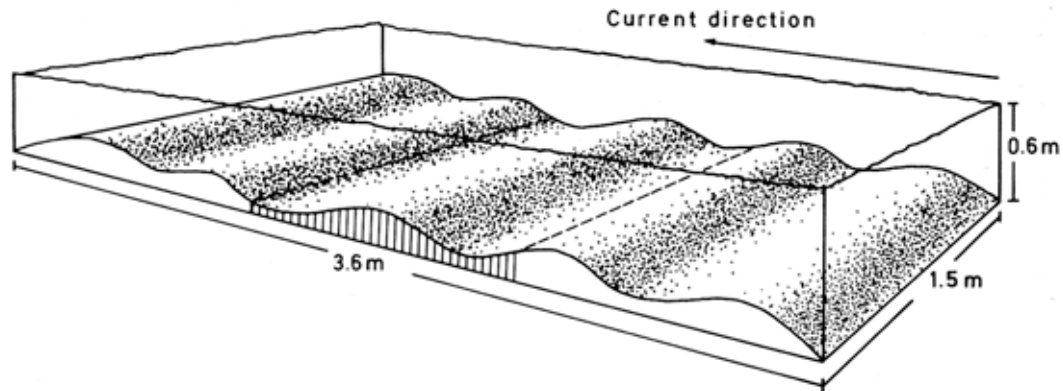


Fig. 8. Sketch of model used in flume experiments. Current velocities were measured across mound no. 3 (hatched).

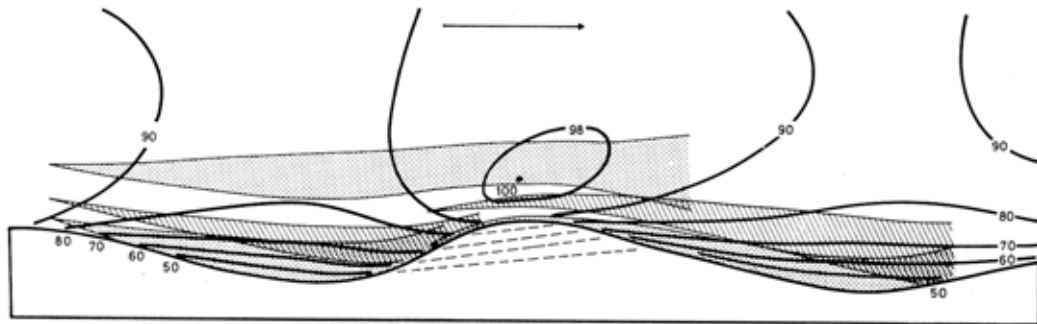


Fig. 9. Current regime across the investigated mound reconstructed on the basis of flume experiments (see appendix). Current velocities relative to the maximum velocity near the summit of the mounds are shown by equal velocity contours. The lines across the mound connect points on the upcurrent and the downcurrent flank with equal bottom current velocities. Motion of dye injected into the water at various points across the mound is shown by the hatched and dotted areas.

the present day profile at Karlby, which, as noted earlier, is perpendicular to the longest axes of the mounds. In the reconstruction of the current regime shown in Fig. 9 the steep SE flanks face the currents. The relative current velocities across the mound will first be considered. Minimum velocities occurred on the lower part of the NW flanks and in the basins. The velocities increased gradually up the SE flank and reached a maximum across the summit. From here the velocity rapidly decreased down the leeward NW flank. Velocities in the basins were approximately 40–50% of the velocity across the summit. Current velocities were higher on the upstream SE flank than in points at the same vertical level on the NW flank. For example, centrally on the NW flank velocity was 60–70% of that on the SE flank.

Water movement was everywhere forward, and there was no recirculation in the lee of the

mounds. The flow was always highly turbulent, but study of dye injected into the water at various places across the mound indicates that the upstream SE flank was the region of most intense mixing (Fig. 9). Faster moving water from higher levels in the flow mixed with slower moving water from the basins. This water then flowed as a smooth continuous layer across the summit.

With the less steep NW flanks of the model facing the currents the pattern of flow across the mound is in several respects different from that described above. First of all the experiments showed that the flow would separate immediately behind the summit, and a separation bubble with recirculating water would develop in the basins. Water here would be slow moving, or stagnant, and the difference in velocity between the summit and the basins, and between the two flanks, would increase as compared to the situation with the steep SE flank facing the currents.

Furthermore, on the upstream flank the experiments indicated a rapid change in velocity from slow moving water in the separation eddy to forward moving water on the upper part of the flank. It seems that the flow regime of the second alternative is completely incompatible with the distributional patterns of the bryozoans presented in the foregoing section, and it will not be considered further.

### Growth and development of bryozoan reef-mounds

The asymmetrical development of the reef-mounds is a result of differences in the abundance of bryozoans across the mound. The main purpose of the present paper is to explain these differences with regards to the environmental parameters of the mound. It would appear from the foregoing sections that currents are here considered to be the most important parameter. A large number of physical factors, such as temperature, salinity, light, depth, rate of sedimentation, and availability of substrate are unlikely to have been responsible for the bryozoan distribution observed in the present study. Temperature and salinity would undoubtedly be essentially constant within an area as small as a single mound. Light and depth can be ruled out because the greatest variation in the bryozoans is between samples from exactly the same horizontal level. The rate of sedimentation of pelagic skeletal material was slow since most of the sediments in the mound are grain-supported. Differences in substrate availability are also unlikely to have been a major factor since the bryozoans formed their own substrate. Larvae settled on fragments of dead colonies of earlier generations of bryozoans.

Consequently in order to explain the changes across the mound in the growth and morphology of the bryozoans we are left with factors related to water movement. In the present study it appears that the distribution of bryozoans may be influenced by water movement in two ways. Firstly, the distribution may be determined by the structural strength of the colonies in relation to the physical force of the moving water. Secondly, water movement may affect the distribution by determining the overall availability of food. Bryozoans are external filter feeders and as such are to a large extent dependent on water movements for food supply (Jebram 1977; Buss

& Jackson 1981). Other influences related to currents, such as removal of waste and oxygenation, are regarded as of subsidiary importance.

### Structural strength and distribution of bryozoans

The role of currents on the distribution of bryozoan growth forms has been discussed by numerous authors (Stach 1936; Berthelsen 1962; Cheetham 1963, 1971; Lagaaij & Gautier 1965; Labracherie & Prud'homme 1967; Schopf 1969; Labracherie 1973; Pouyet 1973). The general correlation between current strength and the growth form of bryozoans recognized by these authors agrees well with the estimated relative current velocities (Fig. 9) and the distribution of growth forms in the reef-mounds at Karlby (Fig. 5). Rigid arborescent forms with flattened branches (adeoniform growth) are, in general, more successful in more rapidly moving water than forms with cylindrical branches (vinculariiform growth). The relative abundance of adeoniform and vinculariiform colonies across the mound therefore suggests that current velocities were highest on the summit and the SE flank. The distribution of erect forms with flexible basis (radicelled forms) and of encrusting forms (membraniporiform A) similarly indicates more vigorous water on the summit and the SE flank.

The variation in branch thickness of *Porina salebrosa*, *Floridina gothica*, and *Onychozella columella* (Table 2) is also positively correlated with the estimated current velocities (Fig. 10). From mechanical considerations (Cheetham 1971; Thomsen 1977; Cheetham & Thomsen 1981) such a relationship could be expected, and a correlation between branch thickness and water movement has also been reported from several other sessile arborescent animal groups (Riedl 1972; Grigg 1972; Schumacher 1973; Chamberlain & Graus 1975; Velemirov 1976; Graus, Chamberlain & Boker 1977; Ditlev 1980).

A decrease in branch thickness in recent bryozoans reported from caves (Harmelin 1973, 1976) is possibly related to the absence of currents, but so far only one study has related branch diameter of bryozoans to actual measurement of current strength. Schopf, Collier & Bach (1980) studied the cyclostome *Heteropora pacifica* from four localities with different current regimes near Friday Harbour, Washington. Bryozoans from four different depths were measured at each locality. They found that the average branch diameter of

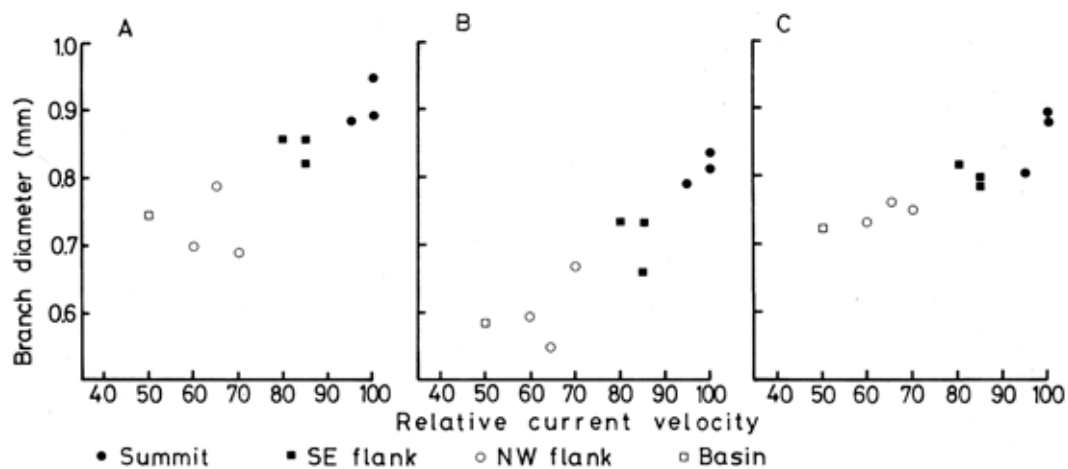


Fig. 10. Mean branch width of *Porina salebrosa* (A), *Floridaia gothica* (B), and *Onychoecella columella* (C) plotted against the estimated current velocities.

*H. pacifica* decreases significantly with depth but at any given depth there is no difference between localities which differ several orders of magnitude in current velocities.

The responses of *C. cribrosa* and *P. lundgreni* from the Danian reef-mounds seem in many ways to be similar to that of *H. pacifica*. *C. cribrosa* and *P. lundgreni* do not change across the reef-mound (Table 2) but both species produced significantly thicker branches at other localities, such as at the poorly fossiliferous Middle Danian locality at Voldum (Table 6). Schopf *et al.* (1980) suggest that the changes in the branch diameter in *H. pacifica* may be a function of differences in light and therefore in food. Such an explanation may also be valid in the case of *C. cribrosa* and *P. lundgreni*, but it cannot directly account for the variation in *F. gothica*, *P. salebrosa*, and *O. columella*. As noted earlier, any explanation related to depth, such as light, can be discounted in the present study. Higher amounts of food on the SE flank and the summit than on the NW flank and in the basins can probably best be explained by the current regime. Therefore the currents may have exerted control over the branch thickness, either directly through the physical force of the moving water, or indirectly by controlling the food supply. The fact that the branches are thickest on the summit and not on the central part of the SE flank where the growth was richest suggests that the first explanation is the most probable (see also next section).

Water agitation seems also to be reflected in the way that the arborescent species are associated. The distribution of the bryozoans was presented in the framework of four different mound habitats: the summit, the upstream SE flank, the downstream NW flank, and the basins. However, the boundaries between the various habitats are transitional (Figs. 6, 7). It seems that the growth of bryozoans across the mound could be regarded as a continuum of populations (cf. Whittaker 1975) rather than as discrete units. Nevertheless, Q-mode cluster analysis of the arborescent species groups together samples in units which closely conform with the empirically formed habitats (Fig. 11). A similar relationship is not present in the encrusting part of the fauna. The dendrogram of the encrusting species (Fig.

Table 6. Branch width (in mm) of *Columnotheca cribrosa* and *Pachytheccella lundgreni* from the Middle Danian locality at Voldum (location, cf. Fig. 1). F-ratios are from comparison between Voldum and all samples in the A sample transect at Karlby.

Species			F-ratio
<i>Columnotheca cribrosa</i>	$\bar{x}$	1.22	100.65***
	sd	0.17	
	N	16	
<i>Pachytheccella lundgreni</i>	$\bar{x}$	0.72	3.32*
	sd	0.10	
	N	25	

\*\*\* significant,  $P < 0.001$ ; \* significant,  $P < 0.05$

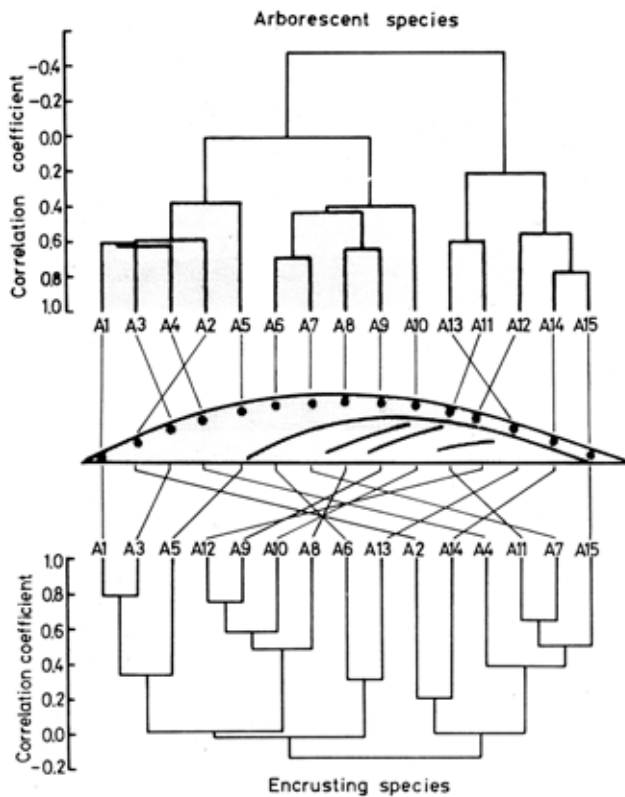


Fig. 11. Q-mode dendrograms of relationships among the 15 samples in the A sample transect. The unweighted-pair-group-method clusterings are based on arcsine-square-root-transformed and standardized weight equivalent percentages of species having at least one abundance of 1.5% or greater or occurring in at least five samples. The upper dendrogram is based on sixteen arborescent species. The lower dendrogram is based on eighteen encrusting species.

11) clusters samples from the upcurrent SE flank (A2 and A4) with samples from the NW flank (A11 and A15). The distinct zonation of the arborescent species and the random distribution of the encrusting ones suggest that the major factors controlling the relative abundance of the two groups were not the same. The most likely factor that would produce a clear pattern in the arborescent species but not in the encrusting ones is current strength. Encrusting bryozoans are not susceptible to the physical force of water movement to the same degree as are arborescent ones. Furthermore, since the encrusting bryozoans mostly settled on dead fragments of erect colonies, they lived in more protected and quieter microhabitats closer to the bottom. Food supply, the other important factor recognized in the present paper, would probably not affect the relative distribution of the two groups differently.

#### *Availability of food and distribution of bryozoans*

The question concerning the differences in the density of the bryozoan fauna between the SE

and the NW flanks (Figs. 6, 7) is important because these differences are responsible for the asymmetrical shape and growth of the reef-mounds. As discussed in the foregoing section it seems possible to explain the changes in the relative abundances of the arborescent species in terms of different mechanical responses of the individual species to the physical force of water movement. However, the direct effect of water, agitation does not seem to have been the most important factor controlling the variation in the absolute abundance. For example, the high density of bryozoans on the upcurrent SE flank compared with the low density on the downcurrent NW flank cannot be explained by differences in the physical stress, as the high density is in the region of high stress (Fig. 12A). Furthermore, the relatively low density on the summit is present in both the encrusting and the erect part of the fauna (Fig. 12B). The decline in the encrusting fauna cannot be directly related to the comparatively high velocities on the summit. Encrusting colonies could not be damaged even by the hydraulic action of the highest current velocities conceivable in the present study. On the

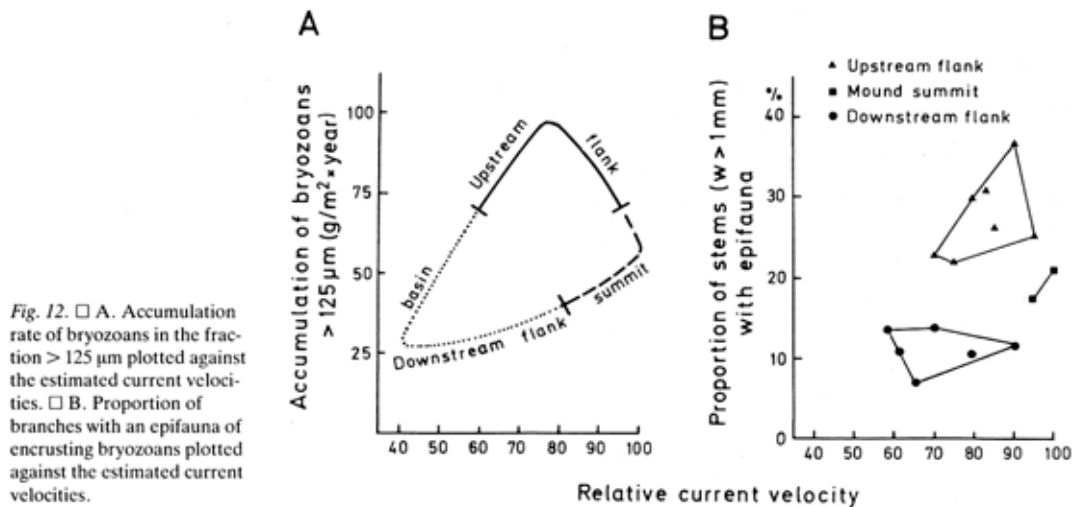


Fig. 12. □ A. Accumulation rate of bryozoans in the fraction > 125 μm plotted against the estimated current velocities. □ B. Proportion of branches with an epifauna of encrusting bryozoans plotted against the estimated current velocities.

other hand, on the summit direct water agitation should not be completely neglected as a possible limiting factor for the density of the erect part of the fauna.

Amongst other factors which are influenced by currents and related to density of filter feeding bryozoans, only food supply seems able to explain the observed differences. There is no doubt that the hydrodynamic conditions are important for the amount of food available for filter feeders (Riedl 1971; Wildish 1977; Lidgard 1981). However, the distributional data from the mounds at Karlby do not unambiguously suggest how these two factors are related in the present case. At least two hypotheses seem relevant to this problem.

According to the first hypothesis the difference in the density of the bryozoans is a result of food depletion. A recent example that may support this hypothesis is given by Buss & Jackson (1981). In a Jamaican coral reef environment they performed a number of experiments allowing measurements *in situ* of food particle depletion as a function of the abundance of suspension feeding sponges and bryozoans. They found that the two groups were highly effective in retaining food particles from the ambient water. The level of food depletion was positively correlated with the abundance of suspension feeders, and with dense growth high levels of depletion might result in competition for food.

An example of significant plankton depletion that in many ways could be parallel to the situation at Karlby has been described by Glynn

(1973a, b). Crossing a 100 m wide reef flat of a coral reef in the Caribbean Sea, the diatom crop of the water entering the reef was reduced numerically by 91% and the zooplankton by 60%. In a similar way, the density of bryozoans on the Danian bryozoan mounds was greatest on the central part of the upstream flank because the water flowing near the sea bottom on this part of the mounds was mixed with food-rich water from the free flow. Downstream from this point water mixing decreased and the food was gradually removed from the water as a result of consumption by the suspension feeding animals. The maximum depletion in the water passing the mound was on the downstream flank and in the basins. Consequently the lowest abundances of bryozoans are found on these parts of the mound.

The Caribbean coral reef environment differs from the Danian bryozoan mound environment in a much shallower water depth for the former (20–40 cm), and it is difficult to ascertain whether the two systems are directly comparable. Because of the deeper water over the bryozoan mounds and because of the turbulent nature of the flow, influx of new nutrients might have occurred in all parts of the mound. Nevertheless, the depletion hypothesis is strongly supported by observations made in the flume experiments (Fig. 9). Study of dye injected into the water at various points across the mound model indicates that food was probably not equally available in all parts of the mound. The observations suggest that near the surface of the upstream flank of the

original mounds, fast-moving food-rich water from relatively high levels in the flow, was forced together with smaller amounts of water from the basins. This water moved as a smooth continuous layer over the summit. Downstream from here the bottom layer gradually moved outward from the mound surface and dissipated, the upper part mixing with fresh water.

The depletion hypothesis explains the distribution of bryozoans independently of differences in current velocities across the mound. This contrasts to the second hypothesis, in which the distribution is interpreted in the light of current action. Increasing water movement normally provides an enriched food supply and is therefore favourable for the growth of filter-feeding animals (Zatsepin 1970; Riedl 1971; Fedra 1977; Wildish 1977; Buss & Jackson 1981). On the other hand, in areas where water is stagnant or movement is very slow the result is often a decreasing population density. These observations are consistent with a high density of bryozoans on the upstream flank and the summit and a low density on the downstream flank and the basins. However, they do not explain why the absolute highest density occurred on the central part of the upstream flank and not on the summit where water velocity was at a maximum. It might be suggested that the relatively low density on the summit is a result of reduced filtering on this part of the mound. It has been shown for scleractinian corals that current strength influences feeding behaviour (Hubbard 1974) and that in many external filter feeding animals, feeding is less efficient if the intensity of the moving water becomes too great (cf. Magnus 1967; Riedl 1971; Mayer 1973; Lidgard 1981). However, this explanation is not convincing, since flow velocities must have been fairly low (a few centimetres per second) in all parts of the mound, and since bryozoans are often particularly abundant in areas with relatively fast ambient currents (Ryland 1970, 1976). That current velocity in itself may not be the most important factor is strongly supported by a comparison of places on the two flanks with the same estimated current velocity. The SE flank always provides a richer growth of bryozoans than the NW flank (Fig. 12).

The general importance of food as a limiting factor is probably also reflected in the fact that the maximum decline in the density of the encrusting species from the SE flank to the NW flank is in the order of 10:1, compared with only 3.3:1 in the erect species. By growing into the

currents, erect species, in the case of competition for food, would tend to gain an advantage over species that encrust substrates directly on the bottom.

Thus, of the three ecological factors – water movement as a physical force, water movement as a transporting agent for food, and food depletion – the density of the bryozoans seems mainly to be controlled by food depletion. The food depletion hypothesis clearly provides the most simple answer to the rather surprising fact that mound growth was most rapid on the upstream flank and not on the summit where current velocity was greatest. Differences in the food supply as a result of differences in the flow velocity may have contributed to the high density on the upstream flank but cannot explain the relatively low density on the summit.

### Palaeoecological conclusions

(1) The asymmetrical Lower Danian Bryozoan reef-mounds were covered with a rich but – in terms of species composition, morphology, and density – variable growth of bryozoans. Density was greatest on the steep SE flank and lowest on the more gently sloping NW flank. The difference in density between the two habitats was for arborescent colonies in the order of 3.3:1 and, for the encrusting colonies, in the order of 10:1.

(2) The environment of the mounds was greatly influenced by currents from the southeast. On the basis of model experiments in a flume the flow pattern and the relative current velocities across the mound are reconstructed. The experiments indicate that a separation bubble downstream of the summit was not present. Mean flow was everywhere forward. Flow velocity was highest near the summit. The velocity in the basins was approximately 40–50% of the velocity on the summit. The velocity on the downstream NW flank was considerably less than the velocity on the upstream SE flank.

(3) The physical force of the currents controlled the relative abundance and the morphology of the arborescent species, whereas the different current velocities are not reflected in the relative abundance of the encrusting species.

(4) The density of bryozoans was highest in areas with intermediate current velocities (the up-

stream SE flank). Habitats with higher (the summit) and lower current velocities (the downstream NW flank) both supported a less dense fauna. Variations in density of the bryozoans were mainly controlled by differences in the amount of available food. Differences in the abundance of bryozoans were responsible for the shape and growth of the mounds.

### Comparison with other patch-reefs and reef-mounds

Modern carbonate sediments rich in bryozoans are prominent on many middle to outer shelves from the tropical to the arctic seas (Wass, Conolly & MacIntyre 1970; Caulet 1971; Milliman 1974; Scoffin *et al.* 1980), but, so far, mound structures comparable to the Danian bryozoan reef-mounds have apparently not been described. It appears to be difficult to find modern counterparts that can be used directly in interpreting the depositional environment of the Danian Mounds, although some of the environmental parameters recognized as important for the development of these mounds also have been discussed in relation to modern build-ups. The effect of low-velocity currents upon reef symmetry and coral distribution are illustrated by Brown & Dunne (1980) in a study of patch-reefs in the Caribbean Sea. A study by Neuman *et al.* (1977) shows that asymmetrical mounds also can be found in deep waters if there are prevailing unidirectional currents. Neuman *et al.* (1977) found numerous discrete carbonate mounds at depths between 600 and 800 m in the Straits of Florida. These mounds differ from the Danian reef-mounds in size, spatial orientation relative to the current direction, and fauna content, which does not include bryozoans. The nature of their growth is only poorly known, but submarine lithification apparently plays an important role. Bottom currents were also recognized to be an important factor in the development of numerous coral mounds found north of Little Bahama Bank (Mullins *et al.* 1981) at water depths between 1000 and 3000 m. Despite great differences in faunal composition, these mounds may be the closest recent analogues to the Danian reef-mounds.

In the geological record, bryozoans, acting either alone or in conjunction with other groups, were important frame-builders in many patch-reefs and reef-mounds, especially of Palaeozoic

age (Cuffey 1974, 1977). The development, growth, and oceanographic regime of these mounds are only known in broad and generalized terms. The model of mound-growth advanced in the present paper for the Danian reef-mounds might provide a useful working hypothesis for these structures also.

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### Appendix

The current regime was reconstructed by model experiments in a free-surface flume which was 12 m long, 1.5 m wide, and 0.6 m deep. Five mounds were modelled in the scale 1:100 (Fig. 8). They were built geometrically similar to the originals, with the assumption, however, that the mounds are elongate ridge-like structures. Studies of flow pattern and current velocities were restricted to mound no. 3. Velocities were measured in fourteen vertical profiles across this mound (Fig. 13). In each profile measurements were made at eleven points located with the closest spacing near the bottom. The current speeds are mean values measured with micropropellers (diameter 6 and 12 mm) over a one-minute period. Experiments were conducted with surface velocities in profile no. 8 varying from 5 to 60 cm/sec. The exact velocities over all parts of the mound could only be determined with micropropellers when the mean velocity in profile no. 8 was above 20 cm/sec. However, differences in the flow velocities with lower currents in the flume could be estimated with a reasonable degree of accuracy by studying the motion of dye injected into the flow at various places across the mound.

In order to ensure that the model-test data applies to the original mounds, it is necessary that the flow in the model and in nature are dynamically similar. The conditions under which similarity of the two systems will be achieved are obtained by analysing the influence of gravity forces and frictional (viscous) forces on the fluid motion (Dailey & Harleman 1966:137). In a system where frictional forces are important, dynamic similarity is realized only when the dimensionless Reynolds number is equal in the model and in nature. If, on the other hand, gravity is an important factor, then the dimensionless Froude number must be equal. The Reynolds number and the Froude number are given by  $R = V L / \nu$  and  $F = V / \sqrt{g L}$ , respectively, where  $V$  is a characteristic velocity,  $L$  is a characteristic length,  $\nu$  is the kinematic viscosity of the fluid, and  $g$  is the gravitational acceleration. Flow in a system with a free surface is generally influenced by both gravitational and frictional forces so that exact dynamic similarity between nature and the model is realized only when both Froude and Reynolds numbers are equal. However, in practice both parameters cannot be held constant unless the scale of the two systems is close to unity. Assuming a water depth of 80 m (Thomsen 1976) and a mean flow velocity over the bryozoan mounds of about 50 cm/sec, the Froude number and the Reynolds number of the original

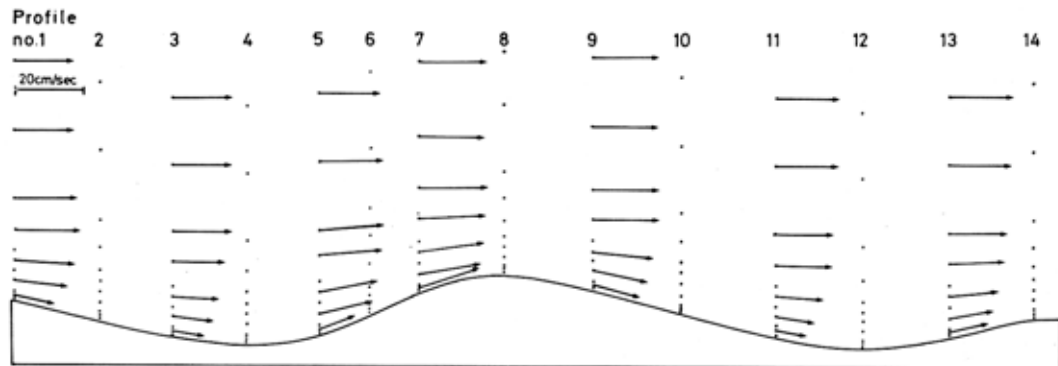


Fig. 13. Transverse shape of mound no. 3 in the model (Fig. 8) showing the location of the fourteen velocity profiles. The velocity was measured at eleven points in each profile. Mean velocities and flow directions of experiment no. 1 are shown for every second profile.

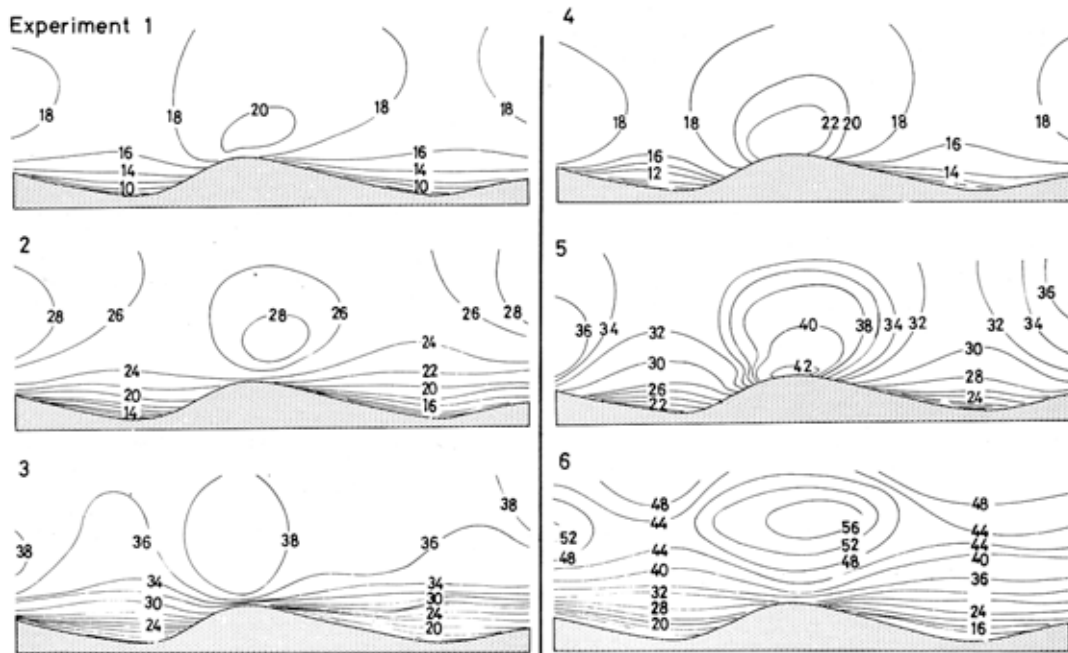


Fig. 14. Current velocity distribution across the mound with 3.5 mm granule as roughness element at different current conditions (experiments 1-3); with smooth bottom surface (experiments 4-5), and with transverse bars as roughness elements (experiment 6). The current velocity distributions (cm/sec) are shown by equal velocity curves.

system are roughly 0.02 and  $4 \times 10^7$  respectively. Equality of the Froude number in the two systems is achieved when the mean flow velocity in the model is about 5 cm/sec. For Reynolds number similarity, however, the velocity should be approximately 50 m/sec. The highest Reynolds number which actually could be obtained in the flume was of the order  $3 \times 10^5$ . Fortunately, experience has shown that in many free-surface flows with significant frictional effects it is necessary to require only Froude number similarity (Daily & Harleman 1966:149). In these cases a reasonable degree of dynamic simi-

larity can be achieved provided that the flow in both nature and the model is highly turbulent with a high Reynolds number, so molecular viscosity effects are negligible.

The question of similarity of frictional effects then becomes one of geometrical similarity of the boundary conditions rather than equality of Reynolds numbers (Daily & Harleman 1966). The flow over the Danian bryozoan mounds falls into this category, because the frictional effects of the bryozoans must have been considerable and because of the high Reynolds number of the flow. Possibly, however, Reynolds number simi-



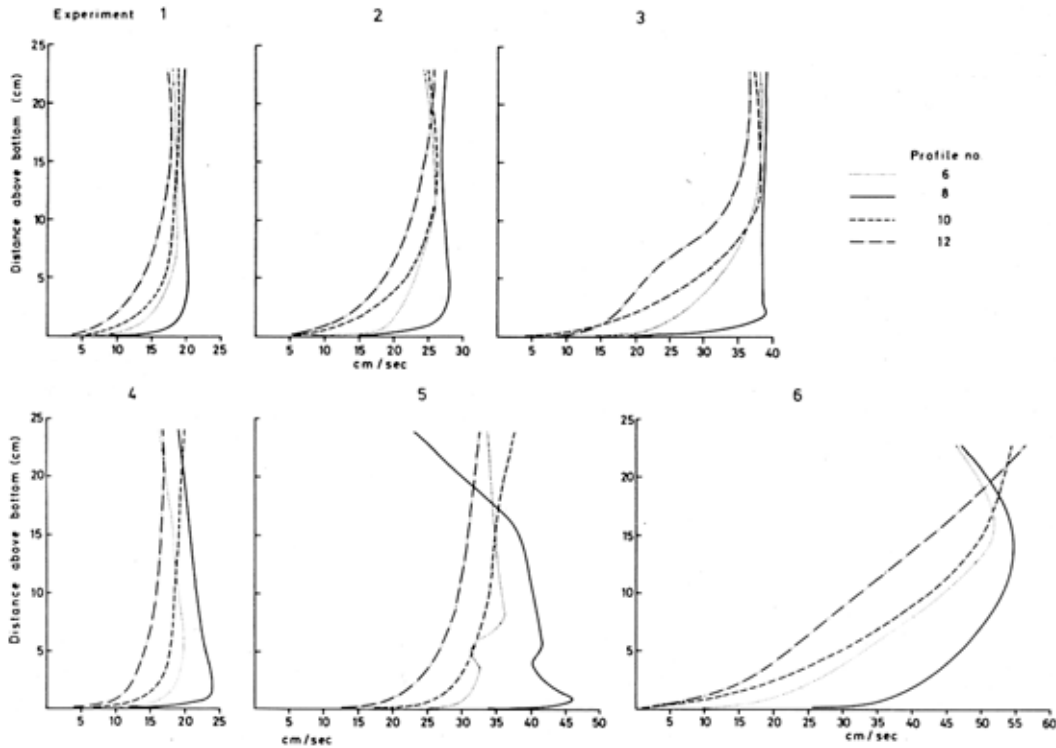


Fig. 15. Velocity profiles (profile nos. 6, 8, 10 and 12) from various parts of the mound under different experimental conditions. Experiments 1, 2 and 3 are with granules as roughness elements. Experiments 4 and 5 are with smooth bottom. Experiment 6 is with transverse bars.

larity should not be completely neglected in this particular case. It cannot be excluded that frictional forces give rise to a separation bubble on the lee side of the mounds if the flow velocity is low (see below).

As noted above, similarity of boundary conditions is important in the type of study conducted here. On the bryozoan mounds the surface irregularities created by the growth of the bryozoans would have been sufficient to extend their effect beyond the laminar sublayer of the flow and thus to disturb the flow in the sea. The surface of the mound was hydrodynamically rough, as can be shown by a few calculations. With sand-grains as roughness element a plane surface is hydrodynamically rough when  $v$ , Karmans number  $K > 1$  (Engelund 1965). This dimensionless parameter is given by the equation  $K = 0.3 k \sqrt{gRl}/\nu$ , where  $k$  is the diameter of the sand-grains,  $g$  is the gravitational acceleration,  $R$  is the hydraulic radius,  $l$  is the slope of the energy grade line, and  $\nu$  is the kinematic viscosity of the fluid.  $\sqrt{gRl} = \bar{U}_f$  in the present study is roughly  $0.05 \bar{U}$ , where  $\bar{U}$  is the mean velocity flow. Assuming a mean velocity over the Danian mounds of approximately 50 cm/sec and an equivalent grain roughness for the growth of bryozoans of 10 cm we have  $K = 0.3 \times 0.1 \times 0.05 \times 0.5/10^{-6} = 767$ . Although this result is subject to a large margin of error, there is no doubt that the surface of the mounds was hydrodynamically rough. A sufficient degree of geometric similarity of the boundary conditions is generally obtained if the surface of the model is also hydrodynamically rough. For grains with a diame-

ter of 3.5 mm as roughness element we have  $K = 0.3 \times 0.0035 \times 0.05 \times \bar{U}/10^{-6} = 52.5 \bar{U}$ . Thus, the surface of the model is hydrodynamically rough when the mean flow velocity in the flume is 0.02 m/sec or higher. This calculation is based on a plane surface but, as will be shown below, it seems also to be valid with a wavy surface.

### Results

Exact dynamic similarity cannot be obtained but the basic requirements for experiments of this kind are fulfilled. Nevertheless, in order to increase confidence in the reconstruction of the original current regime, a number of experiments were performed with various combinations of surface roughness and current velocities. In addition to 3.5 mm granules on the surface, experiments were made with transverse bars with an equivalent sand-grain roughness of 10 mm, and with smooth bottom surfaces. The granule surface is considered to the best approximation to the boundary conditions found in nature.

Study of the flow pattern with a dye streak shows that stagnant recirculating fluids in the basins, separated from the main flow, do not occur (Figs. 9, 13). The mean motion is forward at all locations, although flow appears to become more turbulent near the bottom. This is especially the case in the basins where irregular fluctuations are prominent, and where backward motion may occur momentarily. The mean flow

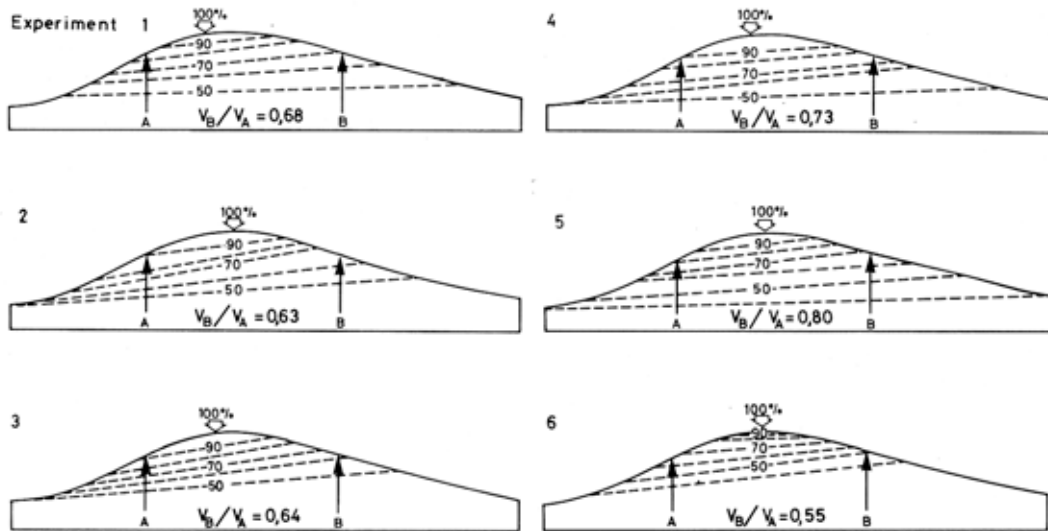


Fig. 16. Current velocities 0.5 cm above the surface of the central part of the mound in percentage of the maximum velocity, which in all experiments occurred near the summit of the mound. The dash lines across the mound connect points on the upstream and downstream flanks with equal bottom current velocities. A and B on the figures are points on the two flanks of the same vertical distance from the summit. The current velocity in B relative to the velocity in A is shown for each experiment.

directions show in Fig. 12 remained virtually constant in all experiments.

Fig. 14 shows the velocity distribution across the mound with 3.5 mm granule surfaces at three different velocity conditions (experiments 1-3); with smooth bottom (experiments 4-5), and with transverse bars (experiment 6). Reliable current velocity determinations with transverse bars could only be obtained with high flow velocity in the flume, because this roughness element, at low velocities, tends to produce high turbulence relative to the forward motion of the fluid. Selected velocity profiles from the various experiments are shown in Fig. 15.

The main interest in relation to the growth of bryozoans is the current-velocity distribution adjacent to the surface of the mound. Fig. 16 shows the flow-velocity distribution 0.5 cm above the surface of the model corresponding to 0.5 m over the real mound. With granule surface (experiments 1-3) the flow velocity in the basins is between 40 and 50% of the velocity on the summit. The velocity on the downstream flank is about 65% of the velocity at a point on the upstream flank at the same vertical distance from the summit. These differences in the flow velocity between the various parts of the model are apparently independent of the absolute current velocity used in the flume. The experiments with smooth surface and with transverse bars show roughly the same relative current distribution. Furthermore, study of the motion of dyes injected into the flow reveals that the near-bottom velocity pattern shown in Fig. 16 remained constant with a mean flow velocity in profile no. 8 as low as 5 cm/sec. This velocity was the lowest used in the present study. The pattern remained unchanged when the mean velocity in profile no. 8 was increased to 60 cm/sec.

On the other hand, it appears clear from Figs. 14 and 15 that the surface roughness influences the vertical velocity distribution in the flume. With a smooth surface (experiments 4, 5) the highest current velocity occurs close to the bottom. When the roughness is increased (experiments 1-3 and 6) maximum velocity is gradually displaced upwards towards the surface of the water.

#### Discussion

The Froude number of the model approached the Froude number in nature when current velocities in the flume were low (about 5 cm/sec). Froude number similarity is generally considered sufficient to ensure that dynamic similarity exists between nature and model if the flow in both systems is turbulent with a high Reynolds number and if the boundary conditions are similar. The first condition of a high Reynolds number was fulfilled in these experiments and it was shown in the previous chapter that the latter requirement was met using 3.5 mm granules as roughness elements when the current velocity in the flume was above 2 cm/sec. While this calculation is based on flow over a plane surface it appears to be valid also in the present case: Experiments 1-3 showed that with 3.5 mm granules as roughness elements and with mean flow velocities in profile no. 8 between 20 and 45 cm/sec, the shape of the velocity profiles (Fig. 15) and the near-bottom velocity pattern (Fig. 16) remained virtually constant, independent of the current velocity in the flume. Furthermore, study of the motion of dye showed that this flow pattern was preserved which velocities as low as 5 and as high as 60 cm/sec. Following Yalin (1971), such constancy of flow pattern independent of the Reynolds number values indicates that the surface in all parts of the mound model was hydrodynamically fully rough.

It should also be noted that a separation bubble was never observed in the model. In general, the points of separation are shifted toward the rear of a body and the separation layer reduced in size with increasing Reynolds number (Rouse 1938:216). Thus, because the Reynolds number of the Danian bryozoan mounds was always much higher than in the model it is evident that flow separation did not take place in nature either. Considering the shape of the mounds this is not surprising.

Hence, it is concluded that the flow pattern obtained in the flume experiments fairly accurately reflects the flow pattern over the original Danian mounds. The low-velocity experiment

with granule surface is considered to simulate the flow pattern in nature most closely (Fig. 14, exp. 1). However, the dissimilarities between the various experiments are relatively small and probably not important in relation to the growth of bryozoans.

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