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CHANGES IN THE MACROFAUNA OF A SHALLOWING SUBTIDAL CHANNEL (SUBATLANTIC, HOLOCENE) IN THE MOUTH OF THE OOSTERSCHELDE (PROVINCE OF ZEELAND, THE NETHERLANDS)

by

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In the deposits of a subtidal channel the macrofauna could be studied from the erosive phase to abandonment and final completely filled channel. The development of the populations of the different species could be studied in deposits formed during several subsequent years. Even the seasonal variations in the macrofauna that lived in the channel are described and explained. During summers much more living specimens were present than during winters, in summers bioturbation is much more intense. At the end of the summer often mass-mortality occurred, evidenced by a shell-layer. Because of the high mortality the fauna varies greatly from season to season and from year to year. The channel was rapidly filled and at the same time the variety in the fauna decreased. The bivalve *Cerastoderma edule* is present in almost the whole sequence, the difference in velocity of growth of this species in the distinguished lithological units is demonstrated.

In channel fill, shoal and 'lagoonal' deposits seasonal layering is present, suggesting that such layering is a normal phenomenon in the mouth of the Oosterschelde.

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Contents:

SAMENVATTING

In een bouwput voor elementen van de stormvloedkering in de Oosterschelde was jarenlang een interessante sequentie te bestuderen. Deze bestond uit sedimenten afgezet in de 16e tot 19e eeuw in een door de ebstroom gedomineerde sublittorale geul (eenheid A-B), en een in de 19e tot 20e eeuw bestaande, door de vloed gedomineerde geul (eenheid C-G). Deze laatste geul werd snel opgevuld. De veranderingen in de makrofauna in die geul werden bestudeerd. Aangezien de geul eerst erosief is komt onderin de geul een rijke, maar grotendeels verspoelde, fauna voor afkomstig uit verschillende milieu's en deels fossiel (tab. 1). Zodra de energie in de geul afnam, stabiliseerde de bodem zodat een aantal dieren zich hier kon vestigen; allochtone elementen komen al snel niet meer voor (tab. 2). De sequentie die dan volgt bestaat uit een afwisseling van zandige, weinig gebiotubeerde lagen met klei-'flaser' die vooral tijdens de winter zijn afgezet en meer kleiige lagen die sterk gebioturbeerd zijn en tijdens de zomer afgezet. Deze coupletten zijn door de hele ontsluiting gemakkelijk te herkennen aan de hand van schelpniveau's die vaak voorkomen in de top van de zomerlagen. Deze schelpniveau's zijn ontstaan doordat tijdens vorstperioden met snelle sedimentatie een groot deel van de fauna massaal stierf. De verschillende soorten reageerden verschillend op de diverse combinaties van kou en snelle sedimentatie zodat steeds een bepaald deel van de fauna massaal stierf en andere dieren de gebeurtenis overleefden. Door deze massasterfte was de hoeveelheid organismen die tijdens de winter in de geul leefde veel geringer dan tijdens de zomer en varieerde de fauna sterk van jaar tot jaar (fig. 4). Uit deze lagen werden monsters genomen en de daarin aanwezige mollusken werden geteld. Aan de hand van jaarringen (tijdens de winter ontstaan) werd de leeftijd van de exemplaren van enkele soorten vastgesteld. Omdat geen erosie optrad konden uit deze gegevens de populaties worden gereconstrueerd welke tijdens elk seizoen in de geul aanwezig waren (tabel 3, 4, fig. 2). Met de snel toenemende sedimentatie verarmde de fauna snel.

De kokkel leefde vrijwel steeds in de geul. De groei van deze soort was tijdens de verschillende stadia van opvulling van de geul sterk verschillend. Met de toenemende ondiepte nam de groei snel toe, de dieren werden in dit gunstiger milieu ook ouder. Extreem grote kokkels (maar ook andere tweekleppigen) komen voor in de afzettingen die werden gevormd toen rond de te graven bouwput een dijk werd gelegd met daarin een inlaat zodat een beschutte lagune ontstond (tabel 5, fig. 5).

Zowel in eenheid D, G als H komt seizoensgelaagdheid voor wat er op wijst dat dit een gewoon verschijnsel is in de monding van de Oosterschelde.

INTRODUCTION

For protection against storm-floods from 1953 onwards many new dikes and barriers have been built in the province of Zeeland. The major project is the construction of a nine kilometres long storm-surge barrier in the mouth of the Oosterschelde (fig. 1). This barrier will be constructed from separate pillars which are built at an artificial island on the intertidal shoal 'Neeltje Jans'. For this purpose a 15 m deep constructionpit was dug, divided in four compartments. During several years the Sedimontology Division of the Institute of Earth Sciences of the State University of Utrecht carried out detailed sedimentological research in one of the compartments. Part of the results is published in van den Berg (1980, 1981) and Visser (1980). In 1979 Dr. S.-D. Nio (Instituut voor Aardwetenschappen, Utrecht) kindly invited me to cooperate in this project by studying the macrofauna of the exposed deposits, particularly those in a rhythmic layered unit in which seasonal layering seemed to be preserved. The paleontological data acknowledged that the layers represent different seasons.

Van den Berg (1980) gives a good introduction to the pit. Seven lithostratigraphic units were

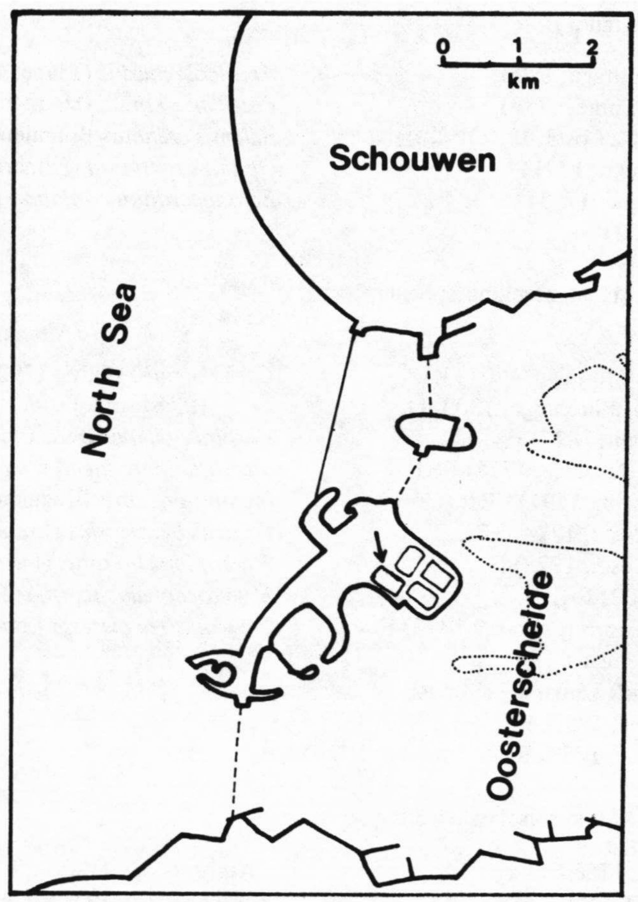

Fig. 1. Position of the exposure (arrow) in the mouth of the Oosterschelde. The interrupted line indicates the position of the future storm-surge barrier, the thin line is a temporary bridge.

Fig. 1. Ligging van de ontsluiting (pijl) in de monding van de Oosterschelde. De onderbroken lijn geeft de ligging aan van de toekomstige stormvloedkering, de dunne getrokken lijn is een werkbrug.

recognized and named A to G. On top of unit G deposits formed after the construction of the dike around the pit are present, herein referred to as unit H. The lowermost units A and B were formed after the 16th century until the 19th century in an ebb-dominated subtidal channel. They exist of megacrossbedded and flaser bedded sands. The units C, to G were formed in the second half of the 19th and in the 20th century in a flood-dominated subtidal channel. The channels ran more or less parallel to the SW-NE wall of the pit.

Unit C is a basal lag deposit. Unit D exists of horizontally, rhythmic beds, deposited during abandonment of the channel. Unit E is a clayey layer which filled the isolated remnant of the channel. Unit F was deposited in a depressed area between intertidal shoals and unit G in small intertidal channels. The sequence shows the gradual abandonment and shallowing of the channel (van den Berg, 1980). In this paper the macrofauna of units D to H will be discussed.

Because many hydrographical maps of the area exist, covering the whole depositional history of the sediments exposed in the pit, and because the sediments were studied in detail the physical conditions during the deposition of the sediments and during growth of the organisms are known very well.

A typical fauna (typische fauna)

Mysella bidentata (Montagu, 1803)
Cerastoderma edule (Linné, 1758)
Spisula subtruncata (Da Costa, 1778)
Angulus fabulus (Gmelin, 1791)
Macoma balthica (Linné, 1758)
Abra alba (Wood, 1802)

Arenicola marina (Linné, 1758)
Pectinaria koreni (Malmgren, 1965)
Balanus crenatus Bruguière, 1792
Ophiura texturata (Lamarck, 1816)
Echinocardium cordatum (Pennant, 1777)

B incidentally washed in (incidenteel ingespoeld)
B1 open sea (open zee)

Tellimya ferruginosa (Montagu, 1801)-RL
Mactra corallina cinerea Montagu, 1803-RL
Spisula elliptica (Brown, 1827)-F
Spisula subtruncata (Da Costa, 1778)-FRL
Angulus fabulus (Gmelin, 1791)-FRL
Angulus tenuis (Da Costa, 1778)-FRL
Donax vittatus (Da Costa, 1778)-F
Abra alba (Wood, 1802)-FRL
Venerupis aurea senescens (Cocconi, 1873)-F (Pleistocene-Eemian)
Petricola pholadiformis Lamarck, 1818-RL
Barnea candida (Linné, 1758)-FR
Zirfaea crispata (Linné, 1758)-R

Corbula gibba (Olivi, 1792)-F (Pleistocene)
Euspira poliana (Della Chiaje, 1830)-FR
Membranipora membranacea (Linné, 1758)-FRL
Balanus crenatus Bruguière-FRL
Pagurus bernhardus (Linné, 1758)-F
Macropipus holsatus (Fabricius 1798)-L
Myoxocephalus scorpius (Linné, 1758)-L
Pleuronectes platessa Linné, 1758-F

B2 Oosterschelde tidal flats (Oosterschelde wadden)

Mytilus edulis Linné, 1758-F
Ostrea edulis Linné, 1758-F
Cerastoderma edule (Linné, 1758)-FRL
Macoma balthica (Linné, 1758)-FRL
Scrobicularia plana (Da Costa, 1778)-F
Littorina littorea (Linné, 1758)-FR

Littorina rudis (Maton, 1797)-F
Peringia ulvae (Pennant, 1777)-FR
Retusa obtusa (Montagu, 1803)-F
Suaeda maritima (L.) Dum.
Aster tripolum L.
Triglochin maritima L.

B3 brackish water (brakwater)

Cerastoderma glaucum (Poiret, 1789)-F
Littorina rudis forma *tenebrosa* Montagu-F

Hydrobia ventrosa (Montagu, 1803)-F
Rissoa membranacea (Adams, 1800)-F

B4 freshwater (zoetwater)

Pisidium sp. - F
Bithynia tentaculata (Linné, 1758)-F
Potamogeton sp.
Nymphaea alba L.
Ranunculus (*Batrachium*) sp.

Menyanthes trifoliata L.
Hippuris vulgaris L.
Scirpus cf. *lacustris* L.
Hydrocotyle vulgaris L.
Carex sp.

B5 terrestrial (land)

Vallonia sp. - F
Catinella arenaria (Bouchard-Chantereaux, 1837)-F
beetle remains

Atriplex sp.
Alnus glutinosa (L.) Vill.

Table 1. Origin of the flora and fauna encountered in unit D, F=fossil, R=recent, L=incidentally living in the channel.

Tabel 1. Herkomst van de flora en fauna aangetroffen in eenheid D, F=fossiel, R=recent, L=incidenteel levend in de geul.

UNIT D: FOSSIL CONTENT WITH SPECIAL EMPHASIS ON THE BIVALVES

Methods

In this well-documented sequence the development of the macrofaunal populations could be studied in detail because the fill-up of the channel is not disturbed by erosion. In the lower part of the rhythmic interval from each seasonal layer a sample was taken. Because not all the samples are of an equal size the numbers of specimens are converted towards a standard sample size of 10 litres or about 25 kg.

The age of the bivalves is estimated from their size and by counting the number of yearrings. These yearrings are darker lines on the surface of the shell, formed during a period of reduced growth. They are generally known as winterrings but according to Jones (1980) at least in several species of bivalves also during the spawning phase such rings can be formed. Three species with well-developed winterrings are studied, in *Macoma balthica* and *Cerastoderma edule* no spawning rings are known, in the specimens of *Spisula subtruncata* from the channel the spawning rings are not developed.

The winterrings are weakly developed in specimens from the channel (unit D), in the younger deposits from a shallower environment (units G, H) the rings are well-developed.

General description of the rhythmic beds

The beds in this sequence are laterally persistent and composed of fine sand with alternately a higher or lower admixture of fine-grained components. The muddy layers are laminated and highly bioturbated. The sandy layers show flaser bedding and sedimentary structures are better preserved because of reduced bioturbation. These sandy and muddy layers form couplets which represent one year, the sandy layers being formed mainly during the winter, the muddy layers mainly during summer (van den Berg, 1980, 1981).

Origin of the fossils

The base of unit D is marked by a shell-lag deposit. The fossil content of the lag is varied because of the variable origin (qua environment and age) of these fossils. A large part of the fossils in the lag is reworked from older deposits cleared away by the channel at the present location, another part was transported towards the location through the channel and part of the fossils lived in the channel. Among the allochthonous fossils are animals and plants from open sea, tidal flat, brackish water, freshwater and terrestrial environments (table 1).

When the erosive stage of the channel had ceased it began to fill up rapidly with fine-grained sediments in which soon a fauna settled, existing of a mixture of species from open sea and tidal flat environments. As can be seen from table 2 the number of species typical for the channel increases

couplet	1	2	3	4	5	6	7	8	9	10	11
typical	7	8	10	8	8	8	7	9	7	5	3
incidental	26	13	10	2	2	3	6	4	2	1	1
total	33	21	20	10	10	11	13	13	9	6	4

Table 2. Number of species of which remains were found in the channel.

Tabel 2. Aantallen soorten waarvan overblijfselen werden aangetroffen.

towards couplet 3 and then gradually decreases again. From the base onwards the number of incidentally washed-in species decreases rapidly what can be explained by a decreasing current velocity in the channel. When the regime changed from erosional to accretional also the source of the sediment changed. From now onwards it was derived mainly from superficial layers in the immediate neighbourhood. Only the easily transported plant-remains were brought in from farther away.

Composition of the fauna

In the deposits remains are found of a fauna poor in species but rich in individuals (table 3).

A	couplet	1	2		3		4		5		6		7		8		9		10		11
	season	s	w	s	w	s	w	s	w	s	w	s	w	s	w	s	w	s	w	s	w
d	*Arenicola marina*																				
d	*Pectinaria koreni*	+	++	+	++	+	+	+	.	+	.	+	+	+	+	+	+	.	.	.	.
s	*Balanus crenatus*	+	+	.	+	+	.	.	.	.	.	+	.	.	+	+	.	.	.	.	+
x	*Ophiura texturata*	++	++	+	++	+	++	+	+	+	.	+	+	+	+	+	+	.	.	.	.
d	*Echinocardium cordatum*	+	++	.	+	+	.	+	+	+	.	+	+	+	+	+	++	+	++	+	+
s	*Mysella bidentata*	50	172	26	15	5	17	5	28	2	.	92	48	8	2	10	6	.	+	.	.
s	*Cerastoderma edule*	.	.	.	62	244	125	1	1	15	.	6	.	80	6	853	2	.	+	.	+
s	*Spisula subtruncata*	8	48	5	28	3	56	123	144	4	.	30	.	34	4	3	.	.	+	.	.
d	*Angulus fabulus*	3	1	6	5	.	1	.	.	3	.	.	.	.	.	.	.	.	.	.	.
d	*Macoma balthica*	6	2	360	179	2	9	6	1	5	.	740	8	2	4	.	8	.	+	.	+
d	*Abra alba*	11	2	38	41	3	1	1	.	.	.	242	.	.	.	18	4	.	.	.	.

Table 3. Frequency of each species of the typical fauna. In column A the mode of feeding of each species is indicated: s=suspension feeder, d=deposit feeder, x= different modes of feeding. In the other columns the couplets and seasons are indicated: s=summerlayer, w=winterlayer. For molluscs the numbers were corrected, two valves representing one individual. +=present, ++=present in large quantities.

Tabel 3. Aantal individuen van elke soort van de typische fauna. In kolom A is de manier van voeden van elke soort aangegeven: s=suspensievoeder, d=sedimentvoeder, x=verschillende manieren van voeden. In de andere kolommen zijn de jaardoubletten en de seizoenen aangegeven: s=zomerlaag, w=winterlaag. De aantallen mollusken werden gecorrigeerd, twee kleppen tellen als één individu. += aanwezig, ++=aanwezig in grote aantallen.

Among the typical species only few allochthonous fossils occur. At least two worms are present: *Arenicola marina* with U-shaped dwelling tubes in the basal part of unit D and *Pectinaria koreni* of which the conical dwelling tubes are found in life position, the larger opening downwards. This latter species is most abundant in the lower part of the channel and is not found above couplet 9. On the shells sometimes barnacles, *Balanus crenatus*, are present. Extremely well preserved specimens of the brittle star, *Ophiura texturata*, are present as well. The species is most abundant in the lower part of the channel and is absent above couplet 9.

Very abundant are the press structures of the heart urchin, *Ecchinocardium cordatum* (pl. 1, pl. 2, fig. 1), of which also complete specimens and isolated spines occur. The species is present in the whole unit.

The shells of bivalves are extremely well preserved, ligament and periostracum are still present and the shells are found in life position. Even burrows, especially of the common cockle, *Cerastoderma edule*, are preserved as V-shaped impressions produced by the foot of the animal. The burrows of *Spisula subtruncata* are preserved mainly in the uppermost part of the muddy layers and are also V-shaped. In the lowermost part of unit D the bivalves *Spisula subtruncata, Angulus tenuis, Abra alba* and *Mysella bidentata* are present with many specimens. Higher in the sequence species appear that are typical for shallower environments, first *Macoma balthica* and later also *Cerastoderma edule* (in couplet 3). Gastropods do not occur.

Observations on the fauna

By means of the winterrings the age of the specimens of some species of bivalves was defined. Of course all living animals burrowed upwards through the newly settled sediment. Since after dying the specimens are not removed by subsequent erosion the amount of specimens in the population could be estimated for all the subsequent seasons. This was done for three species of bivalves (table 4), the results are represented in graphs (figs. 2 and 4). Fig. 2 represents the development of the populations of each species. As can be seen, up to three generations may occur at the same time in a

MACOMA BALTHICA

1923	8/0	8/8							
1922	4/0	4/4							
1921	747/738	9/8	1/1						
1920	3/3								
1919	4/2	2/1	1/1						
1918	28/12	16/8	8/8						
1917	558/360	190/177	13/0	13/9	4/1	3/0	3/1	2/0	2/2
1916	8/6	2/1	1/0	1/1					
1915	2/0	2/0	2/0	2/1	1/0	1/1			
	summer	winter	summer	winter	summer	winter	summer	winter	summer
	1	2		3		4		5	

SPISULA SUBTRUNCATA

1922	41/34	7/4	3/3						
1921	20/20								
1920	13/3	10/0	10/10						
1919	65/63	2/1	1/1						
1918	259/3	256/53	203/60	143/143					
1917	8/0	8/5	3/0	3/3					
1916	94/8	86/83	3/3						
1915	89/0	89/0	89/0	89/12	77/8	77/77			
	summer	winter	summer	winter	summer	winter	summer	winter	summer
	1	2		3		4		5	

CERASTODERMA EDULE

1923	854/852	2/2							
1922	82/80	2/2							
1921	6/2	4/0	4/0	4/4					
1920	19/15	4/0	4/4						
1919	2/1	1/1							
1918	369/244	125/125							
1917	62/0	62/62							
	summer	winter	summer	winter	summer	winter	summer	winter	summer
	1	2		3		4		5	

Table 4. Absolute numbers of living and dead specimens respectively during each season. The first season for all specimens is the summer during which they were born.

Tabel 4. Absolute aantallen van respektievelijk levende en dode exemplaren tijdens ieder seizoen. Voor alle exemplaren is het eerste seizoen de zomer waarin ze werden geboren.

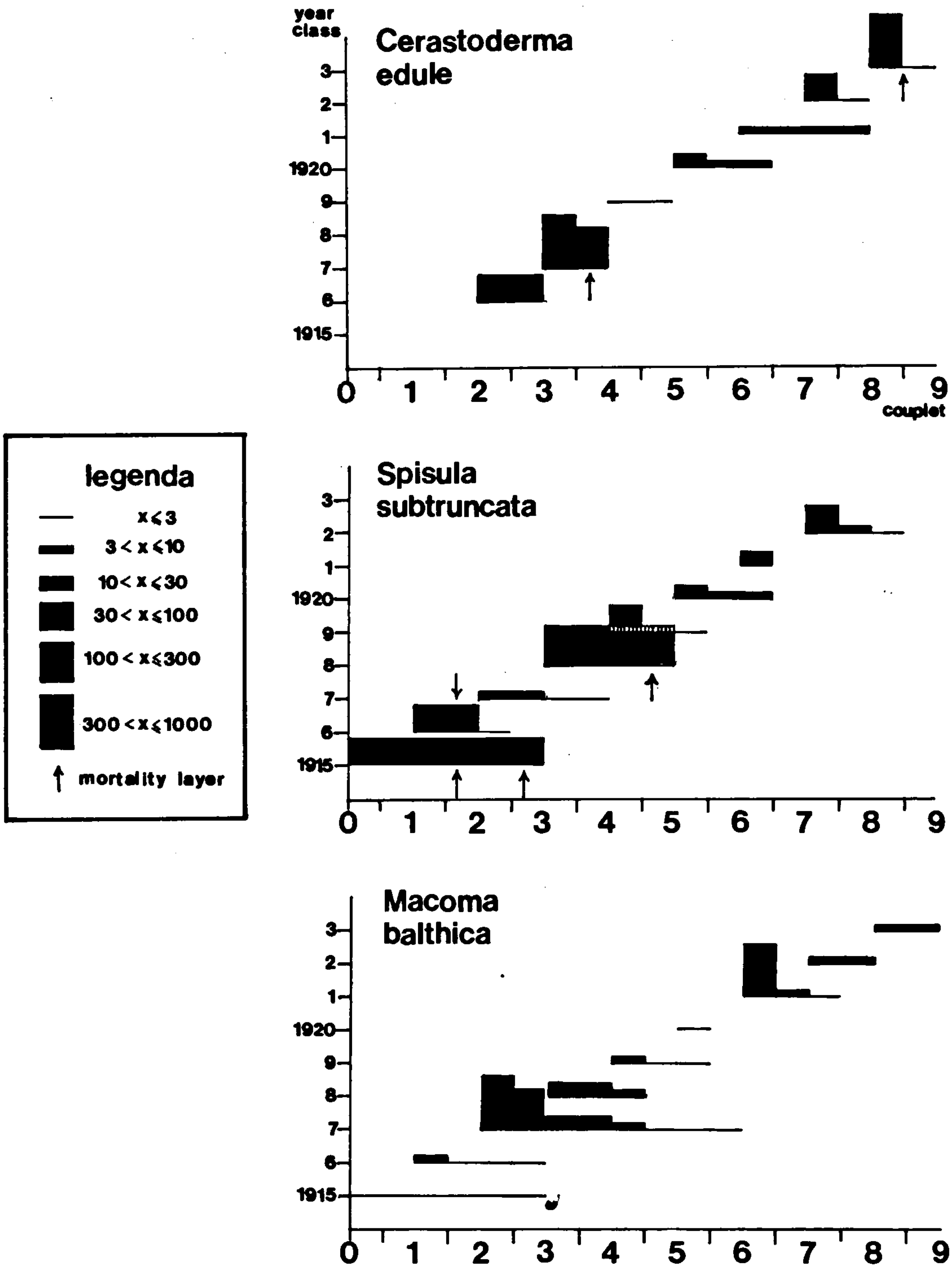

Fig. 2. Composite diagram representing the living populations of the three most important bivalve species in unit D.

Fig. 2. Samengesteld diagram waarop de levende populaties van de drie belangrijkste soorten tweekleppigen in eenheid D zijn weergegeven.

population. But usually only one or two are present, mainly because in this environment most animals died during their first or second year of life (fig. 3).

For cockles Kristensen (1957, p. 32) found that where conditions for growth are unfavourable the animals die young. In the Dutch Waddenzee cockles living in creeks grow slower and die earlier than those from the tidal flats. The cockles in the channel under consideration, however, died extremely young.

In the lower part of unit D near the boundaries between the couplets frequently a mortality layer of bivalves is found. Kristensen (1959, p. 20) found that because of constant homogenisation of the water even in the shallow southern North Sea during frost the mollusc-fauna will perish almost completely. Temperatures down to the freezing point of sea water, however, are not lethal

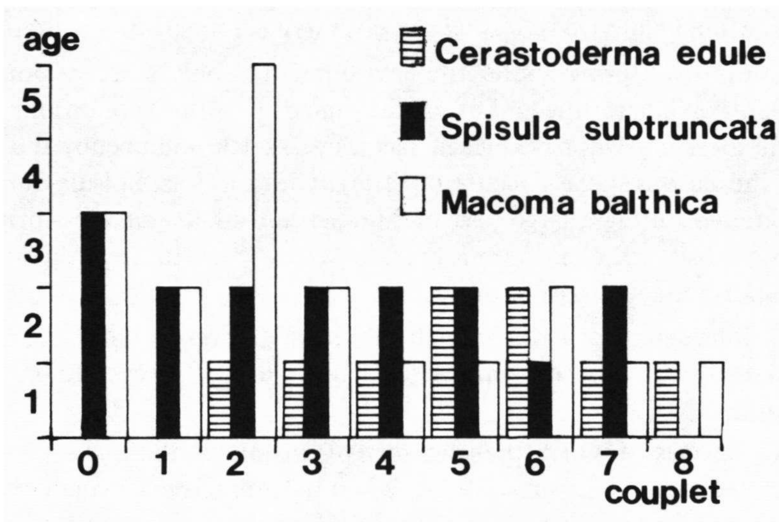

Fig. 3. The maximal age (in years) reached by specimens born in each couplet of unit D.

Fig. 3. De maximale ouderdom (in jaren) behaald door exemplaren geboren in elk der coupletten van eenheid D.

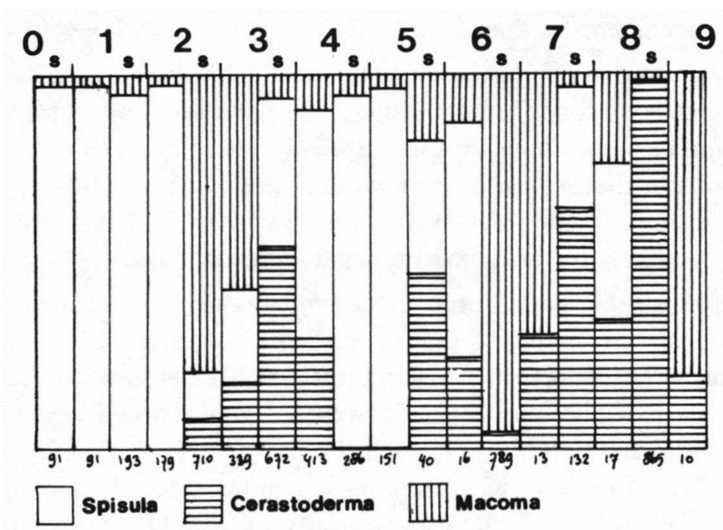

Fig. 4. Relative abundance of the three most important bivalve species in the subsequent layers of unit D. The summer layers are indicated with 's'. Below each column the number of specimens is indicated.

Fig. 4. Relatieve abundantie van de drie belangrijkste soorten tweekleppigen in de opeenvolgende lagen van eenheid D. De zomerlagen worden aangegeven met een 's'. Onder elke kolom is het aantal exemplaren aangegeven.

for most species but at such low temperatures they may become immobilized (Kristensen, 1959, p. 22-23). Because of the rapid sedimentation during winter the animals were covered by sediment, the greater part did not survive and formed a mortality layer.

These mortality layers generally are composed of specimens of one generation of one species, as apparently different generations of the species react in another way on each combination of temperature and sedimentation. For instance cockles, especially the larger ones, are very inactive at water temperatures of 2.5°C or less and active at higher temperatures (Kristensen, 1957, table X). On the other hand *Macoma balthica* especially is active at temperatures between 0 and 5°C and becomes inactive at higher temperatures. The highest mortality in this latter species occurs at temperatures between 20 and 25°C (de Wilde, pers. comm., 1980). After extremely severe winters Ziegelmeier (1964) reported also an increase rather than a decrease of this species. Therefore no mortality layers of *Macoma* occur. While *Cerastoderma* almost never survived a winter (only in the couplets 6 and 7 some specimens survived) *Spisula* usually survived one or two winters.

After such a mass-mortality during winter the environment is only scarcely populated and an ecological niche is available. When (at the end of winter time or in spring) conditions are favourable for spatfall, a species (all these bivalves have pelagic larvae) will settle and occupy the niche densely. Because the spatfall of the various species occurs at different seasons (viz. Spisula during winter and early spring, of *Cerastoderma* during a large part of summer and of *Macoma* in April and May) the composition of the biocoenosis will change rapidly from year to year. In fig. 4 the relative frequences of the three most important species are shown.

Mysella bidentata is considered to be a commensal (see references in Wolff, 1973) but it must have lived here without a host because the animals on which the species was found as commensal do not occur in the channel.

Macoma balthica is a species of which the spat survives mainly at the highest part of the tidal flats in very fine-grained sediment (Beukema, 1973). When the animals reach a length of 6 mm they close their shells at low tide and because of the captured bubble of air with the next low tide current they are transported towards open sea. Therefore the adult animals are most common in the seaward reaches of estuaries (Wolff, 1973, p. 83). In the studied subtidal channel, however, spat of *Macoma* settled successfully and the animals grew up in the channel itself as may be concluded from the presence of many specimens smaller than 6 mm.

Upwards in the sequence the maximum age reached by the bivalves decreases (fig. 3), therefore less generations of each species occur together. Because the settlement of each species differs from year to year the total number of specimens present is highly variable. Adult animals become scarce and most specimens die in their first season. During summer the number of living specimens is about 30 times as high as the number of specimens living during winter. Still higher in the sequence all bivalves disappeared, only echinoderms matched the rapid sedimentation.

In the summer of couplet 10 the spatfall of heart urchins succeeded in a large part of the channel as is obvious from the intense burrowing of that layer. But almost everywhere in the channel the animals disappeared during the same season. They did not die as skeletons are absent. In a restricted area in the southeastern part of the excavation, however, a dense population of heart urchins is present in couplet 11 and the couplets above it (Pl. 1, Pl. 2, fig. 1). It seems most probable that the animals moved towards this location which offers an explanation for the absence of the animals in the other parts of the pit. Probably this site was especially suitable for the species. At this locality also below couplet 10 the heart urchin is more abundant than elsewhere. Also in the southern North Sea the species has a patchy distribution (Buchanan, 1966, op cit.).

The population of heart urchins in the southeastern part of the pit survived several winters but became extinct during the winter of couplet 14, as demonstrated by the high number of skeletons and the absence of burrows in the younger sediments. At the same time also the brittle stars died. Van den Berg (1980, 1981) supposes that this layer originated in the severe winter of 1928/1929 and with this information all couplets can be dated (table 4, fig. 2). The size of the heart urchins may be estimated from measuring the press structures, the velocity of growth is equal to that of specimens living in the North Sea (van den Berg, 1980, 1981). It is obvious that bioturbation was much more intense during summer (Pl. 1, fig. 2). As this species lives up to 10 cm below the sediment surface the intense burrowing may be also present in the upper part of the winter layer.

UNIT G: A COCKLE POPULATION ON THE SHOAL

Of the bivalves which lived in this unit, a population of cockles is most interesting (Pl. 2, fig. 3, Pl. 3). During one summer spatfall was successfull and circumstances were very different from those in unit D: almost all animals survived two winters. While unit D represents channel deposits unit G exists of shoal deposits. During the third winter all animals died, forming a mortality layer in the top of the third summer layer. The whole interval is intensely bioturbated, some of the V-shaped burrows can be traced over large distances, illustrating the digging-upwards movements of the animals (Pl. 3). The size of the burrows increases during summer. From the number of burrows the relative density of the population can be estimated. During the third summer the number of specimens per amount of surface is reduced to about a third of that during the first summer.

The other individuals disappeared by dying (some specimens are found below the mortality layer) and by being washed away by the current. During the whole interval settlement of spat is unsuccessfull, as the population was very dense probably the spat was eaten. There is not enough space for more individuals and therefore the population exists of individuals of one generation of one species.

Towards the end of the third summer all the animals died, forming a mortality layer in the top of the clayey summer layer. The reason for their sudden death is unknown.

Most of the shell have a deformed, irregular lower margin. Such deformations were found also in cockles of unit D and E, in cockles, *Spisula subtruncata* and *Petricola pholadiformis* of the Roggenplaat (Raven, 1980) and in bivalves from the beaches along the Dutch North Sea coast. In the Oosterschelde itself or further seaward such deformations do not occur. Therefore they can not be explained by frost or changes in salinity. It is most probable that the deformations are caused by the density of the populations. Bivalves living in cavities are oftenly deformed in the same way.

UNIT H: DEPOSITS FORMED AFTER DRAINING OF THE PIT

About 1970 the construction works began and the environment was strongly effected by the dike constructed on the shoals, protecting the area behind it. A small inlet in the dike was left open. In the sheltered environment of this artificial 'lagoon' laminated clay was deposited during summers and sand during winters (Pl. 2, fig. 2). Here a biocoenosis completely different from that in unit D settled. It was composed by *Nereis diversicolor* (Müller, 1776), *Membranipora menbranacea* (Linné, 1758), *Balanus crenatus* Bruguière, 1792, *Echinocardium cordatum* (Pennant, 1777), *Cerastoderma edule* (Linné, 1758), *Ensis minor* (Chenu, 1843), *Macoma balthica* (Linné, 1758), *Abra alba* (Wood, 1802), *Venerupis senegalensis* (Gmelin, 1791), *Petricola pholadiformis* Lamarck, 1818, *Mya arenaria* Linné, 1758 and *Crepidula fornicata* (Linné, 1758). The animals died after two or three summers. In this period the animals grew very rapidly. Very well preserved burrows of several species were found. *Mya arenaria* lived in the heavy clay layer and even the burrows of the siphos are preserved. The other bivalves too lived in the clay layer.

Adult specimens of *Echinocardium cordatum* invaded the area immediately after the first winter. The photograph (Pl. 2, fig. 2) was taken near the inlet in the dike. At this location above clean sands suddenly burrows of adult heart urchins appear. The animals did not stay at this location, no skeletons are found. This suggests that the animals only passed through the inlet. At the other side of the 'lagoon' large quantaties of heart urchins survived (J.H. van den Berg, pers. comm.).

THE VELOCITY OF GROWTH OF THE COCKLE

The cockles from unit D are much smaller than those from unit G and even more than those from unit H (table 5). In one summer the cockles from unit H grow even larger than those from unit D after two summers! This confirms the conclusion of Kristensen (1957) that cockles on tidal flats

species	*Cerastoderma edule*										*Venerupis senegalensis*	
unit	D (born couplet 6)		E			G			H		H	
age	1	2	1	2	3	1	2	3	1	2	1	2
n	18	37	21	21	21	13	13	13	28	12	24	24
$\bar{x}$	10.6	21.7	17.7	23.8	28.2	18.1	26.4	30.8	24.0	39.5	20.4	40.8
x (min.)	7.8	17.6	14.8	21.2	25.1	15.0	23.8	26.0	13.5	35.4	15.1	36.1
x (max.)	14.3	25.0	21.5	25.9	32.0	23.6	30.2	35.2	28.2	46.4	26.4	44.0
σ_n	1.70	1.92	1.46	1.24	1.69	2.07	2.04	2.75	3.50	2.66	2.72	2.09

Table 5. Length of the shells of two species after each summer. n=number of specimens, $\bar{x}$= length of the shell, x=mean length of shell, σ_n=standard deviation.

Tabel 5. Lengte van de schelpen van twee soorten na elke zomer. n=aantal exemplaren, $\bar{x}$=lengte van de schelp, x=gemiddelde lengte van de schelp, σ_n=standaarddeviatie.

grow much faster than those in the channels. Also his conclusion (p. 32) that: 'Wherever the conditions for growth are favourable, the cockles live long, while under unfavourable conditions for growth they die young' is confirmed here. The animals from unit H did not die by natural causes but because of the draining.

The mean length of the cockles from each unit was compared with data of Kristensen (1957, table XIX) (fig 5). The animals from the channel vary in size between the values found by Kristensen for creek and tidal flat respectively. The animals from unit H, however, are exceptionally large as a result of the favourable conditions in the protected area. Figure 5 confirms also that the relation which Kristensen (1957, p. 99) found for the cockle: 'The relative rate of growth is, mathematically, a function of the animal's length – not of its age' is valid, as well in the channel as on the flat. Table 5 further demonstrates that the variation in the size of the shells is stronger in the more favourable environments (where velocity of growth is higher). Generally the variation in size decreases during the second summer and increases again during the third summer.

The velocity of growth in cockles is highly dependent from the environment and may be calculated with help of winterrings. The winterrings in bivalves are useful in recognizing seasonal layering. At the studied location such seasonal layering is a common phenomenon occurring in channel fill, shoal and 'lagoonal' deposits (unit D, G and H).

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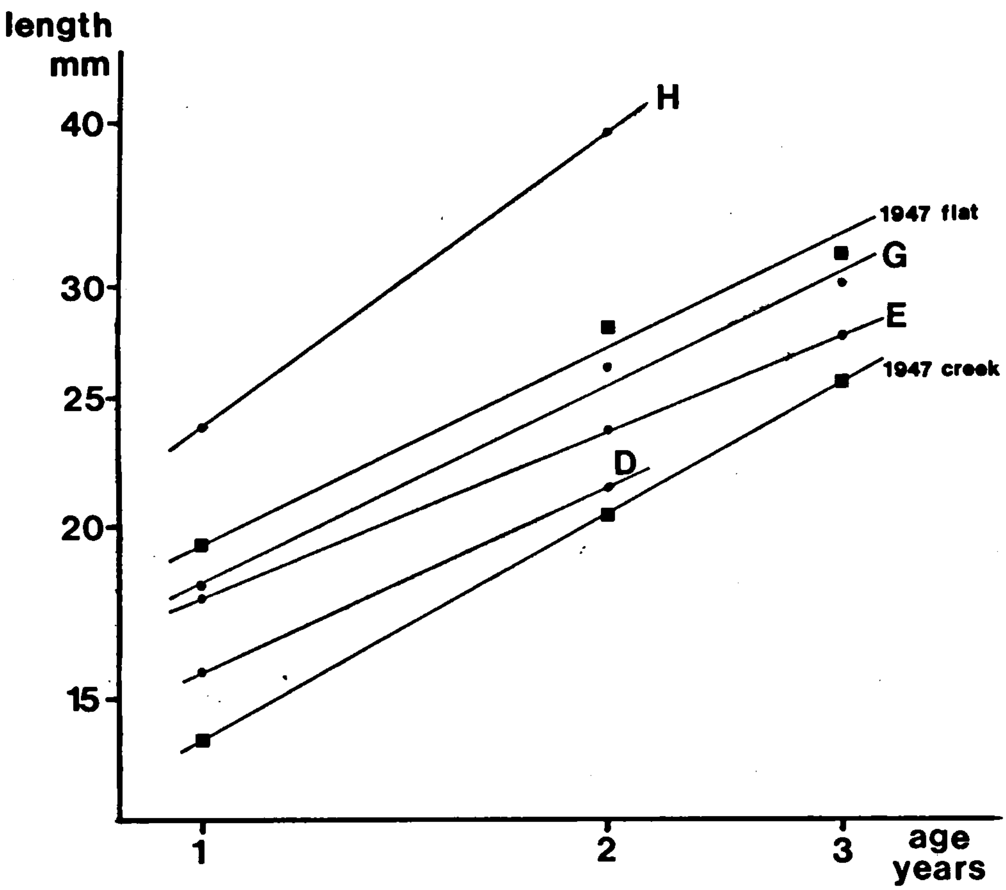


Fig. 5. Growth of populations of cockles in units D, E, G and H. For comparision graphs are given of cockle populations in creek and tidal flat environments in the Dutch Waddenzee (Kristensen, 1957, table XIX). Both axes have a logarithmic scale.

Fig. 5. Groei van populaties van kokkels in eenheden D, E, G en H. Ter vergelijking zijn de lijnen gegeven van kokkelpopulaties in geul en wadmilieu in de Waddenzee (Kristensen, 1957, tabel XIX). Beide assen hebben een logaritmische schaal.

EXPLANATION OF PLATE 1

Figure 1

Press structures of the heart urchin in unit D, couplets 11 to 14, in the southwestern part of the excavation.

The photograph shows the alternation of light winter and dark summer layers. Bioturbation is more intense in the summer layers and also in the upper ten cm of the winter layers. At the base of the photograph is the winter layer of couplet 11, burrowed by adult heart urchins. A younger generation of heart urchins, born in couplet 10, invaded this area during the summer of couplet 11 after death of the older animals. Burrows of these younger animals are present through the subsequent layers of couplet 11 to 14. The size of the press structures increases with the age of the animals. At the base of couplet 14 the animals died.

Figuur 1

Graafsporen van de zeeklit in eenheid D, couplet 11 tot 14, in het zuidwestelijk deel van de ontsluiting.

De foto toont de afwisseling van lichte winter- en donkere zomerlagen. Bioturbatie is intenser in de zomerlagen en ook in de bovenste tien cm van de winterlagen. Onderaan de foto is de winterlaag van couplet 11, doorgraven door volwassen zeeklitten. Een jongere generatie zeeklitten, geboren in couplet 10, trok dit gebied binnen gedurende de zomer van couplet 11 na de dood van de oudere dieren. Graafsporen van deze jongere dieren zijn aanwezig in de opeenvolgende lagen van couplet 11 tot 14. De grootte van de graafsporen neemt toe met de leeftijd van de dieren. In de basis van couplet 14 stierven de zeeklitten.

Figure 2

Press structures of the heart urchin in unit D, couplets 10 and 11, in the southwestern part of the excavation.

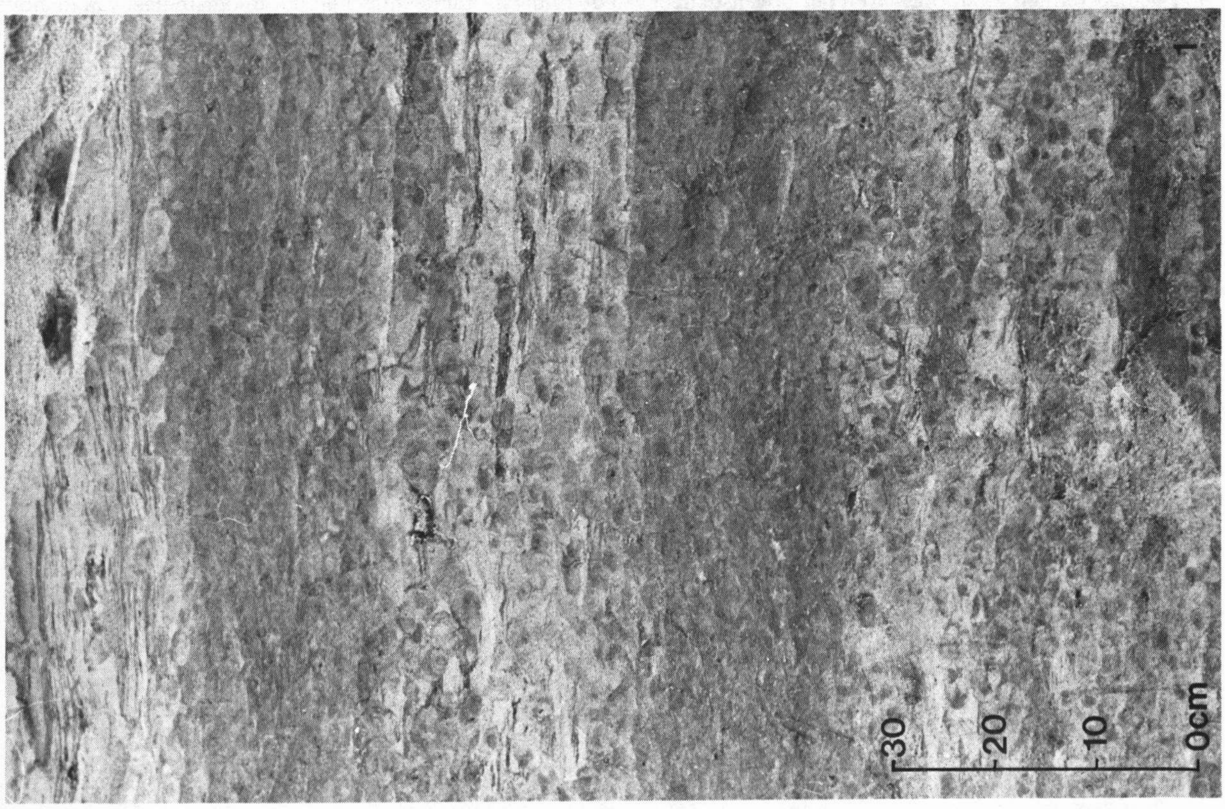
The population of which the press structures are found in these couplets was less dense than that living here from the summer of couplet 11 onwards. Clearly visible is the difference between the intensely burrowed summer layers and the scarcely burrowed winter layers.

Figuur 2

Graafsporen van de zeeklit in eenheid D., coupletten 10 en 11, in het zuidwestelijk deel van de ontsluiting.

De populatie waarvan de graafsporen in deze coupletten worden gevonden was minder dicht dan die welke hier leefde vanaf de zomer van couplet 11. Duidelijk zichtbaar is het verschil tussen de intensief doorgraven zomerlagen en de weinig doorgraven winterlagen.

PLATE 1



EXPLANATION OF PLATE 2

Figure 1

Press structures of the heart urchin in unit D, winter layer of couplet 11, in the southwestern part of the excavation.

Figuur 1

Graafsporen van de zeeklit in eenheid D, winterlaag van couplet 11, in het zuidwestelijk deel van de ontsluiting.

Figure 2

Press structures of the heart urchin in unit H, near the inlet through the dike around the pit.

Well visible are the two clay layers deposited during summers. Below the lower summer layer two sand layers may be distinguished. The lower one of these exists of clean sand, the upper one of laminated clayey sand. The boundary between both is well visible just above the white cockle shell in the middle of the photograph. Probably the deposition of the laminated sand started when the dike around the area was constructed. Then also heart urchins invaded the area and burrowed the upper part of the lower sand unit and the lower part of the upper sand unit.

Figuur 2

Graafsporen van de zeeklit in eenheid H, nabij de inlaat door de dijk rond de put.

Goed te zien zijn de twee kleilagen die gedurende zomers zijn afgezet. Onder de onderste zomerlaag zijn twee zandlagen te onderscheiden. De onderste hiervan bestaat uit schoon zand, de bovenste uit gelamineerd kleiig zand. De grens tussen beide is goed te zien net boven de witte kokkelschelp in het midden van de foto. Waarschijnlijk begon de afzetting van het gelaagde zand toen de dijk rond het gebied werd aangelegd. Toen trokken ook zeeklitten het gebied binnen en doorgroeven het bovenste deel van de onderste zandeenheid en het onderste deel van de bovenste zandeenheid.

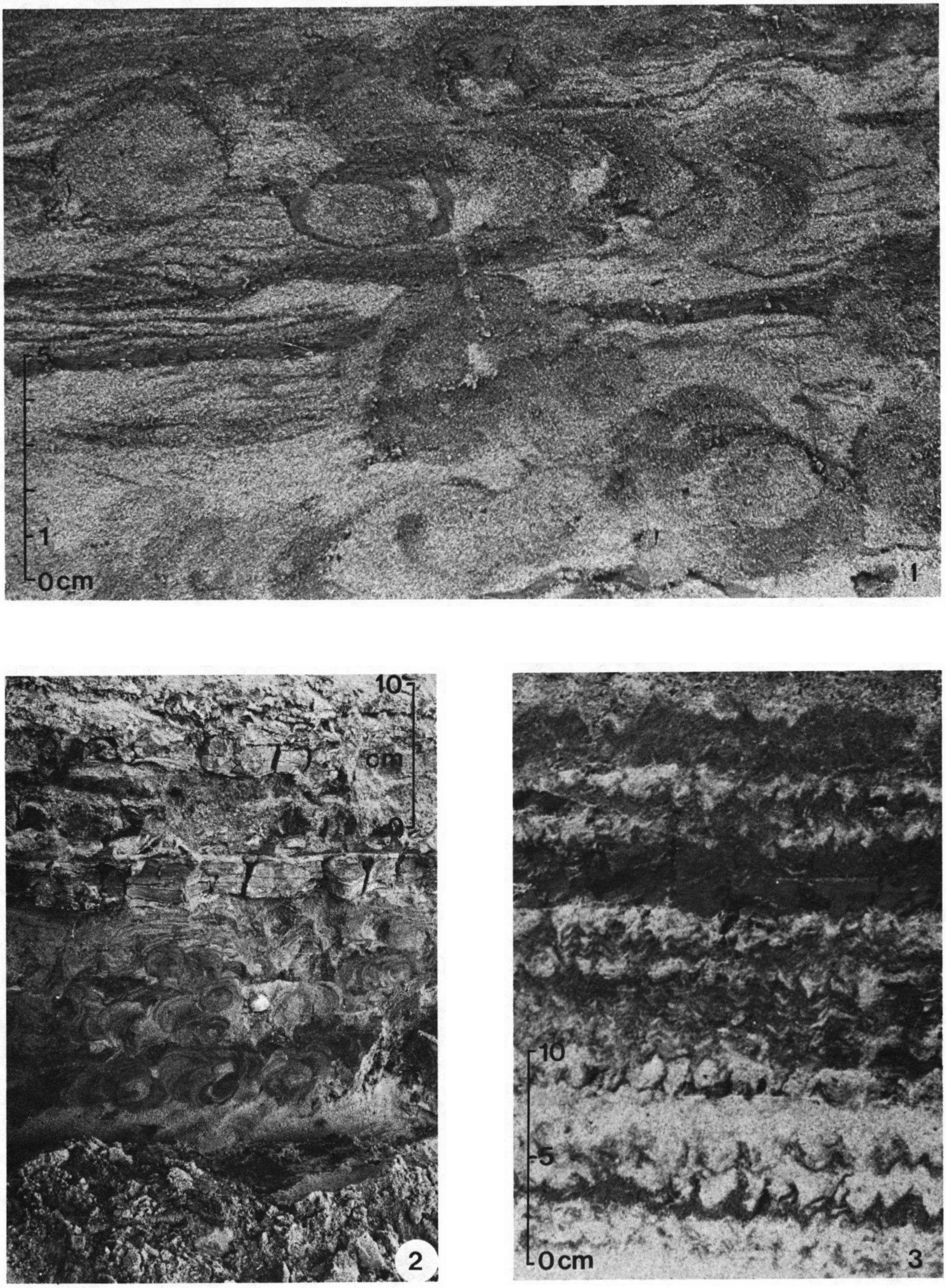
Figure 3

Detail of unit G, burrowed by the cockle.

Figuur 3

Detail van de eenheid G, doorgraven door de kokkel.

PLATE 2



EXPLANATION OF PLATE 3

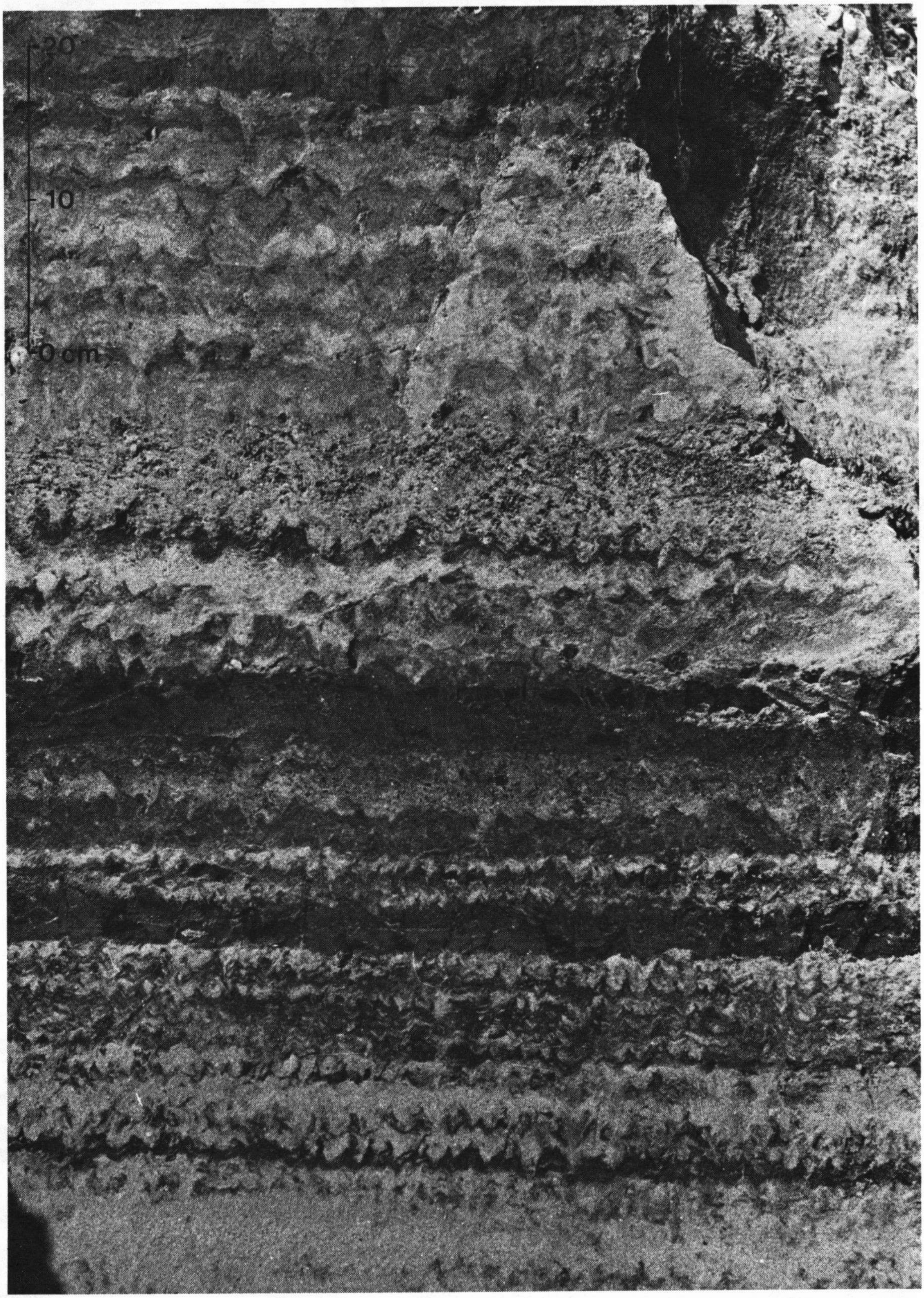
Upper part of unit G burrowed by the cockle.

The dark layers represent the second and third summer after birth of the cockles. The burrows show the digging upwards of the animals. In the second summer layer the size of the burrows suddenly increased, demonstrating the rapid growth of the cockles during summer. At the end of the third summer the cockles died, the shells are present in the clay layer.

Bovenste deel van eenheid G, doorgraven door de kokkel.

De donkere lagen vertegenwoordigen de tweede en derde zomer na de geboorte van de kokkels. De graafsporen tonen het naar boven graven van de dieren. In de tweede zomerlaag nam de grootte van de graafsporen plotseling toe wat de snelle groei van de kokkels gedurende de zomer toont. Aan het eind van de derde zomer stierven de kokkels, de schelpen zijn aanwezig in de kleilaag.

PLATE 3



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