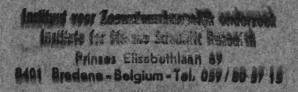# ON THE ECOLOGY OF DISTRIBUTION OF COCKLE AND MUSSEL IN THE DUTCH WADDENSEA, THEIR RÔLE IN SEDIMENTATION AND THE SOURCE OF THEIR FOOD SUPPLY

WITH A SHORT REVIEW OF THE FEEDING BEHAVIOUR OF BIVALVE MOLLUSKS

by

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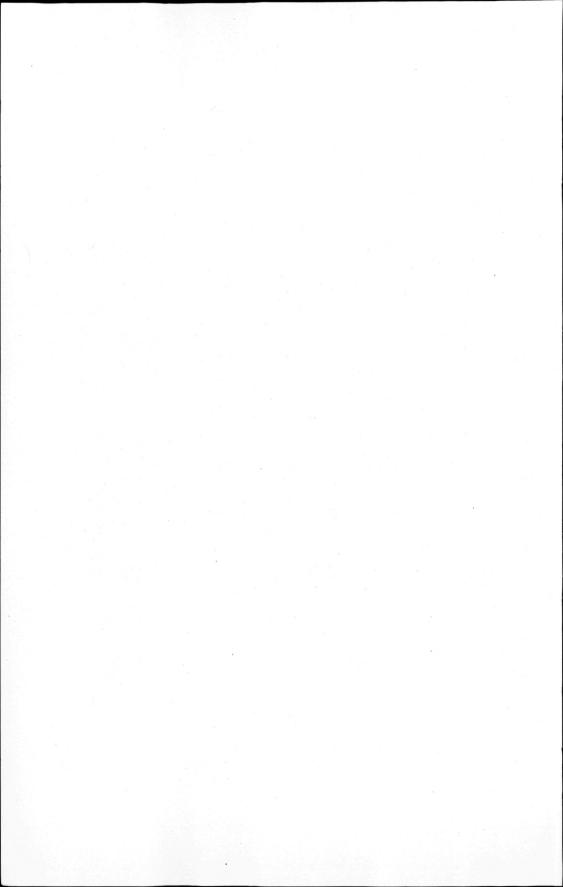
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CONTENTS

I. INTRODUCTION

The extensive sand flats within the coastal areas of the southeastern North Sea, which are so well known under the dutch name of Wadden, are populated by large numbers of polychaetous worms and other species. Since the study of these areas is progressing in many directions the question arises what rôle animals play in their formation or change. This question is easier to put, however, than to answer. I will here try and deal with it in relation to two species of bivalve mollusks, which must be specially important in this connection because of their great numbers: the cockle (*Cardium edule* L.) and the mussel (*Mytilus edulis* L.).

As one cannot expect to gain an insight into the matter before understanding what rôle this special environment plays in the distribution of these mollusks, their distributional ecology will be dealt with first and the influence of the animals on their environment will follow thereafter.

In order to produce a base for useful conclusions the quantity and composition and also the source of the organic and other material suspended in the water, which is of so much importance to these problems, is dealt with in two separate chapters, whereas a special chapter is devoted to the feeding of these animals, which has been (and still is) the subject of many controversies.

I owe many thanks to H. POSTMA, chemist to the Zoological Station, and to Dr C. O. VAN REGTEREN ALTENA at Leiden, for some valuable suggestions made during the reading of the manuscript, and to Prof. Dr PH. H. KUENEN for revision of the English.

Some photographs, originally destined for this paper, were used for illustrating the Waddensymposium (1950) (cf. KUENEN, PH. H., in list of literature). They are referred to at appropriate places in the text.

II. ECOLOGY OF DISTRIBUTION OF COCKLE AND MUSSEL

I. THE ENVIRONMENT (compare map, fig. 6 p. 217)[1]

If an attempt is made to characterize the Waddensea as an environment for marine animals in general matters may thus be stated:

1. Because of the shallowness of the area as a whole light can easily penetrate to the bottom. This opens the possibility for plant growth and the presence of plants means food and cover to animals. Animals can therefore be numerous. But these animals must be able to stand a

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[1] Hydrographic data on the Waddensea are given by POSTMA and VERWEY (1950).

fair quantity of light and they must not be hindered by the plants as might easily be the case on the flats.

2. Generally speaking, currents in the Waddensea are rather strong (up to 4–5 km an hour in the western part) and oxygen and food are therefore easily transported to most parts of the area. But the animals must be able to stand these currents and this is especially difficult on a sandy bottom, which is constantly moving. The distribution of mussels, for instance, is greatly limited by that factor.

3. Currents are valuable, because they transport food. But this transport can only be important, where plenty of food is available. The food consists partly of plankton and partly of other material in suspension. This suspended material consists of organic debris, excrements of organisms, very fine sand, and clay. It forms one whole with the plankton which cannot well be separated from it, so that it is also difficult to distinguish between organic material contained within the plankton and that present as detritus. It is difficult to estimate the total volume of wet organic matter present in plankton and detritus as a percentage of the total volume of plankton and suspended matter, but it may amount to something like 70–90 %. Its importance is for a large part due to the organic detritus, the quantity of which in our coastal waters is very high. Why it is so high has never been definitely established. It is generally assumed, I think, that it is due to plants (especially *Zostera* and algae). In my opinion, however, the mixing of fresh and salt water has also something to do with the matter. Where these meet their plankton is partly killed by the change in salinity, temperature or some other factor. As the quantity of fresh water partaking in the mixing is small compared with that of the sea water the latter must be the chief producer of the organic matter. POSTMA (1951) has pointed out that within the Waddensea it is transported against the gradient and accumulated within the quiet inner parts. It is especially there that sinking takes place, so that the quantity present on the bottom is increased. Since there must be an equilibrium, however, between the large mass present on the bottom and the quantity present in the water in a suspended form, the latter quantity must also be high, notwithstanding the fact that currents there are weak. As the mixing of water goes on constantly the production of debris never stops. The question is dealth with in detail in chapter VI.

I suppose, then, that the mixing of water masses is the chief cause of the richness in food of the Waddensea and of coastal areas generally. The currents, combined with the shallowness of the area, keep much material in suspension, but in quiet places the latter is deposited. It is therefore available to those species which are able to use it suspended, as well as to those, which use it as a deposit. And since the quantity

of matter is so great the number of individuals can also be great.

4. The suspended matter, through its richness in organic material, is valuable as food to those animals which can use it, but at the same time it is detrimental to all organisms which are not able to stand its constant rain. Many species, especially among the hydroids, cannot work it away, except when helped by strong currents, and these are not found everywhere. The number of species is thus reduced because of the deleterious action of the so called silt.

5. The mixing of fresh and salt water during part of the year keeps the salinity relatively low and this is of advantage to those species needing such a condition, but it reduces the number of truly marine species.

6. The water of the Waddensea because of its shallowness largely follows the air temperature, and the temperature extremes certainly cause a further limitation of the number of species.

7. Because of the shallowness, again, part of the flats fall dry at low tide and these are exposed to quite extreme conditions: drying out, great variation in the quantity of light, excessive heat and cold, etc. Changes in water level, therefore, form one of the first factors limiting the number of species.

Summarizing, it may be stated that the Waddensea is inhabited by a small number of species, which can cope with (and possibly need) great differences in the quantity of light and suspended material, salinity and temperature, the strength of the currents and the changes in depth. But these animals have at their disposal extensive areas where competition with other species is less important than elsewhere and where food is abundant; they can therefore be numerous.[1] The distribution of both cockle and mussel should be seen in this light.

What rôle, now, do the factors involved play in relation to the presence and numbers of cockle and mussel?

2. THE NEEDS OF THE COCKLE

Cockles are limited to a sandy bottom, in which the animals dig themselves in. They lie hidden just below the surface, the siphons like short chimneys caring for the supply and removal of the water (fig. 4). The grain size of the sand, generally speaking, is not important (KREGER, 1940; SMIDT, 1951), but the bottom must lie in shallow water, a depth of about 3 metres forming the lower limit in the Waddensea proper,

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[1] SMIDT, in a recent paper on animal production in the Danish Waddensea, which came out after my paper had been written, compares the Waddensea with some other coastal areas and he concludes that the Wadden are extremely rich.

Fig. 1. Cockle fishers at work naar Vlieland. Heaps of shells are lying everywhere around. July 1939, D. KREGER photo.

Fig. 2. Landing on the flats at sunrise. Sept. 1948. D. KREGER photo.

cockles are accumulated in certain areas, where currents are weak. This does not necessarily mean that food conditions are favourable there, for when these cockles grow older, food may become insufficient at the place in question and stronger currents might be of more value; but it does mean that the settling of spat is largely influenced by the current velocity. – Also the depth over the sand is important, however, because current velocity and depth cannot easily be separated. Moreover, less shallow water means a longer period of submergence to the animals, which may result in better conditions for upgrowth and therefore smaller numbers of animals killed.

The thin, rather uniform population over vast stretches of wide flats, finally, must in the first place be due to the uniformity and strength of the currents moving over these areas, for the numbers of animals on such stretches may be higher in the current shadow of osier work than anywhere around. Possibly, the numbers here are also smaller than nearer the creeks, because so many young will have settled along the latter before reaching the wide stretches; this cause, however, I no longer consider of any importance, it could at its most play a rôle on vast stretches of sands like those near the island of Griend (fig. 6).

My former assumption (see KREGER, 1940, p. 188) that dense cocklefields may owe their existence to the presence of tide rips (for description and photographs compare POSTMA, 1950), in which the larvae (as well as the plankton generally) would become concentrated, so that they would settle at such places in enormous numbers, now has to undergo a change. It is now assumed that the weak currents within these tide rip areas permit the young cockles to settle there and they may at the same time be concentrated after their having been carried away from other places. My change of opinion in this respect is especially due to the work of miss BAGGERMAN, which will be published shortly.

The young cockles in the period of metamorphosis must have means to reach shallow water. THORSON (1946, p. 462–463) has drawn attention to the fact that larvae of marine evertebrates generally are positively phototactic when young, negatively when they grow older, in connection with their need after metamorphosis to seek the bottom. Those species inhabiting shallow water, however, would remain positively phototactic also as older larvae, and THORSON mentions as instances among others Balanus balanoides (certainly one of the very best examples), the polychaetous worm Pygospio elegans, the common mussel (the latter after SPÄRCK's observations), and some other species. These species, through their constant positive phototaxis, would be bound to the water surface and thus be able to reach shallow places. It would therefore be natural to suppose that cockle larvae show

whereas they lived up to about 5 metres deep in the former Zuydersea; in the Scheldt estuary they apparently live deeper still and in the North Sea off Den Helder we found them up to about 14 metres deep. The reason for this depth limit is probably given by their need of light, but this has not yet been ascertained. Through this tie to shallow areas the animals on the Dutch side of the North Sea are limited to a narrow stretch of coastal water, including the inlets and the Waddensea.

Whereas their lower and outer limit is thus presumably caused by the absence of sufficient light their upper and inner limit may be caused either by the level of the sands or by salinity. Their upper level on the sands corresponds more or less to that of mean tide. They may occur in large numbers on flats falling dry for some hours every tide, but growth measurements clearly show that conditions are far from optimal where the upper limit is reached. They may also occur in the troughs on the beach of the Dutch west coast. – As to the salinity they stood less than $10\,^0/_{00}$ total salinity in the Zuydersea, but they remained very small there and conditions must have been adverse. When the Zuydersea was closed reproduction of *Cardium edule* still took place at a salinity of about $9-10\,^0/_{00}$, whereas all *Cardium* died when the salinity fell to between about 5.5 and $1.5\,^0/_{00}$ (compare HAVINGA, 1936, and SCHUURMANS STEKHOVEN, 1936).

Within the coastal area with its lower outer and its upper inner limit cockles occur in enormous numbers (figs. 1 and 3), but these vary strongly from place to place. This comes to the fore especially on the shallows of the Waddensea, where locally more than 1000 large cockles per square metre are found, in other places hardly any. One can probably state as a more or less general rule that few animals are found along the southern to western edges of the shallows; that a dense population may occur in stretches more or less parallel to the creeks at some distance from these (except along the southern and western edges); and that the remainder of the sands are thinly populated (see fig. 2).

Several different factors are probably responsible for this capricious ,,minor" distribution. The conclusions here given are based on the work of KREGER (1940), and non-published observations of miss BAGGERMAN, KREGER, KRISTENSEN and myself.

The poorness of the population along the southern to western edges is certainly due to surf action. The bottom here is constantly in motion and there are indications that even larger animals cannot maintain themselves in such places.

The dense population at a certain distance from the creeks must probably be ascribed to the presence of favourable current velocities combined with a favourable depth. As to current influence, the young

a similar innate behaviour. In the summer of 1950 LUCAS at Den Helder has tried to find evidence for this assumption; his observations have not yet been fully worked out, however.

Also the burrowing behaviour of the cockle is interesting from the point of view of these young animals. During metamorphosis the shell measures some 250–300 μ. As the diameter of the sand grains varies from 10 to 400 μ or more, the tiny young creep over and between boulders comparable to those of cairns. These boulders, however large they may be in relation to the young cockles, are exposed to currents, strong enough to overturn and roll them. This may be the reason why the majority of the animals establishing themselves definitely are not 0.3, but some 1–2 mm, the younger ones apparently not getting hold except probably in very quiet places. These young of 1–2 mm, on digging themselves in with the help of their very long foot, disappear entirely below the uppermost sand grains, from where their siphons do not reach the surface. They apparently obtain their water through the grain interspaces.

It was stated above already that the young may easier settle where currents are weak than where they are strong, but that food conditions at places with weak currents are not so good, so that dense populations there may grow poorly or die. Even in places with stronger currents the density may greatly decrease later on for the simple reason that there is not sufficient place. ORTON (1937) and THAMDRUP (SMIDT, 1944, p. 19) found young cockles settling to the number of up to 100.000 per m², SMIDT (1951, p. 82 and 128) found up to 72.000, WOHLENBERG about 70.000 and 40.000 per m². If 40.000 cockles of 1 mm shell length are placed close together they cover a space of no more than 20 × 20 cm. But one year later they need about 16 square metres, so that for the majority there is no place left. The maximum density shown by one year old cockles is about 2000 per square metre. The bottom, in which they live, seems paved then.

In conclusion, it may be stated that the cockle, because of its special needs, is much restricted in the choice of its grounds.

3. THE NEEDS OF THE MUSSEL

The behaviour of the mussel differs much from that of the cockle. Whereas the cockle digs itself in, the mussel as is well known attaches itself by means of chitin-like threads, which can be loosened again. These threads represent a remarkable semi-permanent form of attachment, which is also found in *Chlamys opercularis*, *Ostrea edulis* (KORRINGA and others), *Mya arenaria* (KELLOGG, 1901, SMIDT, 1951) and even *Cardium edule* (JOHNSTONE, 1899, SEGERSTRÅLE, 1928). But in all these

species thread-spinning is limited to early life (in *Chlamys* according to our own observations it may also occur in halfgrown animals), whereas in mussels it remains. Attachment is difficult or impossible on a sandy bottom, which is constantly moving. But where stones or other bivalves cover the ground these form a suitable substratum to the mussel, especially cockles being very important in this respect. Mussels, once settled, may at their turn form a firm base for later individuals.

Like the cockle the mussel is limited to shallow water, from somewhat below high water[1] to a depth of some 6–9 metres. As an exception large banks may occur in somewhat deeper water, of up to 17 metres or perhaps more (northern part of Texelstroom, see map). In the North Sea at some distance from the coast mussels are wanting, except near the surface on the hulls of buoys and lightships.[2] From analogy with the cockle I have always assumed that they do not occur at the bottom there because the latter (at 20–25 m depth) does not receive sufficient light, but proof is still wanting and it must be admitted that they are absent also at the bottom nearer the coast, except where piers, etc. occur. In this connection KRISTENSEN draws my attention to the fact that old mussels can apparently live in the dark, whereas cockles probably can not. The reason for the absence of mussels in deeper water might therefore be that the young do not settle in a dimly lighted environment, where as old animals they would be able to live. This seems unnatural from the viewpoint of the biological significance of such behaviour. – It has more than once been supposed that mussels hardly live outside the tidal zone, because the starfishes (*Asterias rubens*) destroy them there. Whereas this may hold good for certain localities the downward limit of 6–17 metres below low tide level in the Waddensea cannot be caused by starfishes, since the latter occur in great numbers also at 4 metres depth, where mussels may be numerous. Moreover, the cockle, which has a similar depth limit, is not preyed upon by starfishes. Anyhow, one can say that mussels, like cockles, are limited to a narrow coastal zône including the inlets and the Waddensea.

In the Zuydersea mussels diminished rapidly in numbers at the entrance to the southern part, where the salinity fell below $15-20\,^0/_{00}$. After closure *Mytilus* was killed from the moment the salinity fell to $9\,^0/_{00}$ and all animals were dead when the salinity had fallen to 6 (HAVINGA, 1936, p. 10). Judging from the distribution in other areas (Baltic, Danish waters) the extreme lower limit is about $5\,^0/_{00}$, but this

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[1] FISCHER (1929, p. 113) states that in quiet water the upper limit lies somewhat below the low highwaters of neap tide.

[2] SCHRADER (1911) mentions a young individual from a depth of 42 m in the North Sea some 30–40 miles from the coast (Oystergrounds). He supposes that it was carried to that place as a larva.

is far from optimal, and animals found in such salinities remain quite small. Apparently, there is much agreement between cockle and mussel in respect to their salinity needs, but judging from their distribution and behaviour in the Zuydersea the mussel cannot stand such low salinities as the cockle.

SEGERSTRÅLE (1942) mentions $4.5\,^0/_{00}$ as the lower limit for total salinity stood by *Mytilus edulis* on the finnish coast. The more brackish the water there the smaller the animals are. DODGSON (1928), FOX, MARKS and AUSTIN (1936), and FOX (1941) have shown that mussels can only cope with such low salinities if they have quite gradually grown accustomed to them.

FOX (1941) showed that the Californian mussel may grow accustomed to Cl'-concentrations of between about 9.4 and $28\,^0/_{00}$, i.e. about 17 and $50\,^0/_{00}$ total salinity (seawater has about $30-35\,^0/_{00}$ total salinity). Between these values the relation Cl' in tissue water: Cl' in seawater is about $1:1.6$; below 17 and above $50\,^0/_{00}$ this relation is not maintained and Fox believes that the animals do not survive this condition for somewhat longer periods. It follows from these observations that *Mytilus californianus*, which does not occur in bays and estuaries, but inhabits the open coast, has a much higher salinity range than *Mytilus edulis*, which is limited to shallow coastal water. Physiological and ecological differences therefore go hand in hand.

Though *Mytilus californianus* in experiments stands salinities as low as $17\,^0/_{00}$ the species in nature hardly occurs below $30\,^0/_{00}$. FOX (1941) has assumed that it does not occur in water of lower salinities, because for the sexual products and development higher salinities would be needed. This assumption has been tested by YOUNG (1941), who observed that gametes and young larvae live longest in water of 33.5 and $29.6\,^0/_{00}$ and that already in water of $25.1\,^0/_{00}$ conditions are not so good; fertilization may as a rule still occur in $21.5\,^0/_{00}$, but the survival of the larvae at this concentration is distinctly lower. In one experiment, however, Young obtained fertilization of some few eggs in water of only $9.1\,^0/_{00}$ salinity. Though, therefore, it may be true that sexual products and young larvae need higher salinities than the lowest ones stood by the old animals, it is clear that the reason why the old animals in nature do not occur below about $30\,^0/_{00}$ must probably not be sought in the needs of the gametes or young larvae. YOUNG, after citing others, concludes that surf action, common on the open coasts where *Mytilus californianus* occurs, may be needed.

The mussel does not inhabit the whole of the coastal area (in so far it is sufficiently shallow) in equal numbers. In this respect it does not differ from the cockle. The minor distribution of both species, however, is totally different. If one determines the density of cockles over extensive flats it is striking how gradually it mostly changes along a traverse. Nothing like this holds for the mussel. It occurs in patches of large beds or small scalps, in which thousands or some very few animals may be accumulated. There is always local concentration, with areas or patches without mussels between. As to the distribution of these patches as a whole there seems at first sight to be no system in it at all. Observed through the eyes of a geomorphologist, however, two facts are obvious. They are well illustrated in photographs 11 and 12 of the Waddensymposium. The first is that the patches are often

bordering creeks, the second that many of them are lying across the drainage channels of large shallows. Here they may form incomplete dams of up to 200 metres long. The longitudinal axes of the separate musselbeds are lying parallel to the longitudinal axes of the dam. The dam may be several beds broad and the beds forming it are, I believe, distributed in the most haphazard way. The breadth of the dam may amount to some 50 metres. Whereas, in many cases, therefore, the situation of musselbanks in one way or the other bears some relation to that of creeks, there are also patches of banks which cover part of an extensive shallow, apparently without a creek as starting point (Waddensymposium, photograph 10).

Here also, it is logical to ask for the reason of this special distribution.

There is little doubt that it is a question of current velocity in the very first place. KUENEN (1942) has shown that mussels on a sandy bottom cannot maintain themselves where currents are strong and that food conditions are poor where currents are weak. Where mussel beds are situated along the slopes or edges of creeks the influence of currents is clear enough; where dams of mussel banks cross important drains I am inclined to assume that the dams grow up where current conditions are optimal. In the case where a creek is absent, finally, the part of the flats covered by mussels apparently always has currents differing from those over the rest of the flats. All this, however, should be confirmed by more observations, and, if possible, by experiments in the field.

Judging from what is found in the cockle and bivalves generally, one expects that also in mussels the decision where the animals will settle must fall within the first weeks after metamorphosis. The question may be raised, then, how a musselbed can be formed through the action of thousands of mussel larvae more or less uniformly distributed in the water. For there can be no doubt that the distribution of the larvae after a stay of some weeks in the plankton may be called uniform. My original assumption was that the mussel would have a social instinct based on something like smell, and that through it the animals congregate into dense banks. MAAS GEESTERANUS (1942) has shown, however, that this is by no means the case and that banks are formed from mussels, which are accidentally carried over the place in question and find a firm substratum for attachment there. His observations may thus be summarized.

Mussels, because of their method of attachment, prefer to settle in niches. While quite young they can do with small spaces and large numbers settle in the branching of hydroids and algae. I do not think that their preference for such frame work is based on the right niches only, but a certain preference for them is clear. However, they dis-

appear from this substratum after some time, apparently by loosening their hold. This tallies with the fact that large numbers of young mussels of from 0.5 mm and smaller, but up to 10 mm in length or more, are transported through the currents. MAAS GEESTERANUS found more than once 50–60 animals settling on one group of 4 roof tiles (placed on the flats) within one single highwater period. As it is more than improbable that mussels of 0.5–10 mm length would not have passed an earlier period of attached life there is little doubt that the animals found had loosened their hold at other places. Assuming this supposition to be correct it does not seem unlikely that such an alternation between fixation, detachment, transport, and new fixation, may repeat itself several times and new observations, made near Den Helder by miss COOL in the summer of 1950, favour this assumption. It is probable from them that the somewhat older young mussels prefer places, different from those inhabited by the smallest and also from those inhabited by the larger individuals. As to these larger animals, there is probably only one substratum which wholly satisfies their need for niches: the musselbed itself. The animals congregate on them through their need of a suitable place of attachment; it must be assumed that such beds are built up through the action of thousands of individuals, carried over them by chance. T. C. NELSON (1928) described for young *Mytilus* of up to nearly 1 mm in length the formation of a gas bubble by the gills, which would help the animals in floating; but here we are dealing with animals of up to 1 cm and more and it is not clear how such animals can be so easily transported.

In connection with the above facts it is of interest that the process of building mussel beds may show some difference between old, existing beds, and young new ones.

As to old beds, there are a number of places in the Waddensea where these probably exist for many years. Part of them may remain undamaged for several years, others may be broken down again and again during the winter season, but the firm base is not easily destroyed and a certain number of living mussels may remain. The reasons for such damage have been given by FIELD (1923), who mentions storm or strong currents in winter, shifting sand, floating ice, frost, and some other factors working also during the remainder of the year. Such old beds apparently become covered by very few mussels of smallest size; they probably grow chiefly through the arrival of somewhat larger mussels.

There are also localities, where old mussels are absent, but where conditions are quite suitable for the settling of young brood, for instance where a dense field of tubes of dead *Lanice conchilega* covers the bottom or where a cockle bank has entirely died through frost. Here

thousands of young mussels of one and the same size may grow out to extensive patches of some thickness (Waddensymposium, photographs 8–9). They may be well on the way to become true musselbeds when storms come, and most of these patches are rolled up by the action of wind and currents, and their mussels are carried away. The chief reason for their destruction certainly is that these beds are situated in much exposed positions; they can, therefore, grow up in quiet periods, but are destroyed again in stormy ones. So, we cannot say that young mussels do not form beds, but the beds they form are easily destroyed again and make place for new ones. The mussels, which formed them, will gradually contribute to the importance of old beds, which chiefly grow through the addition of somewhat larger animals.

The representation hare given for the younger beds is especially based on observations of KREGER and myself, made in 1939 (compare also KREGER, 1940); that given for old beds is based on the vision of the fisheries surveyor for the western part of the Waddensea, who believes that a number of old beds do remain for years. Probably, however, there are many interstages between one group and the other. KREGER (1940, p. 182–184) described two extensive cockle beds of great density which he found in September 1937 at the Staart van Schieringhals. They consisted almost entirely of cockles born in 1936. Both were recognizable from far as a dark stretch, the dark colour being caused by algae (*Enteromorpha*, *Cladophora*, and others), which found a firm hold on the cockle pavement, chiefly on its dead cockles. In the centre of one of the beds a young musselbank had established itself. Returning there in the summer of 1939 KREGER found that both cocklebeds had been transformed into musselbanks, estimated to be 0.75–1 metre high. Many of the mussels had been killed by the frost of the past winter and here and there heaps of shells had been washed together. A small bank of partly dead cockles and clusters of mussels was found at about 200 m from the first in northeastern direction and it looked as if a southwestern storm had carried them there from the chief bank. In this instance, cocklebeds had grown up on these flats in 1936, a year in which there was an enormous brood fall of cockles everywhere in the Waddensea. These beds had grown to a hard pavement in 1937, when a field of young mussels began its development on the pavement of one of them. In 1938 the second bed also showed a musselfield and both these musselfields grew up to heavy banks in the course of that summer. Notwithstanding the fact that part of the mussels were killed by the frost and carried away the banks next summer had a height of 0.75–1 metre.

This course of events is no more than an instance of the second possibility mentioned above, with the only difference that the mussel-

banks maintained themselves for a longer period. In many places such a course may even be the general rule. FIELD says that musselbanks may disappear entirely 3–4 years after they grew up, to give place to new banks again. In the Waddensea it is not uncommon, I think, that there is a regular alternation between cockle and musselbanks in such cases. The cocklebed is covered by mussels when the cockles are lying dense enough to form a hard pavement. This pavement gives the mussels a firm hold, but when their bank grows higher and higher it is exposed to so many dangers (frost, drying out, shortage of food, increased exposure against currents) that it can no longer withstand them. The mussels are carried away, together with the dead *Cardium* shells, and the sands are lying bare to receive a new cockle population next spring. Because there is ample place a dense bed of *Cardium* can again develop and the whole course of events may repeat itself.

In conclusion, it is more than clear that the needs of the mussel, notwithstanding the fact that the species is so widely distributed, are no less special than those of the cockle and that the mussel, like the cockle, is therefore as restricted in the choice of its grounds.

III. THE QUANTITY AND COMPOSITION OF THE MATTER SUSPENDED IN THE WATER

The different distribution of cockle and mussel must result in a more or less different influence of both species on their surroundings and it may be asked whether this influence is reflected in the formation or growth of the area studied.

Before dealing with this question two series of facts must be considered in some detail. One is concerned with the quantity and composition of the material suspended in the water, which is of so much importance to the animals studied. The second deals with feeding problems, which should form the base for a correct understanding of what happens to the suspended material pumped in by them. The latter chapter has become more detailed than would be necessary in connection with the problems discussed. The biology of feeding in bivalves represents a field with so many points of interest and at the same time so many controversies, however, that a fuller review appeared justified. It follows in chapter IV.

As is well known lamellibranchs obtain their food from organic material in the water or laid down on the bottom. Such species as *Scrobicularia*, *Macoma*, *Angulus* (*Tellina*) and *Abra* by means of their long siphon suck in the material laid down on the bottom, whereas such species as mussels and cockles, like clams, oysters, and many others

Loss on ignition in percentage of total quantity of suspended material and plankton, dried at 120° C

Date	Depth	EBB Total quantity of matter in 1 l, dried at 120°, in mg	EBB Loss on ignition in percentage of total	FLOOD Total quantity of matter in 1 l, dried at 120°, in mg	FLOOD Loss on ignition in percentage of total
1938 June 2	0.5 m above bottom	59	20.2	138	22.9
3		212	13.5	371	16.4
7		205	11.4	186	15.8
8		277	14.2	562	13.4
9		88	15.9	457	26.4
	mean		15.–		19.–
June 21	1 m below surface	23	18.6	37	16.5
22		18	19.–	50	16.–
23		50	17.3	62	19.–
24		47	18.2	47	18.7
27		15	20.4	503 (sand!)	7.7
	mean		18.7		15.6 (without the figure of 7.7 the mean is 17.6%)
Oct. 21	1 m above bottom	61.4 (mean for 14 samples, taken every half an hour of the ebb period)		61.3 (mean for 12 samples, taken every half an hour of the flood period)	mean loss on ignition for ebb and flood taken together 16.5
	1 m below surface	51.2 (mean for 14 samples, taken every half an hour of the ebb period)		44.4 (mean for 12 samples, taken every half an hour of the flood period)	13.9
1940 June 5	1.5 m above bottom	mean 17.5 (beginning of ebb)	17.–	18.4 (beginning of flood)	14.7
		mean 77.4 (strong ebb)	4.4	52.5 (flood)	6.7
		mean 35.9 (ebb)	12.2	21.9 (end of flood)	9.7
		mean 24.0 (end of ebb)	12.6		
	0.5 m below surface	mean 16.0 (beginning of ebb)	5.6	18.0 (low values flood)	9.2
		21.1 (whole of ebb)	11.4	48.8 (high values flood)	8.9
				15.6 (low values end of flood)	17.0
				32.9 (high values of flood)	11.2

take their food directly from the water by pumping the latter in and
retaining the food. Before proceeding to their influence on this food,
we will deal with the food itself first.

It was already stated in chapter II that judging from microscopic
examination the total volume of wet organic matter present in plankton
and detritus may amount to something like 70–90 % of the total of
plankton and suspended matter together; it is only a rough estimate
and therefore without much value. As this organic material contains
much water (perhaps some 95 %) it forms no more than a small per-
centage of the total of a sample dried at 120°, as will follow below.

The figures of table I relate to the water of the Nieuwe Diep, the
harbour of Den Helder. The latter is no more than a creek of the
Waddensea with dams on both sides. Strong ebb and flood currents
run through it as is the case with other creeks, but the quantities of
suspended matter may differ from those of other creeks, because land
with sluices and fresh water are so near by. The figures for the harbour
are the only exact figures available, however. They have been ob-
tained by J. SCHEELE (as a chemist to the Rijks Waterstaat stationed
at the Zoological Station) from samples collected in June and October,
1938. A series of samples from June, 1940, have also been analysed, but
in a less detailed manner, so that only the total quantities of solid
matter, not the composition, are given here. The depth at the place of
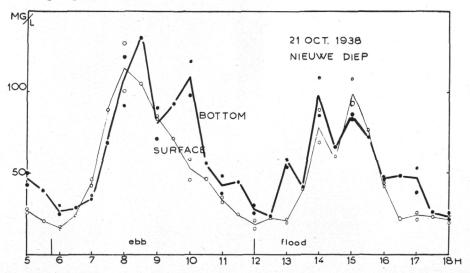sampling was about 6 metres.

Fig. 5. Quantities of total suspended matter (plankton included) in the Nieuwe Diep,
21 October 1938, according to determinations of J. SCHEELE. The figures are expressed
in mg dry weight per litre of water.

The curves for 21 October 1938 (compare fig. 5) show that there exists – as is well known – a direct relation between the total quantity of suspended matter (plankton included) and the current velocity. The figures for 21 October 1938 further show that the total quantity is about the same at one metre below the surface as at one metre above the bottom, in other words, the quantity is rather homogeneous down to about one metre above the bottom. The loss on ignition, in which the organic material is contained, forms some 10–20 % of the total. The loss on ignition tends to be low when the total quantity of matter is high, and inversely. This means that high total figures are in the first place due to an increase in the quantity of *in*organic matter.

The composition of this inorganic material (determined from the same samples) may be deduced from the details of table II. Because the separate samples contained too little material to be analysed separately the quantities of matter of all subsurface samples and those of all bottom samples were mixed and analysed together so that no difference between the quantities present during ebb and flood can be given.

TABLE II

Composition of inorganic constituents of suspended material (plankton included). The figures represent percentages of the ignition residue

Depth	SiO_2	CaO	MgO	Al_2O_3	Fe_2O_3	Total
0.5 m above bottom (June 2, 3, 7, 8 and 9, 1938) .	62.98	10.21	0.42	6.80	19.66	100.07
1 m below surface (June 21, 22, 23, 24, 27, 1938) . .	42.69	6.83	1.41	6.53	38.48	95.94
1 m above bottom (October 21, 1938)	75.6	12.8	trace	2.82	7.65	98.87
1 m below surface (October 21, 1938)	68.8	21.8	0.2	4.21	2.93	97.76

Bij accepting for clay the formula $Al_2O_3 2SiO_2 . nH_2O$ one can calculate how much of the SiO_2 may be considered to belong to the clay, how much to the sand. The above table then reads as follows (table III).

The quantity of sand even in the surface water is quite variable, and, relatively speaking, nearly always important. The quantity of shell material (in any case that of lime) may be as variable as that of the sand. The percentage of clay (determined as $Al_2O_3 2SiO_2 . nH_2O$) is rather low through the high figures for sand; quite remarkable, finally, is the great quantity of Fe_2O_3 (probably present as iron hydroxide), which may amount to nearly 40 % of the residue remaining after ignition, or some 32 % of the dried total, the loss on ignition included. Up to

1950 I have always been of opinion that this high percentage of iron-hydroxide in the suspended matter of the Nieuwe Diep might be due to the fact that the creek is used as a harbour, with many ships and all kinds of steel work, and that the suspended matter in the Waddensea itself would contain much less of this material. This vision was supported by the fact that SCHEELE found similar high values (27.5–30 % of ignition residue) for the suspended matter in the water of the harbour of Zeebrugge (Belgium). Before this paper went to press, however, POSTMA – doubting the correctness of this assumption – determined the percentage of Fe_2O_3 in the suspended matter of water samples collected June 1949 at Texelstroom. He found values of 20–35 (average 25) % (expressed as percentage of the dry weight). – SCHEELE found much lower values for October than for June. Since this might indicate an important annual variation POSTMA also determined the percentage present in winter. As winter samples from the Waddensea were not available at that time he used samples collected in the Nieuwe Diep. These samples (taken February 9, 1950) gave the same high percentage of Fe_2O_3 for the suspended matter as the summer samples from Texelstroom: 26–33 % of the dry weight.

TABLE III

Composition of inorganic material. The figures represent percentages
of the ignition residue

Depth	Sand	Shellsand (CaO + MgO)	Clay	Fe_2O_3	Total
0.5 m above bottom (June 2–9)	57.20	10.63	12.58	19.66	100.07
1 m below surface (June 21–27)	37.14	8.24	12.08	38.48	95.94
1 m above bottom (October 21, 1938). . .	72.3	12.8	6.14	7.65	98.89
1 m below surface (October 21, 1938). . .	63.8	22.–	9.17	2.93	97.90

The determinations of SCHEELE and POSTMA, combined, show that some 55 % of sand, 12 % of shellsand (CaO + MgO), 10 % of clay and 23 % of Fe_2O_3 may be considered a rough average for the composition of the ignition residue. Because of the wide variation in the percentages involved, and the small number of determinations carried out, this figure is rather arbitrary, but it has some value for further calculations. Besides, the average loss on ignition amounts to some 17 %, but this percentage does not refer to the residue after ignition, but to the material dried at 120° C.

Numerous observations made in the Western Waddensea by H. Postma during the years 1946–'51 have shown that the average total of suspended matter (plankton included) may be estimated at about 25 mg per litre (dry weight at 120° C) and that the average loss on ignition amounts to 5.– mg. The CO_2 from the shellsand is contained in the loss on ignition and according to Postma's observations its weight is about 2.– mg, so that about 3.– mg remain. These represent organic material, since the water from the ironhydroxide – as has also been shown by Postma – is driven out through drying at 120° C.

The result is that the average quantity of organic material (3 mg) represents about 12 % of the total quantity of plankton and suspended matter together (25 mg per litre).

Accepting these figures as an average for further calculations and using the percentage for sand, shellsand, clay and Fe_2O_3, which were given above, the water of the western Waddensea may contain on an average:

Organic material	3
Sand	11
Shellsand (CO_2 included)	4.4
Clay	2
Fe_2O_3	4.6
Total	25 mg per liter.

The figures refer to the weight after drying at 120° C.

If the different constituents are expressed as percentages of the dry total of all suspended matter (plankton included) we find the following figures:

Organic material	12%
Sand	44
Shellsand	17.6
Clay	8
Fe_2O_3	18.4

It should constantly be kept in mind that these figures represent rough averages and that they may show variation from place to place and in different periods of the year. The average figure of 12 % for the organic material is based on a large number of data, however.[1]

[1] Linke (1940) remarks the following: "Die Strukturanalyse zahlreicher Schlick-proben (bottom samples) hat ergeben, dass 35 bis 70% Diatomeenschalen, 3 bis 12% organogener Kalk und ebensoviel organische Substanz im Schlick enthalten sind; die minerogenen Anteile treten oft stark zurück. Eine ähnliche Zusammen-setzung haben auch die Sinkstoffe im Wattenmeer, nur dass hier die organogenen Anteile einen etwas höheren Anteil an der Gesamtzusammensetzung haben." This would mean that, Diatom shells included, at least 40–94% of the suspended ma-terial in the Waddensea is organic. This seems a very high percentage and one would like to know what the word "Strukturanalyse" means and in how far these figures are comparable with ours.

IV. THE FEEDING BIOLOGY OF BIVALVE MOLLUSKS

We now come to the difficult question what exactly happens to this material through the activity of the animals. One cannot gain an insight into their actual rôle in matters of sedimentation without some fundamental knowledge of their feeding behaviour and the latter has been the subject of much controversy.

A number of points, which have already been enumerated in the general contents of this paper, are of interest in connection with this chapter.

They are dealt with below.

Research has chiefly concentrated on two groups of species: mussels and oysters. Very little work has been done on the cockle. As the principle involved is more important, however, than the actual facts, data on the oyster will be used whereever they may be of value.

1. HOW MANY HOURS A DAY DO THE ANIMALS PUMP?

This number has never been accurately determined, but a great many observations have been made on the times the shells are kept open or closed. Strictly speaking, open or closed shells are not representative for actual pumping, because pumping may go on while the shells are nearly closed and as an exception may stop when the shells are open.[1] On the whole, however, pumping goes on as long as the shells are open. This even holds for mussels at very low temperatures.

LOOSANOFF and NOMEJKO (1946) registered opening and closing of the shell in a number of specimens of *Ostrea virginica* in the field. They found that the animals kept their shells on an average open for more than 22.5 hours a day. NELSON (1921 and '23) and GALTSOFF (1926) found an average of 20, GALTSOFF (1928) of about 17 hours, due to the fact that in a few instances oysters failed to open during the 24-hour period. GALTSOFF's animals were kept in aquaria, however, those of LOOSANOFF and NOMEJKO and those of NELSON in the field. It should be added that the water temperature in all these experiments was rather high.

HOPKINS (1931) found for *Ostrea lurida* that the animals on an average kept their shells open for over 20 hours, LOOSANOFF (1939) found for *Venus mercenaria* a period of about 21.5 hours, LOOSANOFF

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[1] For literature see DODGSON 1928, GALTSOFF 1928, HOPKINS 1933, and LOOSANOFF and ENGLE 1947. Whereas there is agreement about the fact that pumping may be stopped while the shells are open the data on pumping with nearly closed shells are controversial. HOPKINS stresses the point, however, that in *Ostrea gigas* no pumping takes place unless the shells are a little distance apart. "This distance represents the thickness of the mantle at the edge of the shell."

(1942) for American *Mytilus edulis* periods varying between 18.5 and 24 hours per day.

All these determinations show that, if possible, bivalves keep their shells open for more than 80 % of the 24 hours.[1]

Shell movements are little or not influenced by the annual change of temperature, except that the shells may be closed at low temperatures and according to HOPKINS' observations (1933) also at high ones. HOPKINS (1933) observed that *Ostrea gigas* is open most of all at about 20° C and that it often closes below 6 and above 24° C, a point to which I return further on. Closing at low temperature was also observed by him (1931) in *Ostrea lurida*.

In this species HOPKINS (1931, p. 8–10) has shown that between about 7 and 17° C the temperature *as such* is of no influence on shell closing, though the influence of temperature *changes* is striking. The influence of one and the same temperature change (in this case of 2° C) is the greater the more the water temperature, in which the change takes place, approaches 7° C. HOPKINS gives no data for still colder water.

I think, his observations, combined with those of others, show that the temperature *as such* causes increased closing below 7–8°, whereas temperature changes of 2° are still active (though to a slight extent) in water of up to 17°.

That the shells may be closed at low temperatures has also been proved clearly by LOOSANOFF (1939) for *Venus mercenaria*, a species which closes constantly below about 3° C and is more or less constantly open above about 8° C. There is a clear relation between closing and temperature between 3 and 8°, and no relation between 11 and 28° C. – Closing at low temperatures was further shown by GALTSOFF (1928) to take place in *Ostrea virginica* (compare also page 196), whereas DODGSON (1928, p. 208) for *Ostrea edulis* described cessation of functioning below about 3° C. In the latter case extrusion of faeces and pseudofaeces was used as a criterion.[2]

According to the observations of DODGSON (1928) and LOOSANOFF

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[1] HOPKINS (1931) found that one *Ostrea virginica*, tested for nearly two months (October–November) in running water, opened only 14.5 hours a day; two others, tested for 78 hours in summer, were open an average of only 10.4 hours a day; four others, in artificially aerated water, remained open an average of only 6.6 hours daily. He assumes that various factors may have been responsible for these low figures.

[2] NELSON (1923) states that a sudden drop in temperature may result in temporary decrease in the daily number of hours of activity. Between 4 and 6° C there is a sharp decrease in the ciliary activity of oysters, normal feeding occurs above this range, while almost no food is taken when the temperature of the water is below 4° C. Though these remarks give the impression that the *ciliary activity* was watched I suppose that conclusions were based on shell movements, since NELSON worked with an apparatus recording the shell movements of oysters in the sea. I did not see NELSON's publication of 1921, which probably gives further details.

(1942) *Mytilus edulis* behaves quite differently. DODGSON (p. 194) states that it has been observed to function normally at all temperatures between 0 and 26° C.[1] "At no particular temperature, or range of temperature, between the above limits, have they been noted to function especially actively or especially passively." DODGSON's further data (p. 194–207) go on to show that mussels may continue feeding and ejecting faeces and pseudofaeces in water temperatures sinking below zero. It will appear below, however, that mussels in water of about zero according to DODGSON may close during the day and open during the night only, and that in such cases active pumping takes place only at night.

LOOSANOFF found that American *Mytilus edulis* did not close their shell more than 25 % of the total time even at 1° C, that at temperatures between 0 and 1° a current of water was produced, that the cilia propelled small solid particles and that the stomachs of mussels removed from such cold water contained food.

It is clear from these observations that *Mytilus edulis* can cope with much lower temperatures than *Venus mercenaria* and *Ostrea virginica* and *lurida*. *Mytilus edulis* is a shallow water species with a northerly distribution and in connection therewith it must be able to stand great temperature differences and especially very low temperatures.

It was stated above that *Mytilus edulis* at low temperatures may close during the day and open at night only. DODGSON stresses the fact, emerging from a long series of observations, that mussels can be relied upon to open and function in the dark or in very subdued daylight, but not always to open during the day, especially when the temperature is low (p. 178, 187, 193–194, 201–202). They are as a rule open during the day when the temperature is 4°, frequently function in daylight at 1–2° C, and are usually closed in daylight if the temperature is at or below zero; in the dark, however, they are active in all these cases.

Such a difference between day and night was not found by LOOSANOFF (1942) in American *Mytilus edulis*, but LOOSANOFF (1939) found a similar behaviour in *Venus mercenaria*. The latter also closes its shell somewhat more during the day than during the night, especially between 5 and 15° C. It may perhaps be assumed that light and low temperatures cause closing, that high temperatures cause opening of shells and that at high temperatures the influence of temperature exceeds by far that of light.

The above observations show that oysters fully close at low temperatures, whereas mussels may close at low temperatures during the day only. In both cases there is increased closing at low temperatures. In

[1] Even at 26° C mussels were on one occasion seen to be actively feeding and passing faeces and pseudofaeces at a rapid rate.

this connection it is of interest that *Ostrea lurida* according to Hopkins (1931) closes more during the daily hours of low than during the hours of higher temperatures, the average daily curves for water temperature and shell closing showing complete parallelism.[1] It is therefore clear that, especially in the oyster, decrease of temperature under all conditions gives increased closing.

When the temperature is not extraordinarily low shell movements are apparently little or not influenced by the rhythmic change of light during day and night. This is shown by observations of Galtsoff (1928) for *Ostrea virginica*[2], of Webb (1930) for *Ostrea edulis* and of Loosanoff (1942) for *Mytilus edulis* in America. Loosanoff cites Wenrich (1916) and Chipman (1931) to the effect that also freshwater mussels show no different behaviour during night or day and Loosanoff concludes (1942, p. 233): "It indicates nature's provision enabling the mussels to keep their shells open at any hour of the daily cycle. If, because of the light, the mussels were compelled to keep their shells closed during the day, their feeding time would be confined to the hours of darkness only."

Especially sudden changes of temperature and also sudden changes of light may have a definite influence on closing (Dodgson, 1928: mussel; Galtsoff 1928 and Hopkins 1931: *Ostrea virginica* and *lurida* resp.). That Loosanoff (1939 and 1942) found no such effect in *Venus mercenaria* and American *Mytilus edulis* is not in contradiction to these findings, because the animals are apt to behave capriciously and hard and fast rules in this respect cannot be given. Dodgson, moreover, states that mussels show little or no response to artificial, only to natural light.

There is also an influence of mechanical and chemical factors, changes in Ph or gas content, etc. (Galtsoff, 1928). Especially the observations of Galtsoff c.s. (1947) on the influence of pulp mill waste on the times of shell closing in *Ostrea virginica* are interesting, as are also those of Loosanoff and Engle on the rhythm of contraction of *Ostrea lurida* in high concentrations of micro-organisms with presumably toxic products. How Dodgson's observations (p. 191) on the influence of the changing tide on mussel activity must be interpreted I dare not say.

In such species as cockles and mussels, which may fall dry for con-

[1] Hopkins supposes that also light may have had some influence on this phenomenon and his observations for *Ostrea virginica* seem to point in the same direction. His observations make probable, however, that temperature in this respect is far more important than light.

[2] Nelson (1921) was of the opinion that oysters (*Ostrea virginica*) are open les sat night than during the day. Possibly, temperature influenced his results, but I did not see his publication.

siderable lengths of time, the number of hours of daily activity may be lower than those for bivalves which live constantly under water and for that reason a very low average, of no more than 12 hours of pumping per day, will be used as a base for the calculations following below.

2. WHAT QUANTITIES OF WATER DO BIVALVES PUMP PER HOUR?

The most complete details on this point are those of LOOSANOFF and NOMEJKO (1946), LOOSANOFF and ENGLE (1947) and GALTSOFF, CHIPMAN, ENGLE and CALDERWOOD (1947) for the oysters *Ostrea virginica* and *lurida*. They actually measure the quantities of water pumped. LOOSANOFF and NOMEJKO for *Ostrea virginica* found an average of 12.5–18, GALTSOFF c.s. (1947) an average of about 6–12 litres per hour. Nothing is remarked about the fact that these values are so much higher than those found after the same method by GALTSOFF (1928), with a maximum of only 3.9 litres per hour. The higher figures may be more correct than the lower ones, however, and the studies of 1946 and 1947 are of admirable thoroughness. Whereas the values mentioned above represent average ones, the maxima may be still much higher. LOOSANOFF and ENGLE mention one animal (*Ostrea lurida*) with a maximum of nearly 26 litres per hour for a short period, while 4 others pumped from 21 to 22.5 litres for a similar period of time. LOOSANOFF and NOMEJKO mention some animals (*Ostrea virginica*) pumping 25–27 litres per hour on an average, with a maximum of 31-34 litres per hour. The temperatures in the latter experiments were 19.1–25.8° C. LOOSANOFF and ENGLE stress the fact that very high values may be attained when clear water is available again after the animals have been in highly concentrated suspensions of micro-organisms for some time. This water apparently has the function of cleansing the animals (see especially p. 49 of their paper).

For the Californian sea mussel the quantity has been determined by FOX, SVERDRUP and CUNNINGHAM (1937). They used, contrary to GALTSOFF c.s., and LOOSANOFF c.s., an indirect method and their figures must be considered minima: they may be too low, but can not be too high. They find that at temperatures of 20–23° C mussels of 60–82 (average 74) mm pump 0.5–2.1 (average 1.4) litres per hour, that mussels of 95–130 (average 102) mm pump 2.2–2.9 (average 2.6) litres, whereas the 4 largest animals of 174–182 (average 178) mm pumped 1.8–18.1 (average 6.4) litres. *Mytilus californianus* becomes much larger than *Mytilus edulis*, which grows to about 90 mm only. Animals of 60–82 (average 74) mm may well be compared with about fullgrown Dutch mussels, and according to these investigations such animals would pump about 1.4 litres per hour.

JÖRGENSEN (1949), using the same indirect method, but somewhat simplified, finds some 0.16 litres per hour for *Mytilus edulis* of about 15 mm and some 0.75 litres for *Mytilus* of about 30 mm length. Temperatures for these experiments are not given. WILLEMSEN (1952) used this simplified indirect method at Den Helder. He gave me permission to mention that mussels of 67–80 mm on an average pumped 1.8 litres per hour at a temperature of 12–15° C, whereas the maximum for an individual of 81 mm (at least for a short period) was 4.6 litres per hour.

A summary of some of these values is given here:

Length of animals	Number of litres pumped per hour	
15 mm	0.16	(JÖRGENSEN)
32	0.75	,,
48	1.1	(WILLEMSEN)
67–68	1.7	,,
77–80	1.9	,,

JÖRGENSEN, in an earlier investigation (1943), found a value of about 0.04 litres per hour at 11–22° for small *Mytilus edulis* of about 0.2 g. In his table V he compares the quantity of water they pump with that of mussels of other sizes, neglecting the fact, however, that the youngest animals are no mussel but oyster larvae, and that the other observations relate partly to *Mytilus edulis*, partly to *Mytilus californianus*. These figures, therefore, should not be compared, but comparison of those for *Mytilus californianus* (taken from FOX, SVERDRUP and CUNNINGHAM) shows the same principle as that stressed by JÖRGENSEN: younger animals per gram of weight pump relatively much faster than older ones. Dr P. H. L. TAMMES drew my attention to the fact, however, that in these animals there is a linear correlation between the quantities pumped and the relative value for their inner surface, for which he takes the square of the cube root of their weight.

WILLEMSEN also determined the quantity of water pumped by the cockle and he found an average of about 0.5 litres for old individuals of 30–40 mm length at 17.3–19.5° C. The maximum found was 2.5 litres.

It is of importance that the quantities of water pumped by one and the same animal may show much variation. MAC GINITIE ascribes this to the contraction of the gills. Complete contraction according to him shuts off the current of water entirely. But the quantities of water pumped also depend on other regulating mechanisms, which have well been summarized by LOOSANOFF and ENGLE: The rate at which the water passes through the oyster is controlled by the beat frequency of the laterial cilia of the gills, by the expansion and contraction of the gill ostia, the position of the edges of the mantle, and by the activity of the adductor muscle (which closes the shell). This is an admirable summary, to which one should add the expansion and flattening together of the gills in *Ostrea* (described for *Ostrea gigas* by HOPKINS, 1933,

see small print below) and the functioning of the velum in the inhalant and that of the septa in the exhalant opening in *Mytilus*, described below (small print this page, and p. 204). One should finally realize that all these forms of control are probably influenced by different factors, of which temperature and chemical (possibly also mechanical) influences may be the most important.

A good impression of the delicacy of the regulating mechanisms can be obtained from the detailed descriptions of DODGSON for the mussel. Three such instances are cited here.

DODGSON (p. 169) describes how at the base of the exhalent siphon two thin membranous septa occur, which may open and close the entrance to the siphon from within. "If the septa be watched (by artificial light) in a feeding mussel, they will often be seen to be performing more or less rhythmic movements of extension and retraction. The projection of fine suspended particles against the fimbriated margin of the inhalent opening may be followed by sharp extension of both septa, with almost complete momentary occlusion of the basal-slit." DODGSON (p. 170) could also observe that the movements of the inhalent velum (compare p. 204 of this paper) may be influenced by opening or closure of the exhalent septa.

On p. 170–172 DODGSON describes observations on the movements of the gills, which make it probable that the continuity of the walls of the suprabranchial chamber may be interrupted, so that the subpallial chamber is no longer subdivided. In such a case the inhalent and exhalent orifices become almost coterminous. The whole mechanism reminds one strongly of what may happen in the wall between the lower and upper branchial chambers of crabs (VERWEY, 1930, p. 226–228).

Again, on p. 166, DODGSON states: "There may be a definite reflex arc between the rectum or anus and the adductor muscle, as closed mussels, lying in water, have been noted to open a few millimetres, pass a faecal ribbon in the exhalent stream, and then quickly close again, and remain closed. In mussels taken out of water, after a "full meal", that is, with a full alimentary canal; and stored for some time, the rectum has been found to be engorged, apparently almost to bursting point, but no extruded faeces have ever been found in the mantle cavity."

Also HOPKINS (1933, p. 487–488) gives some detailed observations relating to *Ostrea gigas*: "When the most rapid current is being produced the gills are fully expanded and separate from one another. Then two of the demibranchs may be observed to flatten together, either partially or completely, and there is an immediate reduction in rate. Very frequently it was observed that the two medial demibranchs would flatten together and the two others press themselves against the right and left mantles, respectively. Sometimes this reaction would be momentary; at other times it could last for hours to a greater or less degree."

"Accompanying a sudden shell movement, the gills often contract far back as if to close completely the gill chambers. Such a contraction either alone or in conjunction with shell closure causes complete cessation of flow. GALTSOFF (1928a) noted marked changes in the rate of pumping which were probably due largely to movements of the gills. It may be also, as suggested by GALTSOFF, that mucus forms a layer over the gills, clogging the pores and impeding or stopping the current. Actually to observe this, however, is difficult."

There is a striking shortage in such detailed observations in the literature dealing with this subject and in invertebrate literature generally.

The quantities of water pumped may depend on quite a number of different factors.

Temperature influence on the rate of pumping in oysters has especially been studied by GALTSOFF (1928) and HOPKINS (1933 and 1935). GALTSOFF paid much attention to the influence of temperature on ciliary movement (compare in this connection also the footnote on p. 190 of this paper). Ciliary movement in *Ostrea virginica* may continue to below zero, but it becomes very slow and irregular then, and in the majority of oysters the current according to GALTSOFF stops when the temperature sinks below 8°, this being due to the lack of coordination of the ciliary motion. Generally speaking, the quantities pumped are highest at high temperatures (25–30° C), and they are lower at 10 than at 20° C. The importance of this fact is well demonstrated by such work as that of SAVAGE (1925), showing that the quantities of food obtained by *Ostrea edulis* on the Suffolk coast are negligible during the period January–April, whereas appreciable quantities are taken from July to October, with a short period of brisk feeding in August and September. The temperature during these observations ranged from zero to 23° C.

HOPKINS observations on *Ostrea gigas* are of special value, because they give an analysis of temperature influence on both shell closing and ciliary movement. He finds that the quantity of water pumped depends on ciliary movement and the degree of openness of the shell and mantle. At a certain temperature there is a direct relation between the degree of openness of the shell and the quantity of water pumped. Temperature changes, however, have a different effect on shell opening and ciliary movement. Ciliary motion increases up to 27–28° (as also found in *Ostrea virginica* by GALTSOFF), but the shells open widest at about 20° and a change of temperature from 20° to 25° causes a tendency for the shells to close, but produces at the same time more rapid action of the gill cilia, with the result that the effect on pumping is antagonistic. Below 20° an increase in temperature has more effect on pumping than one would expect from the increase in ciliary activity, but above 20° the effect on pumping is less. HOPKINS adds that both high and low temperatures (above 20° and below about 6°) appear to stimulate the oyster through sensory channels. It is quite difficult to keep a specimen open for experimentation either below 5° or above 25°; the further from the optimum, the more difficult it becomes.

Also the mantle margin shows movements which influence the current. HOPKINS supposes that its tentacles have a function as receptors for stimulation by temperature, just as they possess receptors for stimulation by chemicals (HOPKINS, 1932 *a* and *b*). Mantle, adductor muscle and ciliary movement appear to be directly affected by temperature, but they all seem to act with a high degree of independence of one another, "with the result that variations in the rate

of flow are tremendous." HOPKINS finally refers to GRAY (1928), who noted that the amplitude of beat of *Mytilus* cilia decreases above 33° while the rate of beat continues to increase up to about 37.5° C. "This suggests a comparable difference in temperature optima concerned in the activity of single cilia, and emphasizes the complexity of the activities resulting in a single curve of gross activity at different temperatures."

LOOSANOFF's and DODGSON's observations on the state of affairs in the mussel were mentioned already. In this species the current goes on even below zero, but this need not mean that the quantities pumped cannot be smaller at low than at high temperatures. Observations in the aquarium at Den Helder, where living mussels are used for filtering the aquarium water, have given me the impression that they work little efficient at temperatures approaching zero.[1] Further, also the observations of VON HARANGHY (1942) are important from this point of view. He compares the capacity of *Ostrea edulis*, *Mytilus edulis*, *Spisula solida*, and *Cultellus pellucidus* to clear suspensions of a certain concentration at different temperatures. The activity of the oyster is lower at 10 than at 20° C, that of the mussel apparently somewhat lower, whereas *Spisula* and *Cultellus* at 10 and 20° C according to his results show no difference.

Chemical influences on the quantities of water pumped are also important. It follows from VON HARANGHY's observations that mussels and oysters are less active in clearing suspensions from their suspended matter when the salinity of the water is low than when it is high. The results of GALTSOFF c.s. prove that solved products of pulp mill waste in higher concentrations decrease the quantities pumped and that the latter directly depend on the waste concentration. This effect, too, is certainly due to a direct action on the cilia. – LOOSANOFF and ENGLE show that also the concentration of the suspension within the water in which the animals live is of much influence and that very high concentrations may even bring pumping to a standstill. They assume that high concentrations work chemically and mechanically. That they may work chemically has been proved by the fact that the filtrate of their cultures had the same effect as the cultures themselves or the cells only.

[1] It follows from determinations made at Den Helder in 1951 by miss HEIKENS that the quantities of water *Mytilus edulis* pumps at or near 0° C are indeed small and of no importance when compared with the quantities pumped at 10–15°. The data will be published in Archives Néerl. de Zoologie.

DODGSON (p. 178) states that under similar temperature conditions mussels clear tank water more quickly in September–October than in February–March. He seeks the explanation in gonadial development or some other influence. Such an explanation does not hold for the observations at Den Helder, where temperature clearly is the operative factor.

This chemical influence is wholly comparable to that of pulp mill waste. That they also work mechanically has, I think, not been proved with certainty, a conclusion apparently also reached by KORRINGA (1949, p. 240). This does not mean that mechanical influences cannot be of importance, of course. It is probable that they do play a rôle.

3. WHAT PART OF THE SUSPENDED MATERIAL PRESENT IN THE WATER IS PUMPED IN?

Is the water pumped in with all the material suspended in it or does selection take place at the margin of the siphon?

So many observations have been made on so many species now that there can no longer be any doubt that selection at the siphon entrance is of hardly any importance. It is certain that the animals do take in all particles below a certain size without any selection, if they are not chemically or otherwise dangerous. Very little attention has been given to the point what is actually refused, however. COE and FOX (1944, also COE 1945) state that relatively large and spiny objects are prevented from entering the inhalent opening, but what size is refused by what animals is unknown. According to COE (1947) the inhalent siphon of the Pismo clam (*Tivela stultorum*) is provided with an elaborate filtering mechanism, with sensitive branching papillae which prevent the entrance of larger particles into the mantle cavity. Similar tentacles are found in *Cardium, Mytilus, Ostrea*, and certainly in other species, but it would be worth while to give this mechanism more attention, especially as it also contains the sensory mechanism which gives the stimulus for contraction of the mantle and adductor muscle of the shell, as was remarked by ALLEN (1921) and HOPKINS (1932, 1933). HOPKINS studied it in *Ostrea virginica* as to chemical stimulation.

It is well known that in plankton investigations it is not so easy to obtain a good idea of the true composition of the plankton present in the water, because fine meshed gauze throws part of the water out, coarse nets do not catch the small animals, whereas the narrow opening of the hose attached to a plankton pump may give such animals as Copepods the opportunity to escape. In this connection the following remarks of SAVAGE (p. 15) are important. "It will be observed that during the summer months when the temperature was high, and the feeding activities of the oysters were at their maximum, quite considerable quantities of metazoa (by volume) were captured. After October they disappeared from the food contents, and this was doubtless due, as MÖBIUS (1877) and NELSON (1920) have suggested, to the weakening of ciliary and muscular action caused by the fall in temperature, with the result that the oysters had no longer the power to capture the larger

organisms." This possibility, that the Copepods, etc. in August–September could no longer escape because the oysters pumped so very fast, should certainly not be neglected. A second possibility, however, may be that the larger animals were caught in greater numbers, because so many litres were filtered; also the diatoms and detritus show high maxima in the same months. I have not tried to analyse SAVAGE's figures in respect to the two possibilities mentioned. It is clear from his data that the large summer-numbers of Copepods, etc. were not due to the greater numerousness of these animals in the water during these months.

Speaking generally, it is quite probable that nearly all the material reaching cockles and mussels as suspended matter is pumped in. This is important in connection with the calculations, which follow below.

4. WHAT PART OF THE MATERIAL PUMPED IN IS RETAINED?

Next comes the important point what part of the food is retained from the water before the latter leaves the animal again. This point is full of controversies.

MAC GINITIE has defended the view that pumping need not mean feeding, as a lamellibranch may be pumping without retaining back the food suspended in the water pumped, because the layer of mucus over the gills, which according to MAC GINITIE is necessary to feeding, is not always present as a continuous sheet. COE and FOX (1942) also state that experiments at Scripps Institution, California, showed that the mussel *Mytilus californianus* does not feed all the time it is actively pumping water through the gills.

There are indeed a number of observations, showing that all the matter pumped in need not be retained (GALTSOFF, 1928; LOOSANOFF and ENGLE, 1947), though in other cases it is, and this is one of KOR-RINGA's arguments (1949) for believing that MAC GINITIE's view is right. "We should say with MAC GINITIE: certainly it never should be said that a pelecypod is feeding just because it is pumping or maintaining a current through the mantle cavity." It must be said that GALTSOFF's observations (1928), according to which larger particles like small diatoms seemed to be retained, anyhow, whereas small particles gave quite variable results, could be explained by the assumption that small particles can pass the gills more or less unhindered when the mucus layer is incomplete, whereas larger ones could then be retained through the fronto-lateral cilia. This is what MAC GINITIE, KORRINGA, and also JÖRGENSEN actually suppose. JÖRGENSEN has tried to prove the correctness of this assumption. His results, however, are not convincing, since he does not reckon with the possibility that the mussel itself

interferes by either retaining material or letting it through in another way than through secreting mucus. Moreover, his experiments with flagellates are partly in contradiction to his conclusions.

The whole question of retaining food may remain doubtful as long as no better experiments have been made. MAC GINITIE himself is of opinion that the ingestion of such substances as carmine and carborundum never takes place in normal feeding. But so many non-nutritive kinds of material, carmine included, have been found to be readily ingested, that we must at least trie to bring the numerous former observations into line with the new ones and not discard them without more.[1]

It is certain that all kinds of material, at least down to the size of large colloids, can be retained. ZoBELL and FELTHAM (1938) have shown that *Mytilus californianus* can live for long periods on nothing but bacteria and on this food can gain somewhat in weight. They even kept mussels alive for two years on a diet of bacteria. DAMAS (1934) concludes on good grounds that cockles strain the colloids from the water. We are probably allowed to say that the same happened in the experiments of Fox, SVERDRUP and CUNNINGHAM, and those of JÖRGENSEN. Fox and COE (1943, p. 236), finally, proved in "preliminary experiments" the mussel's ability to remove from its medium very fine, uncentrifugable colloid material such as Congo Red or boiled "soluble starch" in highly diluted dispersions, ingesting some of this material and expelling the rest as pseudofaeces. They even believe that colloids may be a quite valuable source of nutrition. Its value must remain uncertain, however, as long as the quantity of such matter present in the sea is not known.

Not only can lamellibranchs retain material down to the size of colloids, they can strain this off so efficiently that the material can apparently be eliminated completely during one single passage of water through the gills. Fox, SVERDRUP and CUNNINGHAM conclude that in their experiments a constant amount of water passed through the mussel chamber in unit time and that virtually all suspended (and colloidal) calcium in this amount of water was removed.

On the other hand, the observations of LOOSANOFF and ENGLE show that in dense concentrations of micro-organisms high percentages of the suspended organisms may pass through the gills without being retained.

These controversial results could be explained through the supposition that the animal can change the quantity of material it retains

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[1] Thus mussels have been observed to gorge their alimentary canals, so to speak, with chalk; not only for hours, but for days on end (DODGSON, 1928, p. 165); compare also DODGSON, p. 182–185.

more or less "at will". This could be effected through the secretion of mucus, as supposed by MAC GINITIE, or perhaps in another way: through the action of the fronto-lateral cilia, by opening the wall between both branchial chambers, etc. It would mean that, as a re-action to the presence of unsuitable material not only the shell or mantle could be closed, or the siphon shut off, but also mucus pro-duction could be stopped, the action of the cilia changed, etc. It follows from the experiments of GALTSOFF c.s., and of LOOSANOFF and ENGLE, that the stimulus which leads to shell closure can be quite different from that which causes ciliary standstill. Highly concentrated suspensions might cause ceasing of ciliar straining or of mucus secretion, though pumping might go on. In such cases large quantities of sus-pended material might pass the animal partly unhindered, though a certain percentage of them would be retained. The latter might be partly rejected, but another part might find its way to the intestinal tract. In such cases large quantities of the suspended matter could be found in the outgoing current, as well as in both faeces and pseudo-faeces. This is what actually happens. If the water would contain suitable and unsuitable material at the same time, now one, then the other stimulus would predominate and matters would become still more complicated. Mucus secretion, the action of the fronto-lateral cilia, contraction of the gills, opening the chamber walls, would all form means to deal with suitable as well as unsuitable food through the control of the innate reaction mechanism of the species. Feeding would not be restricted to periods when these mechanisms cooperate, but their cooperation would lead to greater efficiency in the capture of food.

5. HOW DOES A SEPARATION BETWEEN USEFUL AND UNUSEFUL TAKE PLACE?

The next point is the selection of particles on their way from the gills to the mouth. Numerous details on the ciliary mechanism of the gills and mouth palps have been given for many species, see especially D. ATKINS in Quart J. Micr. Sc. 1936-38. YONGE cites NELSON (1923 b) who concludes that feeding in the oyster is accomplished "through the delicate coordination of nervous, muscular, ciliary and mucous secreting elements in which mechanical sorting of the materials plays the most important part": "an admirable summary of the state of affairs".

The particles are divided by the movements of different kinds of cilia into two groups: one that is refused, the other that is accepted as food.

YONGE, in his first paper on this subject, dealing with the feeding of

the soft clam, *Mya arenaria*, supposed that the principle of this separation was based on weight of particles, not on size. His argument was that in the clam's stomach he found thin filamentous strips of algae up to 1 mm in length, though the largest solid particles (sand, etc.) were no more than 200 μ in diameter, and the majority no more than 20 μ. YONGE seems to have dropped this supposition when studying the oyster. Though he is not quite clear on this point he considers from then on size of particles apparently more important than weight; I think, because he found that conglomerations of particles are rejected, though separate ones are carried to the mouth. This in itself is no evidence, of course, and I, personally, am not convinced that weight is unimportant. Perhaps, however, there is a combined principle of weight *and* size.

COE (1947) finds for the Pismo clam that more than half of the stomach-contents may consist of sand, the coarsest grains of which measure 200–300 μ longest diameter. That may mean that the sand coarser than that is refused. Thin fragments of periostracum and chitin, however, of nearly 1 mm in length and filamentous algae 1.5 mm long do also occur, they being the largest objects observed. He further finds that solitary diatoms of 50–200 μ and smaller are accepted, but colonial and spiny species are usually refused. I can only understand all these facts through the assumption that both weight and size play a rôle, but the matter remains uncertain.

The point, whether there is other selection than that according to weight and (or) size, for instance according to organic and inorganic particles, hardly appears to need consideration here, because nearly everyone now agrees that the latter selection is out of the question. In connection therewith the following should be mentioned, however. BULEY (1936) has stated that he found hardly anything but dinoflagellates in mussel stomachs, though in the sea water in which they lived he found very few. According to his counts the sea contained 2.4% of dinoflagellates and 97.6% of diatoms against the mussel stomachs 97.4% of dinoflagellates and 2.6% of diatoms. This would mean selection and it tallied with Fox' belief (1936) that dinoflagellates are valuable as food. In 1942 COE and Fox still cited these observations.

But from 1943 on Fox and Coe came to the conclusion that dinoflagellates do not form a valuable food. Since then they no longer believe in selection and BULEY's observations are no longer mentioned (COE and Fox, 1944; COE, 1947). The possibility can probably not be excluded that in this case dinoflagellates may have exceeded diatoms in the bottom water, which reached the mussels, though in the higher layers diatoms exceeded dinoflagellates. – Also LOOSANOFF and ENGLE (p. 50–51) consider the possibility of selection, and their vision cannot be

neglected, because they had an enormous practical experience.[1] On the other hand, it is clear from such work as that of SAVAGE (1925) and others that there is a striking agreement between the composition of the plankton and that of the stomach contents of mollusks living in the water from which the plankton is taken, also in cases where much apparently undigestible material is taken in (oyster larvae for instance).[2]

The most important point in connection with the problem of selection is that of the influence of the concentration of the suspension pumped in. It was remarked already that even high concentrations may be pumped in, but this does not mean that they are favourable to the animals, anyhow, and that most of the material in question would be carried to the mouth. KELLOGG (1915) was of opinion "that a lamellibranch is able to feed only when waters are comparatively clear, when diatoms are brought to the gill surface a few at a time, and that in muddy waters, all suspended particles, of whatever nature, are led to outgoing tracts". This view has become the subject of much discussion (see LOOSANOFF and ENGLE, 1937) and DODGSON and others were cited (see DODGSON, p. 175), who in mussels found the largest quantities of faeces in the muddiest water; in other words, the food from this water had been ingested notwithstanding the high concentration of the silt. We may expect, however, that mussels may behave quite differently from oysters and that the different species of oysters behave by no means the same. In all kinds of animal groups we find species able to cope with large quantities of silt and others which cannot work the silt away, especially the sponges, anemones, corals, and hydroids embracing numerous instances. "ELSEY (1935) found that *O. gigas* withstands existence in turbid water much better than *O. lurida*, which closely resembles *O. edulis*" (LOOSANOFF and ENGLE, 1947). But LOOSANOFF and ENGLE even defend the view that through this cause scarcity of plankton may be better for oysters than its rich development and few biologists will probably accept this. Nevertheless the principle itself may be right.

If large quantities of silt or other suspended matter are pumped in they may clogg the gills, so that oxygen intake may become difficult.

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[1] SMIDT (1951, p. 111) refers to LOOSANOFF (1949), who "states that feeding *Ostrea* are capable of choosing between different flagellates".

[2] There is an interesting observation of DODGSON (p. 187), who describes how mussels in very hot weather, although open and discharging vigorous streams from their anal siphons and manufacturing pseudofaeces in large quantities, refused to ingest any of the suspended material through the mouth. "The water at the beginning of the experiments was 66° F, but rapidly rose, reaching 72° F in the course of an hour. A day or so later, the same mussels resumed their normal feeding in water at 64° F." But this is no instance of selection, of course.

Further, it must cost large amounts of mucus to work such quantities away. This may be sufficient reason for working the silt away along the shortest possible route, that of the pseudofaeces. Moreover, dense masses of small particles will easily clot together and then be dealt with as heavy or large particles, which are ejected as pseudofaeces. This was what KELLOGG (1915) meant and his viewpoint may be right.

LOOSANOFF and ENGLE conclude from their experiments with suspensions of micro-organisms of different concentrations that high concentrations in the oyster give many pseudofaeces and few faeces, and the reverse.[1] – COE and FOX (1944) say about the Californian mussel: "The excess, if not too great, may pass unchanged through the digestive system, but in case of a very great surplus most of the material is rejected by the palps and is discharged from the mantle cavity as pseudofaeces." – COE (1947) states that the matter pumped in is largely refused "in dense suspensions of micro-organisms, spermatozoa, ova, yolk or oil globules, or starch particles".

Because these statements agree there will be little doubt that they are right. Details on these observations have not been given, however, and one would like to know whether the statements are based on a general impression or on more. It is well known that concentrated suspensions produce large quantities of pseudofaeces, but this is only natural. In view of the fact, that there has been so much controversy on this point, it should be established beyond doubt that not only do the quantities of pseudofaeces on feeding of concentrated suspensions increase, but also the quantities of faeces decrease.

In connection with the problem of the refusal of material in the presence of concentrated suspensions the observations of DODGSON on the movements of a membrance in the inhalent opening of *Mytilus edulis* are of much interest; DODGSON gave it the name of velum. These observations form an extension of earlier ones of KELLOGG (1915) and ORTON (1912). KELLOGG was the first to suppose that the velum might have the function described below.

It is usually assumed that refusal of pumped in material is wholly due to the activity of the cilia of gills and palps, which carry the refused material to the place of ejection of pseudofaeces. DODGSON describes, however, how the velum is lowered when there is much suspended matter in the water, with the result that the current entering the inhalent opening is directed to the posterior part of the mantle margin, from where much material is discharged forthwith as pseudofaeces.

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[1] The limit for high concentrations, in producing a high percentage of pseudofaeces, would differ for different micro-organisms, and LOOSANOFF and ENGLE remark that matters must become quite complicated when, as in nature, all kinds of organisms and material occur together.

The reader is referred to Dodgson's full description (p. 172–176) and figures of the velum for a right understanding of this fact.

It means that the mussel has more means than ciliary activity alone to dispose of excess matter and a similar state of affairs may hold for other bivalves (Kellogg described the velum for *Schizothaerus*).

The question whether high concentrations would influence the velum movements both mechanically and chemically remains open. It was stated above already that high concentrations may have a chemical (toxic) effect on pumping and they might have a similar effect on the velum movements as well. Judging from Dodgson's description we are further allowed to assume that mechanical influences are important, anyhow.

Dodgson (p. 174) supposes that the velum not only functions in keeping excess of suspended matter from entering the inter-branchial spaces and anterior parts of the mantle cavity, and in facilitating their rejection in the recurrent marginal stream, but that it also exerts a certain selective function, the degree of diversion of suspended matter varying with its amount, and possibly with the size or irritating properties of the suspended particles (e.g., in the case of sharp sand grains, etc.).

6. WHAT PART OF THE MATERIAL RETAINED IS ACCEPTED, WHAT PART IS REJECTED?

Stomach contents have given us much insight into this question.

The stomach of *Mytilus californianus* and *Mytilus edulis* contain all kinds of phytoplankton (algal spores, dinoflagellates, small diatoms, other algae, and bacteria), zooplankton (flagellates, ciliates, other protozoa, spermatozoa and ova of invertebrates, etc.); further fine material which is considered detritus; and finally fine sand and shell material (Fox, 1936; Coe and Fox, 1942; Fox and Coe, 1943; Coe and Fox, 1944; Coe, 1945). Coe (1947) finds for the Pismo clam, which occurs on sandy coasts, that more than half of the stomach contents may consist of sand. He further finds dinoflagellates in fair numbers: especially *Prorocentrum* (40–50 μ long), *Gymnodinium*, *Peridinium*, *Gonyaulax*, *Dinophysis*, and many others of 40–60 μ. Spherical algal cells of up to 100–300 μ diameter, slender multicellular algae of up to 600 μ, with longest filamentous algae of up to 1.5 mm. Crypto- and phytomonadines and other flagellates. Diatoms of 50–200 μ long and smaller forms often in great numbers. "Other living cells include algal zoospores and the gametes of nearly all the invertebrates of the vicinity, including those of the clam itself." It certainly is an uncommon achievement of Coe to distinguish all of them. – The stomach contents

of the soft clam, *Mya arenaria*, according to YONGE "consist of very
finely divided particles of organic debris, sand and micro-organisms,
e.g. diatoms, singly and in chains; Foraminifera; minute, probably
larval, bivalves; ostracods and other microscopic Crustacea, with parts
of larger specimens; spores and eggs of various kinds; sponge spicules,
and spines of all sizes. The great mass of material consists of small
sand grains".

Many data have been published on the stomach contents of oysters,
for which the reader may be referred to detailed work like that of
SAVAGE (1925).

It is evident from the numerous observations given that the stomachs
of different species always more or less reflect what is found in the
vicinity. One gets the impression that simply all material below a
certain size is ingested. Even large quantities of sand are dealt with as
if they had nutritional value, this simply being due to the simpleness of
the selection mechanism. In connection therewith there is little reason
to assume that organic detritus present in the water should not be
ingested in the same way as fine sand and this is what certainly happens,
as was shown by PETERSEN and BOYSEN JENSEN in 1911 already.
SAVAGE came to the conclusion that more than 90 % of the food con-
tained in the gut (stomach and intestinal tract) of the oysters he
investigated consisted of organic detritus. This detritus has a certain
food value to those organisms which can digest it. The point is, how-
ever, whether the different species of mollusks indeed can digest it, a
problem, which is further dealt with below.

The stomach investigations, together with a direct study of the
material that is rejected as pseudofaeces[1], give at the same time an
impression of what is refused. COE (1947) says that among the dino-
flagellates *Ceratium*, which are spiny and 200–300 μ long, are not
ingested; diatoms of 50–200 μ long and smaller forms are often found
in great numbers, but colonial and spiny species are usually refused. –
Most sand above a certain grain size is certainly refused, but little is
known about the actual grain sizes. Surely, larger pieces of detritus,

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[1] The name pseudofaeces has been given to the refused material by DODGSON, to
whose description and photographs of mussel-pseudofaeces is here referred. He
already draws attention to the fact that their rejection "takes place at a point im-
mediately posterior to the exhalent siphon – that is to say, at the apex of the arch
formed by the fusion of the edges of the mantle folds". This means that they issue
from the part of the inhalent opening next to the exhalent aperture (compare also
Fox and COE, 1943, p. 233). DODGSON adds: "In virtue of the fact that this solid
matter is mixed with a varying amount of mucoid secretion, it tends to be discharged
in formed masses or strings, rather than in separate granules." Only in case the
suspended matter is excessive do the pseudofaeces lose their coherent form. The
resistence of pseudofaeces to disintegration according to DODGSON is striking. The
reader is referred to his description on p. 162–164 for further details.

though they would represent much better food than fine sand, are rejected because of their size (weight). Fox and COE (1943) found that the pseudofaeces may also contain large micro-organisms, ova, larvae, etc. They say they "are usually returned to the sea while still in a living condition", but unpublished observations of KRISTENSEN point to the possibility that since they are enveloped in mucus they may partly die afterwards.

The quantities of pseudofaeces are large when the water contains much sand or many shell fragments (Fox and COE, 1943). They also depend, of course, on the total quantities of material pumped in; they are small when the water contains little matter in suspension.

In *Mytilus* the pseudofaeces simply drop beside the animal together with the true faeces, compare especially DODGSON's description. In other species they may be ejected with force. MAC GINITIE (1941) describes how the gaper clam, *Schizothaerus nuttallii*, ejects material by a sharp contraction of the adductor muscles, which quickly brings the valves together and squirts the water out through the incurrent siphon. This activity according to MAC GINITIE undoubtedly accounts for some of the squirting by clams on mud flats when the tide is going out. When the flats are nearly bare a considerable amount of sand and other material may have accumulated and this is rejected. Longnecked clams usually eject water much more forcibly than those with a short siphon; *Schizothaerus* squirts the water from 3 to 5 feet high. Squirting according to MAC GINITIE is also more frequent when the tide is first coming in. – We can observe this squirting regularly in *Cardium edule*. The water is ejected here up to some decimetres.

7. WHAT PART OF THE ACCEPTED MATERIAL IS REALLY DIGESTED?

Though the selection mechanism of lamellibranchs is complicated enough, it works according to a very simple principle: that of separation of material by weight or (and) size; with the result that such undigestible matter as sand enters in large quantities. One cannot therefore consider the stomach contents as representative of actual food.

Data on the food value of the material pumped in have been collected in the very first place by studying the action of digestive enzymes. Especially YONGE studied the oyster and he also examined the soft clam (*Mya arenaria*), GRAHAM the razor clam, Fox and MARKS (1936) the Californian mussel, COE (1947) gave some notes on the *Pismo* clam. These investigations all led to the result that amylase and glycogenase are produced in significant amounts in the style of the digestive tract, while the same polysaccharidases as well as disaccha-

ridases, proteases and lipases would be produced intracellularly. COE (1947) further found in the Pismo clam a weak cellulase, apparently produced by the style.

The majority of investigators are therefore of opinion that digestion is largely intracellular and that only minute particles, especially plants, can be attacked. On the other hand, the minority are represented by a number of notable exceptions, among whom the MANSOURS rank first. Their work is chiefly concerned with some tropical species, especially *Tridacna*. They are of opinion that extracellular digestion is not to be neglected.

NELSON (1933) cites an instance in which an *Ostrea edulis* yielded 0.75 cm³ of stomach contents, consisting mostly of a free-living nematode (*Chromadora* sp.). Analysis showed 160 worms alive and active, 471 dead but intact, and 5842 partially or wholly disintegrated. Such and other cases (among others many data in SAVAGE, 1925, for the oyster, in publications of COE for other species) do not furnish direct evidence that such animals can be digested, but there is no reason to assume the contrary in view of the fact that after disintegration has started small particles can be attacked further. The uncertainty in this field is well demonstrated by the contents of KORRINGA's paper (1949).

Largely because of YONGE's influence the chief food of lamellibranchs has thus for a long time been considered to be chiefly represented by phytoplankton in the form of flagellates, small dinoflagellates and small diatoms, whereas there was much differense of opinion not only as to the value of multicellular animals, but also to that of detritus. Particles of detritus cannot be identified in the stomach, intestine or faeces with the same certainty as can diatoms, dinoflagellates, etc. None the less, ever since PETERSEN (1911) stressed the importance of detritus as food for lamellibranchs the latter has been considered of more or less importance by a number of investigators. None of them, however, have given themselves so much trouble to show what value detritus may have as food as Fox and COE. It therefore is to be deplored that a number of inaccuracies in the papers of the latter have detracted from the value of their results.

In short, the reasoning of COE and Fox is: the total quantity of food contained in dinoflagellates, diatoms, flagellates, bacteria, etc. is so small that a mussel pumping the year round would only capture a dry weight of them, comparable to one fifth of what it needs. Therefore, another source of food must play a rôle and since there is no other source of particles small enough for digestion than organic debris, the latter must be of much more importance than all these organisms together.

This reasoning is based on the number of litres a mussel pumps in the course of a year, the average content of dinoflagellates and other

organisms present in the water, their weight, and the gain in weight of the mussel within a year. Taken as a whole, this reasoning may be more or less correct (the same standpoint was apparently held by MOORE, 1913), but it loses through inexact argumentation.

In 1936 Fox holds the view that dinoflagellates are a very valuable source of food. He attempts to prove this by observations on their digestibility, and his findings tally with those of BULEY already cited, who finds that they are apparently especially selected. Still in 1942 COE and Fox hold the view that dinoflagellates are readily digested, but because of their small mass can be considered *one* of the principal food supplies only. In 1943 they come to the conclusion that dinoflagellates pass the digestive tract largely undigested and from then onward they no longer attach much value to them as food. This is most natural, but they neglect their former findings (those of BULEY included) without recanting them. This can only lead to confusion, for even when one reads their papers in the right order it is not easy to understand the true state of affairs. The difficulty is still enhanced by the fact that in COE's papers it is not always easy to make out what are new facts and what old ones already dealt with in an earlier paper.

Fox and COE conclude that one large Californian mussel within a year may pump some 22.000 litres of sea water. Now, in 1943, they calculate that such a volume, if it contains 9570 specimens of the dinoflagellate *Prorocentrum micans* (measuring $30 \times 57 \mu$) per litre, contains 4.2 g of dry weight, or some 10 % of the mussel's annual gain in weight, if it could all be digested and directly changed into mussel weight. In 1944 they state that the years 1940–'43 gave averages of 10.000–55.000 dinoflagellates per litre. In these years, therefore, 22.000 litres must have contained some 4–23 grams dry weight of dinoflagellates, and one would think that these must have been at least of *some* value. But COE and Fox now say that the dinoflagellates occurred in such dense swarms that few may have been ingested, whereas the rest were possibly rejected as pseudofaeces. Since the ingested ones must have been largely undigestable, very little remained. This is a somewhat arbitrary argumentation.

A large part of the work of COE and Fox concentrates on a comparison of mussel growth in the sea and the number of organisms present in the water. This work has been continued for more than four years and an enormous amount of labour has been involved. Their observations on growth may serve as an example how such work should be carried out. No correspondence is found between mussel growth and the quantities of diatoms or bacteria, but they do find some correspondence between mussel growth and the dinoflagellate populations. Since, however, dinoflagellates, when very numerous, according to COE

and Fox are largely ejected as pseudofaeces, since they are largely undigestible, and since a four fold increase in abundance according to COE and FOX (1944) is associated with an increased growth rate of the mussels of only 42 per cent, the correlation does not in itself furnish evidence that dinoflagellates are important as food. It may show no more than that both mussels and dinoflagellates thrive under the same environmental conditions. This in itself is not impossible, but it is used as an argument for the value of detritus and as such it is without value. It is clear from the experiments of COE and FOX (1944) that high dinoflagellate figures correspond with rapid growth of mussels; COE and FOX have shown that the dry weight of the ingested dinoflagellates in periods that they are numerous must be very important also in relation to the annual gain in weight of the mussel; FOX (1936) has made it probable that dinoflagellates are at least partially digested. If, nevertheless, one wants to assume that dinoflagellates are unimportant as food and that detritus should be considered of much more value one should at least suppose that the dinoflagellates already during their maximum abundance produce so much detritus that the latter apparently causes an increased growth of mussels. This conclusion is the more obvious since COE and FOX themselves assume that increased mussel growth may coincide with the periods of propagation of *Balanus tintinnabulum* and other species because the latter may furnish detritus to the mussel. Even such a conclusion, however, somewhat neglects the possible value of the *living* dinoflagellates as food for the Californian mussel.

There may be little doubt that suspended organic detritus is one of the valuable sources of food for certain bivalves, as has been assumed by many ever since PETERSEN in 1911 emphatically drew attention to this possibility. SAVAGE (1925), who obtained a great practical experience by his research, found that his oysters had their stomachs and intestine filled with about 25–100 times more detritus than plankton (both counted by volume). He therefore (and also because of the work of JENSEN, 1914) was of opinion that detritus must be taken seriously into consideration as a source of food for oysters, but that "fattening" of oysters may be due to a great consumption of small diatoms. I think it is about this same opinion which is held by most specialists: that the best food for oysters probably is small diatoms, but that detritus may be quite valuable as a cheaper food of lesser value. If we want to prove this, a direct, experimental method seems indicated. This is no easy task. One cannot feed natural detritus, because it cannot be separated from the plankton. GAVARD, however, fed an artificial detritus, according to KORRINGA (1949) with very good results. – The value of detritus will certainly differ for different species,

I am inclined to suppose that it may be more valuable to the mussel than to the oyster. It is clear, however, that very few workers sufficiently command all facts collected in this field up till now; in this respect a critical revision of our present knowledge in this field, not for one, but for several species, would be of much value. WERNSTEDT's conclusion (1943), his experiments would indicate that the food value of detritus is only small, is certainly unjustified.[1]

Some remarks should still be added on the times the ingested material needs to pass the intestinal tract, as they increase our insight into matters of digestion. They refer to oyster, mussel and cockle.

LOOSANOFF and NOMEJKO (1946) say that oysters kept in water of 20.0° C under laboratory conditions passed the particles of food through their entire digestive system in from 1 hour and 20 minutes to approximately 2 hours and 30 minutes.

As to the mussel, numerous observations have been given by DODGSON (p. 182–188), who experimented with "substances such as carmine, chalk, flour, Prussian blue, etc." It was found that material ingested at the mouth may appear at the anus within 1 ¼ hours. Moreover, an alimentary canal engorged from end to end may be completely evacuated in a similar period. "If open, and passing good siphon currents, they appear never to fail to ingest the suspension, but 3, 4, and even 6 hours have been observed to elapse before the passage of the index faeces. In the last case, however, the mussel had been stored for a week in one of the tanks, during the early part of which the weather was hot, prior to the experiment." And though a full tract may be emptied in 1 ¼ hour it may also need a longer time, up to several hours. – Observations of ZoBELL and FELTHAM (1938) gave results, which do not essentially differ from those of DODGSON. They found that bacteria disappeared from the intestinal tract of mussels within six hours after being fed. Their mussel was *Mytilus californianus*.

Finally, JÖRGENSEN (1949) found that 30–60 minutes after the pre-

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[1] WERNSTEDT worked with *Cardium edule* and *Macoma baltica* and his conclusion could only hold for these species. It is probable, however, that the value of detritus for a detritus feeder like *Macoma baltica* cannot be small. His experiments are unsufficient to prove or disprove this.

The value of detritus must be quite different to different species of one and the same animal group. Among crabs many species certainly cannot make use of detritus, whereas others, e.g. the tropical *Uca* species and *Eupagurus bernhardus*, feed on hardly anything else. That the latter species should have such food seems to follow from the fact that it prefers rotten meat (for instance, that of fish) over fresh meat. Such detritus feeders are to be found in many animal groups. This fact is not at all new, of course, but it should constantly be kept in mind to make one realize that it is not the small food value of detritus, which makes detritus valueless to some animals, but the impossibility of such animals to use detritus for food (for the food value of detritus see BOYSEN JENSEN, 1914).

sentation of graphite suspension to mussels large amounts of graphite faeces were ejected through the exhalent siphon. Since JÖRGENSEN worked with rather young *Mytilus edulis*, his observations, again, are more or less in agreement with those of DODGSON. – In all these cases undigestible or presumably easily digestible matter was used and the times it needs to pass the intestinal tract is short.

It follows from the observations of AUSTIN on the stages of digestion of stomach contents of mussels at various times after feeding natural food that digestion had commenced one hour after feeding, but that more than five hours elapse before diatoms in the stomach may have lost their chlorophyll and that the skeletons of diatoms and dinoflagellates were still present 24 hours after the diatoms had been fed. This probably shows that slowly digestible matter passes the tract much slower than undigestible or presumably easily digestible material. The observations of COE (1945) apparently show the same. "That minute diatoms are readily digested is shown by the fact that within 20 hours after the mussels have been fed cultures of small species the faeces consist mainly of chloroplasts, with only a few intact cells." COE considers this a short time, but it is long compared with the other times mentioned.

Finally, the data of Fox and COE (1943) show that mussels brought from the sea into the laboratory may give off undiminished quantities of faeces for three succeeding days. Only after the fourth day the quantity decreases. This means that it takes several days for a tract filled with natural food to lose all its material. In this connection it should not be forgotten that *Mytilus californianus* is a very large species.

As to the cockle I am acquainted with one observation only, that of DAMAS. He says the following. "L'activité nutritive de ces *Cardium* est en effet énorme. Des individus tenus en état d'inanition prolongée et dont le tube digestif vide ne fournissait plus d'excréments reprennent la reproduction de boudins après 12 minutes si on les replace dans une eau vaseuse. Il ne faut donc à la nourriture que ce laps de temps pour parcourir le tube digestif tout entier." It is not probable that real food would need such a short time and it would be of interest to pay some attention to this point.

8. WHAT IS KNOWN ABOUT THE QUANTITY AND COMPOSITION OF THE FAECES?

Generally speaking, the faeces of mollusks are excreted in the form of pellets, the size and form of which are different for different species, compare especially MOORE (1931 a, b, and c, and 1939). They are large and long in the mussel (for description see DODGSON, 1928, p.

161–162) and small and more or less globular in the cockle. MOORE (1939) says that "in general, carnivorous animals tend to produce faeces of loose consistency, vegetable eaters firmer ones, and deposit eaters (like our lamellibranchs) the most resistant of all." "The pellets of deposit eaters will stand (MOORE, 1931a) fairly rough handling, and can even be boiled with sulphuric acid or strong caustic soda without breaking down." MOORE (1931a) found them in bottom deposits, at least a hundred years old and they showed no evidence of breakdown. He ascribes their resistency to the high mineral content of the food of the animals producing them and considers it probable that progressive glauconization may cement and strengthen the pellets so that they may well be preserved permanently (MOORE, 1939).

The quantity of faecal pellets produced is more or less known for cockles. DAMAS counted one pellet issuing every 8 seconds. That would make 10.800 pellets a day. According to DAMAS their size is 0.3 mm³ and the animals therefore would produce 3240 mm³ of faecal matter a day.

Counts in July, 1949, on the sands in front of the Zoological Station, Den Helder, gave the following results:

Number of counts	Extremes of lapse of time between two successive pellets (in seconds)	Average lapse of time between two pellets (in seconds)
± 8	14–23	19
± 8	7–20	12
4	8–27	19
2	13–14	14
8	14–23	19
5	6–37	18
17	8–32	15
21	10–40	27
4	9–16	12
12	10–97	23
Total ± 89		Average 18

These observations show that a total of about 90 observations on 10 different animals gave on an average one pellet every 18 seconds. This was in the middle of summer. It may be assumed that the number is perhaps higher in spring, but certainly much lower in winter, so that 40 seconds may be considered a better average for the year than 20. The *Cardium* had been born in 1947, they were two years old and measured about 30 mm. Older animals may work slower than young ones and DAMAS may have observed younger cockles. The figures show that there is much individual variation.

It should be added that one cockle, after having given off 8 pellets with lapses of time of 14–23 seconds, retained all material for 450 seconds and then gave off a complete string of pellets. There then was a pause of another 60 seconds, thereafter about the old rhythm was taken up again.

If the faecal pellets of cockles of the size mentioned would have a size of 0.3 mm³ as given by Damas and if these cockles would produce one pellet every 40 seconds they would produce 648 mm³ of wet faecal matter per day. As their specific weight is somewhat higher than that of sea water their wet weight must be some 648 mg at the least.

For the mussel similar observations are not available, but Fox and Coe (1943) have determined the dry weight of faeces given off by individuals of different length and they find 7.5, 45, 95, 176, and 281 mg dry weight a day for mussels of 20, 40, 60, 80, and 120 mm length. If I understand them correctly, however, they have decanted part of the sand before drying and weighing the material, so that all these values would be too low. – Also Blegvad (1915) gave some values. They refer to the quantity of faeces, produced by 100 g *Mytilus edulis* during 24 hours. The animals were apparently brought from the sea into an aquarium again and faeces and pseudofaeces were probably measured as one. Since, however, the production of faeces in the aquarium will continue and that of pseudofaeces will stop within a short time because new food is not available, most of the material produced must be true faeces.[1] 100 g mussels produced in one case 1870, in another 3080 mg (dry weight) of material. Blegvad does not mention the size of his mussels, but if they were large they would represent 2–3 animals, so that one large mussel would produce 800–1200 mg (dry weight) of matter per day. Since part of it may have been pseudofaeces, the faeces may have weighed maximally some 1000 mg (dry weight) per animal per 24 hours.

Finally, Kamps made exact measurements of the quantities of suspended material laid down by mussels along the coast of the province of Groningen in the Netherlands. He used small boxes with 80 mussels each and control boxes with similar mussels filled with concrete. The water had free passage through the walls. The boxes were laid out in the sea and they were controlled every fortnight from March to November. It should be added that the water along the coast of Groningen contains several times more suspended matter than that in the western part of the Waddensea, where the work of the Zoological

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[1] It is not wholly correct to consider the quantities mentioned as representative for 24 hours, because the mussels were taken from the sea and their faeces collected over the first 24 hours when they got no food. According to the observations of Fox and Coe, however, mussels taken from the sea may give off undiminished quantities of faeces for 3 successive days.

Station was mostly carried out. KAMPS, who permits me to mention his results (see also KAMPS, 1950, p. 112), found that 80 large mussels within 2 weeks produced quantities ranging from 2600 to 4200 g, with an average of about 3300 (13 determinations). This gives an average production of about 3000 mg (dry weight) per large mussel per day, a quantity 3 times that found by BLEGVAD, but including both faeces and pseudofaeces. The relation between pseudofaeces and faeces within that amount is not known, but a large part of the material may represent pseudofaeces and it is assumed that the true faeces did not exceed 2000 mg per large animal per day at the very most. Assuming a water content of the faeces of about 75 % the wet weight would be some 8 g per large mussel per day, i.e. some 9 times more than that found for the cockles near Den Helder. It should be added once more that the figure is certainly very high and that a faeces-production of half that amount may be more normal.[1]

Fox and COE (1943) determined also the composition of mussel faeces. Here, again, however, "as much sand and shell as possible was separated by comminution and subsequent decantation from the samples at each collection". Apparently, this sand is not contained in the results of their analysis. They find some 70 % of ash ("chiefly sand and shell"), somewhat more than 1 % of N and some 0.5 % of PO_4. If, as assumed, the decanted sand was not calculated, the true ash figures become higher. COE (1945), basing himself on these figures of Fox and COE (1943), says that mussel faeces consist for some 30 % of organic matter, but this quantity would become lower.

TAKAHASHI and YAGI (see MOORE, 1939) found 0.21–0.42 % of P_2O_5, i.e. 0.28–0.55 % of PO_4 in recent faecal pellets[2]; this value is not much different from that of Fox and COE. – Fox and COE multiply their nitrogen figures by 6.25 – "commonly accepted as applying to the

[1] Assuming that the animals pumped 1.8 litres per hour for no less than 20 out of the 24 hours the water pumped must have contained more than 83 mg dry weight of suspended matter per litre plus the quantity digested, a total of at least 100 mg per litre. If they pumped for shorter periods or if they pumped smaller quantities per hour the quantity of suspended material present in the water must have been still greater. The quantities are therefore at least 4–5 times greater than those in the western Waddensea according to POSTMA's determinations. This is in agreement with direct measurements of the quantities of suspended matter per litre, as carried out in the eastern Waddensea by KAMPS. Nevertheless, the mussels (and also the cockles) in the eastern part of the Waddensea remain small. As the salinity of the water there is as high or higher than that in the western part the composition of the suspended material may be less optimal in the eastern than in the western part. In this connection the question of the possibly adverse influence of concentrated suspensions (p. 203–204) is of much interest.

[2] The phosphate content seems to increase as a result of fossilisation; MOORE found values of up to 30.7 % P_2O_5 in old layers.

proteins of marine origin" –, and thus obtain some 7 % for the protein content. This value would also become lower.

It is well known that lamellibranch faeces may contain fair quantities of undigested (partly even living) organisms. These have therefore passed the digestive tract undamaged. It is generally assumed that their presence is due to the absence of enzymes which can attack them. NELSON (1933) is of opinion that in the oyster they are the result of the incomplete separation of food particles from undigestible matter, inherent to the feeding mechanism. COE and FOX, however, in most instances ascribe their presence to excess of food (COE and FOX, 1942; FOX and COE, 1943; COE and FOX, 1944; COE, 1945, and 1947), an opinion apparently going back to FOX (1936). Even after their discovery (FOX and COE, 1943) that so many dinoflagellates remain undigested they ascribed this at first to overabundance of food. Only in 1944 (or later) did they mention incomplete attack through the absence of the right enzymes as a possible cause. But overabundance of food was still held to be the chief reason for unattacked material in the faeces in other instances even now.

The descriptions of COE and FOX (see especially FOX and COE, 1943, p. 232) make the impression on me that excess of food may indeed lead to large numbers of unattacked organisms in the faeces. "When algal zoospores are abundant the phagocytic cells of the digestive diverticula are distended with these reproductive cells. At such times they also form the principal constituent of the faeces, since the mussel is able to assimilate only a small proportion of the vast numbers ingested." The same impression is given, for instance, by the description of Loosanoff and ENGLE (1947).

If, however, living or undamaged organisms in the faeces can be due to two different causes: overabundance of food (eventually due to increased incomplete separation as meant by NELSON) as well as inability to attack the food, their presence in the faeces can no longer be used as evidence that the right enzymes for their digestion are wanting. In the experiments of LOOSANOFF and ENGLE high concentrations of microorganisms produced large quantities of pseudofaeces as well as large numbers of living organisms in the faeces. It has been suggested that these organisms may have been partly unsuitable as food. If they may have been due to overfeeding the supposition that the food was unsuitable may be wrong. The most we can say at present apparently is that in certain cases we see digestion fail to break down the food.
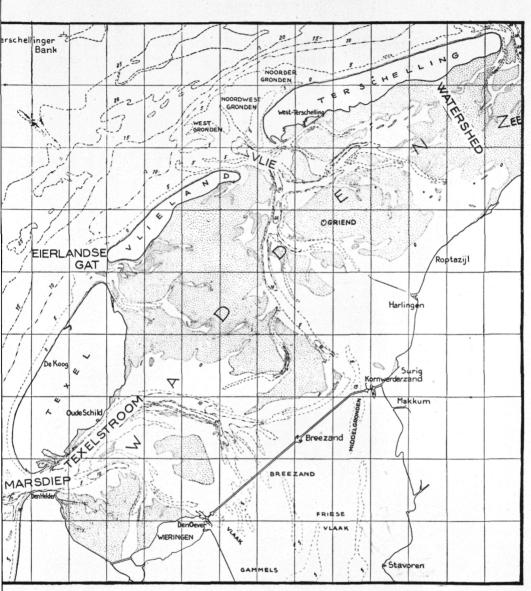
Fig. 6. Western part of the Waddensea west of the watershed between the island of Terschelling and the coast of the province of Friesland. Dotted areas represent the sands falling dry at lowest low water of spring tide.

V. THE ACTIVITY OF COCKLES AND MUSSELS WITHIN
THE WADDENSEA

The mollusks of the Waddensea may cause changes to their environ-
ment in two ways: first, by changing the geomorphological aspect of
the whole, secondly, through their influence on the character of the
material from which the area is built up.

The firstnamed influence, that on the geomorphological aspect, can
only be small. The general morphology of the Waddensea, with its
configuration of main channels and wide flat areas, is in no way
dependent on the presence of mollusks, and the influence of the latter
is only quite secondary and relates to morphological details. In fact, I
am acquainted with one good instance of such an influence only.
Where mussel beds develop over the drainage channels of large
shallows the course of these creeks can be changed under the influence
of such beds as it may also change through accumulation of sand. For
the configuration of the Wadden as a whole this fact is of quite
secondary importance, of course.

One may ask whether the creeks did not rather develop as a result of the presence
of mussels instead of the mussels as a result of the presence of creeks. This is not the
case. The large flats possess a number of drains. Many of these are favourable as a
habitat for mussels, which may form a dam of beds across and a series of beds along
them. In growing heavier the dam becomes an obstacle to the current and the water
partly begins to flow around the dam so that a new creek is developed. This new
creek results from the presence of mussels; yet, one cannot say that the creek owes
its existence to them, as in a somewhat different form it was there already before the
mussels came.

The second way in which mollusks cause a change in the whole is
that they alter the character of the substratum. In this respect the
animals may be of importance in two ways: by altering the quantity,
composition and structure of the bottom material, and by the accumu-
lation of lime in their shells. Having ascertained in the foregoing
chapter the details necessary for a correct understanding of the con-
version of suspended material into faeces and pseudofaeces we may
now see of what importance the activity of these mollusks is in these
respects.

I. THE ACTIVITY OF THE COCKLE

According to WILLEMSEN's observations dealt with above a cockle of
two years old pumps about 0.5 litres of water per hour. Assuming that
the average time of pumping per day for the cockle may be comparable
to that of oyster and mussel, the value of 20 hours found for the latter
species may be taken as a suitable mean for submerged cockles. Since

the quantities of water pumped, however, may decrease at low temper-
atures and cockles may fall dry a certain period every tide the average
number of hours of pumping per day is here estimated at 12, this
presumably representing a very low figure.

The water of the Waddensea according to POSTMA's determinations
contains on an average some 25 mg (dry weight) of suspended material
(including plankton) per litre. During windy weather the quantity
increases. On the other hand, it may be especially low over the sands
where the cockles are living, since the water layer is rather easily
depleted there. The mean figure for the water of the Waddensea as a
whole may therefore be lower, and 20 instead of 25 mg is therefore
taken as a starting point. As very little material is refused at the siphon
entrance, practically the whole of this material is fixed in the form of
flesh, energy, faeces or pseudofaeces.

A cockle pumping 12 hours a day at a rate of 0.5 litres an hour may
fix, then, some 120 mg per day or 43.800 mg a year.

Part of this material is digested, part is rejected as pseudofaeces,
another part is returned as faeces. It was stated above already that one
faecal pellet issuing every 40 seconds may be considered a low average.
That makes per day of 12 hours 1080 and per year 394.200 pellets.
DAMAS estimates the volume of one pellet at 0.3 mm³. His cockles may
have been smaller than ours, but the same figure will be used here.
That comes to 118.260 mm³ of pellets a year. I conclude from MOORE's
paper (1931a) that the water content of this material is some 85 %,
expressed by volume. Assuming a specific weight of somewhat more
than 1 (the pellets are heavier than the sea water) their dry weight
would be at least 17.000 mg.[1]

If the above assumptions should more or less hold good one cockle
in the course of a year would take in and fix at least 44.000 mg (dry
weight) of suspended matter (plankton included) and reject at least
some 17.000 mg of faeces.

The difference between these two figures would represent materials for the cockle's
gain in weight, and for its sexual products, the energy for its metabolism, and its
pseudofaeces.

According to our calculations the dry weight of the organic material makes about
12 % of the total dry weight of plankton and suspended matter. The 44000 mg
pumped in may therefore contain some 5000 mg (dry weight) of organic material

[1] It makes much difference whether the percentage of the water is expressed per
volume or per weight. MOORE expresses the water content per volume, HÄNTZSCHEL
(citing STOCKFISH and BENADE) by weight. Weight figures are much lower than the
corresponding volume figures, how much depends on the relative proportion of sand
and other material. If the faecal pellets consist for 50 % of their volume of sand with
a specific weight of 2.5, and the other 50 % are clay, organic material and water,
with a specific weight of about 1, their specific weight is about 1.3 and the dry weight
here calculated then becomes about 23000 mg.

and this is divided over the pseudofaeces, the food that is taken up, and the faeces. Because nothing is known for certain about the average percentage of organic material within the pseudofaeces and faeces it is impossible to say what percentage of the material is actually digested. Should some 1200 mg be contained in the pseudofaeces, some 1800 mg be digested and as much as 2000 mg make part of the faeces, the latter would contain some 12 % of organic matter. Should occasionally as much as 3000 mg of the organic material make part of the faeces the percentage of organic matter within the latter would amount to 17.5. These figures differ so much from the 30 % mentioned by Fox and COE (1943) for the Californian mussel, that in themselves they form an argument against the usefulness of their figure which – it be remembered – was acquired after decantation of the sand. We are very far, however, from being able to give a provisional metabolic balance sheet of the cockle, as Fox and COE have so admirably attempted to do for the mussel.[1]

If one wants to judge the influence of the cockle population on the fixation of suspended matter in the Waddensea as a whole the number of cockles should be known. It is difficult to estimate the average number of *Cardium* per square metre of sands since there are – as already described – stretches with 2000 adult individuals and also sands (around the island of Griend for instance) with very few or even none. In order not to arrive at too high an estimate 10 cockles per square metre will be taken as an average.

N. PIJL, analyst to the Zoological Station, has determined the total surface of the western part of the Waddensea west of the watershed between Terschelling and the Friesian coast. It amounts to about 1557 km². About 600 km² (38 % of the total) fall dry during the lowest low waters of spring tides and this is about the area inhabited by the cockle. These 600 square kilometers may therefore be inhabited by a total of at the very least some 6000 million adult cockles, but twice that figure is probably more correct.

As one adult cockle would pump in and fix some 44.000 mg (dry weight) of suspended material in the course of a year 6000 million cockles would fix 264 million kg (dry weight) of suspended matter. Assuming a water content of 75 % (by weight) the wet weight may amount to 1000 million kg or a volume of some one million cubic metres.

These same cockles would produce at least some $6 \times 10^9 \times 17.000$ mg dry weight of faeces a year. This makes some 100 million kg. Expressed in volume units they would produce (see above) some $6 \times 10^9 \times 118.260$ mm³ or some 0.71 million cubic metres of faecal pellets a year.

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[1] The above percentages of organic matter (12 % in the material pumped in and perhaps 12 % in the material ejected) both relate to the dry weight at 120° C. They are not comparable, however, since through ejection of sand with the pseudofaeces the percentage of organic material in the stomach contents will first become higher than 12 % and then decrease again to for instance 12 % in the faeces.

This amount may be assumed to be spread over an area of 600 km². It thus would form a layer of some 0.12 mm high. Should the average number of cockles per square metre be 20 instead of 10 (a possibility which may be nearer the truth) the annual layer would be some 0.24 mm. Its thickness would gradually decrease through water loss. It follows from numerous values obtained by J. SCHEELE for the harbour of Ymuiden that the water content of its bottom sediment may decrease from above 70 % by weight (some 86 % by volume) to 60 or even 50 % (some 72 % by volume) towards 1 m depth. MOORE finds a decrease from about 85 to about 77 % (by volume) for the deeper layers of the Clyde mud, which according to him are some 5–25 years old. Such a decrease would cause a decrease of the thickness of the annual layer of 0.12 to about 0.10 mm.

To the volume and weight of the faecal material must be added that of the shells. The shells of 100 well grown Waddensea cockles of about two years old weigh some 750 grams. This means that the lime production of one cockle per year may amount to something like 3–4 g and that 6×10^9 cockles produce some 18–24 million kg of shells. 2000 cockle shells of the above size occupy a volume of about 0.01 m³. If it is assumed that 10 cockles of two years old grow up on a square metre of flat every 2 years, they produce a layer of lime of some 0.025 mm. The layer of faeces would therefore have more than four times the thickness of the layer of lime. The layer of faecal material would contain much water, however. – To this layer of faeces and shells must be added the pseudofaecal material, the quantities of which are difficult to estimate through want of data.

In reality, the assumption that a layer of faeces would be spread over an area of 600 square kilometers of sands is untrue, since the pellets are probably largely transported to the creeks and through them to quiet areas.

Part of the shells are carried to the creeks, but many (I think most) flats show dense layers of cockles, clams and mussels at some depth below the surface and these must be of some influence on the growth of the flats. Where the quantity of sand available for building should be small, shells cannot be without some importance. It is true, they are partly dissolved again through the action of carbon dioxyd, especially in a bottom rich in organic matter, but this is a very slow process and it certainly stops after some time, because there is so much lime in comparison to the quantity of organic material.

The combined effect of the activity of 6000 million cockles in the western part of the Waddensea would be that they withdraw from the water one million cubic metres of wet or some 264 million kg of dry suspended matter (plankton included); that they produce something

like 0.7 million cubic metres or some 100 million kg (dry weight) of faecal material and a quantity of pseudofaeces that is at present difficult to estimate. Further, the amount of shells produced by 6000 million cockles must amount to some 18–24 million kg or some 18–24 thousand cubic metres. Assuming that at least 90 % of this material is $CaCO_3$ the lime production amounts to some 16–22 million kg. Shells, faeces and pseudofaeces together may represent at the very least some 140 million kg dry weight and a wet volume of some 0.85 million cubic metres.

All figures here given represent minima, as they are based on low estimates. It is well possible that they must be doubled. It is unprobable, however, that they should be thrice as high as here given.

DAMAS (1934) came to the conclusion that the quantities of mud deposited in the neighbourhood of Zeebrugge would amount to one and a quarter million cubic metres per year. His estimates were based on one faecal pellet issuing every 8 (instead of 40) seconds and 1000 (instead of 10) cockles per square metre over an area of 250 hectare or 2.5 square kilometres. This would mean that an area 240 times smaller than the western part of the Waddensea would produce nearly double the quantity of 0.7 million cubic metres calculated for the latter. Though this seems a rather high estimate the fact need not be quite impossible, because everything depends on the density of the population. The estimate of 1000 cockles per square metre for the Waddensea would be much too high, for though there are stretches with 2000 fullgrown cockles per square metre the extensive sands with only a few per m² reduce the average.

2. THE ACTIVITY OF THE MUSSEL

Before proceeding in order to see what may be the final conclusion as to the general importance of the above facts the mussel should be dealt with.

The chief difficulty in the mussel is to make a more or less trustworthy estimate of the number of individuals. It is not so difficult roughly to estimate the number of cockles present in the area under consideration, because they are restricted to the flats and fairly regularly distributed there. The population, moreover, is often restricted to one single year class, so that the estimation of the number of old individuals is little disturbed through the influence of large numbers of younger animals. With the mussel matters are quite different. They are not restricted to the flats, but occur also within and along the creeks. The largest bank occurring in the Waddensea in the years 1945–'50 was about 3 kilometres long, about 1 kilometre broad, and it

was lying about 4 metres deep. How many mussels may inhabit such a bank? Moreover, one always finds large numbers of younger and older mussels in the same area at the same time.

For these reasons another method has been followed here for estimating numbers, namely that of using the results of the fisheries. This would not have been possible without the help of Dr B. HAVINGA, director of the Institution for fisheries research, Amsterdam, the fisheries inspector, Mr VAN HENGEL at Amsterdam, and the fisheries surveyor, Mr DE VLIEGER at Den Helder.

In 1949 2.280.000 kg of consumption mussels were fished in the western part of the Waddensea studied here. These are mussels of about 6–8 cm length. As 1 kg contains about 25 specimens their total number may have been some 57 million individuals. To this figure must be added some 271.000 kg of mussels, "cultivated" south of Terschelling and near Griend. They represent some 6.8 million individuals and bring the total at 63.8 million.

Further, some 9.563.000 kg of smaller mussels, of about 3–6 cm length, were fished. They are used as food for ducks and about 50 of them are contained in 1 kg, so that the number of individuals may have been 478 million.

Finally, some 3 million kg of young mussels (so called seed) were fished. One kg of these according to PIJL contains some 500 specimens of from 5 to 30 mm length and the total number of individuals may have been 1500 million.

Now, DE VLIEGER, who is better acquainted with the Waddensea than anyone else, is of opinion that the total fished in 1949 represents about one third of the total present. He believes that the catch consisted of less than half the total and that it was certainly more than one fourth. In other words, the Waddensea in 1949 would have contained some 191.4 (say 200) million consumption mussels, some 1434 (say 1500) million halfgrown mussels, and some 4500 million small mussels.

As 1949, however, was a very good year, these figures should not be considered averages, and one third is therefore taken here. That gives some 70 million old, some 500 million halfgrown, and some 1500 million young mussels of about one year old.

The mean quantities of water pumped by the individuals of these three different groups (see p. 194) will be estimated at 1.5, 1.–, and 0.1 litres per hour pumping. It may again be assumed that the animals pump 12 hours a day and that they take in practically the whole of the suspended material, which will be estimated again at 20 mg.

The animals of group I then pump in: 70×10^6 (number of mussels) $\times 12$ (hours) $\times 1.5$ (litres $\times 365$ (days) $\times 20$ (mg) $= 91.980 \times 10^8$ mg $= 9.2$ million kg of suspended matter.

The animals of group II pump in: $500 \times 10^6 \times 12 \times 1.- \times 365 \times 20 = 43.8$ million kg.

The animals of group III, finally, pump in: $1500 \times 10^6 \times 12 \times 0.1 \times 365 \times 20 = 13.14$ million kg.

So that the combined mussels of the western part of the Waddensea, which are estimated at 2000 million individuals, would annually withdraw from the water a total of some 66 million kg of suspended material.

Should the relation between the quantity of suspended matter pumped in and the quantity of faeces produced, and also the water content of the faeces, be the same as in the cockle, the mussels would produce $\dfrac{100}{264} \times 66 = 25$ million kg (dry weight) of faeces or some 0.18 million cubic metres. If, however, a faeces production of 1000 mg dry weight per large animal per day is taken as a starting point (compare p. 214–215), the quantity of faeces produced by the large mussels alone (say 70 million individuals) is already 25 million kg. Since the quantity of material pumped in by all mussels together is supposed to be about 7 times the quantity pumped in by the large mussels the quantity of faeces produced by all mussels together would also be 7 times the quantity produced by the large animals alone, i.e. 175 million kg (dry weight). The great difference between the first and the last figure (25 and 175 million kg respectively) must be due to the fact that in the first calculation 12 hours of pumping per day and 20 mg of suspended matter per litre of water pumped were taken as a starting point, in the second case a *faeces*-production of 1000 mg for 365 days per year. It may be assumed that the former value is rather low, whereas the latter for the western Waddensea is certainly too high. It was stated already that conditions in the eastern Waddensea differ much from those in the western and they will probably differ much even at neighbouring places. Nevertheless, the figure of 25 million kg as an average for the annual faeces-production by mussels in the western part of the Waddensea will be maintained here.

The weight of the shells of the 2000 million mussels may represent some 4.7 million kg. This figure has been obtained by assuming that the average weight of the shells of the individual mussels of groups I, II and III may respectively be 10, 5, and 1 g.

3. THE ACTIVITIES OF COCKLES AND MUSSELS COMPARED AND COMBINED

Before proceeding, the figures found for the mussel should be compared with the corresponding ones for the cockle.

It has been supposed that the western part of the Waddensea, west of the watershed between Terschelling and the Friesian coast, on an average would contain 6000 million cockles and some 2000 million mussels, both estimates certainly representing rather low figures. The 6000 million cockles would withdraw from the water some 264 million kg (dry weight) of suspended matter. The 2000 million mussels would withdraw some 66 million kg. Cockle and mussel activity in the western Waddensea would therefore be related as 4:1.

It is assumed that the quantities of faeces and pseudofaeces produced by cockles and mussels show a similar relation.

The weight of the shells of 6000 million adult cockles may be estimated at about 21 million kg. The weight of the shells of the 2000 million mussels may represent some 4.7 million kg. This would contain that the cockles produce 4–5 times more shell weight per year than the mussels.

Adding the values for cockles and mussels these animals in the western Waddensea would annually withdraw from the water some 330 million kg dry weight of suspended matter (plankton included), representing some 1.3 million cubic metres of wet material. A very large part of this material, say two thirds at the very least, will be converted into faeces and pseudofaeces. Further, the animals would annually produce some 25 million kg of shells. Shells, faeces and pseudofaeces may at the very least represent some 250 million kg (dry weight) of material, which is not easily carried away.

It has been described above how the mussels, contrary to the cockles, occur in beds, where many thousands of individuals may occur together. The faeces and pseudofaeces of all these animals fall between and around them, filling all interspaces. The mussels are gradually covered by them, and they work themselves out of the sediment where this is possible. Part of them die and form a firm hold for others and they thus build a bank of silt and shells, the upper surface of which is covered by the living animals. The accumulations of silt in large beds may take enormous proportions. It is a general belief among mussel fishers that the layer of silt may reach a height of several decimetres within a year, and this is certainly true.

The reason why this material largely remains where it is produced and, contrary to what is the case in cockles, is only partially carried away, may be found in the form of the faecal bands, which are long, and also heavy (for figures see DODGSON, 1928; MOORE, 1931b; SCHWARZ, 1932). One also gets the impression, however, that the mussel produces more mucus than the cockle, so that the material adheres more firmly. Finally, the faeces can be carried away less easily, because they fall *between* the animals and are not ejected on sand as

are cockle pellets. Nevertheless, large quantities of this material are carried to the lee of the beds, where they may form extensive patches of a very soft sediment. Where dams of mussel beds cross the drains of large shallows this lee seems always to lie at the side of the beds turned away from the shallows.

When the musselbeds are broken up one regularly finds on these sites banks of a very consistent material, which has the appearance of clay and certainly contains a high percentage of the latter. These banks or patches are interspersed with shells. They are not easily destroyed and in musseldams across important drains one may find a number of such patches keeping stand in strong currents.

The difference in sedimentation between cockles and mussels, then, is that the cockles are regularly distributed and therefore produce pellets over wide areas, from where they are easily carried to the creeks; whereas mussels are distributed quite irregularly and produce their faeces locally; these faeces are not so easily carried away. The photographs given by SCHWARZ (1932, fig. 1-4) can well serve to illustrate the differences in question.

What, now, is the result of this combined activity of cockles and mussels?

That they annually convert more (perhaps much more) than 330 million kg (dry weight) of suspended matter into pseudofaeces, flesh and faeces and thus contribute to the fixation of the suspended material on a large scale. In this connection especially the great resistance of the faeces to disintegration is of much interest. MOORE (1931 a and b) has drawn attention to their long life. He found them in the Clyde area unattacked in muds of a century old. They may live shorter in shallow areas, where they are easier attacked, but even here their life may be very long. MOORE (1931) already drew attention to the fact that, biologically, the process of fixing the unconsumable remains into a form, which is unfit for further use, may be very important. Such species as cockles and mussels, which feed by pumping the water, and which must pump constantly so to speak, because their food gaining mechanism works according to a very simple principle and rather inefficiently (an idea especially expressed by Fox and COE), would be in a very adverse position if the water were to contain all the food remains of their neighbours. The "disadvantage" (if we are allowed to use such a word here), however, is that part of the organic material is fixed and therefore withdrawn from the cycle for a very long time. It is shunted on a side line so to speak, from where it may return after many years.

The result is that a large part of the material lies constantly unused. We found that the combined populations of cockles and mussels at least pump some 330 million kg (dry weight) of suspended matter

annually, containing some 12% or some 40 million kg of organic material. Should our former supposition (p. 219–220) hold good that up to two fifths of this material would be excreted within the faecal pellets about 16 million kg would be fixed in the latter per year. If they would resist disintegration for 25 years their deposit would contain some 400 million kg of organic material. Assuming that the other three fifths, or 24 million kg, contained in pseudofaeces and animal flesh, would have an average life cycle of at the very most three years, their total should be about 70 million kg. The value of such figures is very restricted, of course, but they may emphasize the fact that the depot lying unused for long periods may indeed be very important. Within this long period much of the material will, moreover, have a chance to be carried from the western part of the Waddensea to the eastern, whereas accumulation of this material in quiet parts may withdraw it from the cycle for much longer periods or even for ever.

Before leaving this chapter one would like to deal with the question of what influence cockles and mussels are on sedimentation within the Waddensea generally. We found it must be assumed that material in suspension is constantly carried from the North Sea to the Waddensea, where it is retained through sedimentation. To this process of retaining material cockles and mussels contribute on a large scale. The difficulty, however, is to compare this scale with that of the whole. At present, it seems hardly possible to say anything definite on the point, but the question deserves much attention.

VI. THE SOURCE OF THE ORGANIC MATERIAL

The question is of much interest what may be the chief source of the organic matter, which forms the base for the activity of these millions of animals. What may be the relation between the quantities of organic matter present in the Waddensea itself and brought to the latter from outside? Though a decisive answer to this question cannot be given, some general considerations may be of value.

Two processes are at work. One is concerned with the life cycle of the organic material within the area dealt with, the other with the interchange of material between the Waddensea and the surrounding waters. Though these processes cannot be separated, they will be dealt with one after the other.

Assuming, first, that the Waddensea would be self-supporting and received no material from outside (which is not the case, of course), the Waddensea could be treated as if it were a closed body of water. This closed body, then, would contain 6×10^9 cockles, pumping at

least 12 hours a day 0.5 litres per hour, i.e. 0.036 km³ a day. The data, already given for the mussels, show that the adult mussels would pump 0.00096 km³, the halfgrown ones 0.00225 km³, the young ones 0.00135 km³ a day. The total quantity of water, pumped by cockles and mussels of the western Waddensea, would amount, then, to 0.041 km³ a day.

According to determinations of N. PIJL and H. POSTMA the mean depth of the Waddensea west of the watershed Terschelling–Friesian coast at lowest low water of spring tides is about 2.54 m. Mean sea level is for the neigbourhood of Den Helder 1.13 m higher (for Terschelling more than that), so that the mean water height would be 3.7 m or more. As the surface of the western part is about 1560 km² the volume at mean tide would be about 5.8 km³.

As the total populations of cockles and mussels pump at least some 0.041 km³ a day they would pump a volume of water comparable to that of the western Waddensea in about 140 days or 2.6 times that volume in one year.[1] This does not mean, of course, that they would pump the whole water mass of the area 2.6 times a year, since they would pump part of the water again and again, and another part of it not at all. The result, however, would be all the same: that after not too long a period of time the water would have been largely deprived of its suspended organic matter, and how much material would be available to the animals would depend on the relation between the time necessary for its depletion and that necessary for the production of "new" organic material. In other words, the duration of the lifecycle of the organic matter would govern the whole as is the case in any closed body of water.

Now, it is difficult to believe that a population, which is so large that part of it may deprive its water mass from all food within 140 days, could do without a supply of food from outside. It may therefore be assumed that such a supply is necessary to maintain the population at such a high level. There is the more reason to suppose so, because there often may be a transport of organic material from the western Waddensea here studied to the east. The basin as a whole is very shallow and

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[1] LINKE (1940) says that "allein auf der Wattfläche zwischen Juist und dem Festland, die etwa 150 qkm gross ist und bei Tidehochwasser einen Wasserinhalt von 250 Millionen cbm hat, von den dort lebenden Miesmuscheln täglich über 5 Millionen cbm Wasser durch Filtration restlos von Sinkstoffen befreit werden". It would mean that the mussels there would pump the whole watervolume in 50 instead of 140 days. This is not at all impossible, because so much depends on the quantities of mussels in relation to the watervolume. Moreover, our own estimation may be too low. LINKE does not mention the data, however, on which his calculations are based: one would like to know the average quantities of mussels present in the area in question as well as the average quantities of water supposed to be pumped per mussel of a certain size per day.

southwestern winds are dominant; transport may therefore easily take place and this must mean a constant loss. A second loss of organic material is caused by the fisheries. Whereas the quantities of cockles fished (for description see KREGER, 1939) are as a rule small, the quantities of mussels may be quite important and represent several millions of kilograms. A closed body of water without an import of food from outside could never continue producing such large numbers of animals for a series of years.

All this means that the second process mentioned above, that of the interchange between the Waddensea and the water surrounding it, must be very important.

A certain quantity of fresh water, on an average about 10^{10} m^3 per year or 0.014 km^3 per tide, is discharged into the Waddensea and mixes with the water of the Waddensea itself and with that entering every tide from the North Sea. According to measurements of the Rijkswaterstaat the latter quantity (entering through Marsdiep, Eyerlandse Gat and Vlie) is about 2 km^3, so that at high tide, when the total volume of the Waddensea is about 6.8 km^3, the latter are composed of 2 km^3 of water from the North Sea, 0.014 km^3 of fresh water and some 4.8 km^3 of water of the Waddensea itself. The relation between the water entering from the North Sea and the fresh water is about 140:1, the North Sea water must therefore be of much more importance to the Waddensea than the fresh water. It must be realized, however, that part of the 2 km^3 of water from the North Sea entering the Waddensea every tide left the latter during the foregoing ebb. Those 2 km^3 do not, therefore, represent true North Sea water, but a mixture of water from the North Sea and the outer part of the Waddensea, in which the quantity of North Sea water increases outward and increases more and more as high tide is approached. The fact remains, however, that the influence of the North Sea water must be many times greater than that of the fresh water. Therefore, if it is the interchange between the Waddensea and its neighbouring waters, which makes food production possible on a large scale, the source for such food must in the very first place be found in the North Sea.[1]

[1] LINKE (1940), whose paper I saw after my paper had been written, is apparantly of opinion that the suspended matter present in the German Waddensea is chiefly formed within the latter. "Für die Emsmündung konnte nachgewiesen werden, dass Flusseinspülungen keine Rolle spielen. Unsicher ist hingegen noch der Einfluss von See her, besonders aus den grossen Schlickgebieten, die in der Nordsee vor den friesischen Küsten liegen. Damit ist für einen grossen Teil des Schlickes die Bildungsstätte bekannt, so dass die Frage der in einem bestimmten Zeitraum neu gebildeten Schlickmenge untersucht werden kann." As long as it is uncertain, however, whether the North Sea may not be an important source for the material in question, we should not suppose that the latter is chiefly formed within the Waddensea itself.

It is not at once clear how the North Sea water entering the Wadden-sea may cause such favourable conditions in the latter. One is inclined to believe that its *direct* influence must be small. Though 2 km³ of mixed North Sea and Waddensea water enter the Waddensea every tide the combined populations of cockles and mussels according to our calculations do not pump more than 0.041 km³ a day or only some 0.020 km³ per tide. Even if this figure would be too low the quantity pumped can only be small compared with the quantity entering from the North Sea. Further, only part of the total mollusk population comes into direct contact with the "new" water, so that the quantities of North Sea water pumped must be quite low, even if the fact is taken into account that the feeding activity of such largely intertidal animals is greatest during the hours of high water, when the influence of the North Sea is maximal. The favourable influence of the water from the North Sea must therefore be largely an indirect one.

In the chapter Environment the opinion was expressed that the mixing of water masses of different character from the point of view of food production may be especially valuable, because organisms in-habiting these masses may be killed, together with detritus from that water may sink to the bottom and enrich the bottom water. I suppose this to be an important cause for the richness of coastal water generally. Within the Waddensea this material is transported inward and much larger quantities of food must thus become available to the mollusks than would be the case along the direct way alone. Food is here meant to include plankton from the North Sea, disintegrated plankton, detritus from the North Sea, detritus formed within the Waddensea from disintegrated North Sea plankton, and, finally, plankton organ-isms which grew up on the chemical compounds after mineralization of the organic material originating from the North Sea.

Summarizing, these suppositions come to the following.

The Waddensea, if it were a closed basin, could never produce such large amounts of animals as actually do exist and are fished there. It owes part of its organic matter, forming the base for its food supply, to the fresh water and especially to the water from the North Sea entering it. Part of this material will be used directly, but the greater part will gradually move inward and then become available to the animals indirectly. Through the simpleness of the sieving mechanism of the mollusks part of the organic material is refused, whereas part of it is excreted with the faecal pellets. The latter are not easily broken down, with the result that part of the organic material returns into the cycle only after a long lapse of time. A large quantity of it is thus accu-mulated. Another large part of the organic material brought in from the

North Sea will be stored in the flesh of the millions of animals. This part too returns into the cycle after a certain lapse of time, but this lapse must be much shorter than that of the faeces and this food is therefore earlier available again.

The above conclusion, however, that the Waddensea, if it were a closed basin, could never feed such large numbers of animals as actually do exist there, does not mean that the organic material of the Waddensea itself would not be important also. It goes without saying that both kinds of food sources cannot be separated and that they are used as one whole. It is further clear that within this whole the Waddensea-material itself cannot be neglected. If, namely, thanks to the favourable influence of the North Sea, a large population of animals is built up, in which great quantities of organic material are accumulated, the niveau of organic material within the Waddensea reaches a high level, so that a constant flow of organic material and a constant production of new material from it must be the result. Cockles and mussels themselves may be taken as an example. We came to the conclusion that their total within the Western Waddensea may amount to some 8000 million individuals. If one individual on the average would represent only 2000 mg (dry weight) of organic material their total represents at least some 16 million kg. If the average life cycle of these mollusks, as supposed above, would be about 3 years, 5 million kg of organic material at the very least would be furnished annually by cockles and mussels alone. Since, according to our earlier calculations (p. 227) the combined populations of cockles and mussels may pump some 40 million kg of organic material a year it is obvious that the quantities formed "by the Waddensea itself" must represent a considerable part of the whole, even if the fact is considered that much of the above 5 million kg is lost in the cycle. We can probably best say, therefore, that, though the high niveau of the organic material reached within the Waddensea is certainly due to the favourable influence of the North Sea, the latter does little more than regularly adding to the large amount of material already present, thus counteracting its losses.

VII. SUMMARY

The paper means an attempt to evaluate the rôle of bivalve mollusks, especially cockles and mussels, in matters of sedimentation in the western half of the Dutch Waddensea. It deals with the ecological needs of both species and their dependence on environmental factors, and also with the quantity and composition of the material suspended in the water and the source of its organic part, which is used for food.

It contains a concise summary of the feeding biology of bivalve mollusks and finally tries to evaluate the influence of the latter in matters of sedimentation.

1. The Waddensea is inhabited by a small number of species which can cope with (and possibly need) great differences in the quantity of light and suspended material, salinity and temperature, the strength of the currents and the changes in depths. But these animals have at their disposal extensive areas where competition with other species is less important than elsewhere and where food is abundant; they can therefore be numerous. Cockle and mussel should be seen in this light.

2. Cockles are restricted to a sandy bottom in shallow water. The larvae during or after metamorphosis presumably find the latter through their need of rather strong light. They can only settle where currents are weak. Since food conditions may be better where currents are stronger the places of easy settling need not be the best places for growth, with the result that the favourable areas for young and old animals are not always the same. Generally speaking, cockles are quite regularly distributed over the sands, their numbers changing rather gradually with the change of current velocities.

3. Mussels need a more or less firm substratum in shallow water. Their larvae too probably need a fair amount of light during the time of attachment. They settle especially on algae, from which, however, they loosen their hold after some time, to exchange them for another substratum. The byssus threads are quite valuable from this point of view, since they represent a semi-permanent form of attachment. After loosening their hold the young mussels have themselves carried through the currents. During this transport mussel banks catch them at haphazard. Mussel banks form the best substratum for settling since they contain so many niches. The congregation of thousands of mussels in mussel banks is not a result of social behaviour based on smell, but of the fact that there are no better niches for mussels than those between mussels. Mussel banks are especially lying along and over creeks. The reason is that not too weak and not too strong currents are optimal for them.

4. The matter suspended in the water of the Waddensea, averaging about 25 mg (dry weight) per litre, has about the following composition: sand about 44, shellsand 18, clay 8, Fe_2O_3 18, organic material 12 %. These figures are percentages of the dry total at 120° of all suspended material, plankton and organic detritus included. Especially the quantity of sand may show great differences from place to place and from one moment to the other. From the point of view of mollusk activity especially the 12 % of organic material are of interest.

5. The feeding biology of bivalves is dealt with in some detail in chapter IV under the following heads: 1. the number of hours the animals pump per day; 2. the quantities of water which are pumped; 3. the part of the suspended matter, which is pumped in; 4. the part of the material pumped in retained as food; 5. the way in which a separation between useful and unuseful takes place; 6. the part of the material retained which is rejected or accepted; 7. the part of the accepted material which is digested; 8. the quantity and composition of the faeces.

This chapter represents a review of the literature (with some new additions), which serves as a base for the calculations and conclusions following thereafter.

6. Chapter V deals with the activities of cockles and mussels within the Waddensea and with estimates about their rôle in sedimentation.

One cockle in the course of one year may be assumed to take in and fix at least some 44.000 mg (dry weight) of suspended matter (plankton included) and to reject at least some 17.000 mg of faeces. The remaining 27.000 mg are partly ejected as pseudofaeces, whereas the rest represents food. The number of cockles in the area dealt with is estimated at 6×10^9 individuals of 2 years old at the very least. They take in at least some 264 million kg (dry weight) of suspended matter a year and give off some 100 million kg of faeces. They further produce some 18–24 million kg of shells annually.

The mussel population of the area is estimated at about 70 million old, some 500 million halfgrown, and some 1500 million young mussels of about one year old, some 2000 million in all. This certainly is a very low estimate.

The quantity of suspended matter withdrawn from the water may be about one fourth that withdrawn by the combined cockles. The mussels produce 4–5 times less shell weight than the cockles.

Shells, faeces and pseudofaeces of cockles and mussels combined may at the very least represent some 250 million kg (dry weight) of material per year. This material is less easily carried away than before it had passed the animals, but in this connection there is much difference between the two species of bivalves dealt with.

It is difficult to say anything on the relation between the influence of cockles and mussels on sedimentation and sedimentation as a whole.

7. The source of the organic material, on which the millions of individuals inhabiting the Waddensea are built up, is found in the very first place in the North Sea. If the Waddensea were a closed basin it could never feed so many animals. At the same time, the quantity of organic material present in the water per unit of volume is smaller in the North Sea than in the Waddensea. It is accumulated in the

Waddensea through processes, of which mollusk activity represents one. Material from the North Sea is constantly laid down here. Nevertheless, the favourable influence of the North Sea on the Waddensea is certainly chiefly indirect, the North Sea doing little more than regularly adding to the large amount of material already present. For detailed argumentation the reader is referred to chapter VI.

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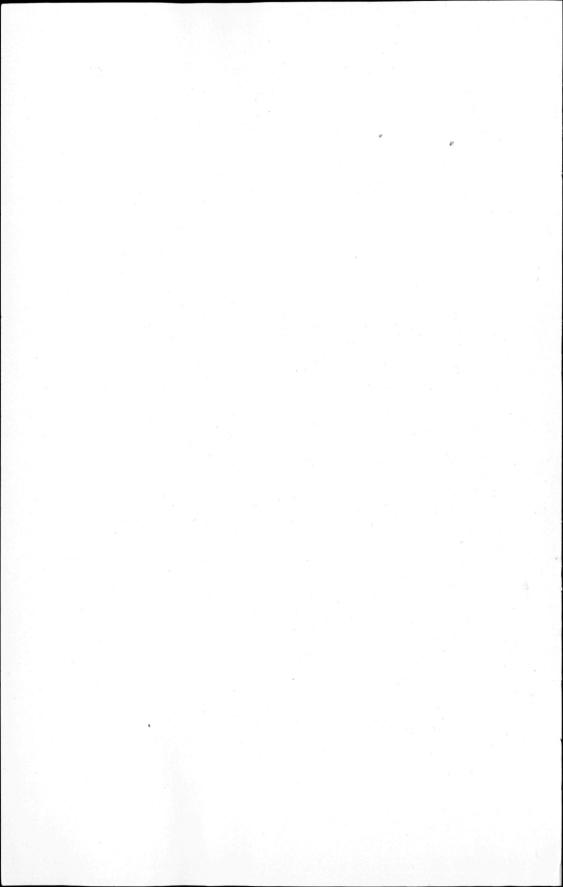[1] Papers denoted by an asterisk have not been studied.

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