The Coastal Waters of the Netherlands as an Environment of Molluscan Life

by
INGVAR KRISTENSEN
(Zoological Station, Den Helder;
Laboratory of Animal Physiology, University of Amsterdam) *)

CONTENTS:

INTRODUCTION

In the Dutch coastal waters there are relatively few mollusc species. On the other hand, most of the species present in this area are rich in individuals. This holds not only for the littoral fauna, but also for the whole fauna of the southern North Sea.

Dutch territorial waters do not extend to more than three miles beyond the coastal line. However, in 1927 the Editor of the "Fauna van Nederland" took another criterion concerning the limits of what can still be labelled as "Dutch". A zone of about 25 km was chosen because the Dutch light-vessels were lying at a distance of some 25 km from the coast at that time. In this paper the discussion is not confined strictly to this area of 25 km, although the main point of discussion will concern the fauna within these limits.

The general nature of the substratum in the Dutch coastal area is rather uniform: for miles and miles only sand is found. The only firm substratum is formed by artificial works, such as dikes, harbour piers, etc.

I shall not try to give a complete picture, either of the different environments or of the molluscs. Empty shells, specimens cast ashore and other allochthonic animals will not play any role in the discussion — only specimens living in their own habitat will be taken into account.

The data in this paper on the detailed distribution are partly derived from the Mollusc volumes in the series "Fauna van Nederland" by VAN BENTHEM JUTTING (1933, 1936 and 1943) and ENGEL (1936), and from the papers of JAECKEL (1952, 1958). Further I have used many published and unpublished observations from the Zoological Station, Den Helder, and from the Laboratory of Animal Physiology, Amsterdam.

*) Present address: Dierfysiologisch Laboratorium, Waterlooplein 24, Amsterdam.

Concerning the nomenclature of Gastropods and Bivalves, I have strictly followed the "Fauna van Nederland". Unfortunately, no volume containing the Cephalopods has yet been issued. JAECKEL (1958), however, has published a fine monograph on the subject and I have followed the nomenclature used by him.

I owe a debt of gratitude to Mr R. H. BAIRD, Conway, and to Dr H. POSTMA, Den Helder, for their advice on the manuscript.

THE NORTH SEA AREA

A stroll along the sandy beaches of the Dutch coast will soon give a clear picture of the paucity of species by the cast up shells. This is just a reflection of the poorness of the mollusc fauna of the southern North Sea compared with the adjacent areas. Although the whole area south of the Dogger Bank is relatively poor in this respect, the Dutch area is exceptionally poor as we know from bottom sampling and dredging results.

The structure of the bottom along the Dutch coast is very uniform. As may be seen on the bottom chart on p. 24-25 sand is found almost everywhere. In the southern part the median grain size is a little higher than in the northern part. Locally, scattered moraine stones are found, for instance to the northwest of the Island of Texel, called "de Stenen". Small peat ridges are found here and there, especially northwest of IJmuiden.

The relief of the bottom is very plain; sand ridges are present just outside the zone of surf and more ridges are present further seaward. From the coast to about 25 km off-shore the depth increases to no more than 25 m, and at 75 km from the coast the depth may reach some 35 m.

Nowhere is soft bottom found — the tidal currents are too strong. The maximum speed reached by the currents is about 4 km per hour at the surface and about half of that near the bottom. The flood tide, according to measurements of "Rijkswaterstaat" on the Dutch light-vessels and of "Deutsches Hydrographisches Institut", takes the water some 10-11 km northeast along the Dutch coast and the ebb takes the water back for some 8 km per tide. As a result of the difference between flood and ebb tide the water moves with a speed of about 7 km per day in a northeastern direction along the coast. This water comes directly from the Channel. The influence of the English North Sea coastal water is small, although the water of the Thames can be traced at points more than half way between the Dutch and English coasts (KALLE, 1953). Of course, the influence of the continental rivers Scheldt, Meuse and Rhine on the constitution of the water near the coast is very important. Fresh water from the rivers causes a lowering of the salinity, but this influence is restricted to a rather narrow strip of perhaps 30 km along the coast, probably because the CORIOLIS force presses to the east the water coming from the south. In this strip an intensive mixing takes place as a result of the strong turbulence caused by the tides and the waves in this shallow area. Therefore, even along the shore the salinity is not very much reduced — the freshwater component can be seen only in the regular decrease of the salinity from 35‰ at 30 km distance from the coast, to about 31-30‰ near the shore. These figures give a rough mean, of course, and rather large fluctuations occur.

The shallowness of the southern North Sea causes some other remarkable hydrographic phenomena. As the water is constantly homogenised, even one or two cold days may exercise great influence on the bottom fauna, especially on some Cephalopods, but also on the other molluscs. In the winter the temperature at the bottom may drop considerably in the course of two days. During a period of frost the temperature can drop to values of about zero and even below that if the winter is a severe one. This is of the utmost importance for the mollusc fauna, which perishes almost completely at such low temperatures. More to the north, at a depth of 35 m or more, the high column of water causes the temperature fluctuations to be much less, and, moreover, the mixing of the surface water and the bottom water is less extensive, so the bottom temperature never drops below zero, not even during the coldest period of an ice-winter.

Another consequence of the shallowness of the area investigated is the great turbidity, since the silt brought into the sea by the rivers cannot settle. The SECCHI-disc which, near Plymouth, can still be seen at a depth of 40 m, vanishes in the centre of the southern North Sea at 10 m and, near the Dutch coast, at 5 m or less.

As we have stated already the mollusc fauna of the southern North Sea is poor and this holds especially for the Gastropods. The reason is not difficult to trace: most snails do not tolerate a substratum of moving sand grains. They need either a firm substratum or a soft, quiet one. Some species find these conditions in the deeper parts of the northern North Sea and also in shallow water there if the area is protected against wave or current action, but they cannot thrive

in the southern North Sea. To this group belong *Acmaea testudinalis*, *Calliostoma conuloide*, *Gibbula tumida*, *G. cineraria*, *Turritella communis*, *Clathrus clathrus*, *C. clathratulus*, *Aporrhais pes-pelecani*, *Colus gracilis*, *Lora turricula*, *Crepidula fornicata*, and many Nudibranchs. It is for the same reason that *Dentalium entalis* and *Lepidochiton cinereus* cannot maintain themselves in and on the sand of the southern North Sea. In fact, there are only three common Prosobranch species here: *Natica catena*, *N. poliana alderi*, and *Buccinum undatum*. Both *Natica*'s live under the surface of the sand during most of the day, and also *Buccinum* may dig itself into the sand; it is even capable of moving forward with only its siphon above the sand, as we have observed in our aquarium. If it does so in the coastal area it will be protected against any non-voluntary transport.

The three Prosobranchs mentioned are carnivorous. This, certainly, is one of the necessary conditions because browsing is not in any degree possible in this environment, and there is plenty of food for these animals because of the abundance of Bivalves of all sizes.

As we shall see below when discussing the Lamellibranchs, perhaps the most dangerous period of life is immediately after metamorphosis when they have to settle. *Natica* and *Buccinum*, however, do not have pelagic larvae. *Natica* produces the well-known plastic-like ribbons which are not harmed by lying under the sand for some time, nor by transport along the bottom. The same holds for *Buccinum*: this species attaches its sponge-like egg-clusters to a firm substratum if available — if there is none, they use the shell of a neighbour, or an empty one, for attachment. It often happens that the clusters are torn away from their attachment and are transported by the tidal currents over long distances — even from the Channel coast, as indicated by epibiontic organisms — without damage to the development of the young inside their capsules. It always takes a long time before the young ones inside have reached the stage of leaving their capsules. After copulation of the adults in November the first clusters may be laid in December-Januari. Production of one cluster takes about two weeks — each night new capsules are added. Then it takes another 2½-3 months before the young appear. Due to the presence of nurse-eggs the young have by that time reached a length of 3 mm, so they may possess some resistance against the transporting power of the currents. During this stage there are many predators, as one can deduce from stomach contents of many species, especially starfish (*Astropecten* as well as *Asterias*) and flat-fish. After having reached a length of about 1½ cm the young whelks are only preyed upon by big fish such as cod, ray and dogfish (*Scyllium* and *Mustelus*) , but these predators are rarely very numerous in this part of the North Sea. Crabs — hermit-crabs included — are not capable of destroying a whelk, as we think we may conclude from aquarium-observations.

Other Gastropods than the above mentioned are rare and are mostly compulsory visitors belonging to the Channel fauna or to the fauna of one of the estuaries and carried to the area by the tides. Only *Neptunea antiqua* and some Opisthobranchs may have a foothold in the "Stenen", northwest of the island of Texel.

The Lamellibranch fauna is not so sparse as the Gastropod fauna. The Lamellibranchs have, by their mode of life, a natural protection against current transportation.

The population of Lamellibranchs off the Dutch coast does not represent one of the "communities" as drawn up by PETERSEN (1918 and previous years) for the Danish waters. Later on, others found that PETERSEN's system was not very well suited for use in the waters in the neighbourhood, and, therefore, some amendments were made (BLEGVAD, 1922; HAGMEIER, 1925; STEPHEN, 1933; JONES, 1950). Although the communities are not sharply bordered and only represent statistically different groupings, the Dutch coastal Bivalve fauna cannot be registered under one of the "communities" as may be seen from the following facts.

The bottom just outside the zone of surf contains many *Macoma balthica* and *Cardium edule* ("*Macoma*-community"). In the whole coastal area *Angulus tenuis* and *Donax vittatus* too are very common ("*Tellina tenuis*-community") and also *Venus striatula*, *Angulus fabula*, *Mactra corallina atlantica*, *Spisula subtruncata*, *S. solida* and *Montacuta ferruginosa*, and, a little further offshore, *Ensis ensis*, *E. siliqua*, *Phaxas pellucidus*, *Abra prismatica*, and *Mya truncata*; most of these belong to the "*Venus*-community", but other species in the same area are representatives of the "*Syndosmya*-community": *Abra alba* and *Mysella bidentata* f.i. Seen from the "community"-point of view the Dutch area is a transitional area, although a rather large and homogeneous one I think. (DAVIS, 1923, 1925, has come to about the same conclusion when considering the Dogger Bank fauna.)

The species of the Dutch coast have some characteristics in common: they all thrive on rather fine as well as on rather coarse sand, they can stand rather heavy currents, they tolerate salinity fluctuations between at least 30 and 35‰, and they can stand the high summer temperatures of 17° C and the low winter temperatures of 2° C and even less.

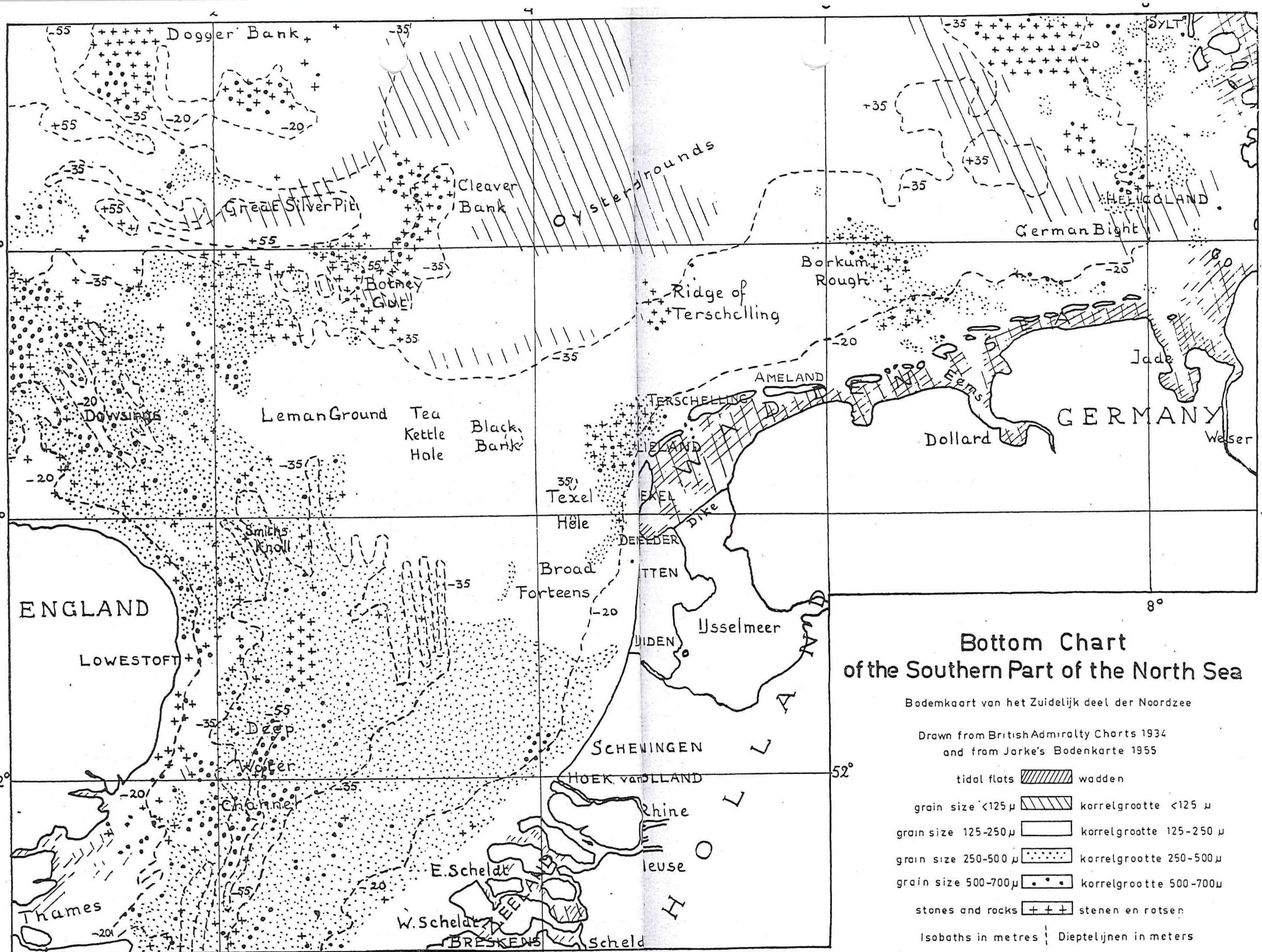
In ice-winters, however, the whole coastal population succumbs. Experiments with some of the most common species — *Macoma balthica*, *Cardium edule*, *Angulus tenuis* and *Angulus fabula* — have

shown that very low temperatures, down to the freezing point of sea water, are not lethal for these species. But at such low temperatures the animals become almost immobilized. They no longer dig themselves in and they close their shells only very slowly. This, of course, is disastrous in a bottom of moving sand: the animals are washed out of the bottom, and sand grains may enter their mantle cavity. That this is actually happening can be seen during any period of frost when the wind is easterly. In this situation an eastward water current along the bottom transports a huge mass of dying Bivalves to the shore, and the stronger the wind the greater the mass of animals washed ashore.

Some species may be a little more sensitive to cold than others. Most sensitive in this respect seems to be *Ensis siliqua*. Along the Dutch west coast this species never reaches an age of more than 3-4 years, with a length of 10-13 cm. The same species reaches a length up to 20 cm in the deeper water north of the island of Terschelling. It has been suggested that these larger *Ensis* should belong to a subspecies different from the stunted ones of the west coast, but one can deduce from the length of the winter rings that the rate of growth is exactly the same in both — only the animals in deeper water reach a much greater age — up to 10 years (KRISTENSEN, 1957). A similar difference — not in rate of growth but in age — is found in *Ensis ensis*. They, too, are very sensitive to cold. Off the west coast the dying bodies of both species may form the principal food of flatfish after a period of frost, as we found in March and April of 1947.

Although sand is found almost everywhere along the coast, for the sake of completeness it should be stated that there are some other much smaller biotopes: first, the sand bottom with stones and pebbles near the island of Texel, but as far as we know the Bivalve fauna there is much like that of the pure sand bottom. Another biotope is formed by the peat ridges off Petten at some 20 m depth. In this peat one can find *Petricola pholadiformis*, *Barnea candida* and *Zirfaea crispata*.

What, now, may be the reason for the relative poorness of the Bivalve-fauna? It might seem to be not too difficult to indicate the environmental factors that are responsible for the absence of many species in the southern North Sea, but the job is not as easily done as one would think. For example: salinity may be of importance: everywhere we observed how the number of species diminished with a decline in salinity. Many species, apparently, do not tolerate salinities below 35‰. But at the same time the stenothermic tendenc[y] of the species concerned can also play a role, together perhaps wit[h] their preference for a more stable substratum. In many cases the onl[y]



For the size of the sand grains the median grain size has been given.
+35: deeper than 35 m — dieper dan 35 m.

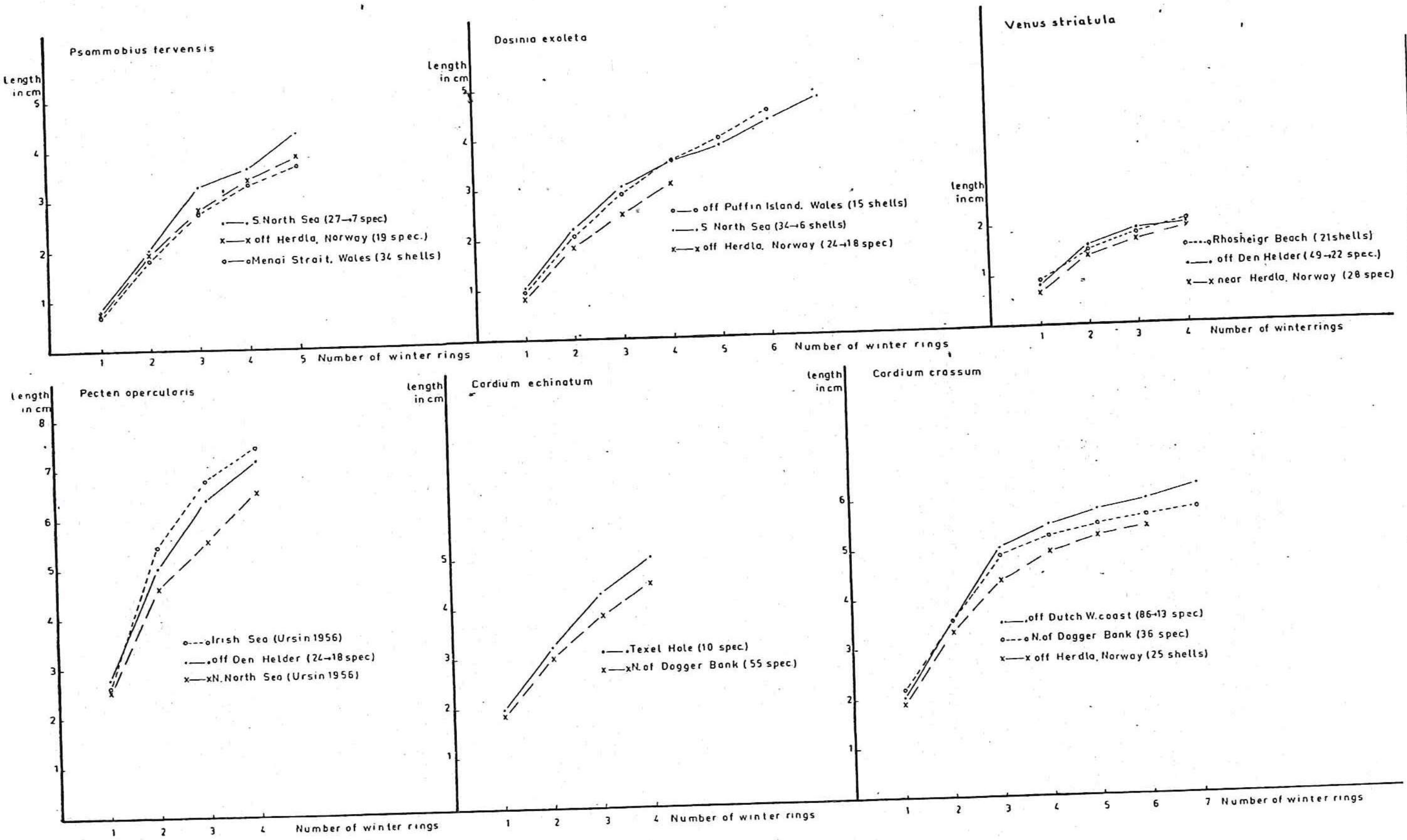
Voor de grootte der zandkorrels is de mediane korrelgrootte opgegeven.
—35: less deep than 35 m — minder diep dan 35 m.

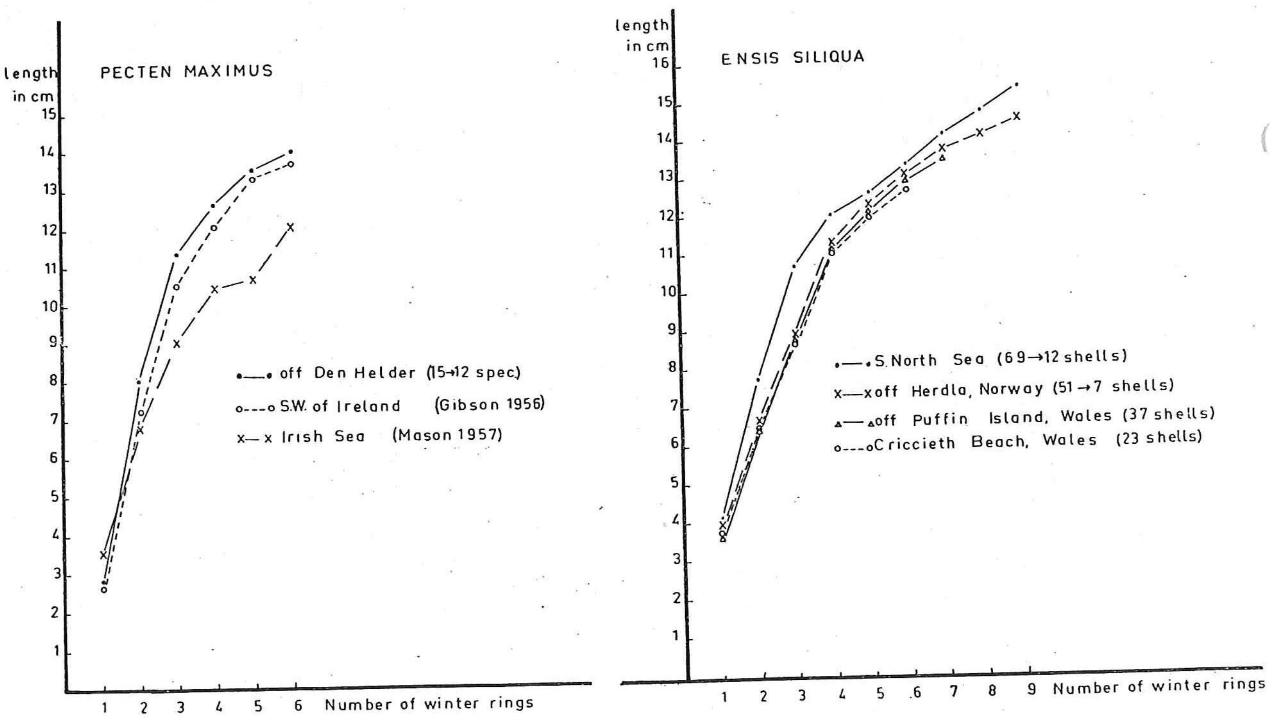
thing one can find out with certainty is which factors can n o t have been of importance. If we compare the fauna of the Baltic (incl. the Belt Sea) and the northern North Sea with the fauna of the Dutch coast we can enumerate several species which never or seldom occur near Holland. For instance: *Leda minuta, L. pernula, Musculus discors, M. niger, Nucula tenuis, Macoma calcarea*, a.o. Their presence in the Baltic shows that they must be rather euryhaline and that they can withstand salinities down to 30‰. They all have, however, a northern, almost arctic distribution and it is not impossible that they cannot tolerate the high summer temperatures in the southern North Sea. But if we indicate that factor as decisive one wonders why they do not occur along the Jutland coast where the water temperature does not reach such high levels as it does near Holland. Perhaps the species mentioned have an aversion to an unstable bottom. It seems, therefore, reasonable to conclude that for the distribution of the species cited salinity plays no role, and that bottom conditions are more important. This conclusion cannot be absolutely certain without doing experiments, as there still remains the possibility that the animals can not stand a wide range of salinity together with high temperatures.

There is another group of Bivalves which are common in the middle and northern part of the North Sea, but which are rare in the southern part and still more infrequent along the Dutch coast: *Cyprina islandica, Cardium echinatum, C. crassum, Dosinia exoleta* and *Psammobia fervensis*, and also the epibiont *Pecten opercularis*. It is a remarkable fact that, in certain years, these species are much more numerous in the southern North Sea than in other years when they may be wholly absent (vide v. REGTEREN ALTENA, 1953, and KRISTENSEN, 1956). There are some years with a relatively dense settlement of spat compared with other years almost without spatfall. We found that the whole population of one species can consist of just one year class. One of the most notable years in this respect was 1947, a year of good spatfall too for many common Bivalves and other species in the shallow parts of the whole North Sea and also in the Baltic. The year of 1947 started with an exceptionally cold winter when most of the sessile fauna died off. In the following spring the spatfall was abundant so that in the summer only one year class was present. After an ice-winter, as a rule, the spatfall of many species is unusually abundant. After the cold winters of 1929 and 1939 the summer showed a rich settlement of many species along the Dutch coast, and in Danish waters the cold winters there of 1909, 1917, 1928, 1929, 1942 and 1947 were also followed by a summer rich in spat. One of the reasons for this phenomenon is, I think, that the bottom has become a virgin one. That means more room for settlement and, what is much more important, less predators before, during and after settlement. In the southern North Sea the summer of 1947 was the richest one we have observed ourselves. This was partly due to the preceding cold winter, but in addition the summer was exceptionally warm and the salinity along the coast was extremely high during the time of the pelagic stage of the young. A second summer rich in spat was 1952 and a third was 1957, both years with a hot summer. On the other hand, the cold summers of 1948, 1949, 1954 and 1956, all preceded by a mild winter, were bad years for spatfall. Although SMIDT (1951) states that a rich spatfall is not always followed by good survival, we may certainly say that as a rule there is a distinct correlation. We found every time that the richer the settlement the richer the year class at the end of the summer.

As mentioned some rare species can establish themselves only in those years which are also successful for the more common Bivalves. In other years they hardly succeed in propagating, so they seem to live here at the limits of their habitat. One would think that such animals would not thrive here as well as in the centre of their area of distribution. However, the animals do not seem to be stunted or handicapped in any way. This becomes evident from their rate of growth if compared with the rate of the same species from other localities (vide graphs on p. 28-29). For a good picture of the yearly rate of growth the different winter rings were measured. "Growth" was taken as the difference between two rings measured from the anterior to the posterior margin. If possible only living specimens taken by trawl or dredge were used, but if these were not present empty shells were taken (see graphs). As the first winter rings are often more easily seen than the later ones the mean size of the first rings is sometimes based on more measurings than that of the later rings as indicated in the graphs by two numbers separated by an arrow.

For *Cardium crassum, Dosina exoleta* and *Psammobia fervensis* material has been collected from the Dutch area, from the Norwegian west coast (Herdla near Bergen, 1939) and from the northwestern coast of Wales (1958). These localities show great conformity, in general, concerning the rate of growth of several c o m m o n Bivalves as may be seen from the curves of two species, *Venus striatula* and *Ensis siliqua*, both also very common in the southern North Sea. The differences in growth rate between the three localities are as small in *Venus* and *Ensis* as they are in *Cardium, Dosinia*, and *Psammobia*. From this it may follow that the growth of the rare species in the Dutch area is not at all stunted as one would perhaps expect; it seems to be even better.





Growth of Bivalves construed from the length of the winter rings.
Groei van Bivalven geconstrueerd uit de lengte van de winterringen.
27 → 7 spec.: of 27 living specimens the smaller rings have been measured, and of only 7 specimens the larger rings.

Another species which is extremely rare along the Dutch coast and which is quite common a little more to the north is *Cardium echinatum*. The rate of growth of some specimens trawled off the west coast shows almost no difference from that of specimens from the northern North Sea — if there is any difference, then again the growth is better in the southern North Sea.

The growth of *Pecten opercularis*, also a rare species in the southern North Sea, has been compared with the growth data from the northern North Sea given by URSIN (1956) and from the Irish Sea as measured by GIBSON (URSIN, l.c.). Here again the southern North Sea seems to be an excellent area for growth. The same holds for *Pecten maximus*, a species that is extraordinarily rare in the whole North Sea. Since 1947 some specimens were caught here, all belonging to the year class of 1947. Only a few specimens could be obtained for measurement; their growth has been compared with data from Ireland published by GIBSON (1956) and MASON (1957).

The conclusions based on growth are supported by some determinations of shell weight. The shells of specimens of the southern North Sea show exactly the same weight as those from other locations. And all species possess ripe gonads in May or June, even *Pecten maximus*.

It is clear that the southern North Sea is a biotope far from unfavourable to the species just mentioned, but for some reason there is almost no spat, or the spat does not succeed in surviving. At all events there must be some larvae present in the spring, partly because of spawning of the local stock, partly because the larvae must be brought into the southern North Sea by the currents from the adjacent areas, especially from the south. That the local stock may be of some importance in this respect may follow from the fact that some spat and young animals are always found from the moment that a new, abundant year class in the area has reached maturity.

All species in question live in the Channel area too, although they are more common in the western part of the Channel than in the Dover area. Some larvae, however, must reach the southern entrance to the North Sea, carried by the north-going current, as the pelagic stage of the Bivalves lasts for at least three weeks.

A second current runs into the southern North Sea from the north-west. This current runs along the English coast from the north to the vicinity of East Anglia and then turns eastward. Its influence near the Dutch coast is not very great, but as it brings a lot of herring larvae from the north-west to the Dutch coast it will also bring some Bivalve larvae from that direction.

The only species of which we know with some certainty how the transport of the young takes place is *Pecten opercularis*. With some regularity the fishermen of Den Helder bring in dense masses of tangled Hydroids (*Laomedea* spec.) full of other organisms: Algae, Crustacea, Tunicata and other species all originating from the Channel coasts. Between the threads of these Hydroids small *Pecten opercularis* of about one cm are often found. I suppose these *Pecten* are brought here as settled spat and not as larvae. It is possible that the Hydroid masses floated, to begin with, because of the presence of Fucoids and other bladder weeds, but as the algae degenerated and the bladders collapsed the Hydroids sank to the bottom.

Part of these *Pecten* bearing Hydroids were cast ashore along the Dutch west coast, others were found in the deeper parts of the sea, in Texel Hole and even more to the north. Most conspicuous in this respect were the years of 1947 and 1954, two years of high salinity, i.e. of a great influence of Channel water; 1947 was marked by its warm summer, 1954 on the contrary by its cold summer, so the temperature is not likely to be of influence here.

In the warm summers of 1952 and 1957 there was some *Pecten* spat which cannot have been transported by bladder weeds because this spat was found on autochthonic *Tubularia* and other Hydroids; moreover, part of the spat had a length of only 0.5-1 mm, so it had settled not long before.

The other species mentioned have their rich spat years only when the summer is a warm one. I presume they enter the North Sea as larvae during each spring. Only if the environmental circumstances are excellent — and that was not the case in the cold *Pecten* year of 1954 — they manage to settle. It is understandable that a high temperature favours rich settlement because it shortens the pelagic phase which is the most dangerous period of life. On the other hand it seems peculiar that species which are more common in the northern North Sea than in the southern North Sea should be favoured here by higher temperatures than are ever found in the north. Perhaps it is not the high temperature as such that is favourable, but other accompanying circumstances. For instance, during a period of warm weather the absence of strong western winds results in less bottom disturbance in these shallow waters. It is certain that the spat is extremely sensitive to bottom disturbance. For *Cardium edule* it has been shown that this sensitive period lasts until the spat has reached a length of 2 mm; even this species of the tidal zone has great difficulties in settling on a rather exposed bottom (BAGGERMAN, 1953; KRISTENSEN, 1957). In such places the cockle succeeds in settling on a large scale only in years which are also favourable to the settlement of "rare" species along the coast. In places where settlement is difficult, growth is usually excellent; this seems to apply to the cockle as well as to the "rare" species. The optimum conditions for settlement do not seem to be identical with the optimum conditions for growth. I think this may be generalized in the following way: I n a n e n v i r o n m e n t s u c h a s t h e S o u t h e r n N o r t h S e a n o s p e c i e s w i l l m e e t o p t i m u m c o n d i t i o n s i n a l l r e s p e c t s. This does not only hold for species that live here on the verge of their range of distribution, but also for those species of which the southern North Sea is just the centre of their habitat. Euryokous sessile species will always have to accept some compromise — and this may even be taken as one of the characteristics of euryoecy.

From the foregoing one may deduce that the paucity of species in the southern North Sea is partly caused by the spat's inability to settle. As may be expected this is of special application to the coastal zone, and it is quite understandable that the small zone of surf, where sand movement is many times greater than elsewhere, is completely uninhabitable even to larger individuals. It is true that the bottom current may carry some molluscs from deeper water, and these are able to maintain themselves during the summer months, but the first autumn gales bring about the total disappearance of the molluscs in this area.

Having discussed the Gastropod and the Lamellibranch fauna we have to consider the Cephalopods of the Dutch coast.

If compared with the adjacent areas the southern North Sea is also poor in Cephalopods. For this fact, however, the moving substratum can hardly be responsible because most Cephalopods are not bound to the substratum as are the other molluscs. Even a bottom linked species such as *Sepiola atlantica* does not show a particular preference for a special type of bottom. It is only *Octopus vulgaris* that shows a marked preference for stones and shells because of its urge to make a shelter.

No species of Cephalopod is present along the Dutch coast for the w h o l e of the year. Most species show a long-distance migration twice a year. They appear in the southern North Sea in spring and they disappear again in the autumn. Only *Sepiola atlantica* and *Eledone cirrosa* do not leave the southern North Sea.

In April *Sepiola atlantica* moves from deeper water to the shallow water of 15—2 m depth. At the same time a similar migration is shown by some Crustacea and by several fish species such as some Syngnathids and the small flatfishes. In a cold spring the *Sepiola* migration is delayed, so it is certain that it is the high temperature of the coastal water they like. When they arrive in April two

size groups can be distinguished: the adult ones full of eggs and spermathophores, and the smaller ones that are not yet quite ripe. The adults spawn immediately or in May, the smaller ones do not become mature before May-June and spawn in the summer. After spawning no adult animals are to be found. We do not know whether they leave the coastal area at that time or whether they die. It is likely that the species reaches an age of only one year.

The small, yellow clusters of *Sepiola* eggs are attached to Hydroids (*Tubularia* e.g.) and other small objects. The young grow very fast and have partly reached maturity when they disappear from the coastal area in September-October. From the contents of fish stomachs we know that the animals stay at some tens of kilometres from the coast during the whole winter. The migration to deeper water can hardly be caused by lack of food near the coast as there are still lots of small crustaceans (small shrimps, *Gastrosaccus*, etc.) that have not yet left the shallow water at that time. The temperature therefore seems to be the principal factor that governs both the arrival at, and departure from, this region.

The second Cephalopod species that may stay in the southern North Sea in the winter is *Eledone cirrosa*. This species is common in the Mediterranean, along the Atlantic coast of Europe, in the Channel and in the northern North Sea, but is rare in the southern part of the North Sea. In the northern part it keeps mainly to the deeper water outside the 40 m isobath, the area where no total water mixing takes place and where neither the temperature nor the salinity show large fluctuations. In the aquarium of the Zoological Station, *Eledone* never thrives and mostly dies after a week or so. Their death is often preceded by serious lesions of their skin originating from unknown causes. But even if the animals remain free from lesions they die within a few weeks. Perhaps it is the low salinity of 33-28‰ they cannot withstand. That would mean that their presence in the southern North Sea might be limited by the salinity.

The same may hold for other species which are found along the coasts of the northern North Sea but not in the Dutch area: *Rossia macrosoma, Allorossia glaucopis, Sepiola pfefferi* and *Sepietta oweniana*. A second reason for their absence along the Dutch coast may be the constant transport of sand along the bottom from which no shelter is to be found.

Most Cephalopod species leave the southern North Sea during the winter. In general, migrants form the south — both fishes and Cephalopods — appear off the Dutch coast again in April or May (VERWEY, 1949). *Loligo vulgaris* is caught in the neighbourhood of Zeeland in the middle of April; more to the north, near Den Helder, they appear about one week later. *Sepia officinalis* comes two weeks later than *Loligo vulgaris*. The distance from Zeeland to Den Helder is about 175 km, so *Loligo* and *Sepia* have to move northward with a speed of 15 to 25 km per day. That proves that their "migration" cannot be a passive transportation by the current; it seems to be based on active swimming to the northeast. *Loligo vulgaris* and *Sepia* keep to the shallow, warm water of a zone of about 15 km along the coast. It is remarkable that the date of the arrival of *L. vulgaris* is hardly affected by the local water temperature while the arrival of *Sepia* can be earlier or it can be delayed by temperatures higher or lower than normal. The northern limit of their migration is at about 54° N, although there are always some individuals that move farther to the northeast, especially in a warm summer. After their arrival in the North Sea spawning starts and then they do not seem to migrate farther to the north. If the spring is a rather cold one, as in 1956, the adult *Sepia* reach Zeeland in rather large numbers, but as the temperature farther to the north was below normal the adult *Sepia* started spawning near Zeeland and did not appear at all at Den Helder in that summer. The young ones always arrive some weeks later than the adults, but in 1956 they arrived only a little later, and in smaller numbers than usual. *Loligo vulgaris* on the other hand is much less affected by the temperature (TINBERGEN & VERWEY, 1945).

Sepia attaches its eggs to a twig or other corpus alienum, *L. vulgaris* forms big clusters of eggs almost without any attachment. *Sepia* spawns but once a year; as the spent animals always seem to be in a bad condition we think many of them succumb within a few days or weeks. *L. vulgaris* spawns several times with intervals of a few weeks, and even then they do not seem to be in a bad physical condition.

In July the adult *Sepia* and all *L. vulgaris* disappear from the North Sea. Whether this is caused by mortality or by a southward migration we do not know. Among the spawning *Sepia* we find specimens of three year classes, and *L. vulgaris* spawns as well in its first as in its second year. Therefore, it seems to be unreasonable to presume that they die after spawning, but sufficient data are not yet available.

The egg clusters remain on the sand bottom quite unprotected for many weeks, but the gelatinous masses are not eaten by any animals as far as we know. The young hatch in the summer months and form a food much sought after by all fishes. Warm summers yield a rich year class. Very successful years for *Sepia* were those of 1937, 1947, 1949, 1952 and 1955. Among these only the summer of 1949 was not a warm one — it was even a cold summer — but in that year the extremely abundant year class of 1947 reached maturity and produced an enormous quantity of eggs.

One year old *Sepia* show much the same migration pattern as the adults, but they arrive a little later and they are present during the whole summer. Like the adults after spawning time they dig themselves a little into the sand by blowing away the sand grains and by fluttering with their fins like flatfish. Only occasionally do they leave their holes and often they return afterwards to the same spot, as we have seen in our Aquarium. In the event of danger they do not leave their holes until the very last moment. When the winter sets in and the temperature drops to 7° C and below, the *Sepia* are pale coloured, become sluggish, do not keep to their holes any longer and cannot offer resistance to the currents. They then fall a victim to dogfish and other predators and to the fishing trawl.

A third species coming from the south is *Octopus vulgaris*. This species enters the North Sea only in years in which they are very abundant in the Channel area, as was the case in 1939, 1950, 1951 and from 1955 to 1957. The total number caught in the North Sea is very small and along the Dutch coast it probably does not exceed 10 to 20 a year. One would expect that most specimens would be caught in the summer, but, on the contrary, they are mostly captured in November and even December. Nevertheless, I am inclined to suppose that they might have entered the North Sea during the warm season. That they are not caught by trawl then is quite understandable to anyone who has some experience with these supple and strong animals; they are not easy to remove from their shelter and even if they are caught they may creep out of any fishing gear. However, they do not tolerate low temperatures. If the temperature falls below 7° C the *Octopus* leaves its shelter, becomes pale and behaves itself quite helplessly with its arms curled up, just like *Sepia* under the same circumstances. They are therefore caught only after a period of cold weather.

Two of the most common species, *Alloteuthis subulata* and *Loligo forbesi*, enter the North Sea from two directions. *Alloteuthis* is almost completely absent during the whole winter and then, in March, the animals appear both in the south and in the northern entrance of the North Sea. They swim in shoals of many thousands and are eagerly preyed upon, as we know from the stomach contents, by almost all fish which are not too small. Their egg clusters are found in the whole North Sea from the deeper parts up to the coastal zone. In the autumn the population diminishes, either by migration or by predation.

Loligo forbesi is a common species along the whole Atlantic coast of Europe, and during the summer and autumn they are quite common in the whole North Sea with the exception of the areas with low salinities. In most years they avoid the Dutch coastal waters and only in years or periods of high salinity they come a little nearer to the coast. We do not know from what direction they enter the southern North Sea. Some adults, together with *Loligo vulgaris*, arrive in April or May, so they may come from the south. The juveniles do not arrive before the end of June or in July. That seems to be rather late for a species coming from the south, but their late arrival may be the consequence of their aversion to water of a salinity lower than 33‰ or so. The species migrating early in the year like, I suppose, the high temperature reached at that time by the shallow coastal water, but this water of rather low salinity does not attract *L. forbesi*. Farther from the coast it is not before June or July that the temperature of the water surpasses that of the Channel water and from that moment the North Sea becomes attractive to this species.

In Scotland *L. forbesi* arrives one or two weeks earlier than in the southern North Sea (RUSSELL, 1922), and in the Skagerack they appear at about the same time as in the south (OTTERLIND, 1954). Near Scotland the size of the young squids is smaller than the size of the animals in the Skagerack and in the southern North Sea. As they grow extremely fast, it is not impossible that the whole North Sea population comes from the north, although it is difficult to believe that they should manage to travel a distance of some 600 km in about two weeks.

After the arrival of the squids in the southern North Sea the ventral mantle length of the males increases from 10 cm to 25-35 cm in November when they reach maturity, and to 35-45 cm in December-January. The length of the females is less and hardly surpasses 30 cm. During the whole year two size groups can be distinguished; in the males the difference between these groups is about 10 cm, in the females almost 8 cm. Because of their rapid growth the groups cannot belong to different year classes but, as in *Sepiola*, there may exist two main spawning periods, or there may be two separate spawning areas, perhaps one in the Channel and one in the north. Although in December the females are full of ripe eggs and even show traces of spermatophores on their lips we have never found any egg clusters in the area, not in December nor in any other season. Just after having reached full maturity, in mid winter, they disappear. Some of them may fall victims to low temperatures or to predators such as *Acanthias*, others perhaps may be able to escape to the south as stated by JAECKEL (1958).

All other Cephalopod species are rare in the Dutch area. Now and then *Illex illecebrosus*, *Todaropsis eblanae* and *Ommatostrephes sagittatus* are caught (compare VERWEY, 1953-1958). *Ommatostrephes*, just as other oceanic species, is often found stranded on the Dutch beaches.

THE WADDEN SEA AREA

The Dutch estuaries of Scheldt, Meuse, Rhine and IJssel are not rich in mollusc species which is to be expected after the discussion of the coastal fauna. The Oosterschelde is rather an exception as it does not receive much fresh water, so it has a constant salinity of about 29 ‰, and the wave and current influence on the bottom of this area is comparatively small. That makes it a suitable place for the culture of mussels and oysters (KORRINGA, 1940, 1941), and other molluscs too can thrive there.

The Dutch Wadden Sea gets fresh water from the IJsselmeer in its western part and from the river Ems in the east. The daily amount of fresh water brought into the Wadden Sea varies rather a lot. This is due partly to natural causes and partly to human interference. The salinity mostly fluctuates between 25 and 34‰. Near the sluices of the Dike of the IJsselmeer it can be less, and on the tidal flats the salinity can for a short time be extremely low due to heavy rainfall. During the winter the salinity on the flats can be raised by freezing of the sea water. The average salinity of the whole area may be some 29‰ — that means that the water is not yet brackish, but less saline than the North Sea (POSTMA, 1954).

Locally, the tidal currents are very strong, up to 8 km per hour at the surface.

The Wadden Sea has an average depth of about 3 m only. This makes the temperature fluctuations large. This applies to the differences between summer and winter as well as to the diurnal fluctuations. The summer temperature may rise to 20° C and, on a flat during a sunny day, even to 30° C. In severe winters values of below zero may be reached and the flats may be frozen to a depth of half a metre. The differences between day and night temperatures do not exceed two or three degrees in the gullies, but may reach 10° C or more on the tidal flats.

The bottom structure is very heterogeneous. Very coarse sand and the finest mud can be found at a distance of 100 m or less. The grain size on the tidal flats is determined by the degree of exposure to wind and current action (POSTMA, 1957). The most exposed flats have a median grain size of 100 to 130 micron, the more sheltered ones being built up of muddy sand. The gullies and the larger channels often have a bottom of coarse sand, but the slopes at low water level may consist of mud. Some of the large old channels, which have not had any function since the enclosure of the Zuiderzee, fill up, little by little, with the finest mud.

Before the enclosure of the Zuiderzee vast fields of *Zostera marina* were present in this area. This vegetation yielded a rich substratum to millions of small Gastropods, mainly *Littorina littorea, Lacuna vincta, Rissoa membranacea*, and to many Nudibranchs. After the catastrophic eel-grass disease in the years after 1930 the *Zostera* fields never recovered. We think that the higher salinity of the Wadden Sea after the enclosure may also have influenced this process, because the eel-grass disease is most violent where the salinity is high. At present *Zostera marina* is only found in the brackish inlets of some of the Wadden islands. On sheltered flats the subspecies *Zostera marina stenophylla* and the small *Zostera nana* are still present, but this has not prevented *Lacuna* and *Rissoa* from disappearing completely.

Hydrobia ulvae is very abundant on the muddy flats and even on the muddy bottom of the old channels out of function. On the flats they form an important food for wading birds (Sand pipers a.o.), and in the channels they are preyed upon by *Asterias, Buccinum*, and small plaice. This happens in such an intensive way that in some places the population has almost disappeared at the end of each winter — this in contrast to the areas where the eel-grass still exists and where *Hydrobia* evidently finds a shelter against its predators.

In the muddy sand of the tidal flats *Retusa obtusa* is not uncommon. It preys upon *Hydrobia.*

Where mussel banks are present *Crepidula fornicata* finds a suitable substratum. It also settles on the houses of hermit crabs. Mussel banks also give a foothold to *Hydrobia ulvae, Littorina littorea*, some Nudibranchs and to *Lepidochiton cinereus. Buccinum undatum* is present in the whole area, on sand as well as on mud bottoms, but only below low water level. *Hydrobia stagnalis* is only present where the water is brackish, but if these snails are transported to more saline localities they can live there for some time, although they do not propagate. Why *Nassarius reticulatus* is never found in the Wadden Sea is not clear to us. This snail is found on the muddy bottom of the sea water filled channels of the islands of Zeeland, and empty shells are found along the whole coast. One would think that the muddy bottom of some Wadden Sea channels would furnish a suitable substratum.

The Wadden Sea is very rich in Bivalves, though not many species are represented. *Mytilus edulis* forms extensive beds on the flats and in the gullies. The larvae seek for a substratum providing the following features: it should not be more than 6 metres under the water surface and it must give the spat the opportunity of settling and fastening by means of their byssus threads in such a way that they cannot be dragged away by the current. For the young spat hydroids and red algae (*Ceramium*) form a good substratum (DE BLOK & GEELEN, 1959). As the spat grows the original substratum may become too tiny and fragile, so their attachment is dissolved and again they are swept to and fro by the tidal currents until they reach a more solid substratum where they can fasten themselves in a way that offers better resistance to the currents. The same process may be repeated more than once until they reach the most ideal substratum, the mussel bank. In this way the mussel banks grow in height. The underlying mussels are suffocated by the faeces and pseudofaeces given off by the newcomers. At last the stability of the bank diminishes and a gale may tear away parts of the bank or even the whole bank, and the living mussels have to try again to get a foothold. New mussel banks can be formed by spat settling on the shells of an old cockle population or on the tubes of a dense *Lanice* population (vide VERWEY, 1952, 1954).

In the Wadden Sea mussels are seldom found deeper than 6 metres. The same fact can be observed in the North Sea where they only live on buoys and their chains. On the chains they rarely occur below 6-8 m under the water surface. But in the very transparent water of the Norwegian fjords I have found *Mytilus* in twice or thrice that depth. This makes it probable that not the depth itself is the limiting factor, but the light intensity. From indoor observations we know that mussels grow very well even in complete darkness, but during settlement I think they have a preference for light.

On the tidal flats the mussels show a stunted growth and they do not fatten there. As the time of submersion is shorter the mussels do not succeed in getting enough food. In the gullies their growth is much better and the clearer the water the fatter they are; that is because a large amount of silt in the water prohibits feeding activity. During a severe winter the mussels below the low water line do not suffer very much, but the mussels on the tidal flats succumb completely.

After the disastrous attack of the parasitic copepod *Mytilicola intestinalis* on the mussels cultivated in the Oosterschelde estuary, some 10 years ago, a large scale start with the cultivation of mussels in the Wadden Sea has been made, and with great success.

Another epibiont is *Ostrea edulis* — in former times autochthonic in the Wadden Sea but since many years completely fished out. In the Oosterschelde estuary they are cultivated in large numbers for human consumption.

Among the digging bivalves *Cardium edule* is the most numerous species, although its occurrence is almost limited to the tidal flats. The more they are exposed to wave action the better is their growth, but in such areas they have difficulty in settling; when less than 2 mm they are washed away. Successful settlement occurs more easily in sheltered areas, but there their growth is much less. Even when a high density is reached the growth of the animals is seldom affected by competition, unless they lie packed together. The stunted growth in these areas is probably caused by the amount of silt that settles during the time of slack water. Then the cockles do not take in enough food for a rapid growth (KRISTENSEN, 1957). In the Wadden Sea the cockles do not thrive below the low water line, though they show excellent growth in the North Sea at some 15 m depth. I think the great turbidity of the Wadden Sea water may be the principal cause of their absence below the tidal zone. It cannot be the lack of light, for cockles can grow excellently in almost complete darkness (ORTON, 1926). It must be the silt layer on the bottom that is noxious to the cockles, and where no settlement of silt takes place the currents are too strong.

Other Bivalves common on the flats are *Macoma balthica* and *Mya arenaria*. Much less common are *Abra tenuis* and *Scrobicularia plana*. In the gullies only *Macoma balthica* is always found. Sometimes *Venerupis pullastra*, *Angulus tenuis* and *Mysella bidentata* are also present.

Here and there peat covers the bottom of the channels and there *Petricola pholadiformis*, *Barnea candida* and *Zirfaea crispata* are found. *Barnea* and *Zirfaea* can also be present where a sticky clay bottom is found.

It is a well known fact that during an ice-winter the whole population of Bivalves on the flats may succumb. Some species, such as *Cardium edule*, vanish completely from the Wadden Sea and also from the coastal region of the North Sea. Nevertheless the repopulation of such species is not a question of years, but is completed already during the following summer. Apparently, even a decimated stock produces enough larvae. I think this may hold for all species in the area investigated: the density of the population is never of any importance in this respect. The only exceptions are the "rare" species: they show they have more chance of successful settlement when the stock is larger than usual. In the Wadden Sea only *Scrobicularia plana* shows difficulty in its repopulation after an ice-winter. I think the reason may be that this species is strictly bound to the tidal zone and has a rather small egg production. When, after a cold winter, the Wadden Sea bottom is virgin other species also produce some spatfall here, for instance *Ensis ensis*, *Ensis siliqua*, *Phaxas pellucidus* and *Angulus fabula*. But after having reached a length of about 1 cm they vanish again.

Cephalopods are not seen much in the Wadden Sea. Only *Sepiola atlantica* can be numerous and they can even propagate here. *Alloteuthis subulata*, *Loligo vulgaris* and *Sepia officinalis* enter the Wadden Sea in small numbers only, the greater part of them being males, whilst the females keep themselves outside the influence of the Wadden Sea water. Only in years of high salinity, as was the case in 1954, the females too may enter the Wadden Sea in fairly large numbers and in such years even spawning takes place.

THE DIKES AND OTHER ARTIFICIAL WORKS

Natural rocks are not found along the Dutch coast. The mainland is protected by dunes. Where they form an insufficient protection or are lacking, dikes have been built. Beaches and harbours are often protected by piers.

In rocky areas artificial works possess almost the same fauna as the surrounding rocks, so one would expect the Dutch dikes and piers to show a fauna comparable to the rock fauna of the Channel coasts. Indeed, if one sums up all the species ever found on the Dutch dikes the list is almost the same as the list of the Boulogne coast in northern France. But when collecting along the Dutch dikes one finds only a small number of species because there are only a few that really are resident there. And this number is still decreasing as the stony dikes, one after another, are covered by a layer of bitumen.

On the dikes one can always find two or three Gastropod species: *Littorina saxatilis*, *L. littorea* and, if Fucoids are present and the place is a sheltered one, *Littorina obtusata littoralis* (vide BARKMAN, 1955). In some locations, mainly in the southern part of the area, *Nucella lapillus* is often present. *Patella vulgata*, *Littorina neritoides* and many others are rare and just temporary visitors. Nudibranchs are often overlooked, but they are present in a variety of species and even in large numbers now and then as can be seen from the contribution to this volume by SWENNEN.

Dikes, of course, are not the most suitable place for Bivalves. The epibiont *Mytilus edulis* can be present in fairly large numbers. On exposed dikes their shells become thick and stunted, but the animals within seem to be in excellent condition. It appears that the shell growth is hampered by the mechanical force of the waves without causing any harm to the "fish" inside. Only in the most exposed localities is the increase of weight affected. Mussel spatfall can be very abundant on the dikes, but the winter storms restrict survival to the more sheltered places.

Other more or less regular inhabitants of the dikes are *Anomia squamula*, *Modiolus modiolus* juv., *Ostrea edulis* juv., *Kellia suborbicularis*, *Saxicava arctica* and the spat of a lot of other species which, however, vanish in their first year.

Where much wood is used *Teredo navalis* and *T. megorata* may be present. Their destructive work has been notorious for many hundreds of years. In the past harbour installations and ships fell victims to them; nowadays it is the osier matting which is used as a protection of the under water slope of the dikes which is devastated. Since wooden constructions have largely been replaced by iron or concrete ones the damage has become less, but still to be feared is the devastation of matting along the dike bases.

Finally, we shall try to trace the reason why so few species inhabit the artificial rock shore of the Dutch coast. Most conspicuous is the dying off of so many settled animals during a cold winter. *Patella vulgata*, for instance, may live on dikes for months and even for years, but then, in a period of frost, they succumb. In Norway, however, *Patella* is found in places where the winters are no milder than in Holland. There we see that *Patella* is present in places facing the sea, and that they are less numerous or even absent further inside the fjords where during the winter ice is formed and where the pack ice drifts along the rocks at the end of the winter (DONS, 1933). The rubbing ice removes many organisms of the tidal zone so that they fall to the bottom. If the bottom is a rocky one and the tidal current is not too strong, some of the animals — provided they are not crushed — may remain there for the time being and crawl to the surface again when the spring sets in. This is absolutely impossible along the Dutch dikes: if any animal is torn away from a dike it is taken by the current and is inevitably lost. This may be the explanation also for the limited distribution of *Nucella lapillus*. As we have seen on the pier of Hoek van Holland during a period of frost (February, 1954), the animals were heaped together in a crevice at the low water line; they were quite motionless and were partly dead. I do not know whether they had been torn away by pack ice or had only been immobilized by the low temperature and had been moved by the surf. At the tip of the pier all the *Nucella* that had been there during the summer had disappeared. Sheltered places are a vital condition for survival in such winters. The same holds for some non-molluscs such as *Actinia equina*, *Metridium senile*, *Psammechinus miliaris* and others.

Among the few animals that are always present *Littorina saxatilis* maintains itself during the winter by its way of living in crevices at or above the high water line. *Littorina littorea* is found above, in and below the tidal zone and as it manages to crawl even on sand at low temperatures some will always survive. *Littorina obtusata littoralis* is found in a lower zone in the winter than in the rest of the year. As JANSSEN (1959) has found, this species changes from being negatively geotactic to the reverse when the temperature drops to values about zero. This change in their behaviour brings the animals from the middle of the tidal zone to lower regions and even to the sublittoral zone where they are much better protected.

Although the winters play an important role, they are not the only factor that prohibits the settlement of a rich rock fauna on the Dutch artificial substrata. A second factor is that the area is too restricted and its situation is too isolated for the development of a rich and stable population. Then there is a lack of sheltered places unaffected by surf and current action. The absence of a rich flora of algae providing food and shelter is one of the consequences of that lack of shelter. Finally, of course, factors such as low salinities and high silt content may also play an important role.

As we have seen the coastal region of the Netherlands is an environment not well suited to the development of what is called a "rich" mollusc fauna. Few species can stand the rather extreme conditions found there, but these few are mostly represented by a large number of individuals. This makes the area a magnificent field for the study of ecological problems.

SUMMARY

The total number of mollusc species living in the Dutch coastal waters is very small.

Many Gastropod species cannot live there because of the sandy bottom and the strong currents. Only three species can withstand the difficulties.

Some 20 Lamellibranchs are common in the area investigated. Grouping them into any "community" of PETERSEN c.s. does not seem to be possible here.

Many Lamellibranch species present in the northern North Sea are absent in the southern part. The arctic species among them do not tolerate the high summer temperatures in the shallow southern part, other species do not tolerate salinities below 35‰ or cannot settle on the unstable sand bottom. If, however, "rare" species manage to settle, their growth during a series of years proves to be excellent. Warm summers, especially when preceded by a cold win-

ter, favour settlement; cold winters kill almost the whole population, but this seems to be no hindrance to the production of a sufficient amount of spat next spring.

Among Cephalopods only *Sepiola atlantica* is common during the whole year. The other species are only present from spring to autumn. The factors influencing the migration and spawning of *Sepia*, two *Loligo* species and *Alloteuthis* are discussed. *Octopus* is only caught during the winter when it succumbs to the cold.

In the Wadden Sea the number of species is extremely small. *Mytilus* and *Cardium* are numerous, but the optimum conditions for growth are not identical with those for population density.

The dikes too have a poor molluscan population. They do not provide enough shelter from surf and current, especially during the winter. This explains the partial absence of *Patella* and *Nucella.*

LITERATURE

ALTENA, C. O. VAN REGTEREN, 1953. Nog eens: levende Noorse Hartschelpen op het strand. Lev. Nat., vol. 56, pp. 85-87.

BAGGERMAN, B., 1953. Spatfall and transport of *Cardium edule* L. Arch. Néerl. Zool., vol. 10, pp. 315-342.

BARKMAN, J. J., 1955. On the distribution and ecology of *Littorina obtusata* (L.) and its subspecific units. Arch. Néerl. Zool., vol. 11, pp. 22-86.

BLEGVAD, H., 1922. Animal communities in the Southern North Sea. Proc. Zool. Soc. London, 1922, pp. 27-33.

BLOK, J. W. DE, & H. J. F. M. GEELEN, 1959. The substratum required for the settling of mussels (*Mytilus edulis* L.). Arch. Néerl. Zool., vol. 13, suppl. 1, pp. 446-460.

DAVIS, F. M., 1923 & 1925. Quantitative studies on the fauna of the sea bottom. Fish. Invest., Ser. 2, vol. 6 & 8.

DONS, C., 1933. Norges Strandfauna 4. Utbredelsen av *Patella vulgata.* Kgl. Norske Vid. Selsk. Forh., vol. 6, pp. 185-188.

GIBSON, F. A., 1956. Escallops (*Pecten maximus* L.) in Irish waters. Sci. Proc. Roy. Dublin Soc., vol. 27, pp. 253-271.

HAGMEIER, A., 1925. Vorläufiger Bericht über die vorbereitenden Untersuchungen der Bodenfauna der Deutschen Bucht mit dem Petersen-Bodengreifer. Ber. Deutschen Wiss. Komm. Meeresf., N.F., vol. 1, pp. 247-272.

JAECKEL JR., S., 1952. Zur Verbreitung und Lebensweise der Opisthobranchier in der Nordsee. Kieler Meeresf., vol. 8, pp. 249-259.

— , 1952. Prosobranchiaten der freien Nordsee (nach den „Poseidon"-Fängen 1902-1912). Verh. Deutschen Zool. Ges. 1951, pp. 207-220.

— , 1952. Lamellibranchien der freien Nordsee (nach den „Poseidon"-Fängen der Fahrten 1902-1912). Verh. Deutschen Zool. Ges., 1951, pp. 221-241.

— , 1952. Zur Oekologie der Molluskenfauna in der westlichen Ostsee. Schr. Naturw. Ver. Schleswig-Holstein, vol. 26, pp. 18-50.

— , 1958. Cephalopoden. Tierwelt Nord- und Ostsee, Teil 9, b 3, pp. 479-723. Geest & Portig, Leipzig.

JANSSEN, C. R., 1959. The influence of temperature on geotaxis and phototaxis in *Littorina obtusata* (L.). Arch. Néerl. Zool., vol 13, in the press.

JARKE, J., 1955. Bodenkarte der südlichen Nordsee. Deutsche Hydrogr. Z., vol. 9, Tafel 1, 1956.

JONES, N. S., 1950. Marine bottom communities. Biol. Rev., vol. 25, pp. 283-313.

JUTTING, T. VAN BENTHEM, 1933. Gastropoda prosobranchia et pulmonata. Fauna van Nederland, afl. 7, 387 pp. Sijthoff, Leiden.

— , 1943. Lamellibranchia. Fauna van Nederland, afl. 12, 477 pp. Sijthoff, Leiden.

— & H. ENGEL, 1936. Gastropoda opisthobranchia; Amphineura et Scaphopoda. Fauna van Nederland, afl. 8, 106 pp. Sijthoff, Leiden.

KALLE, K., 1953. Der Einfluss des englischen Küstenwassers auf den Chemismus der Wasserkörper in der südlichen Nordsee. Ber. Deutschen Komm. Meeresf., vol. 13, pp. 130-135.

KORRINGA, P., 1940. Rapport over het onderzoek naar den broedval van de oester. Versl. & Meded. Afd. Visscherijen, No. 35, 96 pp.

— , 1941. Experiments and observations on swarming, pelagic life and setting in the european flat oyster, *Ostrea edulis* L. Arch. Néerl. Zool., vol. 5, pp. 1-249.

KRISTENSEN, I., 1956. De Artemisschelp (*Dosinia exoleta*). Lev. Nat., vol. 59, pp. 82-84.

— , 1957. De groeisnelheid van het Tafelmesheft (*Ensis siliqua*). Lev. Nat., vol. 60, pp. 93-95.

— , 1957. Differences in density and growth in a cockle population in the Dutch Wadden Sea. Arch. Néerl. Zool., vol. 12, pp. 351-453.

MASON, J., 1957. The age and growth of the scallop, *Pecten maximus* (L.), in Manx waters. J. Mar. Biol. Ass. U.K., vol. 36, pp. 473-492.

ORTON, J. H., 1926. On the rate of growth of *Cardium edule*. Part I. Experimental observations. J. Mar. Biol. Ass. U.K., vol. 14, pp. 239-279.

OTTERLIND, G., 1954. Bläckfisk och fiske i Skandinavien. Faunistisk Revy, nr. 3, pp. 75-91.

PETERSEN, C. G. J., 1918. Havbunden of Fiskenes Ernæring. Beretning Dansk Biol. Stat., nr. 25, 57 pp.

POSTMA, H., 1954. Hydrography of the Dutch Wadden Sea. Arch. Néerl. Zool., vol. 10, pp. 405-511.

— , 1957. Size frequency distribution of sands in the Dutch Wadden Sea. Arch. Néerl. Zool., vol. 12, pp. 319-349.

RUSSELL, E. S., 1922. Report on the Cephalopoda collected by the "Goldseeker". Fish. Scotl., Sci. Invest., no. 3, 45 pp.

SMIDT, E. L. B., 1951. Animal production in the Danish Waddensea. Medd. Komm. Danmarks Fisk.- & Havunders., Ser. Fisk., vol. 11, pp. 1-51.

STEPHEN, A. C., 1933. Studies on the Scottish marine fauna: the natural faunistic divisions of the North Sea as shown by the quantitative distribution of molluscs. Trans. Roy. Soc. Edinburgh, vol. 57, pp. 601-616.

TINBERGEN, L. & J. VERWEY, 1945. Zur Biologie von *Loligo vulgaris* Lam. Arch. Néerl. Zool., vol. 7, pp. 213-286.

URSIN, E., 1956. Distribution and growth of the Queen, *Chlamys opercularis* (Lamellibranchiata) in Danish and Faroese Waters. Medd. Danmarks Fisk.- & Havunders., N.S. vol. 1, nr. 13, 32 pp.

VERWEY, J., 1949. Migration in birds and fishes. Bijdrage tot de Dierkunde, vol. 28, pp. 477-503.

— , 1952. On the ecology and distribution of cockle and mussel in the Dutch Waddensea. Arch. Néerl. Zool., vol. 10, pp. 171-239.

— , 1953-1958. Annual report of the Zoological Station of the Netherlands Zoological Society for the year 1952; id. for 1953, 1954, 1955 and 1956. Arch. Néerl. Zool., vol. 10, 11 and 12.

— , 1954. De mossel en zijn eisen. Faraday, vol. 24, pp. 1-13.

Zee-mollusken uit het Nederlandse kustgebied

(Samenvatting)

door

INGVAR KRISTENSEN

De nederlandse kustwateren zijn arm aan mollusken-soorten. Daar staat tegenover, dat er onder de soorten die hier voorkomen een relatief groot aantal zeer rijk aan individuen is.

Het „nederlandse" territorium strekt zich eigenlijk niet verder uit dan 3 zeemijl buiten de kust. Reeds in 1927 echter heeft de Redactie van de „Fauna van Nederland" een strook van ongeveer 25 km breedte gekozen als gebied waarbinnen de gevonden dieren als „nederlands" geëtiketteerd zouden mogen worden. In deze verhandeling wordt met geen enkele grens rekening gehouden, al ligt het zwaartepunt wel bij de fauna die binnen de grens van 25 km wordt aangetroffen. Wij hebben niet getracht een volledig beeld van de molluskenfauna in dit gebied te geven. Het voorkomen van lege schelpen, aangespoelde dieren en andere allochthone dieren hebben wij geheel buiten beschouwing gelaten — wij hebben alleen gelet op dieren die levend in hun eigen miljeu aangetroffen zijn.

De gegevens over de detail-verspreiding der soorten zijn ten dele ontleend aan de mollusken-deeltjes van VAN BENTHEM JUTTING en ENGEL in de „Fauna van Nederland" en berusten ten dele op gepubliceerde en ongepubliceerde waarnemingen van het Zoölogisch Station te Den Helder en van het Dierfysiologisch Laboratorium der Universiteit van Amsterdam.

Voor de nomenclatuur der Gastropoden en Lamellibranchiën zijn steeds dezelfde namen gebruikt als welke men vindt in de „Fauna-deeltjes". Wat de Cephalopoden betreft is aansluiting gezocht bij de monografie van JAECKEL (1958) over de inktvissen van de Noord- en Oostzee.

HET NOORDZEEGEBIED

Zoals men kan opmaken uit de bodemkaart op blz. 24-25 bestaat de bodem van vrijwel de gehele Noordzee uit zand. In het zuiden is de korrelgrootte gemiddeld iets groter dan in het noorden van dit gebied. Plaatselijk vindt men moraine-stenen, zoals in de „Texelse Stenen". Veenrichels vindt men vooral NW van IJmuiden.

Het bodemrelief is overal bijzonder vlak. Enkele zandrichels vindt men evenwijdig aan de kust, zowel nabij de brandingszone als daarbuiten. De zeebodem helt slechts zeer geleidelijk en bereikt op 25 km