Extrait des Archives Néerlandaises de Zoologie, Tome X, Livr. 3, 1953.

* present adress
Zoologisch Laboratorium
Rijksstraatweg 78
Haren (Gr.)
Holland

SPATFALL AND TRANSPORT OF CARDIUM EDULE L.

by

B. BAGGERMAN *
(Zoological Station, Den Helder)

CONTENTS

I. INTRODUCTION

For some years it has been a subject of investigation at the Zoological Station, Den Helder, to determine the distribution and growth of cockles in the Waddensea in order to obtain an insight into the factors controlling them. These investigations have shown that the cockles in this region are limited to flats which emerge at low tide, and that the animals are not distributed at random over these flats, but rather in a way which will be described below.

KREGER (1940) assumed that this unequal distribution was mainly due to unequal spatfall. He made most of his observations on flats near the Zoological Station, where, according to him, more spat fell on the lower than on the higher parts. He assumed that the highest parts received little spat because the water would have given off the latter to the lower parts covered earlier. Also the smaller head of water and the shorter time of submersion over the higher parts would cause a smaller spatfall. According to KREGER these factors, considered together, would account for the large amounts of spat he found on the lower parts of the flats.

It was remarkable, however, that the largest numbers of adult cockles found by KREGER on the Zuidwal-flats were present on the higher parts and not on the lower ones. This phenomenon also held for two other areas studied by him, and he attempted to explain this by assuming that on the lower parts spat would disappear in larger quantities, so that, ultimately, more cockles would remain on the higher parts. All other areas examined by KREGER showed the smallest numbers of adult cockles on the higher parts, an observation which was well in agreement with his view.

The weak point in KREGER's investigations was that the youngest cockles found by him measured 1–2 mm, these being the smallest specimens retained by his sieve. It has long been known that the larvae of *Cardium* disappear from the plankton at a size of about 300 μ (THORSON, 1946). Therefore, the possibility cannot be excluded that the animals, during the period necessary for growth from 300 to 1,000 or 2,000 μ, were carried to the area in question from other places. In that case, the place where KREGER found his youngest cockles need not necessarily be the place where the spat settled immediately after metamorphosis.

The purpose of my investigation, therefore, was to separate the *direct spatfall* after metamorphosis from the settling of somewhat older spat, which had been transported for some time. This objective was not fully realized, since, owing to practical difficulties, I, too, did not succeed in obtaining the youngest spat. But the importance of transport of older spat by the current was shown with great certainty, and this transport forms the chief subject of my paper.

My investigations (which were carried out in 1950) not only formed the continuation of KREGER's studies in the years 1937, '38 and '39, but also of work carried out by the Zoological Station in the period of 1947–'50. The latter investigations started after the severe winter of '46–'47, when most cockles in the Waddensea died from exposure. The fine, warm weather of the summer of 1947 favoured the development of a new population, and in the autumn of that year the whole area abounded in animals of one single yearclass. It then seemed worth while to follow the growth and density changes of these animals during the following years. This was done by taking samples along a number of traverses. The purpose of my observations was, at the same time, to determine the spatfall along one of these traverses, where the life-history of an older population was known.

The traverse chosen was one which crossed a flat in the middle of the Waddensea, known as Zeehondenplaat (seal shoal) (fig. I). It is

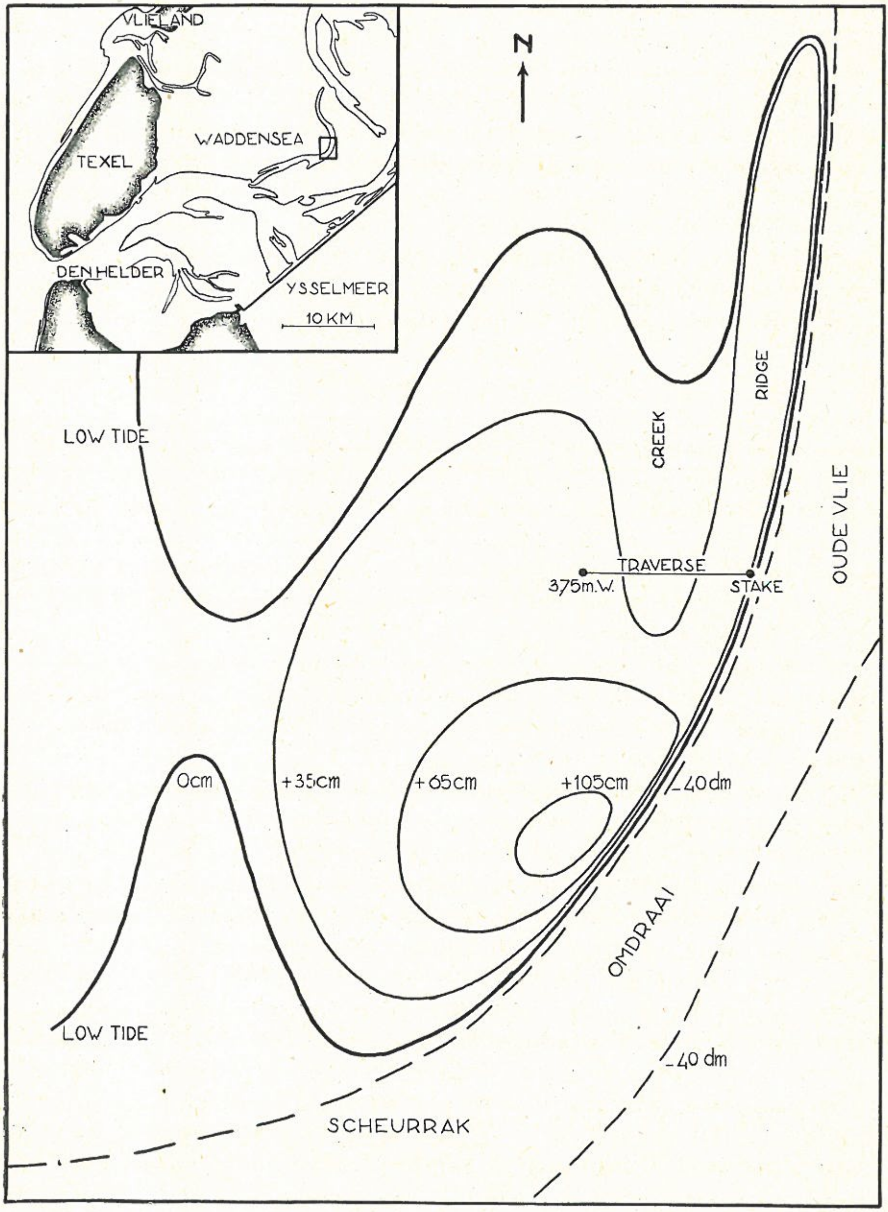


Fig. I. Map of Zeehondenplaat with contour lines and traverse (survey H. POSTMA, June 7, 1950). The zero-contour represents about mean low tide mark. Inset: Western part of Dutch Waddensea with Zeehondenplaat.

bounded by fairways named "Scheurrak", "Omdraai" and "Oude Vlie". On the highest part of the flat, near the "Omdraai", a group of seals usually had their resting place close to deep water.

Because the present investigations formed part of a larger, more extended research program, I was often able to take advantage of the help and experience of others. In this connection I wish to express my gratitude to Dr J. VERWEY, who suggested the subject to me and critically revised this paper, to I. KRISTENSEN and H. POSTMA for their valuable advice and constant help, and to N. PIJL and A. DRAL for much technical assistance. I owe many thanks especially to miss Marg. HUGHES, London, for her help in the translation of the paper.

II. METHODS

As was already mentioned in the Introduction, we hoped to be able to separate the direct spatfall of newly metamorphosed animals from the settling of older spat, which might have been carried to the spot from other places. To this end, small plots of 20 dm^2 were made devoid of cockles and re-examined every few days. The occurrence of animals of 300 μ would be an indication of true spatfall, whereas the occurrence of older cockles would indicate that transport of older spat took place.

Apart from this, the spat population of equal plots, which had not previously been cleared of spat, was studied, in order to obtain an impression – from the comparison of cleared and untouched units – of the tenacity of spat at a certain place.

This scheme only partially succeeded. First, it was impossible to make a quantitative investigation of the plots without using a sieve. This sieve had to have meshes not smaller than 0.5 mm in diameter, because otherwise too much sand would be held back. Even by using a 0.5 mm sieve considerable trouble was occasionally experienced when detritus, in the form of fragments of peat, failed to pass through the mesh. Enormous quantities of this detritus were often present in some places, so that the examination of a single sample frequently took several hours. It resulted from the observations that only animals of 600 μ and larger were quantitatively retained by the mesh, whereas animals of less than 400 μ were not retained at all. For this reason, direct spatfall could not be separated from the settling of animals which had been transported a certain time after metamorphosis.

In the second place, it was often impossible to examine the plots at short intervals, of e.g. 1–2 days. Such a regular inspection had originally been planned, because it was realized that animals of say 300 μ might rapidly reach a size of 500 μ and then would be indistinguishable from animals of 500 μ transported to the plot in question.

Subsequently, it was discovered that the growth rate of the youngest spat was much less than originally expected. Moreover, animals smaller than 600 μ were seldom found. For that reason the second drawback – inspection at longer intervals – scarcely hampered the interpretation of the data. The only disadvantage was that a plot, controlled after e.g. 10 days, was populated almost as densely as the untouched plots.

In the third place, the study of plots not previously examined was later on neglected through lack of time, with the result that only a few data for comparison of cleared and untouched plots were finally available.

For a good understanding of the following work, the methods used must be described in some detail.

A number of plots of 20 dm² along the traverse in question were marked with small poles at their corners. There were 7 of them in all, which are referred to by giving their distance in metres west of a stake placed 40 m from the low tide mark along the "Oude Vlie".

The superficial layer of sand on these plots was removed to the extent of about 2 cm in depth, and sieved. The number of young spat was determined and their length measured. For the shovelling up of the sand a small shovel with 3 turned up sides was used. The latter prevented the water, always present on the sand, from being washed away from the shovel, possibly taking some spat with it at the same time. The residue of the sieved sand was carefully washed over into a glass jar, the contents of which were searched for spat with a 2–3 times magnifying glass. Not only spat of *Cardium*, but also of other bivalves present, were counted, identified and measured under the microscope. Since dead animals can hardly be distinguished from empty shells it was necessary to examine the samples while the animals were still living.

The use of regularly checked plots mentioned above met with some practical difficulties. As a result of the scooping the plots eventually lay somewhat lower than their immediate environment, even in spite of the effort to replace the sand. To some degree the poles, too, were a nuisance by disturbing the regular surface of the sand. Thus it was possible for spat from the surroundings to be washed into these lower lying parts.

Some further experiments were carried out to overcome this difficulty. First, in several places a surface of 2.5 × 2.5 m was cleared of spat by scooping away the superficial layer of sand (a control of this area showed the absence of further spat). In the centre of these cleared patches a small plot of 20 dm² was staked out, in order to ensure that spat could not be washed into the latter from the immediate surroundings. These plots will later be referred to as "isolated plots". The sampling of these plots took place after 12–24 hours.

Another experiment was carried out with pieces of jute (60 × 90 cm), which were spread out and pinned down on the sand. After 12–24 hours the material deposited on these pieces was sieved and examined.

Furthermore, observations were made on the influence of a current shadow on the settling of young spat. To this end screens of irongauze were placed on the flat at a considerable distance from each other, in directions east-west and north-south. The screens were 1.5 m in length and 30 cm in height. On each side of the screen plots of 20 dm^2 were staked out, plus one equal plot lying at some distance from each screen for comparison. These areas, too, were sampled after 12–24 hours. In addition, a larger screen was used, which was made of branches. This screen was 3 m long and 30 cm high. Here, too, control areas as mentioned above were used.

On two different days adult cockles were collected along the traverse on plots which had never before been examined. They were counted and the greatest diameter of each annual growth ring, as well as their greatest length, were measured.

Finally, the Zoological Station carried out grainsize determinations of the sand as well as current measurements. Grainsizes were determined after Van Veen's method (1936), and the figures have been expressed as "median sizes" (Krumbein in Trask, 1939). Current measurements were carried out by timing the passing of floating algae. The heights of the flat were determined in relation to a certain water level.

III. OBSERVATIONS AND EXPERIMENTS

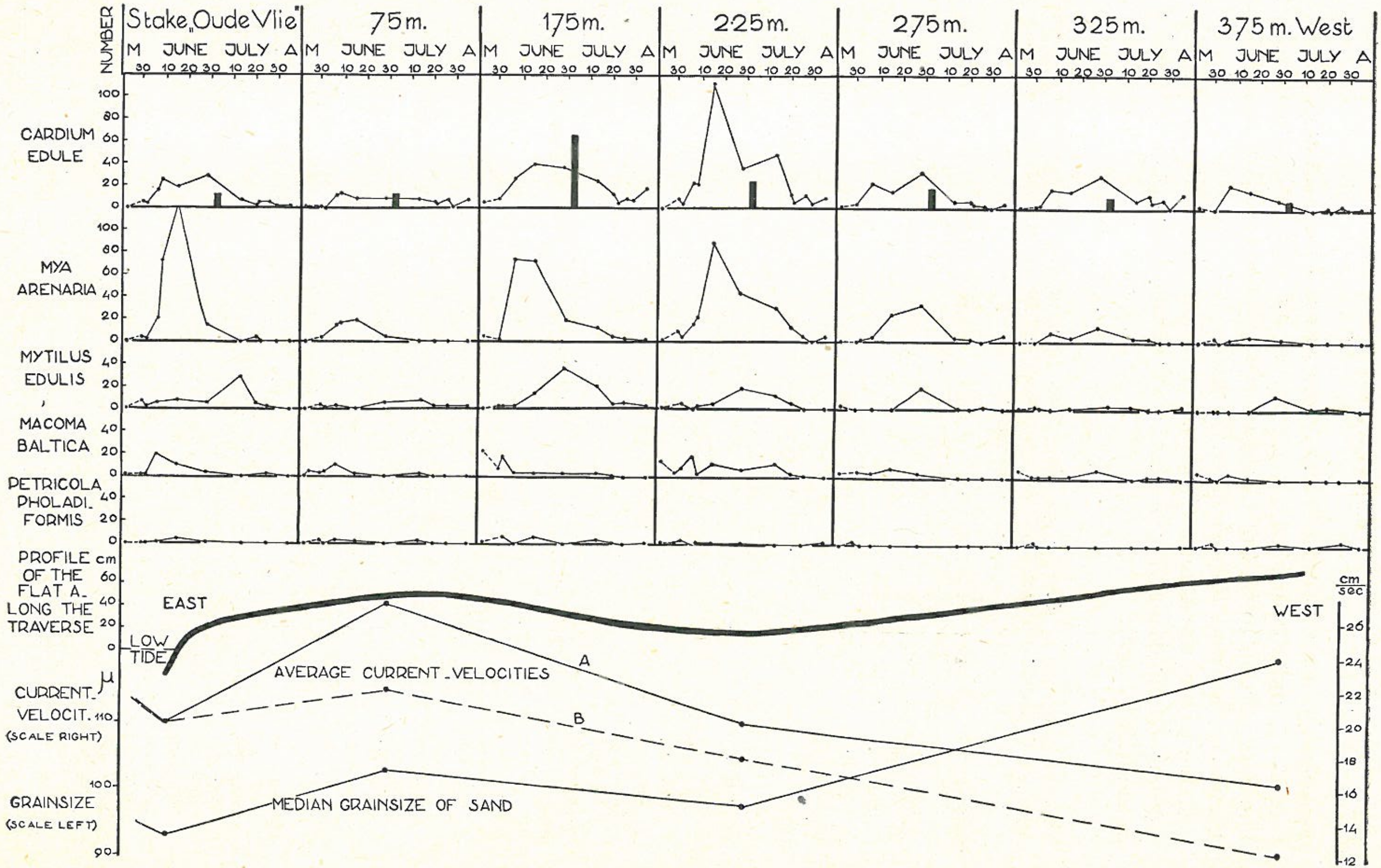
1. TRANSPORT

The data on the occurrence of young bivalves on plots which had been initially cleared are represented in figure II and table I.

In figure II the situation of the plots relative to the stake near the "Oude Vlie" is inserted on top of the columns. The number of animals found is plotted vertically and the different days of sampling are plotted

Fig. II. Numbers of bivalve spat on different plots along traverse in the course of summer. Below: profile along the traverse, average current velocities on June 7, 1950, and median grainsize of sand.

Black columns in *Cardium*-curves denote the quantities of 2 and 3 years old cockles. Average current velocities (mean of average flood and ebb velocities, regardless of direction) relate partly (curve A) to periods of submersion alone, periods of emersion having not been taken into account, partly (curve B) to the complete tidal cycle (periods of emersion included).


NUMBER
Stake „Oude Vlie"
75 m.
175 m.
225 m.
275 m.
325 m.
375 m. West
M JUNE JULY A
CARDIUM EDULE
MYA ARENARIA
MYTILUS EDULIS
MACOMA BALTICA
PETRICOLA PHOLADIFORMIS
PROFILE OF THE FLAT ALONG THE TRAVERSE
cm
EAST
WEST
LOW TIDE
AVERAGE CURRENT VELOCITIES
A
B
CURRENT VELOCIT. (SCALE RIGHT)
μ
cm/sec
GRAINSIZE (SCALE LEFT)
MEDIAN GRAINSIZE OF SAND

horizontally in each column. These days were May 24 and 31; June 1, 6, 8, 15, and 28; July 13, 20, 21, 25, 26, 27, and 28, and August 4. The data pertain to spat of *Cardium edule*, *Mya arenaria*, *Mytilus edulis*, *Macoma baltica*, and *Petricola pholadiformis*.

Table I gives the data of *Cardium* in more detail. Here, not only the number of animals is given, but also their size in microns (we will refer to the italics later).

TABLE I

Numbers and sizes of *Cardium* spat found on different days on investigation and comparison plots. For explanation see text. Numbers for comparison plots are given in italics.

MAY 24	stake	75mW.	175mW.	225mW.	275mW.	325mW.	375mW.	total
400– 600	—	—	*3*	—	—	—	*1*	*4*
600– 800	—	*1*	*2*	—	*1*	—	*1*	*5*
800–1000	—	—	—	—	*1*	*1*	—	*2*
1000–1200	—	—	—	—	—	—	—	*0*
1200–1400	—	—	—	—	—	—	—	*0*
1400–1600	—	—	—	—	—	—	—	*0*
total	*0*	*1*	*5*	*0*	*2*	*1*	*2*	*11*
MAY 31								
400– 600	2	1	5	4	1	—	—	13
600– 800	2	—	3	3	1	2	—	11
800–1000	1	—	—	—	2	—	—	3
1000–1200	—	—	—	1	—	—	—	1
1200–1400	—	—	—	—	—	—	—	0
1400–1600	—	—	—	—	—	—	—	0
total	5	1	8	8	4	2	0	28
JUNE 1								
400– 600	1 *1*	— *1*	*2*	1 *2*	—	*1*	—	2 *7*
600– 800	2 *3*	— —	*7*	2 *5*	*2*	—	—	4 *17*
800–1000	1 *1*	— *4*	—	1 —	*1*	*1*	*1*	2 *8*
1000–1200	— —	— —	—	— *1*	—	—	—	0 *1*
1200–1400	— —	— —	—	— —	*1*	*1*	—	0 *2*
1400–1600	— —	— —	—	— —	—	—	—	0 *0*
total	4 *5*	0 *5*	*9*	4 *8*	*4*	*3*	*1*	8 *35*
JUNE 6								
400– 600	—	—	7	2	2	1	2	13
600– 800	4	4	8	10	6	7	10	49
800–1000	10	6	9	8	10	7	8	58
1000–1200	1	1	2	1	1	2	1	9
1200–1400	—	—	—	1	3	—	—	4
1400–1600	—	—	—	—	—	—	—	0
1600–1800	1	—	—	—	—	—	—	1
1800–2000	—	—	—	—	—	—	—	0
2000–2200	—	—	—	—	—	—	—	0
total	16	11	26	22	22	17	21	135

JUNE 8	stake	75mW.	175mW.	225mW.	275mW.	325mW.	375mW.	total
400– 600	—	2		1				3
600– 800	11	6		8				25
800–1000	8	5		10				23
1200–1400	6	—		2				8
1400–1600	—	—		—				0
1600–1800	—	—		—				0
1800–2000	—	—		—				0
2000–2200	—	—		—				0
total	25	13		21				59

JUNE 15	stake	75mW.	175mW.	225mW.	275mW.	325mW.	375mW.	total
400– 600	—	1	1	7	—	—	—	9
600– 800	2	1	1	21	2	1	1	29
800–1000	10	4	16	52	3	5	3	93
1000–1200	3	1	11	9	3	3	—	30
1200–1400	2	—	5	9	4	2	1	23
1400–1600	1	—	4	10	—	—	3	18
1600–1800	—	—	—	2	—	—	3	5
1800–2000	1	1	1	2	2	3	3	13
2000–2200	—	—	—	—	1	1	2	4
total	19	8	39	112	15	15	16	224

JUNE 28	stake	75mW.	175mW.	225mW.	275mW.	325mW.	375mW.	total
400– 600	2	1	3	2	1	5	—	14
600– 800	2	—	5	1	3	2	1	14
800–1000	5	2	12	3	6	2	1	31
1000–1200	4	—	3	2	1	—	—	10
1200–1400	2	1	5	5	7	7	1	28
1400–1600	7	2	2	7	7	7	1	33
1600–1800	2	—	—	2	1	4	1	10
1800–2000	2	1	1	4	2	1	1	12
2000–2200	1	1	4	7	3	—	2	18
2200–2400	—	—	1	1	1	—	1	4
2500	1	—	—	—	—	—	—	1
3000	—	—	—	1	—	1	—	2
5000	—	—	—	—	—	—	—	0
7000	—	—	—	—	—	—	—	0
total	28	8	36	35	32	29	9	177

JULY 13

400– 600	—	—	—	—	3	—	—	—	1	*1*	—	—	—	—	4	*1*
600– 800	2	—	1	—	6	*2*	9	*1*	1	—	—	*4*	—	—	19	*7*
800–1000	4	—	2	*2*	8	*3*	12	*3*	3	*1*	2	—	—	*1*	31	*10*
1000–1200	—	—	1	*1*	5	*2*	17	*4*	1	*1*	2	*2*	—	—	26	*10*
1200–1400	1	*1*	2	*1*	1	—	5	*1*	—	—	1	*1*	—	*1*	10	*5*
1400–1600	—	—	1	*2*	1	—	5	*1*	—	—	1	*2*	—	—	8	*5*
1600–1800	—	—	—	—	—	*1*	—	*1*	—	—	—	—	—	*1*	0	*3*
1800–2000	—	—	—	—	—	—	—	*1*	—	*1*	1	—	—	—	1	*2*
2000–2200	—	—	—	*1*	—	—	—	*1*	—	—	—	*1*	—	—	0	*3*
2200–2400	—	—	—	—	—	—	—	—	—	—	—	*2*	—	*1*	0	*3*
2500	—	—	—	—	—	—	—	—	—	—	—	*1*	—	—	0	*1*
3000	—	—	—	—	—	—	—	—	—	—	—	*1*	—	—	0	*1*
5000	—	—	—	—	—	—	—	—	—	—	—	—	—	*1*	0	*1*
7000	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	*0*
total	7	*1*	7	*7*	24	*8*	48	*14*	6	*3*	7	*14*	0	*6*	99	*53*

JULY 20	stake	75mW.	175mW.	225mW.	275mW,	325mW.	375mW.	total
400– 600	2	1	1	1	1	2	—	8
600– 800	—	—	1	1	—	4	—	6
800–1000	1	—	2	3	2	4	—	12
1000–1200	—	2	2	3	1	1	—	9
1200–1400	—	—	2	1	1	—	1	5
1400–1600	—	1	2	1	—	1	—	5
1600–1800	—	—	—	1	—	—	—	1
1800–2000	—	—	—	1	—	—	—	1
2000–2200	—	—	—	—	—	—	—	0
2200–2400	—	1	—	—	—	—	—	1
2500	—	—	—	—	—	—	—	0
3000	—	—	2	—	—	—	—	2
5000	—	—	—	—	—	—	1	1
7000	—	—	—	—	1	—	—	1
total	3	5	12	12	6	12	2	52

JULY 21

400– 600	2	—	1	1	1	—	—	5
600– 800	1	1	—	1	—	2	—	5
800–1000	—	1	—	1	2	2	—	6
1000–1200	1	1	1	2	—	1	—	6
1200–1400	—	—	—	—	—	—	—	0
1400–1600	—	—	1	—	—	—	—	1
1600–1800	1	—	—	—	—	—	—	1
1800–2000	—	—	1	—	1	—	—	2
2000–2200	—	—	—	—	—	—	—	0
2200–2400	—	—	—	—	—	—	—	0
2500	—	—	—	—	—	—	—	0
4500	—	—	—	—	—	—	—	0
6500	—	—	—	—	—	—	—	0
6900	—	—	—	—	—	—	—	0
8900	—	—	—	—	—	—	—	0
total	5	3	4	5	4	5	0	26

JULY 25

400– 600	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	*0*
600– 800	1	*1*	2	*2*	3	—	—	*4*	1	—	1	—	—	—	8	*7*
800–1000	3	*1*	2	*2*	2	*4*	5	*4*	1	*1*	4	*2*	2	—	19	*14*
1000–1200	—	*1*	2	—	2	*1*	1	*5*	—	*2*	1	—	2	*2*	8	*11*
1200–1400	—	—	—	*2*	1	—	1	—	—	—	—	—	—	—	2	*2*
1400–1600	1	—	—	—	—	—	2	*2*	—	—	—	*1*	—	—	3	*3*
1600–1800	—	—	—	—	—	—	1	—	—	*1*	—	—	—	—	1	*1*
1800–2000	—	—	1	—	—	*1*	1	—	—	—	—	—	—	—	2	*1*
2000–2200	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	*0*
2200–2400	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	*0*
2500	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	*0*
4500	—	*1*	—	—	—	*1*	—	—	—	—	—	—	—	—	0	*2*
6500	—	—	—	—	—	—	—	—	—	—	1	*1*	—	—	1	*1*
6900	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	—
8900	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	*0*
total	5	*5*	7	*6*	8	*7*	11	*15*	2	*4*	6	*4*	4	*2*	43	*41*

JULY 26	stake		75mW.		175mW.		225mW.		275mW.		325mW.		375mW.		total	
400– 600	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	0
600– 800	—	2	—	—	—	—	—	1	1	1	—	—	—	1	1	5
800–1000	2	1	3	2	—	1	1	3	3	2	3	3	1	1	13	13
1000–1200	—	—	2	—	—	—	1	4	1	1	—	1	—	—	4	6
1200–1400	—	—	3	1	—	—	2	—	1	—	—	1	—	—	6	2
1400–1600	—	—	—	—	—	—	—	—	1	1	1	—	—	—	2	1
1600–1800	—	—	—	—	—	—	—	—	—	—	—	1	—	1	0	2
1800–2000	—	—	—	—	—	—	—	—	—	—	—	—	—	2	0	2
2000–2200	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	0
2200–2400	—	1	—	—	—	1	—	—	—	—	—	1	—	—	0	3
2500	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	0
4500	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	0
6500	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	0
6900	—	—	—	—	—	—	—	—	—	1	—	—	—	—	0	1
8900	—	—	—	—	—	—	—	—	—	—	—	—	—	1	0	1
total	2	4	8	3	0	3	4	8	7	5	4	7	1	6	26	36

JULY 27																
400– 600	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	0
600– 800	—	1	1	—	—	—	—	2	—	—	—	1	—	1	1	5
800–1000	1	2	1	3	3	—	4	1	2	1	1	3	1	1	13	11
1000–1200	—	—	—	—	—	—	3	1	2	—	—	—	—	—	5	1
1200–1400	—	—	1	—	—	1	—	—	—	1	—	1	—	—	1	3
1400–1600	—	1	—	—	1	—	—	1	—	—	—	—	—	—	1	2
1600–1800	—	—	—	2	—	—	1	—	—	—	1	1	—	—	2	3
1800–2000	—	—	—	—	1	1	—	—	—	1	—	1	—	—	1	3
2400	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	0
3000	—	—	—	—	—	—	—	1	—	1	—	1	—	—	0	3
3300	—	—	—	—	—	—	—	1	—	—	—	—	—	—	0	1
4200	—	—	—	—	—	—	—	1	—	—	—	—	—	—	0	1
5400	—	—	—	—	—	1	—	—	—	—	—	—	—	—	0	1
6500	—	—	—	—	—	—	—	1	—	—	—	—	—	—	0	1
7000	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	1
9600	—	—	—	—	—	—	—	—	—	—	—	—	—	1	0	1
11000	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	0
total	1	4	3	5	5	3	8	9	4	4	2	8	1	3	24	36

JULY 28																
400– 600	1	—	—	1	—	—	—	—	—	—	—	—	—	1	1	2
600– 800	1	1	—	3	1	3	—	1	—	—	—	2	—	—	2	11
800–1000	—	—	1	1	5	2	—	3	—	3	—	1	1	—	7	10
1000–1200	—	—	—	1	—	3	1	—	—	—	—	—	—	—	1	4
1200–1400	—	—	—	—	1	—	2	—	—	—	—	—	—	—	3	0
1400–1600	—	—	—	—	—	4	1	—	—	—	—	—	—	—	1	4
1600–1800	—	1	—	—	—	—	—	—	—	—	—	—	—	—	0	1
1800–2000	—	—	—	—	—	1	—	1	—	1	—	—	—	—	0	3
2400	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	0
3000	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	0
3300	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	0
4200	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	0
5400	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	0
6500	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	0
7000	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	0
9600	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	0
11000	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	0
total	2	2	1	5	7	14	4	5	0	4	0	3	1	2	15	35

AUGUST 4	stake		75mW.		175mW.		225mW.		275mW.		325mW.		375mW.		total	
400– 600	—	—	—	—	—	—	—	*1*	—	—	1	—	—	—	1	*1*
600– 800	—	—	1	*2*	4	*2*	4	*12*	2	*3*	6	*2*	—	—	17	*21*
800–1000	1	—	2	*4*	6	*9*	2	*5*	2	*4*	4	*4*	2	*3*	19	*29*
1000–1200	—	—	1	*1*	4	*2*	3	*3*	—	—	—	*1*	—	—	8	*7*
1200–1400	—	—	3	—	1	*3*	—	*1*	—	—	1	—	—	*1*	5	*5*
1400–1600	1	—	—	*1*	2	—	—	—	—	*1*	1	*1*	—	—	4	*3*
1600–1800	—	—	—	*1*	—	*1*	—	*4*	—	—	—	—	—	*1*	0	*7*
1800–2000	—	—	—	—	—	*2*	—	*1*	—	*1*	—	—	—	—	0	*4*
2400	—	—	—	—	—	—	—	*1*	—	—	—	—	—	—	0	*1*
3000	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	*0*
3300	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	*0*
4200	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	*0*
5400	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	*0*
6500	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	*0*
7000	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1	*0*
9600	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	*0*
11000	—	—	—	—	—	—	—	—	—	—	—	—	—	*1*	0	*1*
total	2	*0*	7	*9*	17	*19*	9	*29*	4	*9*	13	*8*	2	*6*	54	*80*

From these data it follows that especially in June large numbers of spat settled on the cleared plots. The number and size of *Cardium* spat found after inspections *within 2 days* are given in table II (this table has been derived from table I, the data of all plots having been taken together).

TABLE II

Date	Total number of *Cardium*	400–600 μ	600–800 μ	800–1000 μ	1000–1200 μ	1200–1400 μ	1400–2000 μ
31-5 — 1-6 . . .	8	2	4	2	—	—	—
6-6 — 8-6 . .	59	3	25	23	8	—	—
25-7 — 26-7 . .	26	—	1	13	4	6	2
26-7 — 27-7 . .	24	—	1	13	5	1	4
27-7 — 28-7 . .	15	1	2	7	1	3	1
Total	111	6	33	58	18	10	7

From the distribution of cockle spat over the different size classes it appears that spat smaller than 600 μ were rarely found; these specimens are likely to have passed through the meshes of the sieve. But it is quite obvious that transport of spat larger than 600 μ took place regularly and that animals larger than 1,000–2,000 μ were also transported.

This conclusion is confirmed by data obtained from the sampling of the so called "isolated plots" (see p. 320). Such plots were made near the "Oude Vlie" and along the traverse at 225 and 375 m west of this point. The results are given in figure III a and among others in table III a. In figure III a both number (vertically) and size (horizontally)

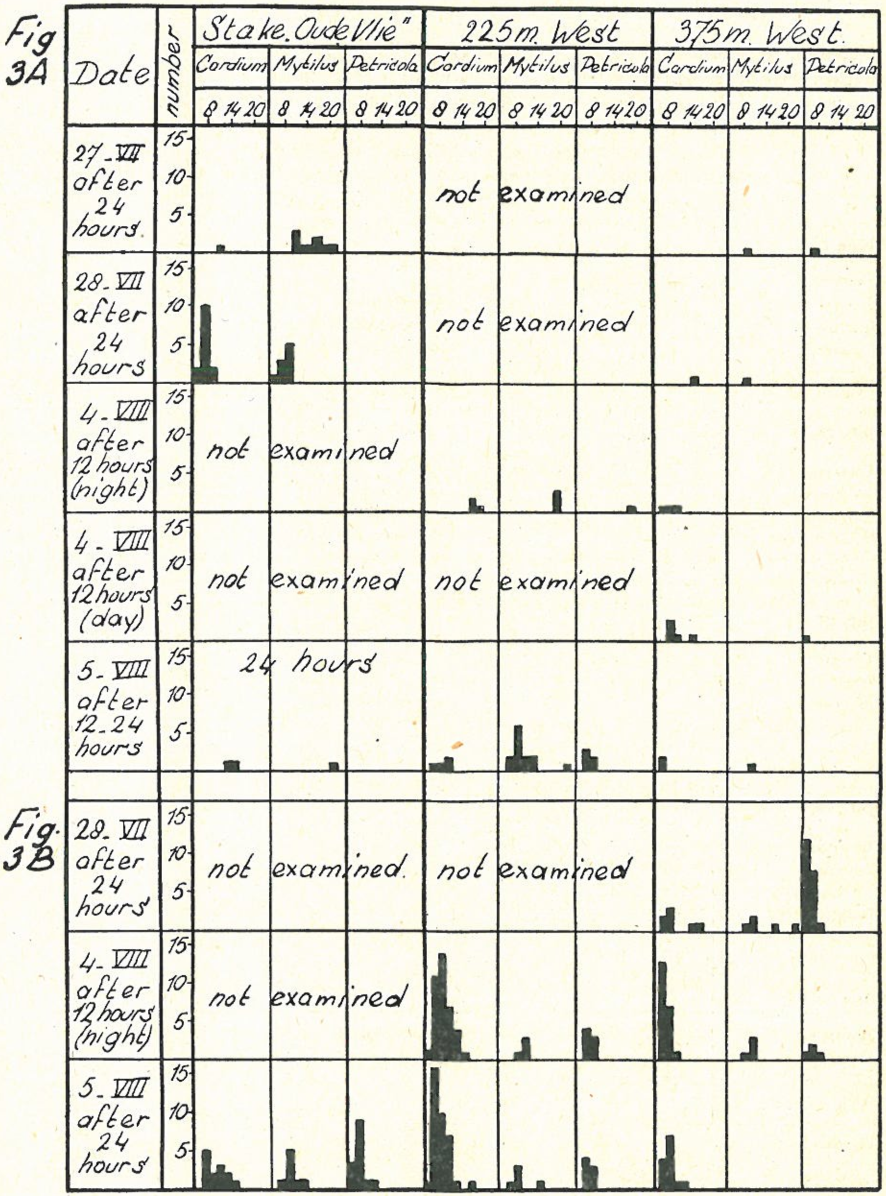


Fig. IIIa. Numbers and sizes of spat settled on isolated plots (for explanation see text). The figures 8, 14, and 20 below the bivalve names denote sizes of 800, 1400, and 2000 μ.

Fig. IIIb. Numbers and sizes of spat settled on jute (60 × 90 cm) (for explanation see text). Sizes of spat as in fig. IIIa.

TABLE IIIa

Numbers of *Cardium* spat of different sizes found on previously cleared plots inspected within 24 hours, compared with those on untouched plots. The figures in the last column indicate the numbers of plots of 20 dm² sampled.

	400–600 μ	600–800 μ	800–1000 μ	1000–1200 μ	1200–1400 μ	1400–1600 μ	1600–1800 μ	1800–2000 μ	2000–4000 μ	4000–8000 μ	9600 μ	11000 μ	Number of plots examined
June 1													
Traverse	2	4	2	—	—	—	—	—	—	—	—	—	3
Screens							not examined						
Jute pieces							not examined						
Isolated plots							not examined						
Compar. plots	8	17	8	1	2	—	—	—	—	—	—	—	7
July 26													
Traverse	—	1	13	4	6	2	—	—	—	—	—	—	7
Screens							not examined						
Jute pieces							not examined						
Isolated plots							not examined						
Compar. plots	—	5	13	6	2	1	2	2	3	1	1	—	7
July 27													
Traverse	—	1	13	5	1	1	2	1	—	—	—	—	7
Screens	4	7	8	4	1	1	3	—	—	—	—	—	14
Jute pieces							not examined						
Isolated plots	—	—	—	1	—	—	—	—	—	—	—	—	2
Compar. plots	—	4	11	5	4	3	3	3	6	3	—	—	10
July 28													
Traverse	1	2	7	1	3	1	—	—	—	—	—	—	7
Screens	14	28	14	2	2	2	1	—	—	—	—	—	14
Jute pieces	—	2	3	—	—	1	1	—	—	—	—	—	1
Isolated plots	2	10	2	—	—	1	—	—	—	—	—	—	2
Compar. plots	1	12	10	4	—	6	1	5	—	—	1	—	10
August 4													
Traverse							not examined						
Screens							not examined						
Jute pieces	1	24	21	8	4	1	—	—	—	—	—	—	3
Isolated plots	—	1	4	2	—	1	2	1	—	—	—	—	3
Compar. plots	1	21	29	7	5	3	7	4	1	1	—	1	7
August 5													
Traverse							not examined						
Screens							not examined						
Jute pieces	1	25	19	11	4	1	1	—	—	—	—	—	3
Isolated plots	—	3	1	2	1	1	—	—	—	—	—	—	3
Compar. plots							same as August 4						

TABLE IIIb

Total numbers of spat of different sizes found on all cleared and comparison plots examined.

Total of spat found on :	400–600 μ	600–800 μ	800–1000 μ	1000–1200 μ	1200–1400 μ	1400–1600 μ	1600–1800 μ	1800–2000 μ	2000–4000 μ	4000–8000 μ	9600 μ	11000 μ	Number of plots examined
Cleared plots	25	108	107	40	22	13	10	2	—	—	—	—	69
Compar. plots	10	59	71	23	13	13	13	14	10	5	2	1	41

are given for 3 species of bivalves, viz. *Cardium edule*, *Mytilus edulis* and *Petricola pholadiformis*.

From this it is clear that sometimes after only 12 hours relatively large numbers of animals had settled down on these plots. Their size varied from 400 to 800 μ.

A similar result was obtained for the spat on the pieces of jute (figure IIIb and table IIIa). The jute had been spread out near the "Oude Vlie" and at distances 225 and 375 m to the west. Again, it is obvious that within a short time (12–24 hours) large numbers of spat had settled down on this substratum. The quantities found here cannot be compared with those on other plots (jute 54 dm^2 and normal plot 20 dm^2). Besides, jute as substratum cannot be compared with sand, as its hairy surface may retain the spat. However, this experiment was not made to reproduce normal conditions, but to show that transport takes place, and it is clear that this transport is, biologically, important.

Eventually, transport of young animals was shown to occur by means of experiments in which screens were used (see p. 320). These screens were placed near the "Oude Vlie" and at a point 375 m to the west (figure IV and table IIIa). In fig. IV the numbers of spat of 5 species of bivalves are represented. Samples were taken on the screen plots (on both sides of the screens) and on plots of the same size some distance away from the screens (so that the plots were not influenced by the latter), both being sampled within 24 hours. The size of spat found on the screen plots is given in table IIIa.

From these data it appears again that transport of young bivalves took place regularly and that *Cardium* was transported up to a size of 1,600 μ. At the same time it follows from these figures that usually more spat are found on the screen plots than on the comparison plots. This is caused by the current shadow near the screens, which enables the spat to accumulate there.

It is apparent from all data mentioned so far that transport of young spat must be considerable.

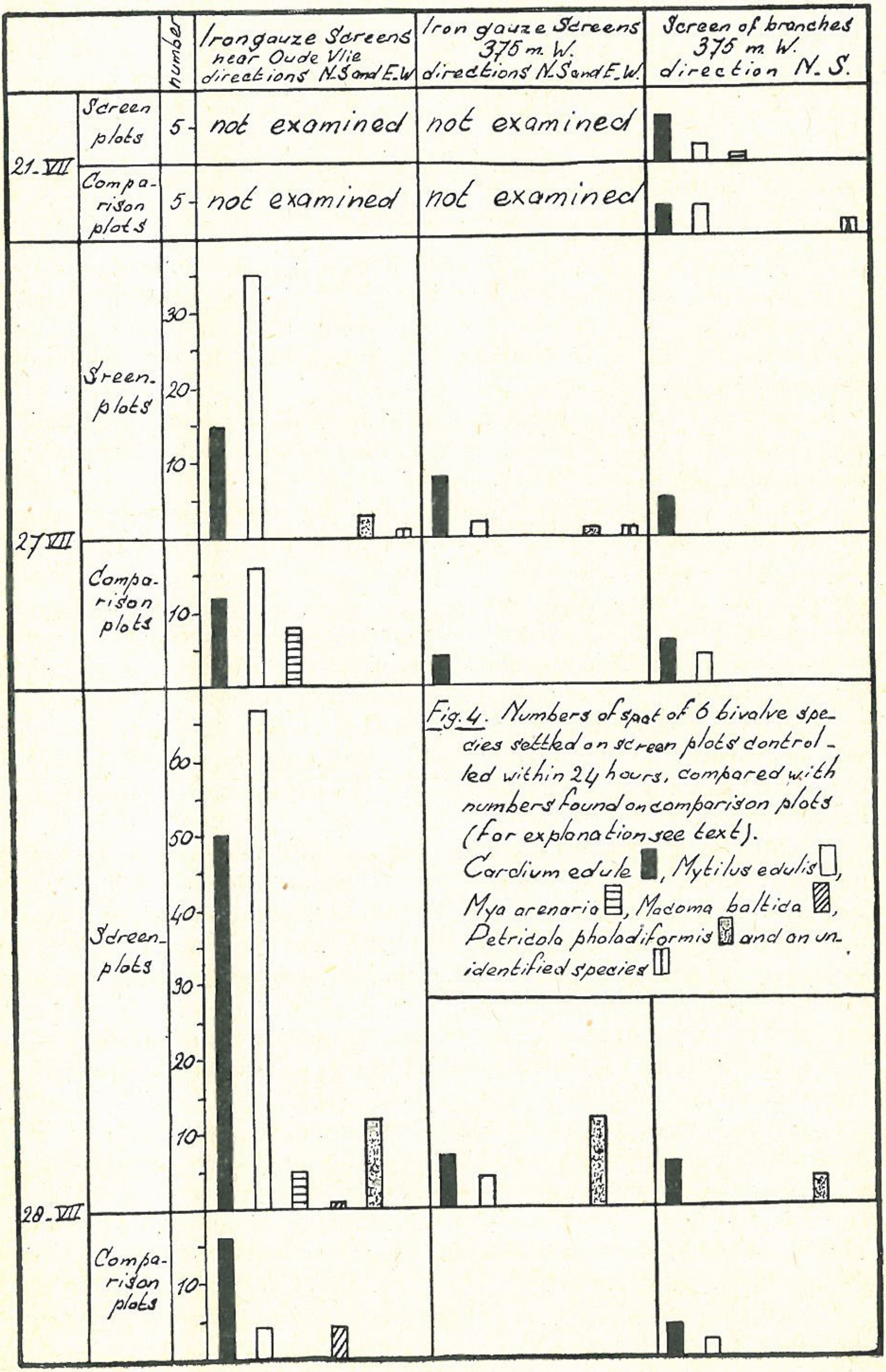


Fig. 4. Numbers of spat of 6 bivalve species settled on screen plots controlled within 24 hours, compared with numbers found on comparison plots (For explanation see text). Cardium edule ▇, Mytilus edulis ▢, Mya arenaria ▤, Macoma baltica ▨, Petricola pholadiformis ▩ and an unidentified species ▥

2. TRANSPORT AND SIZE

All observations have shown that young *Cardium* spat, up to a long time after metamorphosis, are being transported by the current. Now, it is worth while to know at what size the young animals are no longer transported. It was possible to decide this by comparing the sizes of animals found on the regularly cleared plots (so called "transport plots") and those found on places never cleared before ("Comparison plots"), where the young spat had time to grow after settling. Such comparison plots were examined along the traverse (table I, italics) on June 1 and on July 26, 27, and 28; near the screens they were examined on July 21, 27, and 28 (figure IV).

In table IIIa the number and size of spat found on transport plots cleared within 24 hours are given, together with the number and size of the animals found on the comparison plots. The data of the transport plots are obtained from plots along the traverse, near the screens, and from the isolated plots and pieces of jute. The figures in the last column indicate the number of plots of 20 dm^2 inspected at the different places.

In table IIIb the numbers and sizes of all animals found on the transport plots are compared with those of the spat present on the comparison plots. The figures in the last column indicate that a total of 69 transport plots and 41 comparison plots were examined.

In the first place, it appears that on the comparison plots, where the population was able to accumulate up to the day of sampling, we seldom found more spat than on the transport plots. Apparently, large numbers of spat disappear regularly from both transport and comparison plots. This disappearance will have been caused partly by mortality and partly by transportation to places elsewhere. The important rôle of mortality is shown by the decrease in numbers in the course of the season (figure V). Although more spat is being reproduced regularly, the quantity does not increase. In previous years it has also been evident that mortality has a great influence on the *Cardium* population (KREGER, 1940, data Zoological Station, unpublished). During one single day, however, only a few animals will disappear as a consequence of mortality, so that the great disappearence of spat during that time must have been caused mainly in another way: there is a constant supply and removal of spat.

The extent of this transport can be expressed by a certain measure, the rate of transport. We can specify this rate as the ratio of the number of animals found within a certain time on a transport plot to that found within the same time on a comparison plot. Both plots will contain about the same number of newly settled spat and the surplus on the comparison plots may be considered as a remnant of the population, which had settled previously. It should be realized that the rate of transport found will probably be too low, because each individual may have been replaced several times by another one.

On calculating the rate of transport from the figures of table I one obtains for an area of 20 dm² rates of 0.72 (July 26), 0.66 (July 27), 0.43 (July 28), and 0.68 (August 4).

In the second place, it follows from the figures of table III a and III b, that the largest cockles on the transport plots measured 1,600–1,800 μ. On the whole, only 2 animals of 1,800–2,000 μ were found on these plots. On the comparison plots, however, the largest animals were 3,000–9,000 μ. This difference is so striking, that one cannot but conclude that on the "Zeehondenplaat" young cockles up to 1,800–2,000 μ are transported regularly by the current and that cockles are only able to settle permanently when larger than about 2,000 μ.

Unfortunately, during the months of investigation, the numbers of young *Mya, Macoma* and *Petricola* in our samples were so small that they could not be treated in the same way as the numbers of *Cardium*. *Mya* was sometimes found (on transport plots) measuring 2500 μ. *Macoma* was never found larger than 3,000 μ, and *Petricola* never larger than 1,200 μ. The number of *Mytilus* was comparable with that of *Cardium*. Animals larger than 1,800 μ were very seldom found and they were present in equal numbers on both transport and comparison plots. This indicates that in *Mytilus*, too, transport by the current must be considerable. It further seems to suggest that these animals do not settle permanently on the flats, for we never found animals larger than 2,000 μ attached to sandgrains.

The question now arises as to why *Cardium* on the "Zeehondenplaat" is no longer transported by the current on reaching sizes of 1,800 μ and larger. There are two possible answers to this question:

1. The current running over the flats might be too weak to transport animals larger than 1,800 μ.
2. Animals larger than 1,800 μ might be unaffected by the current, because they are capable of burrowing deeply into the sand.

1. With regard to the first possibility an attempt was made to test the hypothesis by comparing the rates of sinking of young cockles and of sandgrains in seawater. Once the maximum grain size of the sand transported by a certain current over the flat is known, it becomes deducible at what size young cockles can still be transported by the current.

On July 20, a day without wind, N. Pijl determined the quantity of sand transported by the current 40 cm above the bottom during both ebb and flood. The quantities varied from 0.3 to 5.1 gr per litre. The median grain size of this sand was 1,00 μ, while a large number of grains of 200 μ and even 250 μ were found in ebb and flood samples.

The rate of sinking of live, young *Cardium* was determined after the method described by Gry (1941). The determination was carried out at a temperature of 20–23 °C, and the results are given in table IV.

There is no close relationship between the sinking rates of cockle spat and sand, and this will have to be ascribed to the behaviour of the animals on falling. They may have their shells open as well as closed and this will have a great influence on their sinking rate.

In spite of the relatively poor correlation, it still follows from the figures that 40 cm above the bottom animals of about 800 μ (corresponding with sandgrains of about 100 μ) can easily be transported, and as numerous grains of 200–250 μ were also found, it is likely that cockles of 1,100–1,600 μ may have been transported at this level. Close to the bottom animals of this size will most certainly have been transported. They can be compared in size with relatively coarse sand.

TABLE IV

Sizes of *Cardium* and sandgrains with the same sinking rates

Temp.	Median size of *Cardium*	Median size of sandgrains
20° C	2000 μ	320 μ
20° C	1900 μ	215 μ
20° C	1600 μ	230 μ
23° C	1140 μ	253 μ
23° C	1110 μ	145 μ
23° C	760 μ	94 μ
23° C	720 μ	60 μ

The result of this experiment is in full agreement with that obtained from table IVa and IVb, viz., that on the "Zeehondenplaat" the current is able to transport *Cardium* spat up to a size of 1,800–2,000 μ.

2. No observations were made with regard to the question whether or not young cockles of a certain size can burrow so deeply into the sand that they are no longer removed by the current. However, very young cockles will almost certainly be washed out. They will always be able to burrow during periods when the water is still, but when the current increases the uppermost sandlayer will be stirred up and very small cockles will be easily washed away.

The same does not hold for adult cockles, which are far more deeply embedded and thus will not be carried off, except, perhaps, in very strong currents or in areas greatly influenced by wind. Without further investigation it is impossible to give a critical current velocity, at which cockles of a certain size can no longer be washed out and transported, but the fact that so many young cockles up to a size of 1,800–2,000 μ are regularly being transported indicates that animals of this size can be removed by the current.

3. TRANSPORT, CURRENT VELOCITY, AND PLACE OF SETTLING

As already mentioned in the Introduction, KREGER supposed the presence of large amounts of cockles in certain places to be caused by 3 factors. The highest parts of the flats would receive little spat because the latter would have remained behind on the lower parts, covered earlier. Moreover, the smaller head of water and the shorter time of submersion over the higher parts would cause a smaller spatfall there. Therefore, the spat would be accumulated on the lower parts of the flats.

In our investigation a great difference in spat population was noticed when comparing the shallow creek (175–225 m west of the "Oude Vlie") with the higher parts of the flat (375 m west). Figure II represents the relative height of the flat along the traverse and also gives the median grainsize of the sand at each of the places examined. It can be seen from this figure – and also from fig. I – that there is a low ridge along the "Oude Vlie" and a shallow creek (being hardly more than a subsidence) behind it. The slope of the creek is steeper east than west. Further westward the flat slopes upwards gradually. The grainsize of the sand is coarser on the ridge than near the "Oude Vlie" or in the creek. Still further west the sand becomes even coarser.

It follows from figure II that the largest amount of spat transported was found in the above mentioned creek and along the border of the "Oude Vlie", whereas the smallest quantities occurred on the ridge and on the highest part. The same holds, in principle, for all other species of bivalves investigated. *Mya* shows a distinct decrease in quantity to the west and a very pronounced increase in number along the "Oude Vlie". It seems justified, therefore, to assume that the presence of large quantities of transported spat in the creek and along the border of the "Oude Vlie" represent the usual phenomenon over this flat. Unfortunately, the quantity of *Cardium* spat close to the "Oude Vlie" could not be determined because of the presence of large amounts of detritus, which made analysis of the samples impossible.

In the case of the pieces of jute and the isolated plots (fig. IIIa and IIIb) there are also indications that the largest numbers of spat were found in the creek. This supports the previous hypothesis.

It is necessary to state once again that these data exclusively concern *transported* animals, which had been metamorphosed some time previously. They do not refer to the *direct spatfall* of newly metamorphosed specimens. It is therefore still unknown whether or not the border of the "Oude Vlie" and the creek are the most likely places to receive *direct* spatfall.

On comparing places with the most prolific settling of transported spat with places of the greatest abundance of adult cockles (born in 1947 and indicated with black columns in figure II), it must be stated that the adult animals are most numerous in the creek and along the "Oude Vlie" (about 30 m west of the stake not indicated in figure II, where their number was 90 on 20 dm²), and that their numbers decrease westward.

The largest quantities of adult cockles are present, however, eastward of the places where the spat are most numerous. The number of adults on the ridge is small and does not increase very much on the outer slope near the stake, where the spat do increase. The adult animals are most numerous at low tide mark of the 'Oude Vlie' (30 m west of the stake), where the quantity of spat could not be determined owing to the presence of much detritus.[1]

On considering the results of these experiments it must be concluded that the creek and the border of the "Oude Vlie" were not only favourable for the young cockles in 1947, but also for transported spat in 1950. Conditions for settling, therefore, appear to be very favourable there.

When we try to account for the accumulation of large numbers of animals in certain places, it seems justifiable to look for a relation between the number of animals and the current velocity. It has been observed that frequently animals up to 2,000 μ are transported by the currents, so that current velocities must be of great importance. The rate of sinking of young cockles in comparison with sand grains also supports this belief. Therefore, it was originally thought that the settling of large numbers of transported animals in certain places would directly depend on the low transporting capacity of the current at those places.

If it is true that the transport of *Cardium* spat may, to a certain extent, be compared with that of sand, it is important to bring the grainsize distribution under consideration. In the drawing up of the following considerations, POSTMA has kindly assisted me.

Current and wind are the two most important factors that stir up the water. The finest sand and mud are found in places where the current is weak and where at the same time the wind gets little hold on the sea bed. Such circumstances are found in quiet places under the lee of land and often at the transition lines between the channels (fairways) and the flats, but not on the flats themselves. There, the

[1] From investigations of the Zoological Station in the years prior to 1950 it is known that in those years the original distribution of young cockles in 1947 was about the same as that found in the present investigation. KRISTENSEN, who carried out the former investigations, supposes that in the winter of 1949–'50 the then two years old animals were carried away towards the east by the very strong west winds. A similar displacement eastward of old animals along other traverses was observed earlier by the Zoological Station.

current is weak enough to deposit fine materials, but the wind has (through the waves) too much grip upon the flat.

From this point of view the grainsize distribution of the sand on and near the "Zeehondenplaat" (figure II) must be considered. On the bottom of the "Oude Vlie" coarse sand is found (median grainsize about 250 μ). This can be understood, because in the "Oude Vlie" strong currents are running. Along the border of the "Oude Vlie" the sand is fine (about 60 μ), but from this place westwards the grainsize increases gradually, except in the creek. This increase goes hand in hand with a decrease in current velocity. It is very likely, however, that the influence of the wind must be held responsible for the greater coarseness of the sand on the higher parts of the flat.

Judging from the current velocities measured it looks as if in the creek a small grainsize is correlated with a greater current velocity. Currents, however, were measured at the surface, and it is probable that in the creek the relationship between surface and bottom currents is not the same as on the flats. During the greater part of the tide the surface water over the creek runs nearly perpendicular to the direction of the latter. Close to the bottom, however, the water may not be able to develop the same velocity as at the surface, because it is caught between the creek slopes. Only when the surrounding area has run dry the water follows the direction of the creek; then, however, currents have become weak. The current, therefore, must have little transporting capacity along the bottom. This supposition also accounts for the presence in the creek of much detritus in the form of small pieces of peat, etc. This material is quite easily transported and can, therefore, only be expected in places where currents are weak. The creek thus forms a kind of accumulation basin for all kinds of easily transportable materials. The presence of large quantities of detritus along the border of the "Oude Vlie" can be explained in the same way.

In view of the preceding discussion it can be understood why such large quantities of young cockles and other bivalves are present in the creek and along the border of the "Oude Vlie". Their presence is caused by the current, which, on losing velocity, drops the young bivalves it has carried from elsewhere. The experiments with the screens also showed that current shadows may cause an accumulation of spat (see p. 329).

There is, however, a second possibility which might explain the presence of large numbers of young cockles in certain places, viz., the *direct spatfall* immediately after metamorphosis. Here we must return to KREGER's point of view. He supposed that more recently metamorphosed spat would fall on places which were deeper than their immediate surroundings (see p. 334). This is still an unproved supposition, but it might be true. In that case, the large numbers of spat in the creek and along the "Oude Vlie" would mainly be due to the fact that these animals had settled there directly after metamorphosis. The presence of so much spat on our cleared transport plots could then also be explained by assuming that these specimens were carried in from the immediate surroundings. Following this train of thought the small numbers of spat on the highest parts of the flats might be due to the fact that but few animals fell there immediately after metamorphosis. The transporting capacity of the current, then, would not be the main cause for the presence of much spat in a certain place, but rather the direct spatfall of newly metamorphosed animals. To reach a definite conclusion on this question the distances should be known over which the animals found in the samples of the cleared plots have been transported.

Unfortunately, the data collected during this investigation are not quite sufficient to decide the matter. Possibly, the direct spatfall plays a certain rôle in the distribution of spat over the flats. On the other hand, transportation by the currents has been shown to be of great importance for the ultimate distribution of cockles over the flats.

It would not be correct to conclude from the foregoing that large numbers of cockles can only be expected in fine sand. Several investigators have already pointed out that there is no correlation between the actual grainsize of the sand and the number of cockles present (KREGER, 1940; WOHLENBERG, 1937; SMIDT, 1951). They often found large numbers of cockles both in very coarse and very fine sand. This seems to contradict the foregoing, but it must be borne in mind that the grainsize of the sand in the present investigation was only used as a *relative* measure, to indicate places with stronger or weaker currents or places where the wind has more or less influence upon the flats. Sand was used as a measure for the transporting capacity of the currents. It is clear that a correlation between the grainsize of the sand and the numbers of cockles present need not be expected.

In using fine sand as an indication for weak currents or little wind influence it must also be realized that the presence of many cockles might be the cause of an accumulation of fine sand. The animals are producing large quantities of faeces and pseudofaeces, which in the long run will form a layer over the cockles. It is therefore necessary, when using the grainsize of the sand as a measure for the current velocity and wind influence, to take this factor into account.

4. DURATION OF TRANSPORT

An attempt was made to get an insight into the rate of growth of cockles by measuring the maximum size of the animals on different days in the course of the season. For this purpose data from plots which had never been cleared before (comparison plots) were used, because only here could animals be expected, which had been able to grow undisturbed. The data have been separated for the lower and higher parts of the flat, because it was known that the growth rate of older cockles on these places was different and, this might hold for the young animals also.

At the beginning of the season the individuals are rather uniform in size, and while the smallest animals are regularly being supplied in the course of the season by settling of new young spat, the shifting to the right of the largest sizes in the length-frequency distribution curve gives a possibility for studying growth. The estimations of the rate were carried out on the basis of daily compound interest. Unfortunately, our data are rather limited in this respect.

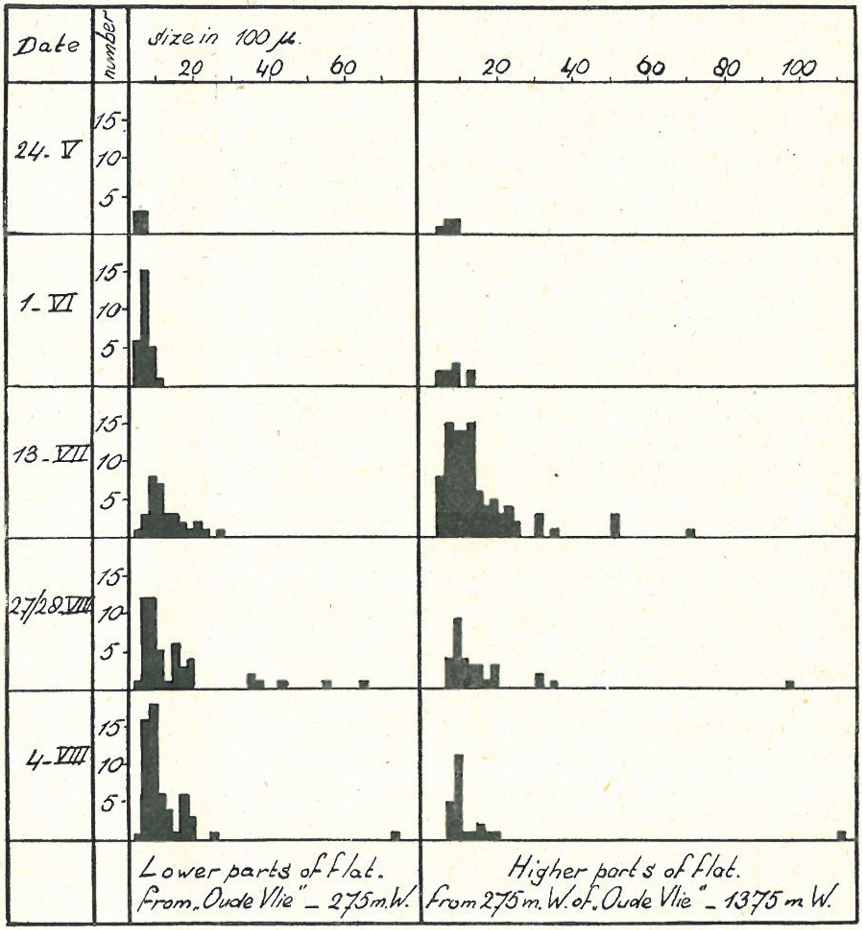


Fig. V. Length frequency distribution of young *Cardium* at different dates on lower and higher parts of the flat. Left: lower parts of the flats between Oude Vlie and 275 m West. Right: higher parts between 275 and 1375 m West. Data refer to plots not previously cleared, compare text.

Later in the season mortality, and also the individual variation in growth, cause the largest animals to be rarely present. The estimation of the rate of growth has, therefore, become less accurate for the older animals (table V and figure V).

These figures show that the young cockles grow fastest on the highest parts of the flat. A similar result was obtained when the annual growth rings and the maximum size of adult cockles were measured. KREGER (1940) has already recorded this phenomenon and given an explanation of it.

TABLE V

		Lower parts of the flat			Higher parts of the flat		
Date	Number of days	Max. size in micr.	Growth in micr.	Growth/day in % of initial size	Max. size in micr.	Growth in micr.	Growth/day in % of initial size
24-5		800			1000		
1-6	8	1200	400	5.2	1400	400	4.3
13-7	43	2600	1400	1.8	7200	5800	4.2
28-7	15	6500	3900	6.3	9600	2400	1.6
4-8	6	7200	700	1.7	11000	1400	2.3

Our data are certainly not sufficient as a reliable source for growth measurements of young cockles of different ages, but they do give an impression of the growth rate. It follows from table V that the length of animals of 300–800 μ most certainly does not increase more than 5 % a day, so that a young cockle of 300 μ must need 10 days to reach a length of 500 μ and at least 20 days to reach 800 μ. SMIDT (1951) gives about the same rate of growth for cockles in the Danish Waddensea. In other words, a large part of the young cockle spat is being transported here and there for weeks, before being able to burrow definitely. Certainly, spat of 1800 μ may have been transported for more than one month. Only very quiet places may form an exception to this rule.

5. TIME OF SPATFALL

The graphs of figure VI represent the average numbers of spat of *Cardium* and other species of bivalves for 2 week-periods between May 15 and August 15. The height of the columns gives the average number of spat falling on 1 plot of 20 dm² per day.

It follows from these data that the largest numbers of *Cardium* and *Mya* spat (over 600 μ) were present during the second half of June. *Smidt* (1951) found the same for *Cardium* in the Danish Waddensea. The largest numbers of *Mytilus* were present from June 15 to July 15, while *Macoma* showed its maximum shortly before this period. For *Petricola* few data are available, so that nothing reliable can be said in this connection. After the middle of June the quantity of *Mya* spat decreases more rapidly than that of *Cardium;* the quantity of *Mytilus* spat decreases rapidly after the middle of July.

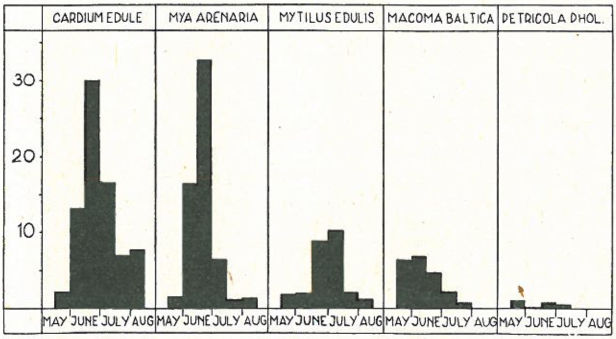


Fig. VI. Average numbers of spat fallen on one plot of 20 dm² per day within periods of 2 weeks between May 15 and August 15, 1950.

Most *Cardium* measured 800–1600 μ during the second half of June. According to previous calculations (see page 339) these animals were at least 20–30 days old, so that the greatest spatfall of newly metamorphosed *Cardium* probably commenced in the second half of May.

On June 2 only a few spat measuring 800 μ were present, and on August 5 much spat still remained. Thus, the first spatfall of *Cardium* must have taken place during the first half of May and the fall was not completed by the second half of June. It is clear that the period of spatfall of *Cardium* in 1950 covered at least 3 months.

IV. CONCLUSIONS

In considering the most important results of this investigation a negative statement must first be made, viz., that it is still unknown as to whether or not newly metamorphosed *Cardium* show any preference for certain places to settle. My attempts to collect the youngest spat were fruitless. KREGER's supposition, that recently metamorphosed animals would come to rest on the lowest parts of the flats, is therefore still unproved.

It could be shown, however, that spat of 600–1800 μ are being transported regularly by the current in large quantities. Strong indications were obtained that these animals, whose rate of fall can be compared with that of sand of 100–250 μ, are deposited especially on places where currents are weak and where winds get little hold on the flat.

In the area investigated this was the case on the lower parts of the flat, which formed an accumulation basin for all kinds of easily transportable material. If KREGER's supposition, that more spat probably fall on the lower than on the higher parts of the flats, would appear to be true, the numbers of such spat would at any rate be much increased by the supply of somewhat older animals from elsewhere by the current. From lack of sufficient data it is, however, impossible to weigh the relative importance of these two phenomena.

It is clear that in the area where the work was carried out the young cockle does not obtain hold directly after metamorphosis (except perhaps in places with a very weak current or with little wind influence), but is being transported for a considerable length of time. Everything points to the fact that the definite settling of spat only takes place when the animals have reached a size of 1000 μ or more. Investigations of SMIDT (1951) appear to show that young cockles are able to settle permanently directly after metamorphosis. It must therefore be assumed that the strong currents in the western Waddensea are the main cause of the long transportation of spat.

V. SUMMARY

Observations and experiments were carried out in the western Waddensea in the summer of 1950 in order to determine the factors governing the settling of spat of *Cardium edule* and other bivalves.

It appeared that young cockles were being transported by the currents for a long time after metamorphosis, until they had reached a size of 1800–2000 μ. It could be calculated from growth rate data that such animals must be at least 4 weeks old.

Strong indications were obtained that most animals are accumulated in quiet places, where currents are not sufficiently strong to carry them away. On the flats investigated these quiet places were characterized by a finer grainsize of the sand compared with that of the surroundings and by the accumulation of all kinds of easily transportable material.

Spatfall of *Cardium edule* took place from the first half of May till, at least, the second half of July. The greatest spatfall took place during the end of May.

VI. LITERATURE

GRY, H., 1931: An apparatus for mechanical micro-analysis of sand. Medd. fra Dansk Geol. Forening København, **10**, 17.

KREGER, D., 1940: On the ecology of *Cardium edule* L. Arch. Néerl. de Zool., **4**, 157–200.

SMIDT, E. L. B., 1951: Animal production in the Danish Waddensea. Medd. Komm. Danm. Fisk.-og Havunders., Serie Fisk., **11**, 1–151.
THORSON, G., 1946: Reproduction and larval development of Danish marine bottom invertebrates. Medd. Komm. Danm. Fisk.-og Havunders., Serie Plankton, **4**, 1–523.
TRASK, P. D., 1939: Recent marine sediments. Tulsa, Amer. Ass. Petrol. Geol.
VAN VEEN, J., 1936: Onderzoekingen in de Hoofden. Diss. Leiden.
WOHLENBERG, E., 1937: Die Wattenmeer-Lebensgemeinschaften im Königshafen von Sylt. Helg. Wiss. Meeresunters., 5, 1–92.