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Quantitative beach research
I. The "left-right-phenomenon": sorting of Lamellibranch valves on sandy beaches

by

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I. INTRODUCTION

During an investigation of the boring activity of *Natica poliana alderi* in July and August 1955 several thousands of valves (with and without a bore hole) were collected from the beach near three places along the Dutch North Sea coast: De Koog on the island

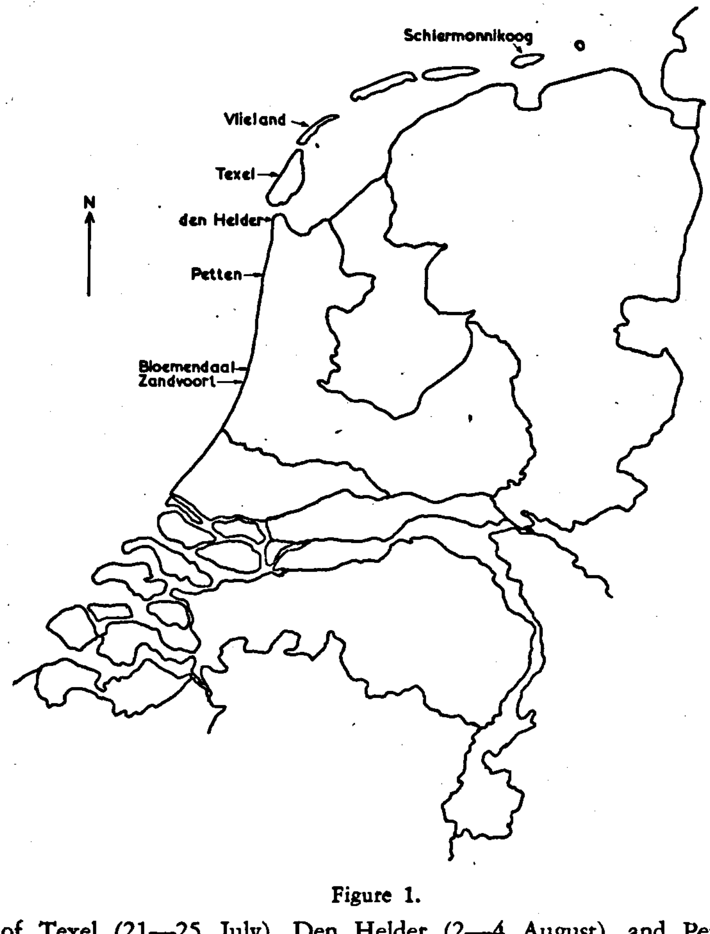


Figure 1.

of Texel (21—25 July), Den Helder (2—4 August), and Petten (6 August) (see fig. 1). These collections were carried out between high and low watermarks. While studying this material we noticed that the ratio between the numbers of left and right valves was different at the three places. Table 1 shows the results.

TABLE 1

The percentages of L- and R-valves of some Lamellibranchs at three places on the Dutch North Sea coast in July-August 1955

	Texel			Den Helder			Petten		
	%L	%R	Total	%L	%R	Total	%L	%R	Total
Sp. subtr.	39.7	60.3	1616	65.3	34.7	1948	52.0	48.0	1681
Sp. solida	44.3	55.7	149	60.7	39.3	56	45.6	54.4	57
M. balthica	47.9	52.1	328	43.7	56.3	213	48.3	51.7	149
D. vittatus	41.0	59.0	178	63.0	37.0	370	46.3	53.7	121

Comparing the percentages of the L- and R-valves of the species *Spisula subtruncata*, *Spisula solida* and *Donax vittatus*, it is evident that at the time of collection R-valves predominated near De Koog on the island of Texel, and L-valves near Den Helder, while near Petten the percentages were almost equal. In the case of *Macoma balthica*, the R-valves were more frequent than the left ones at all these places.

This discrepancy between the numbers of L- and R-valves of Lamellibranchs has often been noted in fossil sediments (RICHTER, 1922, 1924). In recent times this "L-R-phenomenon" has been observed by VAN DER MEULEN (1947) on the so-called "Bosplaat" on the island of Terschelling, where he collected 203 L- and 33 R-valves of various Lamellibranchs (mainly *Cardium edule, C. echinatum,* and *C. crassum*). He supposed that this phenomenon could be explained by a difference in "behaviour" of the asymmetrical L- and R-valves in the movements of waves during ebb and flood.

MARTIN-KAYE (1951) observed the same phenomenon on some beaches on the coast of Trinidad, where he collected valves of *Pitar dione* and of *Arca incongrua.* He writes: "It is thought that the reason may lie in the fact that the right and left valves are, of course, mirror images of one another. Being such they may differ slightly in their response to the forces tending to move them shorewards: the opposite symmetry may favour a slightly different direction of travel in each case" (p. 434).

Both authors, therefore, thought that the *general asymmetry* of the L- and R-valves was the cause of the phenomenon. We shall see that for several species this supposition is almost surely correct.

However, several other explanations are possible. For example:

a. a difference in w e i g h t between the L- and R-valves (cf. *Ostrea edulis*);
b. a difference in s o l i d i t y and thus in f r a g i l i t y between the valves (cf. *Anomia*-species) (compare RICHTER, 1922);
c. a difference between the valves caused by a p r o j e c t i o n f r o m o n e o f t h e v a l v e s, with which this valve can hook in the bottom (e.g. *Mya*-species).

So far as we know no analyses or experiments have been carried out with respect to this L-R-phenomenon, except the observations of RICHTER (1922, 1924) with *Mya arenaria* (see below).

In this publication some observations and experiments which have been carried out on several parts of the Dutch coast will first be discussed. After that an attempt is made to define the phenomenon more exactly, to track the causes, and to make some generalisations.

The author is indebted to Mrs W. S. S. v. D. FEEN-VAN BENTHEM JUTTING (Amsterdam) and Mr P. KAAS (The Hague) for the supply of complete shells; to Dr H. POSTMA and Dr J. VERWEY (Den Helder) for reading the manuscript; to Mr G. THIJSSEN (Amsterdam) who collected near Bloemendaal and also near Falsterbo (Sweden) during an excursion we made for studying bird-migration; and further to the following assistants and biological students who co-operated enthusiastically with the author during our stay on the island of Schiermonnikoog (August 1957): L. J. ANTHEUNISSE, H. H. BOER, Miss M. E. A. v. D. BOSCH, Miss C. M. GAASTERLAND, Miss A. N. GESCHIERE, L. HARTSUYKER, Miss A. JANSEN, A. KESSLER, N. E. KLUNGEL, A. DE LANGE, Miss E. A. MEULEMAN, J. P. OVERDULVE, G. THIJSSEN, R. THIJSSEN, T. A. DE VLIEGER, T. DE VRIES, J. B. VONCK, J. VOS and P. WEDZINGA. Finally the author acknowledges the kind help of Dr. J. EBLING and Dr. F. SEGROVE (Sheffield) in correcting the English text.

II. MORE DETAILS OF THE L-R-PHENOMENON

a. *The extent of the phenomenon*

Table 1 showed that sometimes twice as many valves of the one kind were found as of the other. Later observations demonstrated that the differences can be much more remarkable. Table 2 gives some of the more extreme data.

TABLE 2

Some examples of extreme L-R-sorting

Species	Place	Date	L/R	Total number
Spisula subtruncata	NE-point of Texel	22.7.1957	3.3	124
Donax vittatus	„	„	4.4	65
„	NE-point of Vlieland	24.7.1957	3.3	50
„	Schiermonnikoog (pl. 11)	12.8.1957	8.1	100
„	„ (pl. 14)	„	15.0	64
„	„ (pl. 8)	16.8.1957	8.3	231
Mya arenaria	Falsterbo (Sweden)	23.9.1956	0.09	148

From this table it is clear that the sorting effect can be so intensive that one valve may be as much as 15 times (Schiermonnikoog, pole 14 [1]), 12 August 1957) as numerous as the other.

b. *The inconstancy of the phenomenon*

It must be emphasized that the ratio of the L- and R-valves, which are washed ashore at a given place, is not constant. Table 3 shows some data for collections of *Spisula subtruncata* made on the island of Texel (pl. 20), near Den Helder (pl. 5), and near Bloemendaal (pl. 60).

TABLE 3

Ratio between the numbers of L- and R-valves of *Spisula subtruncata* on Texel (pl. 20), near Den Helder (pl. 5), and near Bloemendaal (pl. 60).

Place	Date	L/R	Total number
Texel	21.7.1955	0.5	417
(pl. 20)	22.7.1955	0.7	141
	23.7.1955	0.5	297
	24.7.1955	0.9	442
	25.7.1955	0.8	319
	17.8.1955	1.1	655
Den Helder	2.8.1955	2.1	331
(pl. 5)	3.8.1955	2.5	757
	4.8.1955	1.5	860
Bloemendaal	26.8.1956	1.2	542
(pl. 60)	27.8.1956	0.9	578
	28.8.1956	1.0	718
	29.8.1956	0.7	781
	30.8.1956	1.1	819

This daily change of the L/R-ratio could always be observed.

c. *Different causes of sorting in different species of Lamellibranchs*

The L-R-phenomenon has a different character in different species of Lamellibranchs. From the foregoing it is already evident that the two species *Spisula subtruncata* and *Donax vittatus* are both sorted to a high degree.

The question arises as to what factor is the cause of this particular sorting effect. In the first place it is possible that there is a difference in weight between the L- and R-valves. To answer this question the weights of the separated valves of complete shells were determined. See table 4.

TABLE 4

Comparison of the weights of the separated valves of complete shells

	L-valve heavier	R-valve heavier	Number of shells
Spisula subtruncata	26	50	76
Donax vittatus	21	14	35
Venus striatula	4	6	10
Macoma balthica	—	62	62

[1]) Along the entire Dutch North Sea coast numbered poles are placed on the beach at intervals of exactly one kilometer.

Excluding for the moment the results for *Macoma balthica*, we get the impression that in the other species there are no consistent differences: in some cases the L-valve, in others the R-valve is the heavier. As each species can show either an L-effect or, at other times an R-effect on the beaches, and as the valves have no remarkable projections and do not show clear differences in fragility, we can suppose that in these species the general asymmetry of the valves is the principal cause of the sorting effect. Later chapters of this publication will support this hypothesis.

In table 5 a preliminary attempt is made to compare some other species with *Spisula subtruncata* and *Donax vittatus*. For that purpose the ratio between the L- and R-valves of some other Lamellibranchs was determined at places where *Spisula* and *Donax* showed a clear L- or a clear R-effect.

TABLE 5

The L-R-phenomenon of some species of Lamellibranchs at places where *Spisula subtruncata* and *Donax vittatus* had a clear left (L) or right (R) effect.
Texel (pl. 20): 3—16.7.1956; Texel (pl. 31 and 32): 22.7.1957; Bloemendaal: 26.8—9.9.1956; Zandvoort: 30.4.1956; Schiermonnikoog: 12—20.8. 1957.

		Effect	L	R	Tot.	L/R
Spisula solida	Texel (pl. 20)	R	602	876	1478	0.7
„	Schiermonnikoog	L	132	68	200	1.9
Mactra corallina	Texel (pl. 20)	R	15	17	32	0.9
„	Schiermonnikoog	L	38	14	52	2.7
Venus striatula	Zandvoort	?	41	57	98	0.7
„	Schiermonnikoog	L	25	17	42	1.5
Macoma balthica	Texel (pl. 20)	R	553	587	1140	0.9
„	Schiermonnikoog	L	1486	1706	3192	0.9
Angulus tenuis	Texel (pl. 20)	R	35	50	85	0.7
„	Schiermonnikoog	L	225	87	312	2.6
Angulus fabula	Texel (pl. 20)	R	12	107	129	0.1
„	Schiermonnikoog	L	41	287	328	0.1
Scrobicularia plana	Texel (pl. 20)	R	45	53	102	0.8
„	Schiermonnikoog	L	18	14	32	1.3
Mytilus edulis	Texel (pl. 20)	R	87	114	201	0.8
„	Schiermonnikoog	L	123	120	243	1.0
Cardium edule	Bloemendaal	R	411	326	737	1.3
„	Schiermonnikoog	R	420	404	724	1.0
„	Bloemendaal	L	246	217	463	1.1
„	Schiermonnikoog	L	674	589	1263	1.1
„	Texel (pl. 31 and 32)	L	132	104	236	1.3

This table demonstrates that the valves of *Spisula solida* behave in the same manner as those of *Spisula subtruncata* and of *Donax vittatus*. The same can be said of *Angulus tenuis*, and, perhaps to a lesser degree, of *Mactra corallina* var. *atlantica* and of *Venus striatula*. The numbers of *Scrobicularia plana* and of *Mytilus edulis* are rather low, but we are left with the impression that the valves of these species are not sorted very much.

The results for *Macoma balthica* and *Angulus fabula* are very remarkable, as (see also table 1) under all circumstances the R-valves are more frequent than the L-ones. It has already been shown (see table 4) that the R-valves of *Macoma balthica* are always heavier than the L-valves. Therefore it is probable that they also have a more solid structure, so that during transport towards the beach and whilst in the surf, they are less likely to be damaged than the more fragile left valves. Hence more R-valves are likely to survive. In principle this does not exclude the possibility that there may subsequently be sorting due to differences in symmetry. In fact, since the L-R-ratio is very constant — Texel (July 1955) 0.9, Texel (July 1956) 0.9, Schiermonnikoog (August 1957) 0.9, Den Helder (July 1955) 0.8, Petten (August 1955) 0.9 — it is probable that little or no sorting occurs.

The same seems to be true of *Angulus fabula*. Possibly the diagonal striations, which are present only on the R-valve, make this valve more solid than the L-one.

The observation on the beach of the Baltic near Falsterbo (Sweden), where, of 148 valves of *Mya arenaria*, only 14 were left ones, shows that the valves of this species can be sorted in a rather extreme manner. Near this beach there are practically no ebb- and flood-currents, while there is only a very slight surf on a faintly rising sea-bottom. This indicates that under such circumstances the very large projection of the L-valve is an obstacle which prevents its washing ashore. (It is interesting that KLÄHN (1932) mentions that the R-valve of *Mya arenaria* is heavier than the L-one.) Most propably we have here an example of sorting due to a p r o j e c t i o n o f o n e o f t h e v a l v e s. RICHTER (1922 and 1924), observed a similar sorting of *Mya*-valves and gave the same explanation.

The observations on *Cardium edule* indicate that the L-valves are usually the more frequent under those conditions when an R-effect is shown bij *Spisula subtruncata* and *Donax vittatus*. As no special research was carried out on this shell on a beach rich in *Cardium*, we are not sure that this suggestion will prove to be correct.

From the foregoing remarks it can be concluded that of the species studied so far, the L-R-phenomenon is shown very clearly by *Spisula subtruncata*, *S. solida*, *Donax vittatus* and *Angulus tenuis*, sorting most probably being due to the general asymmetry of the valves. In *Macoma balthica* and *Angulus fabula*, however, the sorting is due to an entirely different factor, namely the weight and the structure of the valves.

Finally, a possible third sorting-factor was observed with *Mya arenaria*, namely the projection on the L-valve.

During the later parts of this paper the term "L-R-phenomenon" refers only to the sorting due to the general asymmetry.

III. THE PHENOMENON UNDER DIFFERENT CONDITIONS

a. *The effect of the wind-direction on the L-R-phenomenon at the same tidal phase*

The further study of the L-R-phenomenon was continued with an investigation of the influence of the wind-direction. This was carried out during the period 3—16.7.1956 near De Koog between pl. 20 and 21 on the island of Texel. Here all valves, except those of the dominant species *Cardium edule*, lying on a first (most landward) sandbank with a rather constant size and form, were collected daily at low tide. At the same time the wind-direction and wind-velocity were determined with the aid of a compass and a hand-anemometer (Haag-Streit, Bern).

Table 6 shows the total numbers and the percentages of L- and R-valves of *Spisula subtruncata*, *S. solida* and *Donax vittatus*, collected on days when there were winds of constant direction and high velocity. This table also contains the data for calm or nearly calm days when the wind had a variable direction. The numbers collected on days with the same wind-direction have been added together.

TABLE 6

Total numbers and percentages of L- and R-valves of *Spisula subtruncata*, *S. solida* and *Donax vittatus*, collected during 3—16.7.1956 near De Koog on the island of Texel under different wind-directions.

Wind-direction	Number of days	Windvelocity m/sec.	L	R	Total	%L	%R	%R-%L
N	2	8½, 9	646	905	1551	41.7	58.3	16.6
WSW	2	6½, 10	326	346	672	48.5	51.5	3.0
SW	3	7½, 8½, 14	1137	1231	2368	48.0	52.0	4.0
NE	2	7, 7½	988	1597	2585	38.2	61.8	23.6
Variable	5	0.8, 1, 1½, 2.7, 3½	1893	2808	4701	40.3	59.7	19.4

Fig. 2 illustrates the results. It is clear that for all observed wind-directions an R-effect was found. Moreover, it is evident that this

R-effect was much lower with coast-parallel winds from SW-directions than with those from N-NE-directions. It is also remarkable that with the latter winds the R-effect was nearly the same as on calm or nearly calm days. The interpretation of these results will be given in chapter VII.

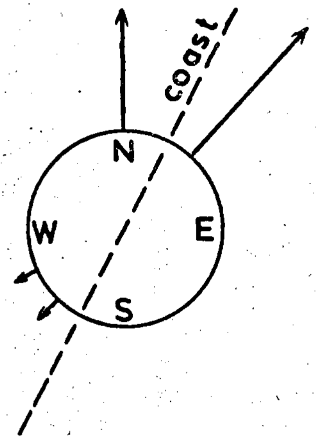


Figure 2.

b. *The effect of tidal changes on the L-R-phenomenon under constant wind-direction*

1. *Preliminary observations*

To study the question of the L-R-phenomenon during tidal changes some investigations were carried out from 12-21.8.1957 on the island of Schiermonnikoog. For this purpose we selected a part of the beach near pl. 8, where the species-composition of the valves washing ashore was favorable for our studies, the frequency of *Cardium edule* being relatively low, whilst that of *Spisula subtruncata* and of *Donax vittatus* was high. During the observation-period the wind constantly came from western directions. Fig. 3 gives an impression of this part of the beach. The coast-line lies approximately W-E. The upper beach (I) and the first sandbank (II) were separated by the first creek (b). This creek, like all creeks on Schiermonnikoog during the period of investigation, had a remarkable structure. Due to the heavy westerly winds blowing parallel to the beach all western parts of the creeks were very shallow, so that in fact they only communicated with the sea at the NE-side (d). The upper surface of the second sand-bank (III) became dry only at low water of spring tides. The second creek (c) had, a similar structure to the first, although the features were less well marked.

As a result of this remarkable structure of the beach, and of the prevailing westerly winds, the flow of the water in the creeks was always the same, namely W-E. It can easily be understood that this must be the case with the eastward flowing flood tide. But during ebb-tide the stream was similarly eastward: due first to the fact that the water transported coastward by the waves could return to the sea only through the eastern exits, and secondly to the fact that water present in the creeks when the banks became exposed could escape only in that direction.

On the first sand-bank four poles were partly entrenched (fig. 3: 1, 2, 3, 4), demarcating a quadrangle of 295 m^2. Once a day at low tide all valves lying on this quadrangle were collected. In addition on some days a large quantity of valves was collected at C, shortly before low water.

Table 7 shows the total number and the L/R-ratio of the valves of *Donax vittatus* collected on the quadrangle and near C, during four successive days.

TABLE 7

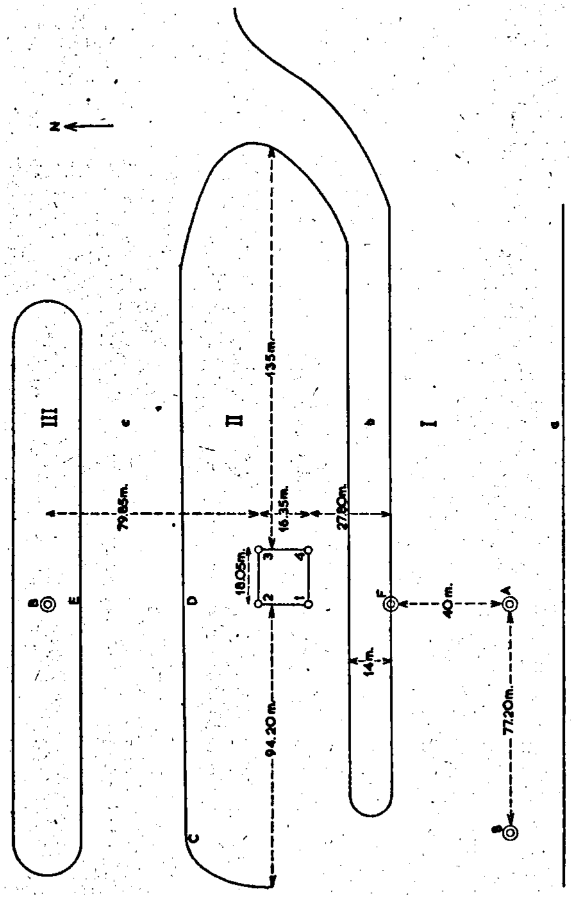
Total numbers and the L/R-ratio of the valves of *Donax vittatus* collected from 14—17.8.1957 on the quadrangle and near C.

Quadrangle		C	
L/R	Total	L/R	Total
1.3	259	5.1	86
1.3	211	6.6	778
1.7	533	6.7	231
1.6	518	4.5	624

This table shows that the L/R-ratio was very different at the two collection-sites. Near C the L-valves were always much more frequent than on the quadrangle. As the valves were deposited on the quadrangle when the sea-level was higher than when the valves were collected near C, it appears that the L/R-ratio changes during the tides.

2. *The phenomenon during flood*

To study these supposed changes in the L/R-ratio during the tides some observations were first made during flood on the part of the beach between pl. 8 and pl. A (fig. 3). Shortly after the water had started to rise up the beach, seven observers started collecting all valves of *Donax vittatus* which were present in that zone which was already continuously immersed. The valves collected in each quarter hour were added together. Thus the


N
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II
I
a
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c
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D
E
F
135 m.
79.85m.
16.35m.
27.80m.
18.05m.
40 m.
14 m.
94.20 m.
77.20m.
1
2
3
4

Figure 3.

collectors followed the rising water for a period of 1½ h. Table 8 gives the results.

TABLE 8

Numbers of L- and R-valves of *Donax vittatus* collected on a rising tide on the slope of the beach during 1½ h. on 17.8.1957.

Time	L	R	Total	% L
10.00—10.15	115	60	175	65.7
10.15—10.30	146	42	188	77.7
10.30—10.45	87	17	104	83.7
10.45—11.00	64	14	78	82.1
11.00—11.15	33	4	37	89.2
11.15—11.30	6	1	7	85.7

Fig. 4 demonstrates the changes in the numbers of L- and R-valves collected during this period. It is evident that higher on the beach (during the rise of the water and thus also of the observers) fewer valves were present.

Fig. 5 shows the percentages of the L-valves. It is clear that at the beginning this percentage increased rapidly, while after about 1 hour it remained rather constant at the high level of 85. This means that at that time about 6 times as many L-valves as R-valves were washed ashore.

This experiment was repeated on 19.8.1957 with three observers per quarter of an hour since it was found that under the given conditions this number was sufficient. Table 9 and fig. 6 give the results.

TABLE 9

The numbers of L- and R-valves of *Donax vittatus* collected on a rising tide on the slope of the beach during 1½ h. on 19.8.1957.

Time	L	R	Total	% L
11.15—11.30	233	88	321	72.6
11.30—11.45	152	24	176	86.4
11.45—12.00	96	20	116	82.8
12.00—12.15	71	23	94	75.5
12.15—12.30	54	11	65	83.1
12.30—12.45	41	20	61	67.2
12.45—13.00	25	6	31	80.6

Again the sharp decline in numbers is remarkable. Moreover the curve for the R-valves is much more irregular than that for the L-ones, which affects the percentages. Clearly the relative decrease of the number of R-valves was not so regular as on 17.8.1957. The only observed differences in the conditions were that the NW-wind had a velocity of 5 m.sec. on 17.8 and of 6.5 m.sec. on 19.8, whilst the number of waves was 8 and 11 per min. respectively.

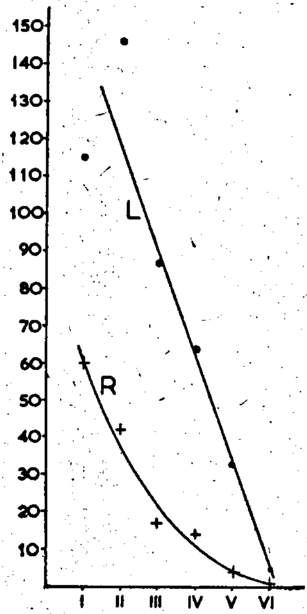

Figure 4.

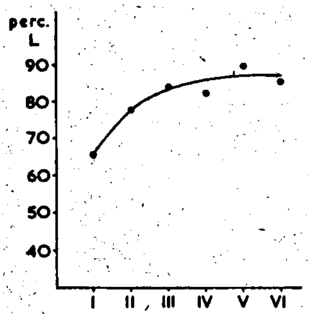

Figure 5.

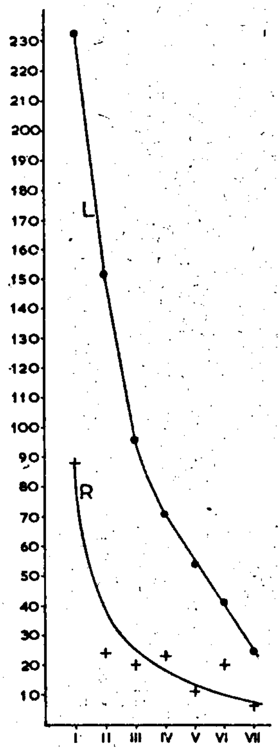

Figure 6.

3. *The phenomenon during ebb*

On the first sandbank (II, fig. 3), in the strip CD, the reverse experiment was carried out. During ebb tide, starting when the top of the sandbank was nearly dry, all specimens of *Donax vittatus* were collected in the manner mentioned above. Three observers

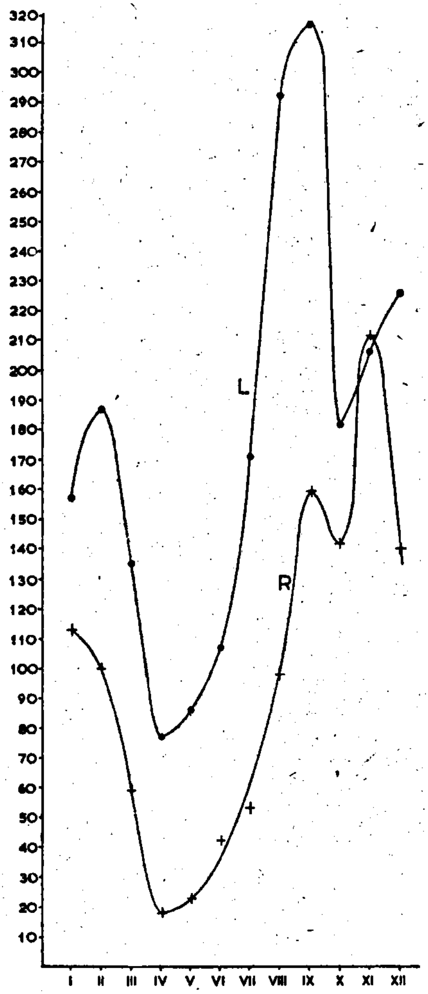

Figure 7.

followed the water for 3 hours. For the last quarter of an hour the tide was flowing. Table 10 and figs. 7 and 8 give the results.

TABLE 10

The numbers of L- and R-valves of *Donax vittatus* collected during ebb tide on the slope of the first sandbank in the strip CD (77 m.) during 3 hours on 17.8.1957.

Time	L	R	Total	% L
17.00—17.15	157	113	270	58.1
17.15—17.30	187	100	287	65.2
17.30—17.45	135	59	194	69.6
17.45—18.00	77	18	95	81.1
18.00—18.15	86	23	109	78.9
18.15—18.30	107	42	149	71.8
18.30—18.45	171	53	224	76.3
18.45—19.00	292	97	389	75.1
19.00—19.15	319	159	478	66.7
19.15—19.30	182	142	324	56.1
19.30—19.45	206	212	418	49.3
19.45—20.00	226	140	366	61.7

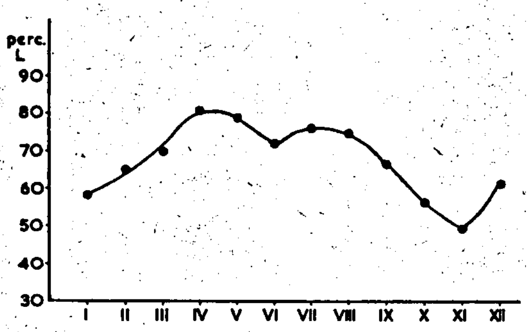

Figure 8.

Fig. 8 demonstrates that at first the L-effect increases, but later decreases until a level is reached where the numbers of L- and R-valves are equal (19.30—19.45). When the water starts rising the L-effect can be observed again immediately (19.45—20.00).

Fig. 7 can be interpreted with the aid of fig. 9 which shows the seaward distances covered by the observers. They started (17.00—17.15) on the plateau of the sandbank. Here the numbers of L- and R-valves were not very different and, clearly, the sorting effect was not very intensive. Near the edge of the plateau the number of L-shells increased, that of the R-shells decreased: the sorting effect was higher (compare fig. 8). This effect was still more apparent on the gradually descending slope seaward to the sandbank, although here the absolute number of valves was small. At the bottom of the slope the sorting effect remained high, while the number of valves (both L- and R-ones) increased, due to the fact that at this level the waves could take large quantities of valves out of the stock present subtidally. Later (19.15—19.30) the wave-action diminished due to the protection afforded by the second sandbank (fig. 3): the number of shells again decreased. At the same time the sorting effect steadily diminished, disappearing during the period 19.30—19.45. As soon as the water started rising the sorting effect could again be observed.

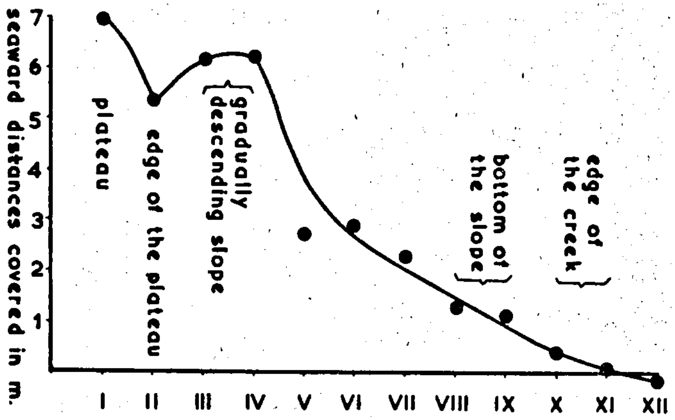

Figure 9.

IV. AN EXPERIMENT WITH VIOLET-STAINED VALVES OF SPISULA SUBTRUNCATA AND OF DONAX VITTATUS ON THE SECOND SAND-BANK

To gain more insight into the movements of the valves in this coast-area, experiments were carried out with valves marked with striking colours. For this purpose several staining methods were tested beforehand in the laboratory at Amsterdam. Valves of various species of Lamellibranchs were kept in staining solutions for some minutes or hours. When the colour was absorbed sufficiently the valves were rinsed with tapwater. Afterwards they remained for one night on a shaking-machine in a glass jar partly filled with sea-water and sand, to imitate the effect of the surf. Table 11 lists the stains and staining-methods.

TABLE 11

Tested stains and staining-methods

aniline blue	haematoxylin	picro blueblack
azo carmine	Indian ink	picro indigo carmine
borax carmine	light green	ponceau de xylidine
congo red	manganese oxide	safranin
cotton blue	methylene blue	silver nitrate (in darkness, afterwards treatment like photographs)
copper sulphate	methyl violet	
fuchsin acid	nile blue sulphate	
fuchsin-paraldehyde	phloxine	sudan 3
gentian violet	picric acid	toluidine blue

In most cases the valves were decolourized the next morning. Methyl violet and toluidine blue gave rather good results. Gentian violet was much the best stain: the valves acquired an intense violet colour.

Very good results were also obtained with the help of the following method, which was developed for us by Mr G. DE VRIES of the Chemical Laboratory of the Free University. The valves are heated in a 5% Pb-acetate solution in water for 2 hours on a water-bath at 90° C. Afterwards they are washed in tap water and then kept for 2 hours at 90° C in a 5% K_2CrO_4-solution in water (made alkaline by adding some drops of NaOH2n). In this way the compound $PbO.PbCrO_4$ is formed, and is incorporated into the structure of the valves, giving them a very marked orange-red colour, so that they can be easily observed on the beach at a distance of several meters.

On 14.8.1957 at six p.m. about 10,000 valves of *Spisula subtruncata* and about 1000 valves of *Donax vittatus*, all stained with gentian violet, were placed on the dry plateau of the second sand-bank (III) near pole B (see fig. 3). The numbers of L- and R-valves were known. We hoped that it would be possible to study the sorting effect by collecting the stained valves on the first sand-bank (II) during the following days.

At the next low water (15.8 at 5.45 a.m.) a track of violet valves could be seen going from B in the direction of pl. 2 of the quadrangle (see fig. 3). The majority of the valves were present in the sand of the rather steep landward side of the second sandbank, approximately at E in fig. 3. On the seaward side of B no violet valves could be found, and also in the second creek (c) they were present neither on nor in the bottom. On 17.8 the situation was identical. The violet valves could be dug out by hand in large numbers near E, but they were absent from the bottom of the second creek. During the entire period of observation (up till 21.8) no single violet valve was found on the first sandbank.

This experiment shows that, under these particular conditions, valves of the species under investigation are transported over the sandbank by wave action and become burried on the landward side by sand which accompanies them. They do not cross the creek, but remain *in situ* whilst the sandbank is carried over them; thus they once again come to lie on the seaward side. Then in one or two leaps they are washed again over the bank. Thus, the landward passage of these shells consists of rapid leaps alternating with long resting-periods during which they lie buried in the sand.

It can easily be seen that the situation must be different near the exits of the creeks. The same phenomenon will occur during storms, or during protracted periods of high winds blowing parallel to the beach, which have the effect of orientating the banks at right angles to the coast in stead of parallel with it.

V. AN EXPERIMENT WITH ORANGE-RED STAINED VALVES OF DONAX VITTATUS ON THE SLOPE OF THE BEACH

From the foregoing experiment it was concluded that in order to study the L-R-phenomenon with the help of marked valves it would be necessary to lay them at another spot, namely to seaward of a bank or of the beach.

Therefore, on 19.8.1957 at 11 a.m., 400 L- and 400 R- orange-red valves of *Donax vittatus* were laid down at the base of the slope of the beach near F (fig. 3), shortly before the rising water arrived at that point. At high water (at about 3 p.m.) we began to divide the beach into quadrangles of 100 m^2 with the aid of poles. This was continued until the entire slope of the beach was dry (7.30 p.m.). In the longitudinal direction of the beach the quadrangles were indicated with letters, in sea-ward direction with figures (see fig. 11). The high-water mark (......) traversed the 1-quadrangles. From quadrangles 1—6 of the series a-E and quadrangles F_6 and G_6 all stranded specimens of *Donax vittatus* (both stained and unstained) were collected; this contrasts with the previous experiments in which valves were taken out of the water. Since the valves were extremely numerous, only a fraction ($\frac{1}{2}$ or $\frac{1}{4}$) of the 7-quadrangles was studied. The 8-quadrangles could not be studied, due to the onset of darkness, but, in any case, due to their situation on the bottom of the creek and the landward side of the first sandbank, they were very poor in valves both of *Donax vittatus* and other species.

Table 12 and fig. 10 show the total quantities of unstained valves found in the series a-E. Each figure, therefore, represents the number collected from 600 m².

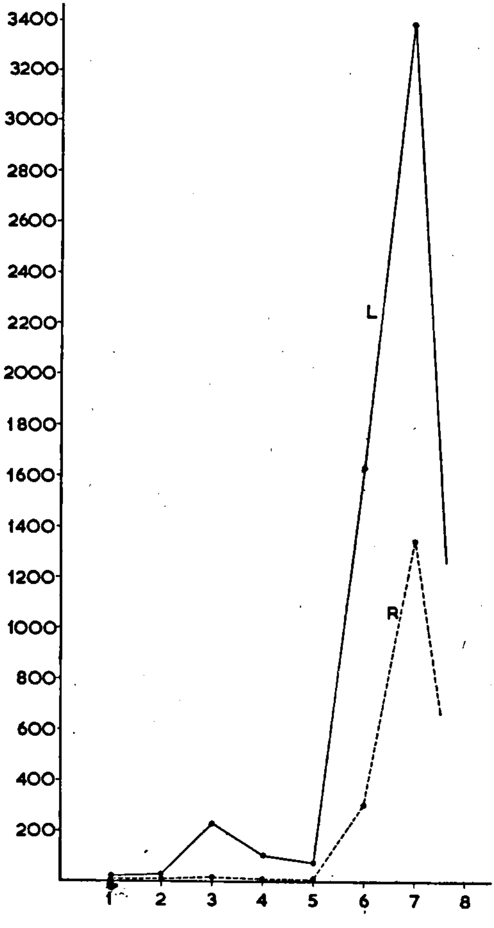

Figure 10.

It can be seen that only a very small part of the enormous stock of valves present at the base of the beach, arrives at the top.

From the percentages it is clear that the L-valves were already more numerous at the base of the beach. But, in accordance with the earlier observations, the L-effect is even more evident higher on the beach-slope.

TABLE 12

Total numbers of unstained specimens of *Donax vittatus* collected in the series a—E.

No. Quadrangle	L	R	Total	% L
1 (high-water mark)	23	5	28	82.1
2	30	7	37	81.1
3	229	15	244	93.9
4	101	10	111	83.5
5	84	7	91	92.3
6	1632	303	1935	83.7
7	3384	1344	4728	71.6

Fig. 11 shows the places where stained valves were collected during the first low-water following the start of the experiment, and fig. 12 contains the results obtained during the three succeeding low-water periods. The observed valves were always removed. (1—2 means: 1 L- and 2 R-valves.)

The following points are of importance:

1. Only very few valves were found some meters to the west of the starting point (F). This again demonstrates that the ebbstream flowed in an easterly direction in the creek.

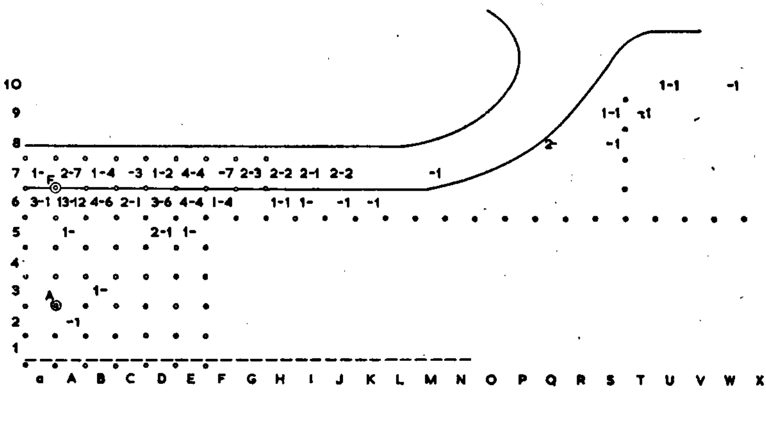

Figure 11.

2. The other valves were observed eastward of F. Some of them were found at a very great distance. During the first low-water, i.e. about 6 hours after the beginning of the experiment, the most distant stained valve was collected in W_{10}. This valve had covered 230 m. During the second low-water one was found in DD_{10}, 295 m. from F. This observation shows that valves of *Donax vittatus* can be transported over great distances along the coast.

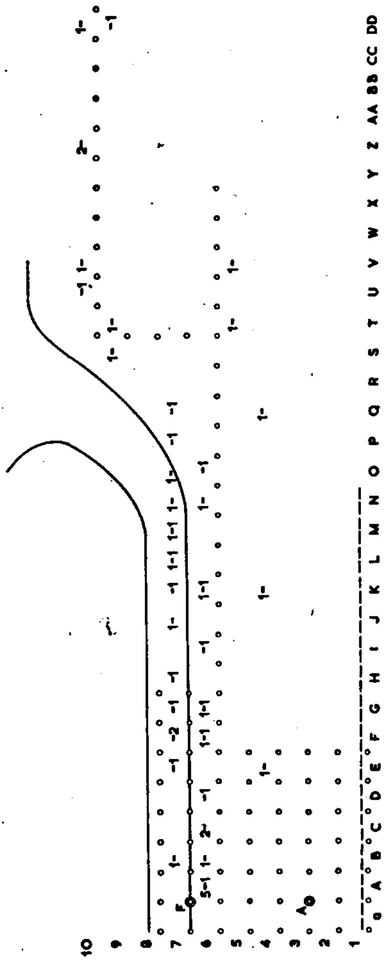

Figure 12.

3. Because in the series O, P, Q, and R the creek curved in the NE-direction, the beach extended seaward in the succeeding series. Table 13 shows the numbers of stained valves found in the creek (quadrangles in row 7 from a to 0) and on the beach.

TABLE 13

Stained specimens of *Donax vittatus* in the creek and on the beach.

Low water after start of exp.	In the creek L	In the creek R	On the beach L	On the beach R
1	17	36	41	44
2 + 3 + 4	6	8	24	11
Total	23	44	65	55

These data indicate a sorting effect; the R-valves (especially at the beginning) were more frequent in the creek, while the L-valves were more frequent on the beach.

4. The distribution of the stained valves suggests that many valves were transported out of the creek via the eastern exit. In the series a-0 the valves were lying mainly in the 6- and 7-quadrangles, while beyond 0 they were lying much more to seaward (see Table 14).

TABLE 14

The numbers of stained valves of *Donax vittatus* in the quadrangles east of O.

quadrangles	numbers	quadrangles	numbers
1	0	6	1
2	0	7	2
3	0	8	3
4	1	9	6
5	2	10	8

It was impossible to collect in the bend of the creek as it contained much water even at low tide.

VI. SOME DIFFERENCES IN "BEHAVIOUR" BETWEEN L- AND R-VALVES OF DONAX VITTATUS

a. *L- and R-valves in to-and-fro moving water*

Seaward of the beach near pl. 8 of Schiermonnikoog a large number of observations were made on the changes in position of single L- and R-valves of *Donax vittatus* in the water flowing up and down the slope of the beach. During the observation-period the angle between the direction of the breaking wave and that of its backwash was small. Fig. 13 gives an impression of the results. At I is shown the position of an L- and of an R-valve (with their convex sides uppermost) in water streaming in the direction to the beach. The valves are then oriented with their pointed ends (indicated by a dot) directed to the land. If the water then starts flowing in the opposite direction it presses against the short but steep side AB, with the result that, if the pressure is sufficient, the valve starts twisting. As can be easily seen the L-valve will turn clockwise, the R-one anti-clockwise (II and III), so that finally the positions shown at IV are reached. During the next wave the L-valve will again turn clockwise, the R-one anti-clockwise (V-VII).

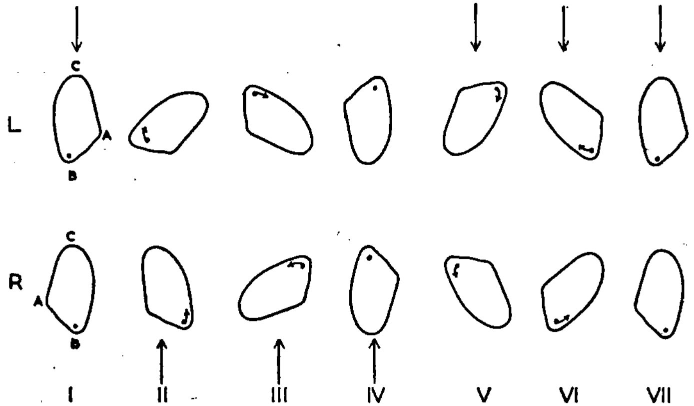

Figure 13.

At suitable places on the beach and with a sufficiently strong action of the waves it is a surprising sight to observe the L- and R-valves turning intermittently in opposite directions.

b. *The orientation of L- and R-valves in relation to the points of the compass*

These observations were carried out at low-water tide on the island of Schiermonnikoog on the slope of the beach and on the first (most landward) sandbank near pl. 8. The wind was WNW. With the aid of a compass the orientation of 541 valves of *Donax vittatus* was determined. The line BC (fig. 13) was chosen as the axis of the valve, while the direction in which B pointed was taken as the direction of orientation.

The results obtained on different occasions were almost identical, so they are summed up in table 15. In this table the smaller number of observations made on R-valves is converted into an equal number as the observations with L-valves.

TABLE 15

The orientation on the beach of L- and R-valves of *Donax vittatus*

Orientation	L	R	Rc (Expected no. of R in a total of 395)	L—Rc
N	11	8	22	—11
NNW	16	4	11	5
NW	11	3	8	3
WNW	14	4	11	3
W	17	1	3	14
WSW	19	8	22	— 3
SW	11	6	16	— 5
SSW	43	13	35	8
S	65	9	24	41
SSE	96	29	78	18
SE	25	18	49	—24
ESE	36	12	32	4
E	9	9	24	—15
ENE	11	14	38	—27
NE	4	5	14	—10
NNE	7	3	8	— 1
	395	146	395	

Fig. 14 shows the results of equal numbers of L- and R-valves (L: drawn line; R: broken line). It is remarkable that the figures obtained by connecting the frequency-points of the L- and the R-valves have an asymmetry comparable to that of the valves themselves.

Considering that the coast lies approximately W-E, it follows firstly from these figures that most valves have a landward orientation. Table 16 illustrates this.

TABLE 16

The general orientation of L- and R-valves of *Donax vittatus*

Directed to	L	R
sea	18.8%	28.3%
W	4.3	0.8
E	2.3	6.1
land	74.6	64.8

Secondly, both table 16 and fig. 14 show that the L-valves are more frequently directed westward or landward, while the R-valves more often are oriented eastward or seaward.

This effect can be seen more clearly in fig. 15, in which the difference L-R_c is shown (an L-surplus is indicated with a drawn line, an R-surplus with a broken line).

The differences between the number of L-and R-valves orientated towards each point of the compass can be explained on the basis of two series of observations. First, as we have just shown, the valves become orientated by water movements. Secondly, all these water movements had an easterly component. This was in part due to the prevailing westerly winds which affect both upsurge and backwash of the waves, and in part to the eastward movement of the ebb stream.

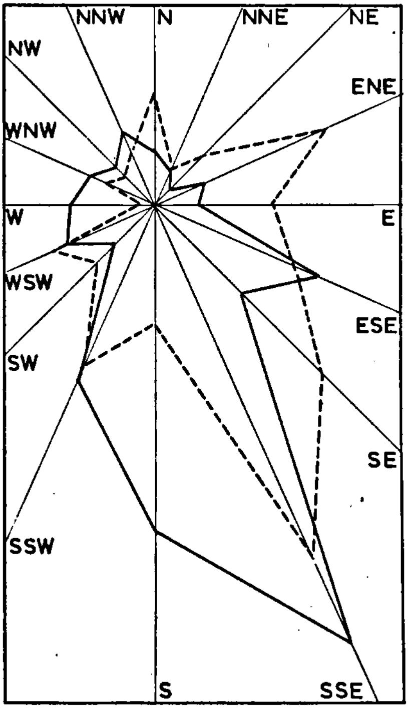

Figure 14.

Taking these facts together the following can be stated:

1. A large proportion of the valves are oriented towards the S, SSE, or SE (L: 47.1%; R: 38.2%) and it can be concluded that this is effected by water movements directed towards the beach (i.e. the upsurge of the waves).

2. As the R-valves are predominantly directed towards the east (fig. 14), with a pronounced surplus in the ENE-direction (fig. 15) it is clear that they were more easily orientated by water flowing seaward (i.e. the backwash of waves) than the L-valves.

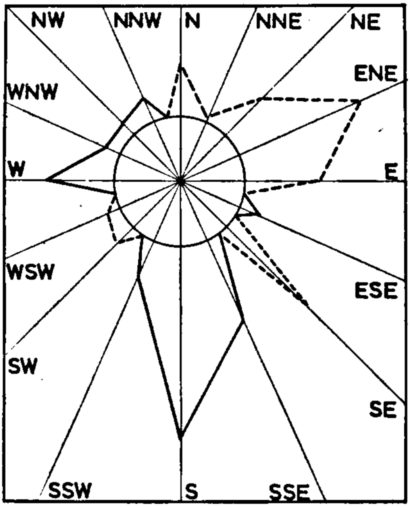

Figure 15.

The causes of these differences are elucidated in fig. 16. The upsurge orients the L- as well as the R-valve in SSE-direction. The backwash has little effect on the L-valve (I) as it lies with its sloping side BC turned towards the water-stream, while the steep sides AB and AC of the heaviest part of the valve are resisted by the sand. Moreover its rotation is clockwise, which would be impossible in the water-flow to ENE.

For the R-valve (II) the reverse is true. R-valves turn anti-clockwise as we have seen, which exactly fits the stream-direction. The water presses against the steep sides of the valve, and if the pressure is sufficient the valve will start turning.

If the valve moves it is probable that it will be transported in a seaward direction. If the valve comes to a rest it will lie orientated to ENE (III). This means that the following upsurge passes easily over it as it has now the same position in regard to the oncoming wave as the L-valve had to the backwash. As the total resistance of the sand against the sides AB and AC of the R-valve is without doubt higher than that against the side AB of the L-valve (which had the added advantage that it fits the stream-direction), the latter will be transported beachward more easily than the former.

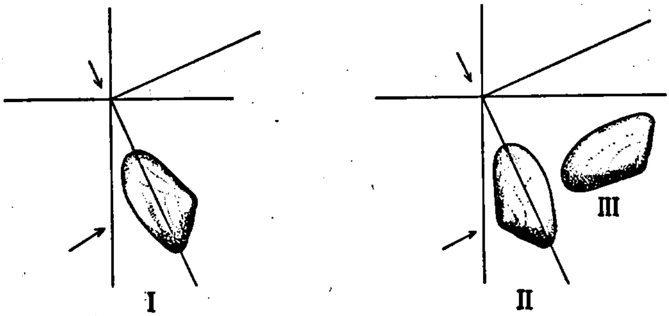

Figure 16.

Summarizing it can be concluded that, under the conditions of our observations, the L-valves had the advantage over the R-ones both during the upward and during the downward movement of the water.

Repeated many times this will result in an L-effect of the kind we discussed above. It is clear that the result will be reversed when the upsurge is southwesterly and the backwash northwesterly.

VII. WAVES AND CURRENTS AT DEEPER LEVELS AS CAUSES OF THE L-R-PHENOMENON

In the preceding chapter the discussion of some facts resulted in the conclusion that obliquely directed water streams flowing up and down a sandy beach will cause a sorting of L- and R-valves.

The first question which arises is whether this theory is in harmony with the results of the previous observations and experiments. Generally speaking this question can be answered in the affirmative. During all the observations on the coast of Schiermonnikoog the waves came from western directions, while both flood and ebb were eastbound in the creeks, so that, in accordance with the theory, an L-effect resulted. Also, the preponderance of R-valves in the creek and of L-valves on the beach during the experiment with the orange-red stained valves is in agreement with the theory. The same applies to the R-effect observed on Texel (table 6) as here we collected at low tide, so that the valves had previously been deposited on the first sandbank during ebb. (During July 1956 at this place the creeks had exits to the sea at both ends).

Secondly, the mechanism of this effect requires discussion. A first possibility is that sorting is effected high on the slopes by the different directions of flow of the upsurge and backwash of the waves, with the wind influencing the angle between the two. MARTIN-KAYE (1951, p. 434) also saw this possibility: "Separation may possibly proceed further on the beach itself as the shells are washed up and down by each succeeding wave". The alternative explanation is that sorting is effected at a deeper level by the combined action of wave-movements and water-currents (ebb and flood), without the wind having a primary influence.

In considering these questions we may start with the observations on the island of Texel relating to the influence of the wind-direction. As was shown in table 6 and fig. 2, with N- and NE-winds an R-effect was observed which was nearly the same as that seen on calm days. These winds, which blew nearly parallel to the beach, undoubtedly caused an increase in the angle between the direction of the upsurge and backwash of the waves. Nevertheless this did not result in an unduly large R-effect. Likewise, notwithstanding their high velocity, WSW- and SW-winds did not bring about an L-effect. (The decrease of the R-effect can be explained by the decreased speed of the ebb with heavy SW-winds.) These facts are strong arguments against the supposition that sorting takes place by wave-action high on the slopes.

A second argument against this supposition is the observation that on 19.8.1957 when the waves were stronger during flow than on 17.8, the curve of the R-valves had a more irregular course (figs. 4 and 6). If the first supposition was right, one would have expected a clearer sorting effect.

In addition the last part of the curve of fig. 8 suggests that surface movements of the water are not very important, as during that time the waves were very low, due to the fact that they could hardly pass the second sandbank (there was a depth of only about half a foot of water).

Again, during inspection of the quadrangles in the experiment with the orange-red stained valves it was observed that only very seldom was one of the stained valves washed away by the receding wave. The strongest argument, however, is the fact that this possibility of sorting was excluded to a great extent during the ebb- and flood-experiments, as the valves were collected deliberately on those parts of the slopes, which were covered by the water.

Because of all these arguments it seems improbable that the sorting process occurs high on the slopes.

The second supposition is more feasible: i.e. that sorting is effected at deeper levels by the interplay of currents and the subsurface effect of waves, while the breaking of the waves, washing up and down on the slopes, carries up the result of this sorting.

In favour of this theory are the results of the ebb- and flood-experiments, and the observation that, in spite of the very strong SW-winds, on Texel the R-effect was maintened during ebb-tide.

The results shown in fig. 8 particularly support this opinion. At the beginning of the experiment (5 p.m.) the top of the first sandbank was not yet dry; under these conditions there was no impediment to the ebb. As the water level continues to fall, the creek becomes narrower, but since waves continue to wash over the second sandbank the speed of the stream is, for a time, increased. Subsequently, as these amounts of water decrease, the ebb flow slackens. A similar pattern is found in the intensity of the L-effect.

During slack water (19.30—19.45) equal numbers of L- and R-valves were found, although the waves were not perceptibly lower than shortly before and after this time.

It may be concluded that the valve-movements are as reproduced in fig. 16, and that the sorting-processes take place under water on the seaward slopes. This sorting becomes visible on the slopes and the banks as the water falls, whilst some of the sorted valves can be raised from lower to higher levels by the breaking waves.

The conclusion is that, along the Dutch coast, on a beach of "normal" construction (i.e. with beach-parallel sandbanks separated by creeks which communicate with the sea at both ends) the ebb-stream will cause an R-, the flood-stream an L-effect. This implies that if at low-water an L-effect is observed the structure of the beach must be "abnormal". Such, for instance, was the case at Schiermonnikoog, where from 12-21.8.1957 the creeks had only eastern exits. In addition, the L-effect during ebb-tide near Den Helder (which was noted from 2-4.8.1955 and also on several later occasions) is due possibly to the presence of jetties, which deflect a SW-directed ebb-stream to a northerly course parallel to the beach.

VIII. SUMMARY

At several places on the sandy beaches of the Dutch coast unequal quantities of L- and R-valves of Lamellibranchs were found to be present. This sorting effect may be due to the general asymmetry of the two valves (*Spisula subtruncata*, *S. solida*, *Donax vittatus*, *Angulus tenuis*), or to a difference in fragility of the valves (*Macoma balthica*, *Angulus fabula*), or to the fact that one of the valves has a projection (*Mya arenaria*).

It was found that the L-R-phenomenon resulting from the general asymmetry shows regular changes in intensity during the tidal phases.

In the tidal area experiments were carried out with stained valves, and studies were made regarding the differences in "behaviour" of single left and right valves in the water near the beach, while on the beach the orientation of left and right valves in the points of the compass was determined. The results obtained lead to the conclusion that the sorting of the asymmetrical valves is effected by water-streams flowing obliquely up and down at the base of the slopes of the beach and the banks; these processes occur underwater by the interplay of water-currents (particularly the tidal streams) and the oscillatory wave-movements near the bottom.

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X. SAMENVATTING

Op verschillende plaatsen aan de Nederlandse kust werd een ongelijke verhouding tussen het aantal L- en R-schelpkleppen van Lamellibranchiata aangetoond. In extreme vorm kan één van beide kleppen zelfs 15 maal meer voorkomen dan de ander. Deze sortering kan veroorzaakt worden door de algemene asymmetrie tussen de beide kleppen (*Spisula subtruncata*, *S. solida*, *Donax vittatus*, *Angulus tenuis*) of door de grotere breekbaarheid van één van beide kleppen (*Macoma balthica*, *Angulus fabula*), dan wel doordat één van beide kleppen een uitsteeksel bezit (*Mya arenaria*).

Het *L-R-verschijnsel* als gevolg van algemene asymmetrie blijkt tijdens de eb- en vloedbewegingen regelmatige veranderingen te ondergaan. Onder anderen aan de hand van experimenten met gekleurde kleppen van *Donax vittatus*, en met behulp van waarnemingen betreffende het „gedrag" van L- en R-kleppen in waterstromen, en na bestudering van de ligging van L- en R-kleppen in de windroos wordt de mening geopperd dat het sorteren geschiedt door middel van schuin tegen strandhellingen heen- en weerlopende waterstromen, welk mechanisme onder water ligt en gevormd wordt door het samenspel van waterstromen (eb- en vloedstromen) en de heen en weergaande golfbewegingen langs de bodem.