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Distribution and ecology of the slugs *Alderia modesta* and *Limapontia depressa* in the Netherlands*)

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INTRODUCTION

This paper deals with the slugs *Alderia modesta* (LOVÉN) and *Limapontia depressa* ALDER & HANCOCK, both very common in the intertidal zone of the Dutch salt-marshes.

VAN BENTHEM JUTTING & ENGEL did not mention them as native species in „Fauna van Nederland" 8, a monograph on Dutch Opisthobranchia, published in 1936. *Alderia* and *Limapontia* do not belong to the order of Nudibranchia, but to a separate order, Saccoglossa (Ascoglossa). They possess an uniseriate radula, the worn teeth of which fall in a pouch (saccus, ascus). Their way of life is different, the Nudibranchs feed mainly on hydroids, sea anemones, bryozoa, sponges, etc.; only a few species e.g. *Polycera quadrilineata* O. F. MÜLLER feed on algae, while all west-european Saccoglossa feed exclusively on algae.

DATA FROM DUTCH LITERATURE

The literature on the occurrence of *Alderia* and *Limapontia* along the Dutch coast is very limited. In 1914 GILSON recorded the first find of *A. modesta* (as *A. scaldiana* NYST) from the Land van Saeftingen in the Westerschelde. His publication, however, remained unnoted by Dutch malacologists. KERBERT (1918) reported the species from Durgerdam, but this find was doubted by VAN BENTHEM JUTTING & ENGEL (1936). In 1939 ENGEL, GEERTS & VAN REGTEREN ALTENA found *Alderia* on „De Beer", a nature reserve near Hoek van Holland. At the same time they found *L. depressa*, which had not been recorded earlier for the Netherlands. In 1940 they published an important study on their observations. In 1952 DEN HARTOG & SWENNEN mentioned a number of localities of the two species in the Waddenzee. After this in the semipopular periodical „Het Zeepaard" *A. modesta* had been recorded from IJmuiden (STOK & MULDER, 13 (3), 1953), „De Bol", Texel (SWENNEN, 15 (2), 1955), Ossendrecht (MULDER, 16 (1). 1956); Tholen, Mosselhoek (BOD-

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DEKE, 16 (4), 1956) and Voorne, Strandhaak („Groene Strand" SMITS, 16 (7), 1956); *L. depressa* from IJmuiden (STOCK & MULDER, 13 (3), 1953) and the „Zwarte Polder" near Cadzand (MULDER & VIERGEVER, 14 (3/4), 1954).

Alderia modesta (LOVEN).

Stiliger modesta LOVEN, 1844
Alderia harvardiensis AGASSIZ, 1850.
Alderia scaldiana NYST, 1855.

A clear description of the Dutch specimens was given by ENGEL, GEERTS & VAN REGTEREN ALTENA l.c. I can add only that the specimens may measure up to 12 mm.

DISTRIBUTION

Alderia modesta is a boreal species, which has been found along the european coast from the Dronthjemfjord to Normandy and the west coast of Ireland. In the Baltic it reaches the neighbourhood of Helsinki. Along the American east-coast it has been observed last century in Massachusetts and New Brunswick *(Alderia harvardiensis* AGASSIZ). Recently it was discovered in two localities along the Pacific coast in California near San Fransisco (HAND & STEINBERG, 1955).

Alderia modesta is not rare along the Dutch coast. The localities in the Netherlands, so far known to the author, are listed below and mapped in fig. 1a.

Province of Groningen

1. Delfzijl, 11-IX-1954. Leg. J. Beukema. 1 specimen on a very muddy salt-marsh with many *Aster tripolium* and *Vaucheria sp.* at the end of the port.
2. Noordpolderzijl, 14-IV-1953. Leg. C. den Hartog & J. Beukema. Many specimens on an extensive clayish salt-marsh in the *Puccinellietum maritimae* on *Vaucheria coronata*. Numerous egg-masses present.
3. Zoutkamp, XI-1954. Leg. A. F. Mulder.

Province of Friesland

4. Schiermonnikoog, Oosterkwelder, 24-VIII-1951. Leg. C. den Hartog. Some specimens in the *Puccinellietum maritimae* on *Vaucheria* sp. (DEN HARTOG & SWENNEN, 1952).
5. Ameland, *a.* 't Oerd, 11-IV-1953. Leg. C. den Hartog & A. S. Tulp. Numerous along the steep edges of a narrow side-branch of the great creek on *Vaucheria* sp. Also spawn-masses were found.
   b. Hollum, Westerstrand, 10-IV-1953. Leg. C. den Hartog & A. S. Tulp. Rather many *Alderia* with egg-sausages in the *Puccinellietum maritimae* on *Vaucheria coronata* and *V. arcassonensis.*
6. Terschelling. *a.* 't Sehaal, 2-IX-1954. Leg. C. den Hartog. Occurring in large numbers in the *Puccinellietum maritimae* and in the vegetation with *Obione portulacoides* and *Limonium vulgare* as dominant species on *Vaucheria* sp.
   b. Dellewal, 19-VII-1951. Leg. C. Swennen. In the *Puccenellietum maritimae* on *Vaucheria* sp. (DEN HARTOG & SWENNEN, 1952).

c. Groene Strand, 3-IX-1954. Leg. C. den Hartog. In the *Puccinellietum maritimae* on *Vaucheria* sp.

7. Noorderleegh, 9-VII-1952. Leg. B. van Huissteden. Very numerous.
8. Westhoek, 9-IV-1953. Leg. C. den Hartog & A. S. Tulp, 3 specimens in a reclaimed salt-marsh, only connected with the sea by 4 little locks; in the *Puccinellietum maritimae* on *Vaucheria coronata* and *V. compacta*.

Province of Noord-Holland

9. Texel. *a.* Slufter, 3-VIII-1951. Leg. C. Swennen. (DEN HARTOG & SWENNEN, 1952).
   b. Eendracht, 23-IX-1951. Leg. C. Swennen ; on salt-marsh. (DEN HARTOG & SWENNEN, 1952).
   c. De Bol, 6-VIII-1954. Leg. C. Swennen. Very many *Alderia* in a brackish pool inside the dike, on submerged *Vaucheria* sp., on spots where the vitality of *Zostera marina* begins to decrease.
   d. Mokbaai, IV-1953. Leg. C. Swennen. A few specimens.
10. Balgzand, 5-VII-1951. Leg. C. Swennen. Very common. As most of our field research has been carried out in this territority, a more detailed description is given on p. 22 of this paper (DEN HARTOG & SWENNEN, 1952).
11. Wieringen, Normer, 1-VII-1951. Leg. C. Swennen. Rather numerous in the vegetation of *Obione* and *Limonium* on *Vaucheria* sp. (DEN HARTOG & SWENNEN, 1952).
12. IJmuiden, 27-VII-1952. Leg. the Gerrits brothers. Rather many on *Vaucheria* sp. on the mudflat at the end of the trailer-port.

Province of Zuid-Holland

13. Rozenburg, De Beer, 24-VIII-1939. Leg. S. J. Geerts & C. O. van Regteren Altena. On the north bank of the Nieuwe Waterweg and in the tidal creeks of the "Rietmoeras" at the southeast-coast. Many specimens on *Vaucheria*-patches. (ENGEL, GEERTS & VAN REGTEREN ALTENA, 1940).
14. Voorne, Strandhaak, 15-VIII-1953. Leg C. den Hartog. Very many specimens in the *Vaucheria*-vegetation, also in the *Vaucheria*-undergrowth of the *Spartina townsendii* and *Scirpus maritimus*-fields.

Province of Noord-Brabant

15. Ventjagerplaat, on the northside of the breakwater in the Hellegat, 21-VII-1952. Leg. C. den Hartog & C. Swennen. Very numerous on *Vaucheria* sp.
16. Woensdrecht, 9-IV-1951. Leg de Coninck. In the *Puccinellietum maritimae* on *Vaucheria* sp.
17. Ossendrecht, X-1951. Leg. A. F. Mulder. Numerous on *Vaucheria* sp.

Province of Zeeland

18. Tholen, Mosselhoek, VIII-1955. Leg. R. Boddeke. On *Vaucheria* sp.
19. Noord-Beveland, salt-marshes near Kamperland, 29-V-1955. Leg. C. den Hartog. Many specimens in the *Spartina townsendii* vegetation on *Vaucheria* sp.

20. Zuid-Beveland, salt-marsh near Waarde, 2-IX-1952. Leg. W. G. Beeftink. On *Vaucheria* sp. in the *Puccinellietum maritimae*, higher up changing into the *Armerieto-Festucetum*.
21. Zuid-Beveland, salt-marsh west of Bath, 3-VII-1952. Leg. W. G. Beeftink. In the *Spartina townsendii* sociation.
22. Zeeuws Vlaanderen, Land van Saeftingen, 31-V-1911. Leg. G. Gilson (GILSON, 1914).

Limapontia depressa ALDER & HANCOCK.
Limapontia nigra (SPENCE BATE, 1850) non JOHNSTON.

The Dutch specimens are excellently described by ENGEL, GEERTS & VAN REGTEREN ALTENA (1940).

The *Limapontia depressa* described by ALDER & HANCOCK was black. KEVAN (1934), finding orange-yellow specimens with light-green translucent hepatic branches, described these as a new variety : var. *pellucida*. This yellow variety has been found repeatedly afterwards (ENGEL, GEERTS & VAN REGTEREN ALTENA, 1940 ; FISHER-MCMILLAN, 1949 ; QUICK, 1950 ; GASCOIGNE, 1952). Most of the specimens found by the author in the Netherlands and all those collected near Wimereux belonged to the var. *pellucida* ; the typical black variety has been found only exceptionally in the Netherland. On the Balgzand it had been observed only on the highest parts of the salt-marsh, whereas the yellow specimens occurred in the whole vertical range of the species. In experiments both types behaved in the same manner. Finally, beside black and yellow many intermediate colours also occur so that the value of the var. *pellucida* must be seriously doubted.

GASCOIGNE (1952) distinguished in *Limapontia depressa* 4 main colour varieties, viz. black, olivegreen, lightbrown and yellow, but the too attached little value to them, and did not give them special names. I have been inclined to consider the black and the yellow variety as the extremes of a colour series within the species. According to GASCOIGNE, however, in several localities along the British coast well-recognizable ecotypes occur.

An inquiry into the colour variation of *Limapontia depressa* in one locality should be very interesting. The darkest specimens have been found by the author on the highest parts of the salt-marsh only and in mesohalinic habitats.

GALLIEN (1929) recorded that specimens, brought into water of high salinity, turned yellowish. Thus the colour of the animals may be dependent on the salinity.

A close ally is *Limapontia capitata* (O. F. MÜLLER), which was found recently in the Netherlands also (SWENNEN, 1956). These two species are often confused. PRUVOT-FOL (1954) does not distinguish between them and, incorrectly, considers *L. depressa* a synonym of *L. capitata*. ENGEL, GEERTS & VAN REGTEREN ALTENA mention the following characters for *L. depressa* :

1. anus nearly at the end of the body.
2. body more or less flat, broadest behind the middle.
3. head very faintly two-lobed.
4. tail obtuse or wanting.

For *L. capitata* are mentioned :

1. anus medio-dorsal, a little behind the centre of the body.
2. body with a medio-dorsal hump.
3. head with two clearly visible crests.
4. tail longer and acuminate.

The third and fourth character should be rather variable. QUICK (1950) mentioned a microscopical difference : *L. capitata* should have 8—9 radula teeth, *L. depressa* 13—15.

Finally GASCOIGNE (1952) paid attention to an ecological difference. He found *L. capitata* only in rock-pools with a dense *Cladophora*-vegetation, just as FISHER-MCMILLAN (1949), QUICK (1950) and some older authors. *L. depressa* has been found by him only on salt-marshes. He doubts the statements by KEVAN (1934) and NICOL (1935), who mention *L. capitata* from salt-marshes. Probably they confused blackish specimens of *L. depressa* with *L. nigra*.

Another species which may be easily confused with *Limapontia* is *Actaeonia corrugata* ALDER & HANCOCK, which is living in tidal pools with much *Cladophora*. It is distinguished, however, by 1. its two tentacles, 2. the absence of the sweet smell, which *Limapontia* always emits when irritated, and 3. the development of the eggs. *Limapontia* has a pelagic larval stage, but in *Actaeonia* the whole development takes place in the egg-capsule.

DISTRIBUTION

Because presumably *L. depressa* has been confused with *L. capitata* repeatedly, the area of distribution is insufficiently known. *L. depressa* occurs in Great Britain, Normandy, (GALLIEN, 1929), Wimereux (PELSENEER, 1893), Belgium (Schelde, unpublished observations of BEEFTINK), the Netherlands and Denmark (Isefjord ; RASMUSSEN ex EVANS,

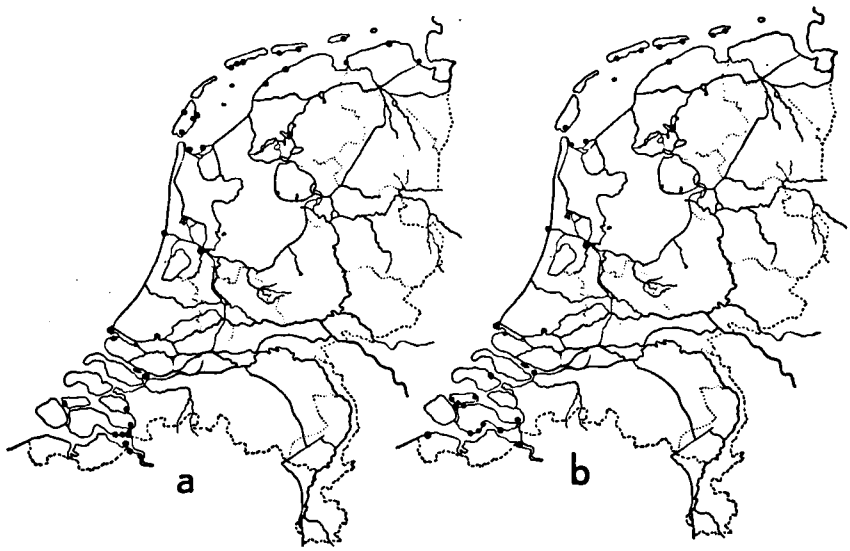


FIGURE 1. Distribution of **a.** *Alderia modesta* in the Netherlands, and **b.** *Limapontia depressa* in the Netherlands.

1953). JAECKEL (1952) considers *L. depressa* as a probably lusitanic species.

To my opinion it is better to consider it a boreal species, on account of the distribution as we know it at present, viz.: around the North Sea. The localities where the species was found in the Netherlands, are listed below and mapped in fig. 1b.

Province of Friesland

1. Schiermonnikoog, *a.* Oosterkwelder, 1-VI-1952. Leg C. den Hartog. A few specimens in the *Puccinellietum maritimae* along the bank of narrow creek ; on *Vaucheria* sp.
   b. Westerkwelder, 13-VIII-1952. Leg C. den Hartog, 4 specimens in the *Puccinellietum maritimae* along a small creek in a reclaimed salt-marsh ; on *Vaucheria* sp.
2. Ameland, *a.* 't Oerd, 11-IV-1953. Leg. C. den Hartog & A. S. Tulp. A great number of specimens along the steep edges of a narrow side-branch of the great creek on *Vaucheria* sp.
   b. Hollum, Westerstrand, 10-IV-1953. Leg. C. den Hartog & A. S. Tulp. In the *Puccinellietum maritimae* on *Vaucheria coronata* and *V. arcassonensis.*
3. Terschelling, *a.* Bosplaat near pile 21, 19-VII-1951. Leg. C. Swennen (DEN HARTOG & SWENNEN, 1952).
   b. Dellewal, 19-VII-1951. Leg. C. Swennen. (DEN HARTOG & SWENNEN, 1952).
4. Noorderleegh, 9-VII-1952. Leg. B. van Huissteden.

Province of Noord-Holland

5. Texel, Mokbaai, IV-1953. Leg. C. Swennen. Hundreds of specimens on the salt-marsh. Also spawn-masses.
6. Balgzand, 5-VII-1951. Leg. C. Swennen. In the *Puccinellietum maritimae* (DEN HARTOG & SWENNEN, 1952).
7. Wieringen, Normer, 30-VI-1951. Leg. C. den Hartog, 1 specimen on *Blidingia minima* and *Rhizoclonium riparium,* but the next day in great numbers on *Vaucheria*-patches in the vegetation of *Limonium vulgare* and *Obione portulacoides* (DEN HARTOG & SWENNEN, 1952).
8. IJmuiden. 27-VII-1952, Leg. the Gerrits brothers, 4 specimens on the mudflat at the end of the trailerport ; on *Vaucheria* sp.

Province of Zuid-Holland

9. Rozenburg, De Beer, 24-VIII-1939. Leg. S. J. Geerts & C. O. van Regteren Altena. On *Vaucheria* sp. in the tidal creeks of the salt-marsh "Rietmoeras", at the Southeast coast. (ENGEL, GEERTS & VAN REGTEREN ALTENA, 1940).
10. Voorne, Strandhaak, 23-VIII-1953. Leg. C. den Hartog, a few specimens on *Vaucheria* sp. in the *Puccinellietum maritimae.*

Province of Noord-Brabant

11. Ventjagerplaat on the northside of the breakwater in the Hellegat, 21-VII-1952. Leg. C. den Hartog & C Swennen. On *Vaucheria* sp. in the undergrowth of a vegetation with *Scirpus maritimus* and *Aster tripolium.*

12. Woensdrecht, 9-IV-1951. Leg. de Coninck. On *Vaucheria* sp. in the *Puccinellietum maritimae.*

Province of Zeeland

13. Schouwen, Dreischor, 21-VII-1952. Leg. the Gerrits brothers.
14. Noord-Beveland, Salt-marsh north of Kats, 4-IX-1952. Leg. W. G. Beeftink.
15. Noord-Beveland, Salt-marshes near Kamperland, 29-V-1955. Leg. C. den Hartog. Numerous on *Vaucheria* sp. in the *Spartina townsendii*-vegetation, but also under *Obione.*
16. Zuid-Beveland, Salt-marh near Oud-Sabbinge (along the Zandkreek), 3-VII-1952. Leg. W. G. Beeftink. In *Obione*-vegetation belonging to the *Puccinellietum maritimae* with much *Vaucheria* sp.
17. Zuid-Beveland. Noord Sloe between the Caland-polder and the Sloedam, 1-IX-1939. Leg. C. Brakman. On fine algae in a tidal creek in the salt-marsh. (ENGEL, GEERTS & VAN REGTEREN ALTENA, 1940).

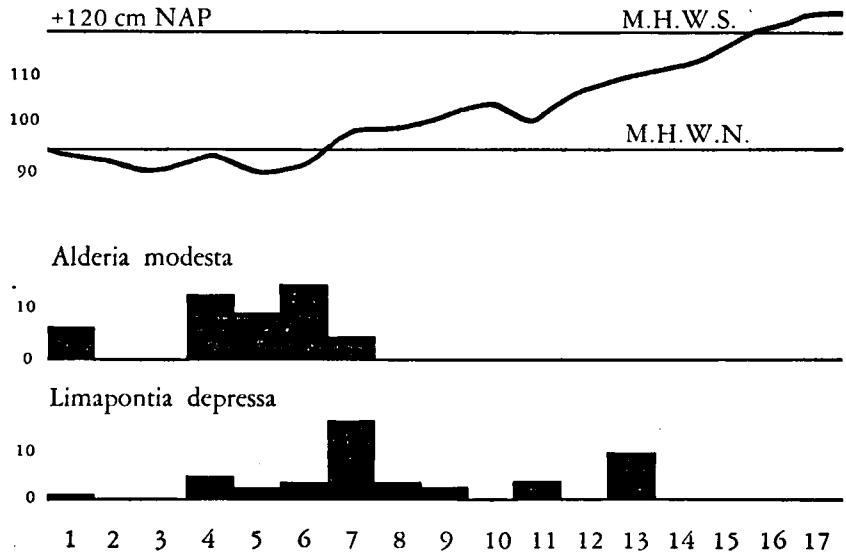


FIGURE 2. Occurrence of *Alderia modesta* and *Limapontia depressa* in relation to the relief of the Balgzand-saltmarsh.

18. Zuid-Beveland, Salt-marsh near Waarde, 2-IX-1952. Leg. W. G. Beeftink. On *Vaucheria* sp. in the *Puccinellietum maritimae,* higher changing into the *Armerieto-Festucetum.*
19. Zuid-Beveland, Biezelingse Ham near 's Gravenpolder, 30-VI-1952. Leg. W. G. Beeftink. In the *Puccinellietum maritimae* with only little *Vaucheria* sp.
20. Zuid-Beveland, Salt-marsh near Baarland, 9-VII-1952. Leg. W. G. Beeftink. In *Obione*-vegetation, belonging to the *Puccinellietum maritimae.*

21. Zuid-Beveland, Salt-march near Ellewoutsdijk, 21-VII-1952. Leg. W. G. Beeftink. In the *Puccinellietum maritimae* with very numerous *Triglochin maritima*. No *Vaucheria* sp. found.
22. Zeeuws-Vlaanderen, Zwarte Polder near Cadzand, 18-IV-1954, Leg. A. F. Mulder & J. Viergever. In a little pool, which can only be reached by the sea during spring floods.

HABITAT

The ecological investigations on *Alderia modesta* and *Limapontia depressa* have been carried out mainly on the Balgzand, the extensive territory of mudflats and salt-marshes between Den Helder and the Amstelmeer. This is not only one of the largest, but for three reasons also one of the most typical salt-marsh territories of the Netherlands:

1. No reclamation works have been carried out there. The human influence is limited to a moderate pasturage by cattle.
2. The salt content of the water is gradually decreasing from the north to the south, without disturbing influences of sluices and culverts.
3. The grass *Spartina townsendii*, introduced around 1925 on the salt-marshes of the province of Zeeland and later also into the Waddenzee, has not yet established itself on the Balgzand. This species pushes away the original vegetation, devaluating the salt-marsh into a monotonous *Spartina*-field.

The territory consists of a very extensive mudflat, a number of miles broad, with four large salt-marshes, situated along the dike. The northernmost salt-marsh is the largest and is continually crumbling off. Sheltered by it lies a second one, the northern border of which is increasing very rapidly; in the near future it may join the great salt-marsh. This part of the territory was chosen for my field-observations. As most ecologists only published summary vegetation descriptions and as the phytocenological investigations of WESTHOFF, BEEFTINK, a.o. showed that the vegetation may give very important indications about the environment, the author has devoted much attention to the vegetation.

Starting from the mudflat, we observe the following belts of plant communities on the salt-marsh mentioned:

1. *Salicornietum strictae*,
2. *Puccinellietum maritimae*,
3. *Armerieto-Festucetum*.

The *Salicornietum strictae* does not establish itself before the mudflat has been sufficiently raised by sedimentation of sand and silt particles. The phytocenologists have highly valued the only phanerogam of the community, *Salicornia europaea* ssp. *stricta*. The short vegetation period of this species, from June to October, however, makes this supposition unprobable. According to my observations the sediment is fixed by diatoms and Cyanophyceae, which cover the soil with a thin film. In the *Salicornietum* the large cushions of *Vaucheria* sp. establish themselves. By its strong growth and its silt fixing power the species strongly contributes to raising the soil level. The *Vaucheria*-cushions form an excellent germinating bed for *Puccinellia maritima*, the sea spear grass.

In general *Puccinellia* appears on the level of mean high water at neap tide (M.H.W.N.), forming very rapidly large tussocks, which within

a few years stool out to large vegetation floes in the *Salicornietum*. Finally the floes unite, incompletely, the borderline being always indicated by a very narrow gully. The difference in height between *Salicornietum* and *Puccinellietum* in the rule amounts to 5—10 cm. The grass mat developed in this way has been described as *Puccinellietum maritimae*. Beside *Puccinellia* this vegetation also contains much *Salicornia europaea*, if only in little, faintly ramified, specimens and especially in holes; *Suaeda maritima* and more rarely *Aster tripolium, Spergularia marginata* and *Atriplex hastata* have been noted in the investigated territory. The density of *Vaucheria* sp. decreases, but the species is always present in the dense algal film formed by *Rhizoclonium riparium* and the Cyanophyceae *Lyngbia aestuarii, Anabaena torulosa* and *Microcoleus chthonoplastes*. This algal film is often scarcely developed however.

On the level of mean high water at spring tide (M.H.W.S.), which coincides with + 120 cm N.A.P.[1]), *Festuca rubra* begins to dominate in a vegetation, characterized by the presence of *Armeria maritima* and *Cochlearia anglica*. In this community, described as *Armerieto-Festucetum*, the plants of the *Puccinellietum* occur but sparsely. In the algal film *Vaucheria* sp. is very rare and is nearly completely substituted by *Rhizoclonium riparium*. This vegetation is submerged during storm-floods and extreme high springtides only.

In the territory already mentioned the author marked out a transect on 30 July 1953, which was studied in the first week of August. From the mudflat up to the dike 14 sample-plots of 1 m^2 surface, at intervals of 10 m have been investigated phytocenologically with the estimating method of BRAUN-BLANQUET (Pflanzensoziologie, 2nd edition, Wien, 1951).[2])

After this the actual numbers of *Alderia, Limapontia* and of the pulmonate snail *Phytia myosotis* were counted. Besides, the sample plots were pictured to express as clearly as possible the structure of the biotopes. The results of these surveys figure in table 1 and figs. 3 to 5.

The position with respect to M.H.W.S. was determined by placing wooden sticks, painted with water-colour. As soon as the ebb stream began, the highest water-level could be read. Thus it was possible to make a diagram of the salt-marsh relief (fig. 2).

[1]) N.A.P. i.e. New Amsterdam Watermark, the Dutch standard level.

[2]) The estimating method of BRAUN-BLANQUET consists in making a complete list of species occuring in a certain sample-plot. Then the abundance and the area covered by each species is estimated and expressed by means of a figure, according to the following scale:

+ = few specimens
1 = rather many specimens
2 = very many specimens, or covering 5—25% of the sample plot
3 = covering 25—50% of the sample plot
4 = covering 50—75% of the sample plot
5 = covering 75—100% of the sample plot.

By the phanerogames a second figure expresses the sociability of the species, according to the following scale:

1 = single
2 = little tussocks
3 = large tussocks and groups
4 = large not closed carpets
5 = homogeneously closed vegetation.

TABLE 1. Zonation on the Balgzand.

Survey no.	1	2	3	4a	4b	5	6	7	8	9	10	11	12	13	14
Herbaceous layer in %	10	< 5	5—10	40	100	15—20	5—10	100	100	100	100	100	100	100	100
Algal layer in %	40	10	20	60	< 5	40	30	25	5	5	5	< 5	< 5	20	< 5
Depth in cm beneath M.H.W.S.	26	27,5	29	26	26	30	28	21	20	18	15	18	11,5	9	6,5
Phanerogames:															
Salicornia europaea	2.2/3	1.2	2.2	3.4	2.1	2.2/3	2.1/2	3.4	3.3	3.3	3.3	2.3	2.2	1.1	1.1
Puccinellia maritima	+.2	+.1	—	+.1	5.3	+.2	+.1	4.4	5.4	5.4	5.3	5.3	5.4	5.5	5.5
Suaeda maritima	—	—	—	—	+.1	—	—	+.1	+.1	+.1	+.1	1.1	1.1	+.1	+.1
Aster tripolium	—	—	—	+.1	+.1	—	—	( )	—	—	—	+.2	—	—	—
Spergularia marginata	—	—	—	—	—	—	—	+.2	—	—	—	—	—	—	—
Atriplex hastata	—	—	—	—	—	—	—	—	—	+.1	—	—	—	—	—
Algae:															
Vaucheria sp.	3	2	2	4	+	3	3	2	1	1	1	+	+	2	+
Enteromorpha sp.	+	+	+	1	+	+	+	1	—	—	—	+	+	1	+
Anabaena torulosa	1	+	—	—	—	1	1	+	—	—	—	—	—	—	—
Rhizoclonium riparium	—	—	—	+	1	—	—	1	+	+	+	+	+	1	+
Ulva lactuca	→ +	—	—	→ 1	—	—	—	—	—	—	—	—	—	—	—
Cladophora fracta	—	—	—	—	→ +	—	—	—	—	—	—	—	—	—	→ +
Mollusca:															
Alderia modesta	7	—	—	14	—	10	16	5	( )	—	—	—	—	—	—
Limapontia depressa	1	—	—	5	—	3	4	17	4	3	—	5	—	10	—
Phytia myosotis	—	—	—	—	—	—	—	2	1	85	14	5	13	—	2

Notes to table 1.

Survey 4 (fig. 3) was clearly divided into 2 parts each with a homogeneous vegetation. Therefore both parts were surveyed separately.

In the table → indicates that the algae have been washed in during high tide and maintain themselves, though they do not really belong to this zone. When a plant or mollusc happens to be absent from the plot investigated though actually occurring in the zone, this has been indicated by ( ).

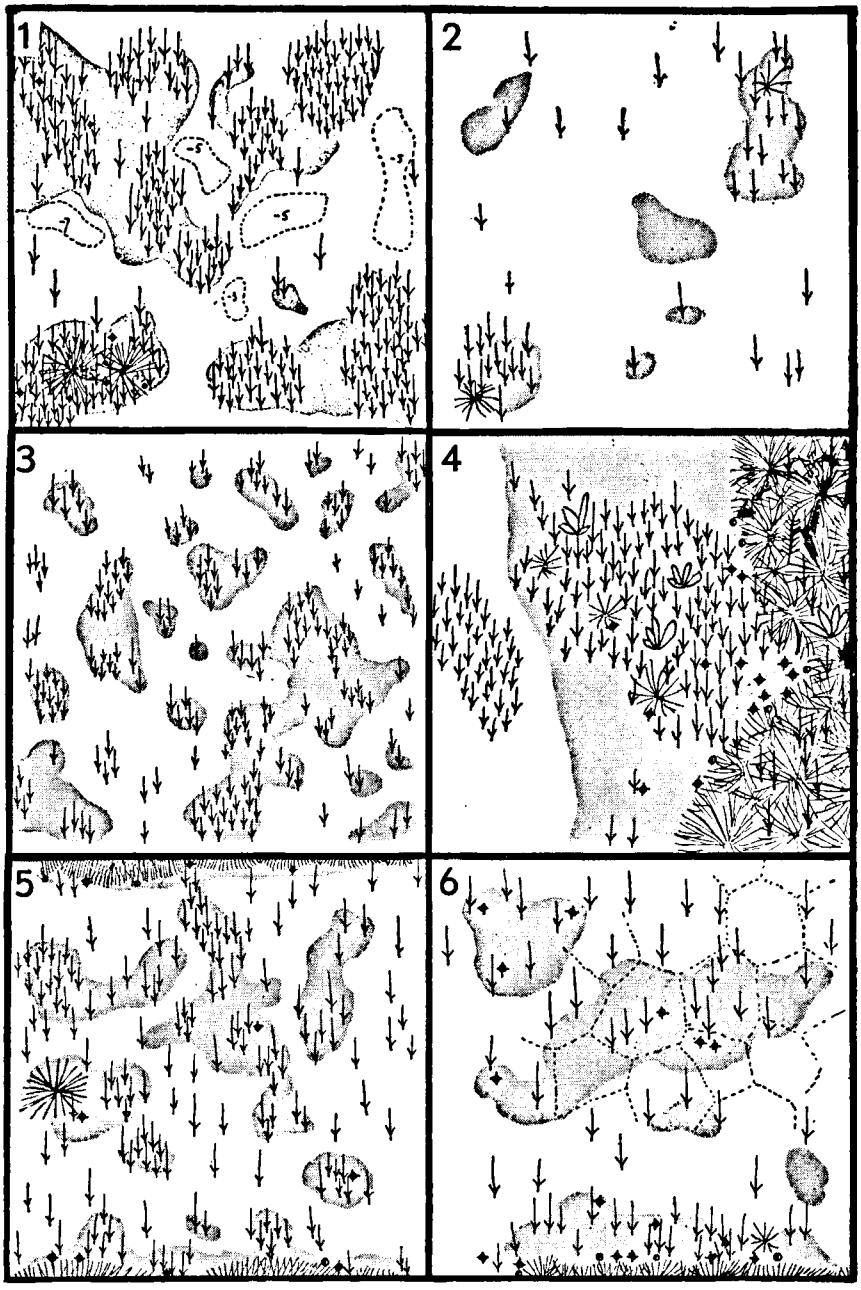


FIGURE 3. Surveys 1 to 6.

The diagram clearly shows, that the vertical range of *Alderia modesta* on the salt marsh is much more limited than that of *Limapontia depressa*. It was found only in the belt between + 90 and + 100 cm

N.A.P., on both sides of the line of M.H.W.N., in vegetations which may be classified into the *Salicornietum strictae* and the initial phase of the *Puccinellietum maritimae*. *Limapontia depressa* on the contrary, occurs in the transect from + 90 to + 111 cm N.A.P. (beyond this it has been found to near M.H.W.S.), thus likewise in the *Salicornietum*, but also in the whole *Puccinellietum*-belt, and with its optimum in the latter association. The distribution on the salt-marsh, as given in fig. 2, however, may easily give rise to misinterpretations. In pure *Salicornia*-vegetations both species are wanting or very rare. It appears that in the *Salicornietum* the animals occur exclusively on the *Vaucheria*-patches and particularly on the cushions situated in the neighbourhood of the *Puccinellia*-tussocks. In the initial stages of the *Puccinellietum* the slugs have been found nearly always at the margins of the vegetation floes.

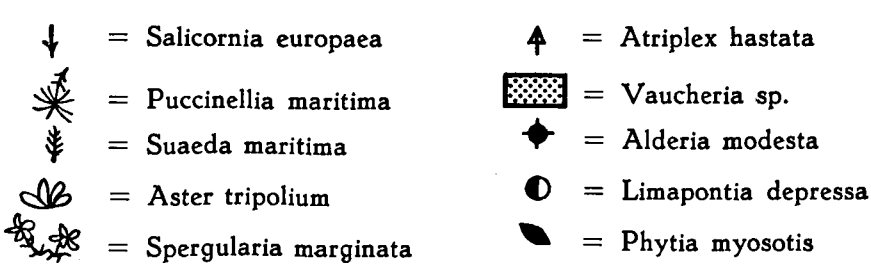
Contrary to *Limapontia*, *Alderia* creeps much farther from this protecting marginal zone, for sunning, as already recorded by ALLMAN (1846). They are, however, dependent on the hiding places in their direct surroundings. The margins of the grass-tussocks, but also the shrinking rents in the bottom of small creeks, dried up during low tide, are utilized by the animals for this purpose. During insolation they are grazing still on *Vaucheria* sp., but they are feeding in the sheltering marginal zone also.

Usually *Limapontia* does not leave the marginal zone, but it occurs in rather large numbers on the algal film under the closed *Puccinellia*-mat. They are evidently more sciaphilous than *Alderia*.

In my laboratory experiments, carried out in glass vessels, in 100% of the cases all specimens of both species crept from light to dark.

Considering the marginal concentration of both species we may conclude that on the Balgzand *Alderia modesta* is a characteristic animal for the initial phase of the *Puccinellietum maritimae*, and that *Limapontia depressa* may be considered as a characteristic animal for this association as a whole. On the Balgzand the slugs were not observed in other communities. In other salt-marshes, however, the animals have sometimes been found in other communities also. On the Normer in the related vegetation of *Obione portulacoides* and *Limonium vulgare*, which is submerged during springtides, both species are common. In the beginning of September 1952 *Limapontia depressa* had been found by W. G. BEEFTINK on a salt-marsh north of Kats in the island of Noord Beveland, in the *Artemisietum maritimae* and in the *Armerieto-Festucetum*, both communities situated above M.H.W.S. As this species has pelagic larvae, it is most probable that they established themselves there during an extremely high spring tide, thus representing an exceptional case.

Symboles used in figures 3 to 5.



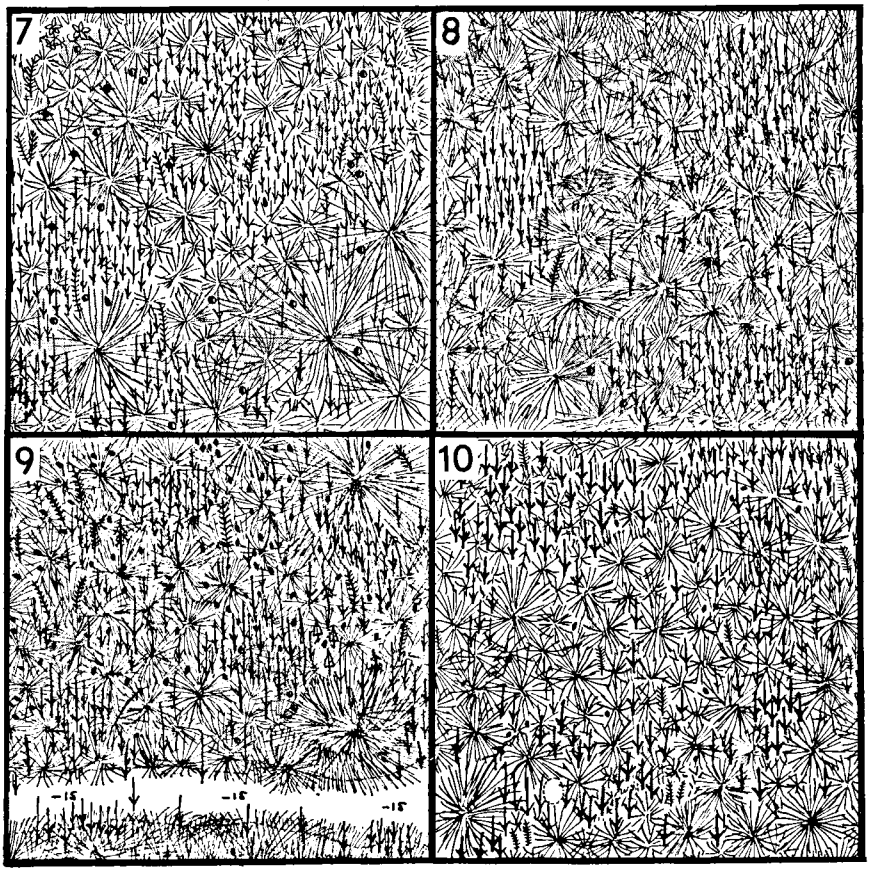


FIGURE 4. Surveys 7 to 10.

The pulmonate snail *Phytia myosotis* occurs on the Balgzand exclusively in the *Puccinellietum maritimae*. It is a detritus feeding animal, which reaches a very high optimum at + 102 cm N.A.P. Although it often has been found on or under plants it is certainly not bound to them, as is evident from the observation of A. F. MULDER and J. H. STOCK, who observed the animal near the sluices of IJmuiden under stones. In captivity the animal dies very soon.

Although *Alderia* and *Limapontia* on the Dutch coast mainly live on salt-marshes, there are also some localities with different conditions. ENGEL, GEERTS and VAN REGTEREN ALTENA (1940) e.g. discovered *Alderia* along the Nieuwe Waterweg in an open *Vaucheria*-field and both species in the *Vaucheria*-undergrowth of a *Phragmites*-vegetation. Such conditions have been found by the author only on the Ventjagerplaat in the Hellegat, on the island of Voorne and near IJmuiden. All these localities have in common a rather large tidal amplitude and a rather low, often very variable salinity.

On 21-VII-1952 the author found on the Ventjagerplaat the following zonation (fig. 6):

1. a bare clayish mud-flat.

2. a closed *Vaucheria*-field with *Fucus vesiculosus* on scattered stones. On *Vaucheria Alderia modesta* was very numerous.
3. the *Scirpetum maritimae*, locally replaced by a *Spartina townsendii*-sociation. In the undergrowth *Vaucheria* sp. was predominant; upon it many *Alderia* and a few *Limapontia* were found.

Alderia occurs on the Ventjager on the extreme westpoint only; eastwards it soon disappears, although *Vaucheria* sp. grows yet very luxuriantly there. Probably it lives here near the limit of its adaptability. Experiments have shown, that it can stand very low salinities for a short time, although the limiting salinities in nature are always higher. On the eastern part of the Ventjagerplaat *Schoenoplectus lacustris*, which has been considered a real glycophyt, occurs in rather large quantities.

On 30-VIII-1953 the mudflat in the trailerport of IJmuiden, near the blast-furnaces was investigated. The following zonation was observed from low to high (fig. 7):

1. sandy mud-flat without any vegetation.
2. a closed *Vaucheria*-field, in the northern corner of the territory continuing unchanged as undergrowth of the *Scirpetum maritimae* and even of a *Phragmites*-vegetation.
3. bare sand without vegetation.
4. floodmark with *Cakile maritima* and *Salsola kali*.
5. dune vegetation with *Ammophila arenaria*.

Alderia modesta was very common in the *Vaucheria*-vegetation, wanting, however, in the *Phragmites*-undergrowth. The *Vaucheria*-belt was c. 10—15 m broad, and situated nearly on one level. Just before the margin of the belt lay some stone-heaps on which *Fucus vesiculosus* reached its upper-limit, which coincided with the lower limit of *Vaucheria* sp., and also with M.H.W.N. This agrees very well with the observations on the Balgzand, where *Vaucheria* sp. settled also near M.H.W.N. While the *Vaucheria*-cover was very closed, it was difficult for the *Alderia*'s to hide. Most *Alderia*'s were concentrated along the margins of the cover, which sometimes was as thick as 5 cm and around open spaces in the vegetation. In the surveys 1 and 2 (Tab. 2) this is clearly shown. Survey 1 was taken in a closed vegetation near the margin of the plot; 20 *Alderia* specimens were collected from it. In survey 2, which had a more open character, 57 specimens had been found. Locally the numbers per m^2 were much higher, e.g. near the stone-heaps the author saw 31 specimens in a dm^2. These extensive *Vaucheria*-fields are extremely

TABLE 2. Habitat of *Alderia modesta* near IJmuiden

Survey no.	1	2	3
Herbaceous layer in %	—	—	10
Algal layer in %	100	60	95
Phanerogam:			
Scirpus maritimus	—	—	2.1
Algae:			
Vaucheria sp.	5	4	5
Enteromorpha prolifera	+	+	—
Mollusca:			
Alderia modesta	20	56	37

vulnerable. In the beginning of September 1953 the whole field had been detached from the bottom, rolled up and washed ashore by a S.W. storm.

In the *Scirpus maritimus*-vegetation only, the field remained unimpaired. By its rapid growth *Vaucheria* sp. is able to repair the damage within a year.

Especially in many localities in Zeeland, the vegetation of the salt-marshes has been disturbed by the mass-occurrence of the grass *Spartina townsendii*, which may be predominant in the whole belt between M.H.W.S. and M.S.L. (mean sea level). *Vaucheria* sp. is one of the few species, which hold out in this vegetation, unless *Spartina* becomes too dense. Especially in spring, when the *Spartina*-vegetation is yellow yet and bare, we may meet with *Vaucheria* as well as with *Alderia modesta* and *Limapontia depressa*.

The habitat descriptions, given by other authors usually are not accurate, e.g. QUICK (1950) wrote that *Limapontia depressa* had been found commonly in the "*Juncus*-vegetation." Nevertheless the descriptions in outline agree with my observations. Nearly all authors found *Alderia* and *Limapontia* on the salt-marshes, where they were exposed to tidal movements.

Nevertheless some dates are known about localities, where the animals live in pools and holes, cut off from the sea and only occasionally reached by exceptionally high floods. LUTHER (1902) collected *Alderia* in a little pool on the sea shore near Helsinki; SCHULZ (1936) found this species along the Kiel Bay in little pits and cattle marks, which the sea reached during storms only. In such a pool *Limapontia depressa* was met with by MULDER & VIERGEVER in the Zwarte Polder near Cadzand. Comparable with these pools are the waters, embanked by men, in which now and then water can be let in. Such a locality was described in England by FISHER-MC MILLAN (1949). In the Netherlands such localities also occur, viz. the "Bol" in the island of Texel (*Alderia modesta*), the salt-marsh of Westhoek (*Alderia modesta*) and the Westerkwelder in the island of Schiermonnikoog (*Limapontia depressa*).

Some specimens of *Alderia modesta* have been found in deeper water, viz. up to 14 m depth. (ODHNER, 1907; RASMUSSEN, 1951). It may be questioned, however, if these animals were autochthonic indeed. Possibly these were specimens, transported by stormfloods from their real habitat. RASMUSSEN (1951) found them in 2—5 m deep water, but lateron in a more typical habitat, on c. 1 km distance from the first locality (EVANS, 1953).

Special reference may be made to the paper of KEVAN (1939) who also found *Alderia* and *Limapontia* on salt-marshes, but who gives a somewhat wunderful hypothesis on the distribution of the slugs over the salt-marsh. Unfortunately his rather obscure description of the habitat hampers the right interpretation of his data. I consider it rather certain, that "low water mark" in his paper, in fact is another line, viz. the limit between salt-marsh and mud flat. He mentions e.g. *Fucus* from below "low water mark", while this genus on the contrary is eulittoral. According to his figure *Alderia* should deposit its egg-masses on the aestuarine mud below "low water mark", while the animals should go

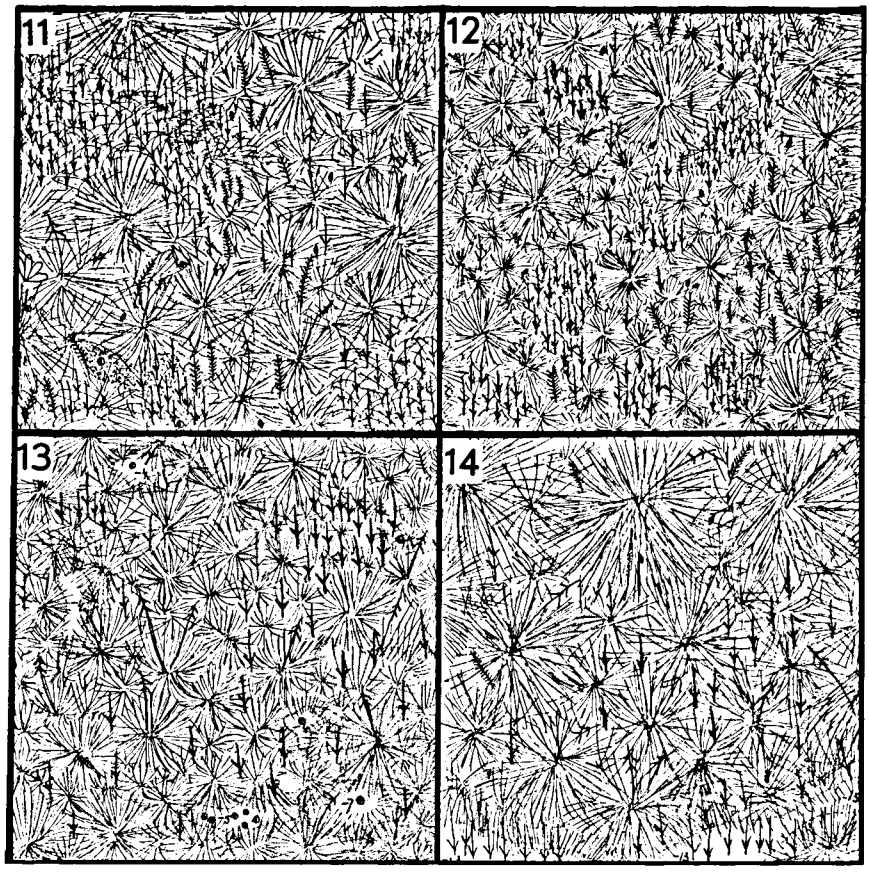


FIGURE 5. Surveys 11 to 14.

and feed nearly up to the spring high water line. This is very improbable, for then the slow animals should have to creep from "high" to "low water mark" for spawning. On the Balgzand the author observed, that *Alderia* deposited its spawn-masses in the total vertical range of its occurrence, without making far excursions over the salt-marsh. KEVAN supposes the veliger-larvae of *Limapontia depressa* to metamorphose into little slugs in the territory below "low water mark"; with increasing growth the slugs should proceed higher, up to the spring high water line. On the highest part of the salt-marsh they should spawn. This idea also is in contradiction to my observations on the Balgzand. Spawn masses have been found in the whole range, inhabited by *Limapontia*.

Summarizing, we may conclude, that *Alderia* and *Limapontia depressa* inhabit 3 different types of habitat:

1. polyhalinous environment with tidal movement, living mainly in the *Puccinellietum maritimae*.
2. mesohalinous environment with tidal movement, occurring in the

Vaucheria-fields and in the undergrowth of the *Scirpetum maritimae.*

3. small pools and pits, which can only be reached by the sea during very high floods; here they have been found occasionally; this type is the only one along the Baltic coast.

Both species show the marginal concentration phenomenon. *Alderia* has a more limited vertical range than *Limapontia depressa.*

PERIODICITY

Alderia modesta was found in the Waddenzee by the author from the beginning of April to the end of December. Mr. MULDER kindly informed me, that at IJmuiden he also found *Alderia* in February. Spawn masses were found during the whole period from April to December. *Limapontia depressa* was observed from the beginning of April to the beginning of November, during the whole period with spawn masses.

At the beginning of April 1953 I did not find the slugs on the salt-marshes of the island of Terschelling, where they are common in summer. Some days later adult specimens appeared to be present in similar localities in the island of Ameland. We may suppose, that the animals had hibernated on the salt-marshes hidden in the mud or covered by the algal layer. Probably the animals appear when temperature exceeds a certain value and then begin to spawn promptly. As the egg-masses were found during a great part of the year in the sea the veliger larvae also occur during a great part of the year. The young, just metamorphosed animals will also arrive in the salt-marsh during the greater part of the year and continually rejuvenate the population. I have never observed sudden increase of young slugs. In the higher parts of the salt-marsh where *Limapontia depressa* mainly occurs, it can establish itself within a fortnight (spring tide). It is impossible, however, to group the rapidly growing animals according to their age, because their length varies a great deal and depends on their condition.

KEVAN (1934) did not find the species as from July on the salt-marshes of Tynningham (Scotland); they appeared again in November. In the winter months they were, however, less numerous than at the end of autumn and in spring. KEVAN wondered whether the animals, found in spring, were the same as those he had found in autumn. Cultures proved this to be the case. (KEVAN, 1941).

In November he found young as well as adult animals; the young animals had no doubt developed from just metamorphosed veligers. The few adult specimens, however, must have aestivated. Probably they were those spring animals which had not spawned before the beginning of the unfavourable season. His finding less animals in March, may be due to the fact that the addition from metamorphosed veliger larvae had not yet taken place.

The complication caused by the summer being a second unfavourable season, may have induced KEVAN to misinterpret his observations, as he supposed to have to do with 2 generation-waves. Moreover he was the first to study the life-cycle of these interesting slugs, so that he could not consult any literature. The yearly life cyles of *Alderia* and *Limapontia* in the Waddenzee agree very much. Also on Tynningham salt-marsh both species had a similar life-cycle.

Since 1951 the author has found *Alderia modesta* every year in considerable numbers; *Limapontia depressa* also, except in the year 1954. In that year some individuals were found on the Balgzand in April. They were missing during the rest of the year; also in other localities, where they were numerous in the preceding years.

I have searched for it at Wimereux, Voorne, Balgzand, Normer, Frisian coast and Terschelling, in vain, however. The cause of their absence is unknown. Perhaps the strong winter 1953—1954 has been disastrous for the hibernating individuals, although a few specimens had been found still in spring. Maybe also, the veliger larvae which remained in the sea did not survive the winter. The dry spring and the exceptionally wet summer also may have been of influence. Perhaps the combination of all these unfavourable circumstances is responsible for this curious absence.

It is remarkable, that *Alderia* on the contrary was common in 1954. The author did not have the opportunity to continue his observations after 1954.

FOOD

With a single exception *Alderia modesta* and *Limapontia depressa* have been found on *Vaucheria* sp., so that it seems very probable, that they feed on this alga. In litterature it is recorded, that *Enteromorpha* sp., Conferva (collective name for filamentous algae) and even *Zostera* sp. should also have been used as food. Malacologists often have described the vegetable or animal substrate on which they found the slugs as food, without investigating whether the animals really utilized it as such. EVANS (1953) described the manner in which *Alderia* pricked and sucked out the *Vaucheria* filaments with remarkable rapidity, up to 10 filaments a minute. According to him *Alderia* should have to be con-

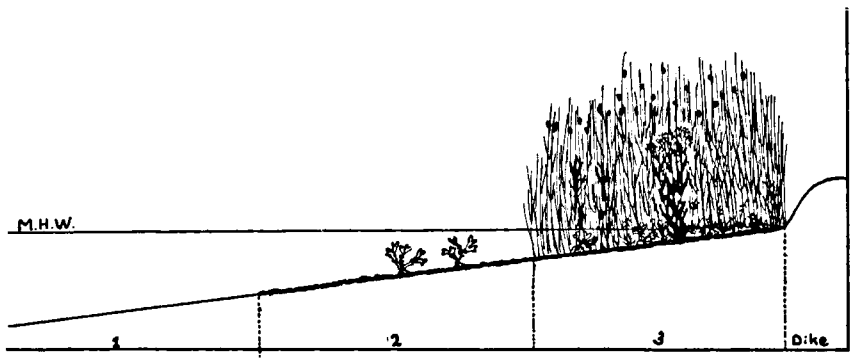


FIGURE 6. Zonation on the westpoint of the Ventjagerplaat in the Hellegat. 1. Bare clayish mudflat. 2. *Vaucheria*-field with *Alderia modesta* and on stones scattered *Fucus vesiculosus*. 3. *Scirpetum maritimae*, with *Vaucheria*-undergrowth, on which many *Alderia modesta* and a few *Limapontia depressa*.

sidered as a specialist on physiological grounds, because *Vaucheria* should have oil as assimilation product and should not possess pyrenoids. The last only partly holds true, for pyrenoids occur in different salt-

marsh species, a.o. in the common *Vaucheria compacta*. RASMUSSEN (1951) dredged his *Alderia* specimens on *Chaetomorpha* sp.; thus when the normal food is lacking it seems possible for *Alderia* to switch over to a Cladophoraceae diet. This however, would be contrary to its food-specialism, for Cladophoraceae do not contain oil. Yet it has by no means been proved that *Alderia* really had eaten *Chaetomorpha* sp.

At the Zoological Station at Den Helder I tried to show in another way, that *Alderia* and *Limapontia depressa* feed on *Vaucheria* sp. indeed.[1]) To this end I used the method, developed by STEHOUWER (1952) and BRAAMS & GEELEN (1953) for testing the slugs *Aeolis papillosa* and *Cratena aurantia* as to their preference for certain sea-anemones and hydroids. The animals were put in a tank and there they had the choice of 2 water currents, of which one had been led through the „food" and the other one served as "check". The experiment consisted of 3 parts. The first time the *Alderia*'s has to choose between *Rhizoclonium riparium* and "check"; the result was that the animals didn't react. After this the animals had to choose between *Vaucheria* sp.[2]) and "check"; finally between *Vaucheria* sp. and *Rhizoclonium riparium*. In both cases the slugs preferred *Vaucheria* sp. This experiment has been repeated with *Enteromorpha compressa* and *Percursaria percursa* instead of *Rhizoclonium riparium*, but *Vaucheria* sp. always was preferred.

This experiment failed with *Limapontia depressa*, because the animals could not creep up against the watercurrents of the siphon. *Alderia* also often could not manage it, although the current was very slow.

In stagnant water the choice tests succeeded for both species, 4 *Alderia*'s were brought into a vessel with a *Vaucheria*-patch and a *Rhizoclonium riparium*-patch. The results were clearly positive.

After	40 minutes :	1	specimen on *Vaucheria*
	50	2	
	95	2	
	125	3	
	145	4	

While creeping about, *Alderia* sometimes came for a short time on *Rhizoclonium*.

The same test was carried out with 7 *Limapontia*'s with the following result.

After	65 minutes :	2	specimens on *Vaucheria* ;	1	specimen on *Rhizoclonium*
	105	3		1	
	135	3		2	
	155	4		1	
	205	6		1	

The choice-test was repeated with 11 *Alderia*'s and 13 *Limapontia*'s, but now a number of algae was used as choice-material viz. *Vaucheria* sp., *Rhizoclonium riparium*, *Percursaria percursa* and *Enteromorpha compressa*. The results have been listed below (table 3).

[1]) EVANS' paper was unknown to me at that moment.

[2]) *Vaucheria* sp. was always sterile, thus not to be indentified. Once *V. litorea* has been collected, but it is by no means sure that the material used for my experiments belonged to this species.

TABLE 3. Results of choice-test with *Alderia* (11 specimens) and *Limapontia* (13 specimens).

Time in hours	1½		2½		3		3½		4	
Alderia (a) and *Limapontia* (b) on some algae	a	b	a	b	a	b	a	b	a	b
Vaucheria sp.	6	5	7	6	9	8	11	10	11	10
Rhizoclonium riparium	—	2	—	3	—	2	—	2	—	2
Percursaria percursa	—	—	—	—	—	—	—	—	—	—
Enteromorpha compressa	—	—	—	—	—	—	—	—	—	—
Creeping about	5	6	4	2	2	3	—	1	—	1

A variation of this experiment has been carried out by using as choice-material *Vaucheria dichotoma*, a species from fresh and brackish water, which I had adapted to sea water, and which the slugs in nature would never meet with. *Vaucheria* sp. from the salt-marsh had been put in the vessel for 5 minutes and after this removed. In the afternoon 6 *Alderia*'s and 7 *Limapontia*'s were put in it. Next morning 5 *Limapontia*'s were found on *Vaucheria dichotoma*, 1 specimen on *Rhizoclonium riparium* and 1 specimen wandered about.

Three specimens of *Alderia* were found on the spot, where *Vaucheria* sp. had been lying, 1 specimen was on *Vaucheria dichotoma* and 2 yet crept about.

From these experiments we may conclude, that *Alderia modesta* is very fastidious, eating certain *Vaucheria* sp. from the salt-marsh only. *Limapontia depressa*, on the contrary, satisfies itself with all *Vaucheria* species, and exceptionally even with *Rhizoclonium riparium*. Ir. W. G. BEEFTINK informed me that on the Zeeland salt-marshes he observed *Limapontia* in absence of *Vaucheria* sp., and, if present, sometimes without any relation to *Vaucheria*. As *Vaucheria* sp. nearly always is present

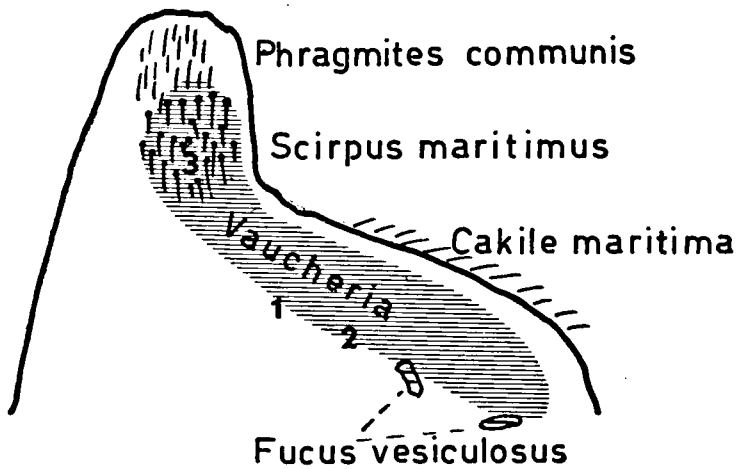


FIGURE 7. Sketch map of the *Vaucheria*-fields in the trailerport of IJmuiden. The figures 1—3 indicate the localities of the surveys 1—3, listed in table 2.

in the algal layer it is difficult to prove this. According to C. SWENNEN, however, *Limapontia depressa* in captivity feeds very well on *Cladophora*, a genus closely related to *Rhizoclonium*, also possessing very large cells.

ACKNOWLEDGEMENTS

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