

Observations on the distribution of land snails in the woods of the IJsselmeer polders

K. REININK

Institute for Ecological Research,
Arnhem, The Netherlands

1. INTRODUCTION

An investigation of the distribution over the IJsselmeerpolders of such animals as terrestrial molluscs, which probably migrate very slowly, seemed worth-while because this distribution might provide indications concerning the rate and mode of colonization. As the main emphasis was put on colonization, it would suffice to make the observations in a single type of terrain distributed over the Noordoostpolder and the polders Oostelijk and Zuidelijk Flevoland. On this basis, the study was restricted to the deciduous woods, which as a rule form the habitat with the greatest variety of species.

The following questions were to be answered:

1. Can migration to planted woods be explained by transportation on plant material when the plantations were established?
2. Can differences in the composition of the mollusc fauna be explained by environmental differences within the woods?
3. Are there indications that either distance from the "old land" or the age of the woods exerts an influence on the number of species present?

2. THE WOODS IN WHICH THE STUDY WAS PERFORMED

The planting of woods in the various polders was started soon after reclamation was completed. In the Noordoostpolder (which was reclaimed in 1942) about 5% of the land is now covered with woods, in Oostelijk Flevoland (1957) eventually about 15%, and probably a still higher percentage in Zuidelijk Flevoland (1968). The woods were planted

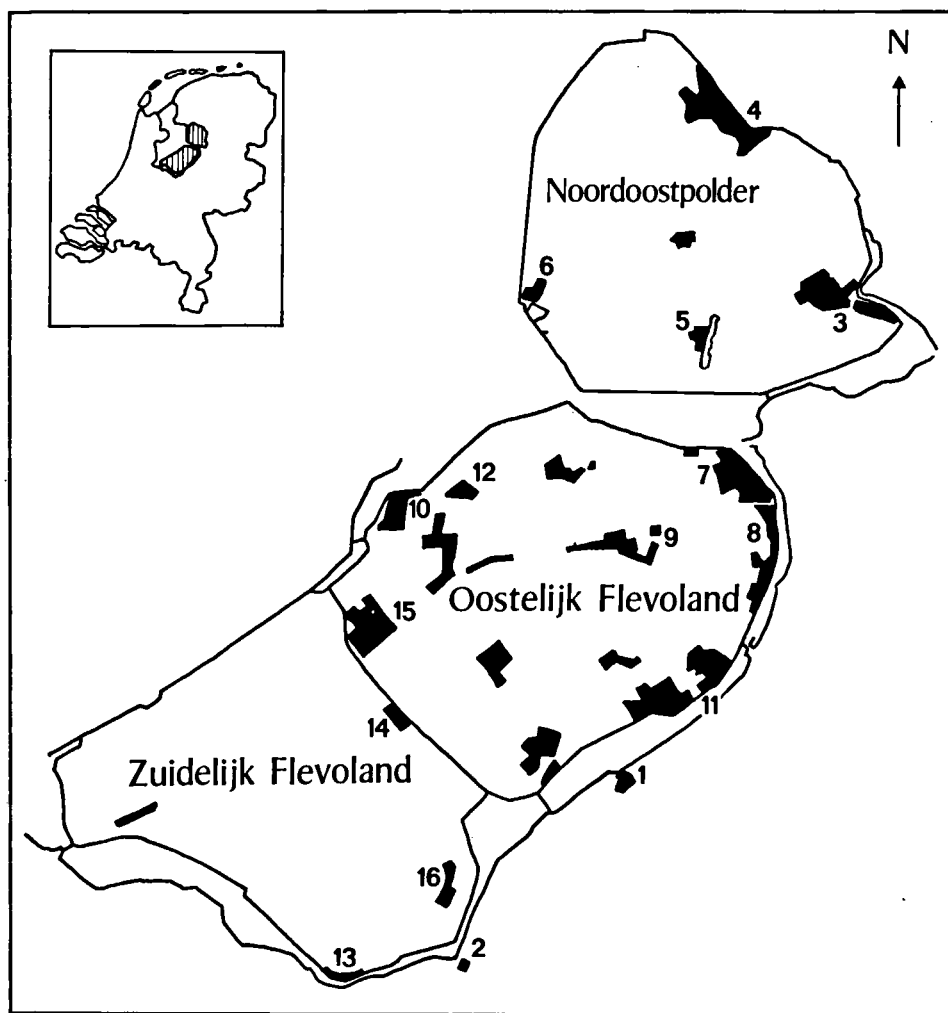


Fig. 1. Location of the woods in the IJsselmeerpolders. The investigated woods are indicated as follows: 1, Hierden; 2, Oldenaller; 3, Voorsterbos; 4, Kuinderbos; 5, Schokkerbos; 6, Urkerbos; 7, Roggebotzand; 8, Revebos; 9, Dronten; 10, Lelystad; 11, Oecologisch Reservaat; 12, Visvijverbos; 13, Laakse Strand; 14, Knarhaven; 15, Horsterwold; 16, Hollandse Hout.

on relatively "new" soils with a high calcium content due to the presence of numerous shells of marine molluscs. Initially such fast-growing species as alders, willows, poplars, and sometimes ash trees, to act as a wind-break, were planted predominantly, and this also helped slower-growing species to survive. The planting material used in the Noord-oostpolder came mainly from a nursery near Vollenhove, the material for the polders

Oostelijk and Zuidelijk Flevoland from a nursery in the Roggebotzand.

The location of the investigated woods is indicated in fig. 1. Two small woods on the adjacent old land were included in the study to find out whether the mollusc fauna there showed any important divergence from that occurring in the polder woods. It was not possible to find places with roughly the same vegetation in all areas; there are appreciable differences in the composition of the tree and herb layers. Table 1 shows the main characteristics of the various sites. The year of planting varied from 1944 to 1968, and classification according to age corresponds roughly with the age of the polders. The only earlier plantation is the one on the Laakse Strand in Zuidelijk Flevoland, which was planted on a dry strip outside the dike within which the polder was still under water. Because of the wide difference in the age of the woods, the cover also differs strongly, the youngest woods still being very open. Almost all of the investigated woods were planted; the only spontaneous growths are the willow wood near Knarhaven and the one on the wet part of the Laakse Strand in Zuidelijk Flevoland, which bears some resemblance to a tidal wood because cowslips (*Caltha palustris*), and angelica (*Angelica archangelica*) have become established between the willows. A few of the older woods have a well-developed moss layer. Some data on the soil and the vegetation are also given in table 1.

Table 1a. Data concerning the sampled wooded areas (September, 1973).

	No.	Area	Year of planting	Origin	Distance to old land in km	Predominant tree species	Predominant herbs
Old land	1	Hierden	1949	planted	-	Ash	Stinging Nettle
	2	Oldenaller	1963	planted	-	Ash	Rough meadow-grass
N.O. polder (1942)	3	Voorsterbos	1944	planted	2.3	Ash	Stinging Nettle
	4	Kuinderbos	1951	planted	0.5	Ash	Stinging Nettle
	5	Schokkerbos	1952	planted	5.6	Ash	Stinging Nettle
	6	Urkerbos	1955	planted	17.3	Ash	Bushgrass
O. Flevo-land (1957)	7	Roggebotzand	1959	planted	1.2	Ash+Poplar	Stinging Nettle
	8	Revebos	1959	planted	1.0	Ash	Bushgrass
	9	Dronten	1964	planted	9.0	Ash+Alder+Popl.	Rough meadow-grass
	10	Lelystad	1964	planted	22.5	Ash+Poplar	Rough meadow-grass
	11	Oec. Reservaat	1967	planted	1.7	Willow	Rough meadow-grass
	12	Visvijverbos	1970	planted	21.0	Alder+Poplar	Rough meadow-grass
Z. Flevo-land (1968)	13a	Laakse Strand dry	1964	planted	0.7	Poplar	Stinging Nettle
	13b	Laakse Strand wet	1962	spontaneous	0.7	Willow	Fiorin
	14	Knarhaven	1968	spontaneous	11.4	Willow	Coltsfoot

Scientific names of plants: Alder *Alnus glutinosa* (L.) Vill.; Ash *Fraxinus excelsior* L.; Poplar *Populus* spec.; Willow *Salix* spec.; Bushgrass *Calamagrostis epigejos* (L.) Roth; Coltsfoot *Tussilago farfara* L.; Fiorin *Agrostis stolonifera* L.; Rough meadow-grass *Poa trivialis* L.; Stinging Nettle *Urtica dioica* L.

Table 1b.

	No.	Tree layer % cover	Herb layer % cover	Moss layer % cover	Soil type	pH-H ₂ O	Calcium content
Old land	1	90	100	-	sand+peat	4.8	< 0.1
	2	90	100	80	light sandy clay	4.9	< 0.1
N.O.polder (1942)	3	90	70	90	sandy clay	8.0	4.2
	4	80	100	60	sandy clay	7.8	0.6
	5	80	50	70	sandy clay	7.8	10.1
	6	40	100	90	sand+boulder clay	7.0	< 0.1
O. Flevo- land (1957)	7	50	100	80	sandy clay	7.5	2.3
	8	80	100	90	sandy clay	7.2	0.3
	9	70	80	2	clay	7.6	2.6
	10	40	70	10	sandy clay	7.9	2.0
	11	90	40	-	sandy clay	7.6	3.6
	12	50	100	-	sandy clay	7.9	3.5
Z. Flevo- land (1968)	13a	20	5	1	sand+sandy clay	7.6	1.5
	13b	90	80	1	riversand+sand	7.3	-
	14	60	30	1	sandy clay	7.6	4.3

3. METHODS

3.1. Sampling

Comparative sampling was performed in September 1973; this month was chosen because, according to the literature (Gittenberger et al., 1970), land snails are most active in the relatively damp autumn and specimens of most of the species are adult at that time. This was verified in 1974 by sampling in four periods (April, June, August, and October) in those woods on the old land and in each of the three polders where the highest number of species had been found in September 1973. In October 1974 a one-year-old wooded plot in the Horsterwold in Zuidelijk Flevoland and a two-year-old plot in the Hollandse Hout in Oostelijk Flevoland (see fig. 1) were also sampled to find out whether land snails occur in newly planted woods.

The sampling procedure was as follows: in a visually selected homogeneous area in a wood, ten sampling points were selected on the basis of random numbers, each measuring 1/16 m². Ökland (1930) took 12 samples from 1/16 m² to compare areas and Mörzer Bruyns (1947) used two or more samples from plots measuring 1/4 m². For sampling, a metal frame (inside length of the sides: 25 cm) was placed over the herb layer. Within this frame, the plants were examined for snails, cut off close to the ground and removed. Next, the litter, the moss layer (if any) and the thin layer of humus were collected in plastic bags and taken to the laboratory, where the samples were dried in an oven at 35°C and separated into fractions with five sieves to simplify examination. In addition use was made of specimens collected in 1971 in a study with funnel traps for ground-beetles (Coleoptera: Carabidae) in a number of the plots.

3.2. Determination of environmental factors

In each plot, ten samples were taken from the upper 5 cm of the soil. In these samples, the pH-H₂O (soil-to-water ratio 1:5) and the amount of free calcium carbonate were

Table 2. Terrestrial molluscs found in the woods under study. The number of individuals is given per 10 samples deriving from 1/16 m² soil surface; † = only empty shells found; x = species not found in October 1974 (applies only for sampling sites 1, 4, 7, 13a).

Land molluscs	old land		N.O. polder						O. Flevoland						Z. Flevoland				presence of living specimens
	1	2	3	4	5	6			7	8	9	10	11	12	13a	13b	14		
<i>Cochlicopa lubrica</i> (Müller, 1774)	1	-	60	32	10	3			197	16	8	-	5	-	5	7	†	12	11
<i>Zonitoides nitidus</i> (Müller, 1774)	13	-	7	-	-	1			5	31	26	46	10	1	11	1	-	11	11
<i>Trichia hispida</i> (Linnaeus, 1758)	26	†	13	36	11	-			14	1	-	9	1	-	4	3	-	11	10
<i>Euconulus fulvus</i> (Müller, 1774)	3	-	†	1	-	-			12	3	-	5	11	-	5	-	-	9	7
<i>Vitrina pellucida pellucida</i> (Müller, 1774)	†	4	3	2	-	7			3	†	12	-	3	-	-	-	-	9	7
<i>Punctum pygmaeum</i> (Draparnaud, 1801)	†	-	†	†	†	†			14	-	2	†	†	-	-	†	-	8	2
<i>Succinea</i> spec.	†	-	†	†	†	†			-	-	†	†	-	-	†	-	-	8	1
<i>Oxychilus cellarius</i> (Müller, 1774)	4	-	42	6	15	-			20	-	-	-	-	†	-	†	-	7	5
<i>Nesovitretea hammonis</i> (Ström, 1765)	7	16	-	11	-	76			-	11	-	-	-	-	†	-	-	6	5
<i>Discus rotundatus</i> (Müller, 1774)	5	†	67	-	32	-			-	-	-	-	-	†	-	†	-	6	3
<i>Vallonia excentrica</i> Sterki, 1892	-	-	†	-	†	-			†	-	15	-	-	-	21	2	-	6	3
<i>Vallonia pulchella pulchella</i> (Müller, 1774)	-	-	†	-	-	2			-	4	-	-	-	-	9	†	-	5	3
<i>Carychium minimum</i> Müller, 1774	-	-	-	17	-	-			84	-	-	-	-	-	-	3	-	3	3
<i>Vertigo pygmaea</i> (Draparnaud, 1801)	-	-	-	2	-	-			3	-	-	-	-	-	†x	-	-	3	2
<i>Helicigona arbustorum arbustorum</i> (Linnaeus, 1758)	5	-	-	†	-	-			-	-	-	-	-	-	(1971)	†	-	3	1
<i>Vitrea crystallina</i> (Müller, 1774)	6	-	-	-	-	-			-	-	-	-	-	-	-	-	-	1	1
<i>Succinea oblonga</i> Draparnaud, 1801	-	-	-	-	-	-			1	-	-	-	-	-	-	-	-	1	1
<i>Carychium tridentatum</i> (Risso, 1826)	†	-	-	-	-	-			-	-	-	-	-	-	-	-	-	1	0
<i>Acanthinula aculeata</i> (Müller, 1774)	-	†	-	-	-	-			-	-	-	-	-	-	-	-	-	1	0
<i>Cepaea nemoralis</i> (Linnaeus, 1758)	-	-	-	†	-	-			-	-	-	-	-	-	-	-	-	1	0
<i>Agopina nitidula</i> (Draparnaud, 1805)	-	-	-	-	-	-			†x	-	-	-	-	-	-	-	-	1	0
<i>Arion intermedius</i> Normand, 1852	-	1	1	2	-	-			-	-	-	-	-	-	-	-	-	3	3
<i>Arion subfuscus</i> (Draparnaud, 1805)	-	-	1	x	26	-			-	-	-	-	-	-	-	-	-	2	2
<i>Deroceras reticulatum</i> (Müller, 1774)	-	-	-	1	-	-			-	-	-	-	-	-	(1971)	-	(1971)	1	1
<i>Arion ater rufus</i> (Linnaeus, 1758)	-	-	-	-	-	-			-	-	-	-	-	-	-	-	-	-	-
<i>Limax maximus</i> Linnaeus, 1758	-	-	-	-	-	-			-	-	-	-	-	-	-	-	-	-	-
Number of living specimens	70	21	193	114	94	89			350	69	51	72	27	4	55	16	0		
Number of species	12	6	12	15	8	6			11	7	6	5	5	4	9	12	1		
Number of species with living specimens	9	3	7	12	5	5			9	7	4	4	4	2	6	5	0		

determined (the latter according to Scheibler). The soil was classified roughly in three types: clay, sandy clay, and sand.

4. RESULTS

4.1. Sampling in 1973 and 1974

Table 2 shows the numbers of species and individuals occurring in the various wooded plots. The slugs were assigned to a separate group, because only living specimens encountered during the sampling were counted; small individuals may be missed under these conditions and they can no longer be recognized in dried samples. This factor may have affected the number of individuals and species found. Since the analyses based on species abundance given below show the same results whether slugs are included or not, they were always included.

With the exception of the two plots on old land, the woods are arranged in table 2 according to age and the snail species according to the number of woods in which they were found. Values between parentheses refer to species found in 1971 in funnel traps but not in the subsequent sampling.

It is evident from table 2 that the greatest number of species (15) was found in the Kuinderbos (Noordoostpolder). The largest number of living individuals (560/m²) occurred in the Roggebotzand (Oostelijk Flevoland). In the literature (Mörzer Bruyns et al., 1959) a density of 100-400/m² is mentioned as normal for nutrient-rich woods. The high number in the Roggebotzand was due mainly to *Cochlicopa lubrica* and *Carychium minimum minimum*.

Table 3 shows the numbers of species and individuals in the various seasons in 1974. These changes were studied in the ash wood near Hierden (old land), a plot with an ash cover in the Kuinderbos (Noordoostpolder), the alder-poplar wood in the Roggebotzand (Oostelijk Flevoland), and the dry part of the Laakse Strand (Zuidelijk Flevoland). The largest number of species (16) was found in April 1974 in Hierden, the largest number of individuals (576/m²) in October 1974 near Kuinre.

The total numbers of viable species and individuals are given at the bottom of table 3. The data show a distinct pattern, i.e., an initial decrease from April to June followed by an increase in August and October. This indicates that sampling should preferably be performed in the late summer or autumn. It is striking, however, that a number of species of slugs were found most frequently in the spring. The relatively dry summer period is the least suitable for sampling.

A total of 25 species of land snails was found, including the 1971 funnel-trap data.

4.2. Migration via planting material

It was not possible in this study to directly observe the ways in which snails disperse. Since it was important to know whether the introduction could have occurred via planting material, a search was made for land snails in the tree nursery of the Rijksdienst voor de IJsselmeerpolders in the Roggebotzand as well as in a few newly planted woods. The search for snails or remnants of snails in the tree nursery did not yield any material. The plant beds in this nursery are regularly cleaned, which means that hiding places and food

Table 3. Terrestrial molluscs found in four woods in four periods of the year (1974). The number of individuals is given per 10 samples deriving from 1/16 m² soil surface; † = only empty shells found; x = species not found in October 1973.

	Hierden (old land) 1			Kuinderbos (N.O. polder) 4			Roggebotzand (O. Flevoland) 7			Laakse Strand (Z. Flevoland) 13a				Presence of living specimens
	April	June	August	October	April	June	August	October	April	June	August	October	Presence	
<i>Cochlicopa lubrica</i>	3	†	7	2	4	†	7	73 ^x	2	8	29	159	3	16
<i>Zonitoides nitidus</i>	11	†	2	2	6	-	-	5 ^x	†	†	1	9	3	13
<i>Trichia hispida</i>	12	†	7	31	6	-	†	44	†	†	†	5	4	11
<i>Euconulus fulvus</i>	1	†	†	5	1	-	†	8	3	†	†	3	†	16
<i>Vitrina pellucida pellucida</i>	†	-	†	†	-	†	†	5	†	†	†	1 ^x	†	15
<i>Punctum pygmaeum</i>	-	-	† ^x	† ^x	-	†	†	19	†	†	-	-	-	10
<i>Succinea spec.</i>	†	†	†	†	-	†	†	3	-	†	†	-	†	9
<i>Oxychilus cellarius</i>	3	†	†	3	1	†	†	7	†	†	†	-	†	10
<i>Nesovitrea hammonis</i>	9	†	13	16	2	†	2	7	†	-	-	-	†	12
<i>Discus rotundatus</i>	4	1	5	34	-	-	-	-	-	-	-	-	†	9
<i>Vallonia excentrica</i>	-	-	-	-	-	-	-	-	6	†	†	†	†	11
<i>Vallonia pulchella pulchella</i>	-	-	-	-	-	-	-	-	-	†	†	†	†	5
<i>Carychium minimum minimum</i>	-	-	-	-	-	-	-	-	-	16	1	3	34	8
<i>Vertigo pygmaea</i>	-	-	-	-	†	†	†	180	3	†	†	†	†	4
<i>Helicigona arbustorum arbustorum</i>	1	†	†	5	-	†	†	7	†	†	†	8	†	12
<i>Vitrea crystallina</i>	1	1	12	11	-	-	-	-	-	-	-	-	-	6
<i>Succinea oblonga</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	7
<i>Carychium tridentatum</i>	†	†	†	11	-	-	-	-	†	†	†	†	†	3
<i>Acanthinula aculeata</i>	-	† ^x	-	-	-	-	-	-	-	-	-	-	-	4
<i>Cepaea nemoralis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	4
<i>Arion intermedius</i>	2 ^x	1 ^x	-	-	-	6	1	-	-	-	-	-	1 ^x	1
<i>Arion subfuscus</i>	2 ^x	1 ^x	-	-	-	-	-	-	-	-	-	-	-	0
<i>Deroceras reticulatum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	2
<i>Arion circumscriptus Johnston, 1828</i>	3 ^x	1 ^x	-	-	-	-	-	-	-	-	-	-	-	4
<i>Deroceras laeve</i> (Müller, 1774)	-	-	-	-	1 ^x	4 ^x	-	2 ^x	-	-	-	-	-	3
<i>Arion ater rufus</i>	2 ^x	3 ^x	-	-	-	-	-	-	-	-	-	-	-	3
														2
Number of living specimens	54	9	47	120	15	10	33	361	14	10	69	290	30	5
Number of species	16	15	14	13	7	12	11	14	11	11	11	11	12	23
Number of species with living specimens	13	7	7	10	6	2	6	13	4	3	8	9	6	7

sources such as herbs, fungi, and algae are virtually absent. Nursery staff could not remember ever having seen snails there. Furthermore, the planting material is lifted mechanically and thoroughly shaken, so that very little soil remains attached to the roots.

In October 1974 a thorough search was made for land snails on a couple of rainy days in a one-year-old wooded plot in the Horsterwold in Zuidelijk Flevoland and in a two-year-old plot in the Hollandse Hout in Oostelijk Flevoland. After a prolonged search, the slug *Deroceras laeve* was found in the former locality and the slugs *Arion ater rufus*, *A. circumscriptus*, *Deroceras reticulatum*, and *D. laeve* in the latter (in all cases only a few specimens), and one individual of the snail *Zonitoides nitidus* in the Hollandse Hout. All of these species can live on open ground. Most of them were also found occasionally in the funnel-traps for ground-beetles in nearby fields, and could therefore have originated from the immediate vicinity or have been present when planting was started. Sampling in 1975 did not yield any new species in either place.

On this basis it may be concluded that introduction via planting material is highly improbable. Therefore, the differences in species composition could be analysed to find out whether they were due to environmental factors, the age of the plantations, or proximity to old land. To simplify the analysis, we shall restrict ourselves here to species abundance in the various woods.

4.3. Correlation between a number of environmental factors and species diversity

The environmental parameters included in the study are shown in table 1:

pH — The low pH (4.9) of both of the woods on old land is striking in comparison with the values for the IJsselmeerpolders (7.0-8.0). This is related to the calcium content of the soil. Ökland (1930) found the largest number of species at pH 6.5 and decreasing numbers at lower and higher pH values. Our data show no correlation with species abundance.

Calcium content — The amount of calcium carbonate differs rather strongly between the woods and also between the polder woods. This may be the result of local differences in the distribution of deposits of marine shells in the soil. According to Ökland (1930), an increasing calcium content is accompanied by an increase in the number of species (up to a certain point), but this correlation was not found in the polder woods.

Vegetation — All of the woods with a thick undergrowth of stinging nettle (*Urtica dioica*) had many land snails. In fact, the six woods where this plant was dominant in the herb layer had the highest species numbers. In the literature (Frömming, 1968) this nettle is reported to be an important food plant for polyphagous land snails.

No significant correlation was found between the amount of cover of the different layers of the vegetation and the species diversity of the snail fauna. The woods are so similar in composition of the tree layer and in soil type that no influence of these factors can be expected.

4.4. Correlation between number of species and distance to old land or age of the woods

This brings us to the discussion of the colonization of the polders, which will be based on a comparison of the snail faunas in terms of location and age of the woods in which they occur. We have restricted ourselves to the number of species because, in our opinion, the number of living specimens in the samples is a better reflection of the suitability of

Table 4. Data on the occurrence of land snails and slugs on and near the former islands of Schokland and Urk; island data according to Van Benthem Jutting (1944).

	Schokland island (before reclamation)	Schokker- bos 1973	Urk island (before reclamation)	Urker- bos 1973
<i>Succinea pfeifferi</i> Rossmmaessler	x	(x) S.spec.		
<i>Discus rotundatus</i>	x	x		
<i>Oxychilus cellarius</i>	x	x		
<i>Vertigo pygmaea</i>	x	-		
<i>Pupilla muscorum</i> (Linnaeus, 1758)	x	-		
<i>Arion circumscriptus</i>	x	-		
<i>Deroceras laeve</i>	x	-		
<i>Vallonia pulchella pulchella</i>	x	-	-	x
<i>Zonitoides nitidus</i>	x	-	-	x
<i>Deroceras reticulatum</i>	x	-	x	-
<i>Trichia hispida</i>	-	x	x	-
<i>Cochlicopa lubrica</i>	-	x	-	x
<i>Vallonia excentrica</i>	-	x		
<i>Punctum pygmaeum</i>	-	x	-	x
<i>Arion subfuscus</i>	-	x		
<i>Vitrina pellucida pellucida</i>			-	x
<i>Nesovitrea hammonis</i>			-	x

the environment for a few species than of the establishment of all species. Because the occurrence of particular species in the woods in various places and of different ages proved to be irregular, we use only the number of species per sampling site. This number includes species of which only empty shells were found, because first we were interested in migration and colonization rather than possible extinction of the species, and secondly because it remains to be seen whether the species of which only shells were found had indeed become extinct locally or occurred only in a very low density or mainly in another period of the year. Comparison of tables 3 and 4 shows that the four places investigated in 1974 had living specimens of most of the species for which only empty shells had been found in 1973.

In general it can be expected that with colonization the number of species will increase with time, depending on distance from the old land as a source area. Such differences can only be established for animals (or plants) that migrate slowly. Lassen (1975) says, partially on the basis of work done by Hubendick (1947), that freshwater snails are dispersed rather rapidly by water birds. Dispersion by birds seems probable for some species of land snails, but it is not known whether this occurs generally (Butot, 1977).

The polder data can be analysed with respect to the influence of time and distance separately. Fig. 2 shows a distinct correlation with the number of species for both. Because of the strongly divergent environmental conditions in the wet part of the Laakse Strand, these data were not included in the calculation of correlation.

Distance — The distance to old land was taken as parameter because it is not known where the nearest locality on old land in which the species occur is located. Until information becomes available on the way in which the species usually travel (via birds or some kinds of motor-vehicle), it is difficult to decide whether the distance should be measured along roads or in a straight line. However, in the absence of large differences in

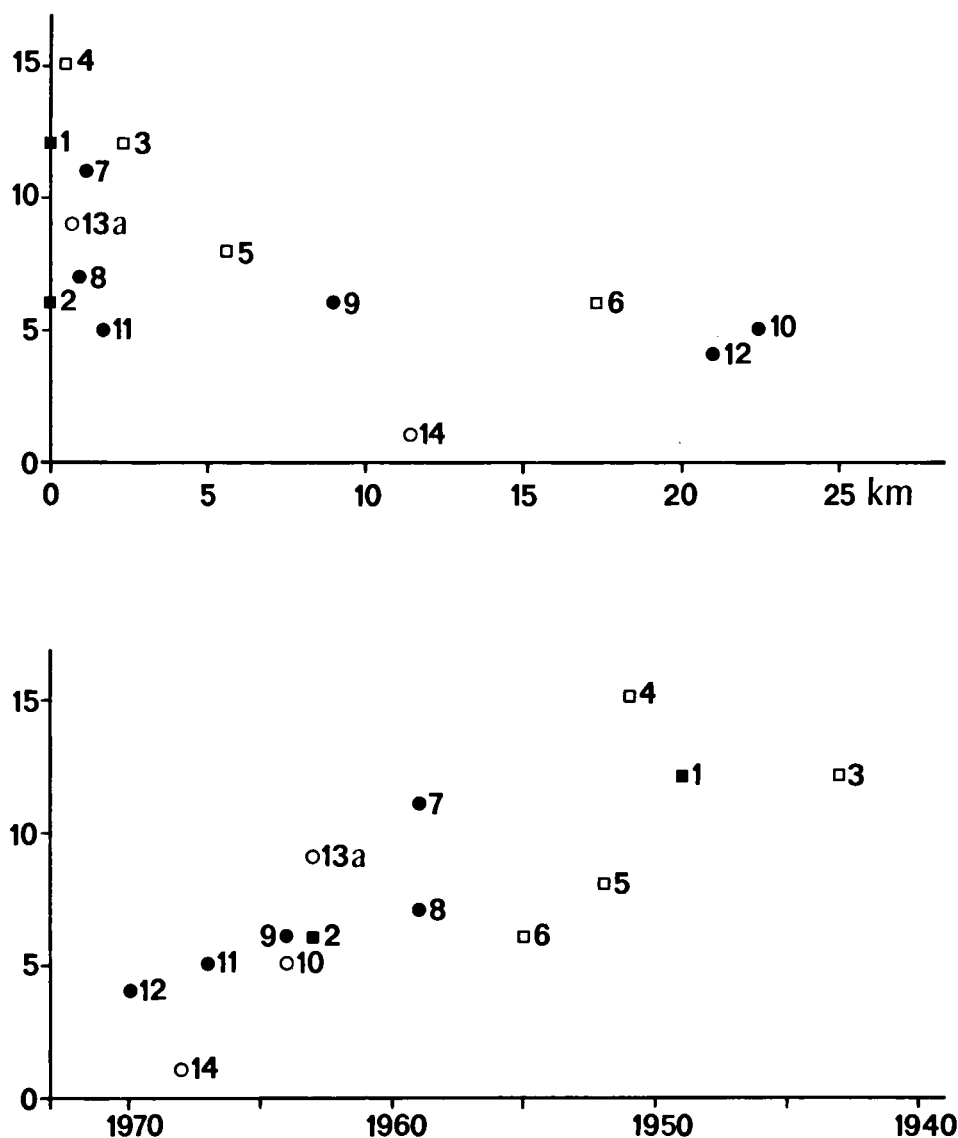


Fig. 2. Correlation of distance to old land (above) and year of planting (below) of the investigated woods with the number of species of land snails occurring in these woods. The numbers in the graphs correspond to those in fig. 1; different symbols are used to distinguish the woods on old land (■) and in the various polders (□ = Noordoostpolder; ● = Oostelijk Flevoland; ○ = Zuidelijk Flevoland).

the correlations, we used the distance in a straight line as the simplest method.

One complication involved here is that the two woods investigated in the Noordoostpolder are situated close to the former islands of Schokland and Urk. Before the reclamation, land snails did occur on the islands, but the places where the investigated woods are located were still under water. An inventory of the species found up to 1942 on the islands of the Zuiderzee, including Schokland and Urk, was given by Van Benthem Jutting (1944). These data are shown in table 4 together with those on the species found in the woods in question in 1973. It is striking that only a few of the pre-reclamation species were found in 1973, whereas many other species were also present then. It therefore seemed justifiable to treat the woods on the former islands in the same way as the others.

As can be seen from fig. 2, there is a distinct decrease in the number of species with increasing distance. The correlation between these two parameters is significant ($r = -0.60$, $P < 0.05$).

Time — If the time available to reach a given place is to be included as a factor in the study, use must be made of the interval since a given polder was reclaimed. It is unlikely, however, that this is a realistic approach, because the environment of a recently reclaimed polder is not suitable for the establishment of land snails, and remains unsuitable for some time. This is confirmed, e.g. by the data for the Hollandse Hout (Oostelijk Flevoland, dry in 1957) and Horsterwold (Zuidelijk Flevoland, dry in 1968), both of them very young woods with a small number of species in 1974 (see page 35).

From the bottom curve in fig. 2 it is evident that the data from the woods in a given polder show a trend consistent with that of the total curve. This raises the question of whether the moment of reclamation of a polder is the most suitable parameter for the demonstration of an increase in the number of species in time. In this context a relationship with the age of the woods seems more logical. Changes in the uppermost soil layer due to the accumulation of litter and humus occur more rapidly in woods than elsewhere. It can therefore be expected that after the planting of a wood the general environment develops more rapidly in a sense favourable to land snails than would be the case in places outside it, even though only a few of the species found in the study are specifically forest species (according to the habitat descriptions given by Gittenberger et al., 1970).

If instead of the interval since the reclamation of the polders we take the time since the planting of the woods for the analysis of correlation with the number of species, the result is much better ($r = 0.79$, $P < 0.01$). It thus seems probable that in the initial period after reclamation no immigrants can survive in the new environment, and that a certain developmental level of the environment must be reached before colonization can occur on an appreciable scale.

For the evaluation of the importance of the observed difference in the correlation between the number of species and the distance to the old land as well as the age of the woods, the negative correlation ($r = -0.41$, $P > 0.10$) between the two latter parameters must be taken into account. This correlation is not unexpected, because the reclamation of a polder is usually begun near the old land. The influence of this correlation can be eliminated in a multiple regression analysis. The partial regression of species number on age of the woods, with exclusion of the influence of distance, is highly significant ($P \approx 0.003$), but partial regression of species number on distance to the old land, with

exclusion of the influence of the age of the woods, is not significant ($P = 0.09$).

This means that the number of species of land snails in a wood in the IJsselmeerpolders can be predicted much more accurately from the age of the wood than from the distance from the wood to the old land. It is, however, not justifiable, strictly speaking, to conclude from this that the number of species is determined by environmental conditions related to the age of the wood (whether or not in association with time). Nevertheless, this is a good working hypothesis for further research.

5. CONCLUSIONS AND SUMMARY

1. In a study in the woods of the IJsselmeerpolders 25 species of land snails were found; 21 of these occurred in the Noordoostpolder and 21 in Zuidelijk and Oostelijk Flevoland. The largest number of species (15) was found in a plot in the Kuinderbos. The highest density was found in 1973 in the Roggebotzand (Oostelijk Flevoland) and in 1974 in the Kuinderbos, i.e., more than 500 living individuals per m^2 .

2. The conclusion of other investigators that the autumn is the best period for sampling of molluscs in forests was confirmed.

3. Introduction of terrestrial molluscs with planting material is not very probable, due to (a) the maintenance of clean plant-beds in the tree nursery from which the planting material originates; (b) the virtual absence of soil around the roots during transportation; (c) the absence in newly planted woods of mollusc species occurring in the older polder woods.

4. No correlation was found between the pH or calcium content of the soil and the number of species present.

5. Deciduous woods with a relatively dense undergrowth of stinging nettle plants have a relatively rich mollusc fauna.

6. A positive correlation was found between the age of the woods and the number of species, and a negative correlation between the distance from the old land and the number of species. Calculation of partial regression coefficients showed that only the former relationship is significant.

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SAMENVATTING

Waarnemingen betreffende de verspreiding van landslakken in de bossen van de IJsselmeerpolders

Een onderzoek naar de verspreiding van landmollusken in de IJsselmeerpolders is interessant omdat hieruit wellicht conclusies over de wijze en snelheid van kolonisatie kunnen worden getrokken. Alleen loofbossen werden onderzocht (fig. 1), omdat deze over het algemeen de meeste soorten bevatten. De volgende vragen werden gesteld: (1) Is migratie naar de aangeplante bossen te verklaren door vervoer van plantmateriaal in de bebossingsperiode? (2) Zijn eventuele verschillen in soortenrijkdom van de molluskenfauna te verklaren uit milieuverschillen in de bossen? (3) Zijn er aanwijzingen voor een invloed van de afstand tot het "oude land" of van de leeftijd van de bossen op de soortenrijkdom?

Bemonstering in de polderbossen vond plaats in september 1973 en op vier tijdstippen (april, juni, augustus en oktober) in 1974. In elk bos werden random tien monsters van 1/16 m² genomen, door een stalen raamwerk met inwendig zijden van 25 cm over de kruidlaag te schuiven. Binnen dit raamwerk werden de planten op mollusken afgezocht en strooisel, mos en humuslaag verzameld. Na drogen bij 35°C en zeven werden de fracties op mollusken onderzocht. Per terrein werden eveneens tien monsters van de bovenste 5 cm van de bodem genomen. Hierin werden de pH en de hoeveelheid vrije koolzure kalk bepaald. De grondsoort werd grof ingedeeld in klei, zavel of zand.

Er werden in totaal 25 soorten landmollusken aangetroffen, nl. 21 in de Noordoostpolder en 21 in Zuidelijk en Oostelijk Flevoland. De grootste soortenrijkdom had een perceel in het Kuinderbos (Noordoostpolder) met 15 soorten. De grootste dichtheden werden in 1973 in het Roggebotzand (Oostelijk Flevoland) en in 1974 in het Kuinderbos gevonden nl. meer dan 500 levende individuen/m² (tabel 2).

De conclusie van andere onderzoekers, dat het najaar de beste periode is voor bemonstering van landmollusken werd bevestigd. Het aantal levende soorten en individuen nam in 1974 van april tot juni aanvankelijk af en steeg weer in augustus en oktober (tabel 3).

Infectie van de bossen door overbrenging van landmollusken met plantmateriaal is niet erg waarschijnlijk (a) doordat de plantbedden in de kwekerij steeds vrij van onkruid werden gehouden; (b) doordat bij transport van het plantmateriaal praktisch geen aarde om de wortels zit; (c) doordat in pas aangeplante bospercelen molluskensoorten ontbreken, die in oudere polderbossen wel voorkomen.

Er werd geen correlatie gevonden tussen de pH, respectievelijk het kalkgehalte van de bodem en het aantal soorten.

De loofhoutpercelen met een dichte ondergroei aan brandnetels bevatten een relatief rijke molluskenfauna.

Er is over het algemeen een toename gevonden van het aantal soorten met toenemende ouderdom van de bossen (fig. 2, onder) en een afname van het aantal soorten met toenemende afstand van de bossen tot het oude land (fig. 2, boven). Leeftijd en ligging van de bossen zijn echter ook onderling gecorreleerd. Een partiële regressie-analyse maakt waarschijnlijk dat het eerst genoemde verband (met de leeftijd van het bos) het belangrijkste is.