Forty years of undisturbed change in the ground dwelling fauna in the Lauwersmeer, a reclaimed tidal estuary of the Dutch Waddensea

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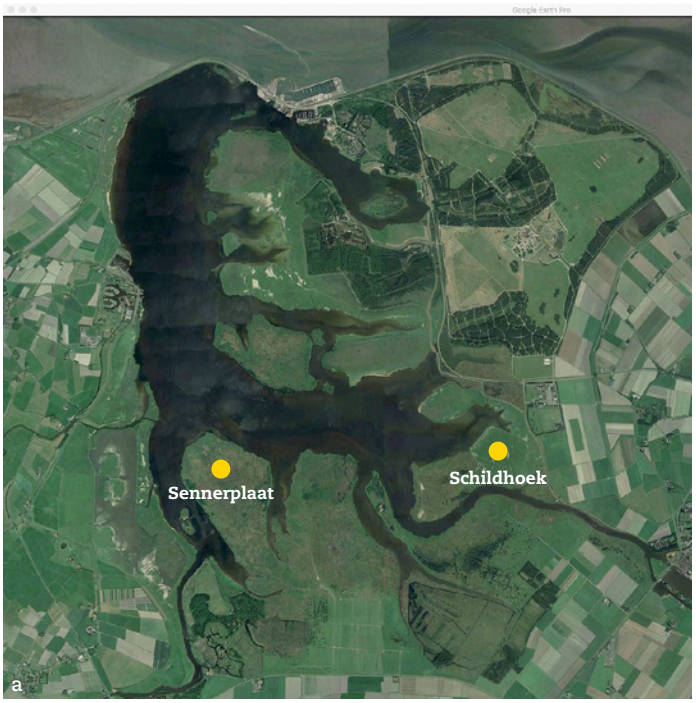
A tidal area of 9,000 ha in the north of the Netherlands was reclaimed in 1969. The presence of carabids, spiders, harvestmen, woodlice and myriapods has been monitored at two locations (Sennerplaat and Schildhoek) in the full period 1969-2008. The ecosystem could develop under undisturbed conditions, and desalinization and vegetation succession are the main processes. The characteristic salt marsh species disappeared after twelve years, indicating the fast desalinization. The succession from open soil (sandy or muddy) to a dense reed marsh with litter layer needed 15-20 years. More than 350,000 specimens have been captured in four series of two traps and identified to species-level; full data are presented in this paper. High numbers in specimens are present in the first years, but also after ten or twenty years in carabids and spiders. The first harvestmen, woodlice and myriapods invaded the system only after twenty years. Analyses in development of the catches in spiders indicate that the catches in the first twenty years are higher in the specimen numbers, the other twenty years remain on one lower level. Analyses in development of the catches in carabids indicate differences between the two locations. In Schildhoek the numbers are higher in 1970-1978 and on a constant lower level later. In Sennerplaat the numbers are higher with peaks around the years 1973, 1983 and 1991, and on a constant lower level later. Higher numbers can be explained with some dominant species. The analyses on the species numbers, including loss and gain in yearly species, indicate that after some years the numbers remain on the same level for carabids at the four sub-locations and for the area as a whole. However, in the spiders the number of species rise from 20 to 45 with all data merged; in the four sub-locations the number remain on a constant level. Although many similar developments can be given for the two locations, some differences can be indicated that are related to abiotic conditions and dispersal. In the discussion, we conclude that during a forty-years period of succession we meet a constant arrival and disappearance of species in carabids, and after fifteen years also a gradual increase in spider species, that might be explained by dispersal capacity.

Introduction

The Dutch society has a standing tradition in reclaiming wetlands by the construction of polders, vast areas with low lying land where water tables are regulated. During the 17th-19th century many shallow lakes have been reclaimed and in the 20th century large parts of the former estuary IJsselmeer ('Zuiderzee', closed in 1932) changed into 165,000 ha. with agricultural polders. In a few years after the reclamation of these areas, the ecosystem developed from a pristine muddy soil into a vegetated area with solid soil. The succession in vegetation was studied for Wieringermeerpolder (Feekes 1936), Noordoostpolder (Feekes & Bakker 1954), oostelijk Flevoland (Bakker 1957) and zuidelijk Flevoland (Clevering & Van der Toorn 2000, Van der Toorn *et al.* 1969,). However, after some years the dewatered soil in the pristine polders was converted into agricultural land or forest and a natural succession was stopped. The vegetation in the maintained nature reserve Oostvaardersplassen was managed strictly for bird species (e.g. Ter Heerdt 1994).

Published research in ground dwelling fauna in these new polders was even far more restricted. Feekes (1936) mentions from Wieringermeer e.g. the frequent spider species *Larinioides*



1. (a) Image of the Lauwerszeepolder showing the location of the study areas. (b-c) Details of the Sennerplaat and the Schildhoek indicating the location of the traps. Foto's: Google Earth images 2005
1. (a) Beeld van de Lauwerszeepolder met de locatie van de studie-terreinen. (b-c) Details van de Sennerplaat en de Schildhoek met de plaats van de vallen.

cornutus (Clerck), *Pardosa amentata* (Clerck) and *Erigone dentipalpis* (Wider) in the first years after reclamation. From the more recent IJsselmeerpolders Mook (1971) reviews the settlement in various fauna species during the first years and Haeck (1971) the immigration of the carabid beetles. Similar research was performed in former salt marshes after the closing of estuaries in the southwest of the Netherlands, starting in 1971. Verschoor & Krebs (1995) monitored nine years the development in carabid beetles of Markiezaat, and on the marshes of Flakkee the carabids were monitored also in an elevation gradient in 1972 (Zijlstra 1973). However, no studies for decades on undisturbed development of the flora and fauna exist in those locations.

Comparably, in the extreme north of the Netherlands was formerly the Lauwerszee (figure 1), an estuary of ca. 9,000 ha. in the saline and tidal Waddensea, that was closed in order for safety to prevent flooding of surrounding cultivated areas and, moreover, to store fresh water from the surrounding agricultural polders. In 1969 the dike to separate the Lauwerszee from the Waddensea was closed at low tide, leaving a polder area with a water level ca. 85 cm below mean sea level, with former sand banks, mud flats, salt marshes and open water. Contrary to the reclamations mentioned before, the new Lauwersmeer polder area was left alone for nature development. This opportunity was used to start a study in succession with the monitoring of the development of some groups in the ground dwelling fauna. In July 1969, a program was started to describe the immigration and development of the carabid beetle and spider fauna in four locations of Lauwerszee polder by means of various types of traps (Meijer 1971, 1973, 1974). After the first author had completed the collection of fauna data for his Ph.D. thesis (Meijer 1980), sampling was continued with eight pitfall traps, at two sampling sites each, in two different subareas. These traps were operational permanently at exactly the same location from July 1969 till October 2008, and the data from this research will be presented fully.

With this paper we show what changed in the ground

Table 1. Soil factors in the trapping stations Sennerplaat (SP) A and B and Schildhoek (SH) A and B (from Meijer 1980).
Tabel 1. Bodemfactoren van de vangstlocatie Sennerplaat A en B, en Schildhoek (SH) A en B (volgens Meijer 1980)

	SPA	SPB	SHA	SHB
$CaCO_3$ [a]	4.0	3.7	5.5	5.5
Humus [a]	0.5	0.2	0.5	0.6
Silt (< 16µ) [a]	3.5	2.1	3.9	4.7
Sand (> 16µ) [a]	89.9	92.4	88.5	88.3
U-value [b]	102	96	138	137
K_2O [c]	26.3	18.6	30.0	32.0
P_2O_5 [d]	5.34	7.75	6.27	8.54
N [e]	4.9	6.3	14.2	10.8
pH $_{H2O}$	8.0	8.1	7.8	7.9

[a] % of dry soil / % droge bodem
[b] U16-value is defined as the ratio between the total surface of the grains and a compact volume of that material (see: Locher & De Bakker 1987, page 78). / De U16-waarde is een relatieve maat voor het oppervlak van een minerale stof bestaande uit zand en silt (zie Locher & De Bakker 1987, pagina 78).
[c] mg per 100 g of dry soil / mg per 100 g droge bodem
[d] mg per litre of dry soil / mg per L droge bodem
[e] Total mineral N mg per 1000 gram of dry soil / totale minerale N mg per 100 g droge bodem

dwelling fauna during that 40-years period with undisturbed succession from a pristine bare soil to a well-vegetated wetland. We investigate the species turnover that reflects the different conditions during this succession and test whether a change from a pioneer phase to a more climax phase can be indicated.

The study area

After the Lauwerszee was closed from the tidal Waddensea in 1969, the resulting 9,000 ha. 'Lauwerszee-polder' consisted of 3,000 ha. water with a large lake (Lauwersmeer) plus tidal creeks and 6,000 ha. of land: the sand bars, mudflats and salt marshes of the former tidal estuary. Nowadays, this polder forms the National Park 'Lauwersmeer'. Arable land and military training grounds surround the National Park. From the study areas by Meijer (1980), two locations were maintained for this 40-years research: the Sennerplaat A & B (Area I, or Fine Sand in earlier publications) on a former sandbar, and the Schildhoek A & B (Area V or Silt) on a former mudflat (figure 1). Table 1 summarizes some data on the soil of the two locations in 1970; Schildhoek appeared to be richer in silt, calcium, potassium and nitrogen.

The water level in the lake can only be maintained by free drainage at low tide of surplus water through a system of sluices into the Waddensea. Whenever the sluices have to stay closed for some time, as due to adverse weather conditions the water level in Waddensea remains too high, the lake may rise to such levels that large areas of the former mudflats are submerged. Such submersions do regularly occur in autumn and winter; the former mudflat Schildhoek is inundated every winter and even incidentally in summer. However, the Sennerplaat, being an elevated former sandbar with ca. 30 cm higher elevation, was never inundated by water from the lake in last decades. Initially the Sennerplaat was rather dry as rainwater could readily run off and/or seep into the sandy soil. Due to the ongoing development of the vegetation and the formation of a layer of litter and mosses, drainage was hampered and the Sennerplaat became more or less marshy too.

An important change was that by the closing of the dike in 1969 the desalination started: as the lake was constantly flushed with the runoff from the agricultural hinterland, within a few months salinity decreased from 17,000 mg Cl/l to 300 mg in winter and 1500 mg Cl/l in summer (Van Rooij & Drost 1996). Desalination of the soil was a process of ten to fifteen years, especially on the low and flat mudflats such as the Schildhoek, where a more or less clayish soil and a high water table prevented vertical percolation of rainwater.

The development in the vegetation follows these physical changes. A selection of photos in figures 2-17 provides an impression from both areas in the period 1970-2000. The Sennerplaat can be described as a sandy area with a quickly desalinated soil, subject to sand drift in 1969 and 1970 (figure 2) and with slower development to closed vegetation. The very flat Schildhoek, having a more clayish soil, was more slowly desalinated: a more or less closed vegetation of halophytic plants developed here quickly. In spring 1970 the Schildhoek was muddy and bare (figure 3), but some months later it had a loose vegetation of well-developed halophytes *Salicornia maritima* and *Suaeda maritima* (figure 4) that produced so much seed that a dense vegetation of small *Salicornia* and *Suaeda* plants resulted (figure 5) in 1971.

Figures 6 to 17 give an impression of the invasion in this halophytic vegetation by various grasses and later the development into reed (*Phragmites australis*) beds with an undergrowth of various herbs such as *Mentha aquatica*, *Angelica archangelica*, *Valeriana officinalis*, *Scutellaria galericulata*, *Lycopus europaeus*, *Eupatorium cannabinum*, grasses such as *Agrostis stolonifera*, and a well-developed layer of mosses and decaying plant material. In the early 1990's, a dense growth of the grass species *Calamagrostis epigejos* developed on the Sennerplaat. However, in 1995 this *Calamagrostis* became very heavily infested by the coccid *Eriopeltis lichtensteini* Signoret (identification by Maurice Jansen), resulting in the virtual disappearance of *Calamagrostis* in 1996. The species did not become a significant part of the vegetation later.

Another major difference between Sennerplaat and Schildhoek is the level of disturbance in both areas: the Sennerplaat was only disturbed by regular visits to empty the traps, while horses and cattle heavily grazed the Schildhoek from 1982 onwards. Livestock grazing affects species in ground dwelling fauna (Van Klink & Van Schrojenstein Lantman 2015). However, around both sets of two traps in the Schildhoek an 80 m wide circular exclosure was fenced off. Figure 13 shows that the vegetation around these patches was reduced to a short turf of mostly *Juncus gerardii* with some *Agrostis stolonifera*. Inside the fences a lush vegetation (up to 2 m high) of reeds eventually developed (figures 15 & 17). These exclosures in Schildhoek can even be recognised in the Google Earth pictures in figure 1.

As the study of the vegetation at the traps was stopped in 1974, no detailed information over the full period is available. Joenje (1974, 1978) presented extensive information on abiotic factors and the development of the vegetation during the first six years after reclamation. Van Rooy & Drost (1996) summarized the hydrological and physical development of Lauwersmeer in 25 years.

Methods in collecting data

In both subareas two sets of two pitfall traps (5 m separated) were operational from July 1969 until October 2008. The traps (cf. figure 4) consisted of a 15 cm wide plastic funnel provided with a small plastic bottle containing a 4% formalin solution. The funnel was placed in a dug-in metal container flush with the ground level. A perspex roof secured by a brick prevented flooding of the funnel by rain. Catches were initially gathered each week, later on, when the functioning of the traps was less

disturbed by blown sand and debris, as a rule each fortnight. Trapping was discontinued in late October and started again in late March. Due to an epidemic of foot-and-mouth disease in 2001, access to both the Sennerplaat and the Schildhoek was denied, hence the gap in the tables and the graphs.

The catches were gathered, sorted and identified to species level by the first author. Initially only carabid beetles (Coleoptera, Carabidae) and spiders (Arachnida, Araneae) were taken into account. Later, other minor groups colonized the area and also were recorded. In this way harvestmen (Arachnida: Opiliones), woodlice (Crustacea: lsopoda: Oniscoidea), myriapods (Diplopoda) and one rove beetle species (Coleoptera: Staphylinidae) were added to the list of species studied.

The overall results of 40 years captures

Table 2 presents a complete list of encountered species in alphabetical order with the nomenclatural data. The names for carabids follow: Muilwijk *et al.* (2015); for spiders: Van Helsdingen (2012); for harvestmen: Wijnhoven (2009); for woodlice: Berg & Wijnhoven (1997); and for millipedes: Berg (2005). In tables 3, 4 and 5, the total number of specimens per year is given for all encountered species; an abbreviated name (table 2) is used to refer to the species concerned. The full yearly data for the four sampling locations (Sennerplaat A and B and Schildhoek A and B) are available at the website of Entomologische Berichten as supplementary data (www.nev.nl/pages/publicaties/eb): annex 1, 2, 3, and 4 for the carabids; annex 5, 6, 7 and 8 for the spiders; and annex 9 for the other groups.

The trapping scheme resulted in a total capture of 350,449 identified specimens of ground dwelling animals, summarized in table 3, 4 and 5. For each species the median value in the numbers had been calculated and each species value with a higher number than the median value is highlighted in the tables. Next, the total species sequence is organized with the species with the highest weight in 1969 to the species with highest weight in 2008. This sequence is partly arbitrary because some species are present in few years, whereas others are represented during many years. The rare species with less than five catches are put separately in the lower part of the table. In the end of the table some characteristics of the yearly captures are added: the number of species (n) as well as the gain and loss of species and total year capture in specimens (N).

Carabids

Over the 40-year study period, a total number of 203,815 specimens of 98 species were caught (table 3). The majority of these 98 species illustrate the succession in Lauwersmeer with arriving of new species and after some years or longer a disappearance. In this continuum some major lines can be drawn. There are pioneer species that disappear after 10-15 years, but other pioneer species remain for 25 years; after ca 6 years from the start there is an increasing group of colonizing species that remain till 2008, but after 35 years a new group of species succeed to colonize the area. Interesting is that there are also groups of species that are mostly less frequent in numbers and are present only for circa 8 years: in the first years, after 10 years and after 25 years.

To illustrate the dynamics in catches, the total yearly number of specimens in carabids for Sennerplaat and Schildhoek are presented in figure 18, showing the growing, thriving and dwindling of the catches. In both areas a rapid increase in catches from a total year-catch of only 22 specimens in 1969 to more than 10,000 specimens in both areas some years later, and a subsequent decrease to a more or less stable level of about 1,000 a year. The high numbers are mainly caused by a very restricted number of species that are represented by many hundreds or thousands. In both areas *Bembidion varium* (Olivier) is dominant in 1970-1971. In Schildhoek *Dyschirius salinus* Schaum reach a maximum of 5300 specimens in 1975 and *Dicheirotrichus gustavii* Crotch a maximum of 8800 specimens in 1978, explaining the highest values in figure 18. In Sennerplaat the maximum with *Dicheirotrichus gustavii* is 8650 specimens in 1973; in 1984 and 1990 the number of specimens in *Dyschirius globosus* (Herbst) and *Bembidion assimile* Gyllenhal is ca. 2000 each. Moreover, in 1981-1984 are high numbers in *Pterostichus vernalis* (Panzer) and *Acupalpus parvulus* (Sturm) and in 1990-1993 the high numbers also derive from *Agonum fuliginosum* (Panzer), *A. theoreyi* Dejean and *Pterostichus diligens* (Sturm).

Data on carabids in detail

Evaluation of the list of represented species learns that five species (out of 98) are very scarce in the Netherlands according to Turin (2000): *Amara majuscula* (Chaudoir), *A. quenseli* (Schoenherr), *Badister unipustulatus* Bonelli, *Bembidion lunatum* (Duftschmid) and *Paradromius longiceps* (Dejean). Also in Lauwersmeer these species are very rare. Especially well represented during the first years in the data are the salt marsh species, almost all characteristic species from literature are given. What changed after ten years of reclamation is that species known from more fresh shorelines entered the system and replaced the former group. After some years the next group with species from vegetated soil with litter layer invaded, in its turn slowly replaced with species known from wetlands with dense vegetation (e.g. *Carabus granulatus* Linnaeus). In 2008 we have the fourth group in species that fully replaced a former group (table 3).

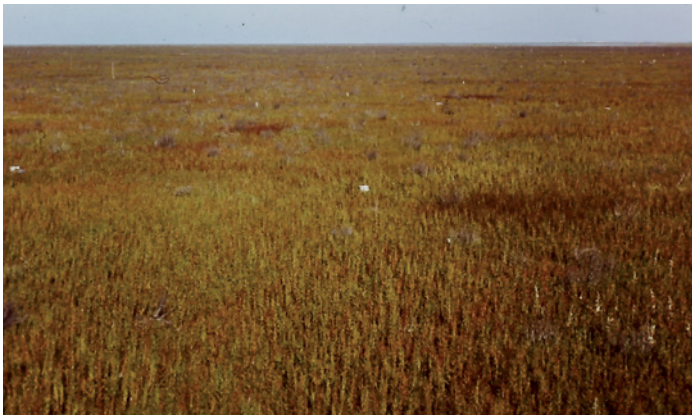
Turin *et al.* (1991) analysed a set of 1616 samples of year catches of carabids in pitfall traps from totally different habitats in the Netherlands. This resulted in a diagram of the carabid habitats along two axes: dry to wet and closed to open vegetation (figure 19). Moreover, for each carabid species present in sufficient numbers in the catches, a set of coordinates was calculated indicating its position on the map mentioned. Since these results are based on Dutch catches, it is evident that the results are only applicable on Dutch carabid catches. The method in itself can be used everywhere, given a sufficiently large body of year catches. Based on these coordinates, an index was calculated for each year catch in the combined four traps in the Sennerplaat and in the Schildhoek. The number of specimens for each species was multiplied by the X- and Y-coordinate. The coordinates for all specimens in the year catch were added and finally divided by the total year catch. This resulted in two yearly coordinates Tx and Ty that could be plotted.

In the Sennerplaat as well as in the Schildhoek a distinct development can be seen in the mapped data (figures 20-21). Initially in both areas the year catches are represented in upper right corner of the habitat map, indicating a saltmarsh like habitat. From 1978 to 1982 there is a rapid transformation to the eurytopic, wet habitats. From then on, the catches remain in that section of the habitat map. The catches in the Schildhoek show roughly the same development with a short interim period (1979-1981) in which the catches are more characteristic for a specific habitat: reed beds. In general, this reflects the desalination of the areas (earlier in the Sennerplaat) and the development of the vegetation. After the early 1980's there is no longer a drift in a certain direction, but the data suggest changes from year to year indicating that the carabid fauna is far from stable in the last 25-year period.

2. Sennerplaat early spring 1970. All following photos: Jan Meijer

3. Schildhoek early spring 1970.

4. Schildhoek 1970.



5. Schildhoek 1971.

6. Sennerplaat 1975.

7. Schildhoek 1975.

8. Sennerplaat 1980.

9. Schildhoek 1980.

10. Sennerplaat 1984.

11. Schildhoek 1984.

12. Sennerplaat 1989.

13. Schilhoek 1989.

14. Sennerplaat 1993.

15. Schildhoek 1993.

16. Sennerplaat 1999.

17. Schildhoek 1999.

Table 2. List of all species incorporated in the research, with in the first column the species abbreviation (in annex 1-9) and second column the full species name. The next synonyms are valid in the carabids (not mentioned in Muilwijk *et al.* 2015): *Agonum emarginatum* instead of *A. moestum*, *Bembidion bruxellense* = *B. rupestre*, *Blemus discus* = *Trechus discus*, *Dyschirius tristis* = *D. luedersi*, *Harpalus affinis* = *H. aeneus*, *Harpalus rufipes* = *H. pubescens*, *Philorhizus sigma* = *Dromius sigma*.
Tabel 2. Lijst met alle aangetroffen soorten in dit onderzoek, met in eerste kolom de soortafkorting (in annex 1-9) en in tweede kolom de volledige soortnaam. Bij de loopkevers zijn sommige namen aangepast in Muilwijk *et al.* 2015, waarbij verklaring hierboven.

CARABIDAE

ACUPEXIG	*Acupalpus exiguus* (Dejean)
ACUPFLAV	*Acupalpus flavicollis* (Sturm)
ACUPPARV	*Acupalpus parvulus* (Sturm)
AGONEMAR	*Agonum emarginatum* (Gyllenhal)
AGONFULI	*Agonum fuliginosum* (Panzer)
AGONMARG	*Agonum marginatum* (Linnaeus)
AGONMUEL	*Agonum muelleri* (Herbst)
AGONSEXP	*Agonum sexpunctatum* (Linnaeus)
AGONTHOR	*Agonum thoreyi* Dejean
AMARAENE	*Amara aenea* (Degeer)
AMARAPRI	*Amara apricaria* (Paykull)
AMARBIFR	*Amara bifrons* (Gyllenhal)
AMARCOMM	*Amara communis* (Panzer)
AMARCONV	*Amara convexiuscula* (Marsham)
AMARFAME	*Amara famelica* Zimmermann
AMARFAMI	*Amara familiaris* (Duftschmid)
AMARFULV	*Amara fulva* (Müller)
AMARLUNI	*Amara lunicollis* Schioedte
AMARMAJU	*Amara majuscula* (Chaudoir)
AMARPLEB	*Amara plebeja* (Gyllenhal)
AMARQUEN	*Amara quenseli* (Schoenherr)
AMARSPRE	*Amara spreta* Dejean
ANCHDORS	*Anchomenus dorsalis* (Pontoppidan)
ANISBINO	*Anisodactylus binotatus* (Fabricius)
ASAPFLAV	*Asaphidion flavipes* (Linnaeus)
BADIBULL	*Badister bullatus* (Schrank)
BADIDILA	*Badister dilatatus* Chaudoir
BADILACE	*Badister lacertosis* Sturm
BADISODA	*Badister sodalis* (Duftschmid)
BADIUNIP	*Badister unipustulatus* Bonelli
BEMBAENE	*Bembidion aeneum* Germar
BEMBASSI	*Bembidion assimile* Gyllenhal
BEMBBIGU	*Bembidion biguttatum* (Fabricius)
BEMBBIPU	*Bembidion bipunctatum* (Linnaeus)
BEMBBRUX	*Bembidion bruxellense* Wesmael
BEMBFEMO	*Bembidion femoratum* Sturm
BEMBGUTT	*Bembidion guttula* (Fabricius)
BEMBIRIC	*Bembidion iricolor* Bedel
BEMBLAMP	*Bembidion lampros* (Herbst)
BEMBLUNA	*Bembidion lunatum* (Duftschmid)
BEMBLUNU	*Bembidion lunulatum* (Geoffroy)
BEMBMINI	*Bembidion minimum* (Fabricius)
BEMBNORM	*Bembidion normannum* Dejean
BEMBOBTU	*Bembidion obtusum* Serville
BEMBPROP	*Bembidion properans* (Stephens)
BEMBQUAD	*Bembidion quadrimaculatum* (Linnaeus)
BEMBTETR	*Bembidion tetracolum* Say
BEMBVARI	*Bembidion varium* (Olivier)
BLEMDISC	*Blemus discus* (Fabricius)
BRADCAUC	*Bradycellus caucasicus* (Chaudoir)
BRADHARP	*Bradycellus harpalinus* (Serville)
CALAMELA	*Calathus melanocephalus* (Linnaeus)
CARAGRAN	*Carabus granulatus* Linnaeus
CLIVFOSS	*Clivina fossor* (Linnaeus)
DEMEATRI	*Demetrias atricapillus* (Linnaeus)
DICHGUST	*Dicheirotrichus gustavii* Crotch
DYSCGLOB	*Dyschirius globosus* (Herbst)
DYSCOBSC	*Dyschirius obscurus* (Gyllenhal)
DYSCPOLI	*Dyschirius politus* (Dejean)
DYSCSALI	*Dyschirius salinus* Schaum
DYSCTRIS	*Dyschirius tristis* Stephens
ELAPCUPR	*Elaphrus cupreus* Duftschmid
ELAPRIPA	*Elaphrus riparius* (Linnaeus)
HARPAFFI	*Harpalus affinis* (Schrank)
HARPLATU	*Harpalus latus* (Linnaeus)
HARPRUFI	*Harpalus rufipes* (Degeer)
LEISFULV	*Leistus fulvibarbis* Dejean
LEISTERM	*Leistus terminatus* (Hellwig)
LORIPILI	*Loricera pilicornis* (Fabricius)
NEBRBREV	*Nebria brevicollis* (Fabricius)
NOTIAQUA	*Notiophilus aquaticus* (Linnaeus)
NOTIBIGU	*Notiophilus biguttatus* (Fabricius)
NOTIPALU	*Notiophilus palustris* (Duftschmid)
NOTISUBS	*Notiophilus substriatus* Waterhouse
ODACMELA	*Odacantha melanura* Paykull
OODEHELO	*Oodes helopioides* (Fabricius)
PANACRUX	*Panagaeus crux-major* (Linnaeus)
PARAALBI	*Paranchus albipes* (Fabricius)
PARALONG	*Paradromius longiceps* (Dejean)
PHILMELA	*Philorhizus melanocephalus* (Dejean)
PHILSIGM	*Philorhizus sigma* (Rossi)
POECCUPR	*Poecilus cupreus* (Linnaeus)
POECVERS	*Poecilus versicolor* (Sturm)
POGOCHAL	*Pogonus chalceus* (Marsham)
POGOLURI	*Pogonus luridipennis* (Germar)
PTERDILI	*Pterostichus diligens* (Sturm)
PTERMELA	*Pterostichus melanarius* (Illiger)
PTERMINO	*Pterostichus minor* (Gyllenhal)
PTERNIGE	*Pterostichus niger* (Schaller)
PTERNIGR	*Pterostichus nigrita* (Paykull)
PTERSTRE	*Pterostichus strenuus* (Panzer)
PTERVERN	*Pterostichus vernalis* (Panzer)
STEMMIXT	*Stenolophus mixtus* (Herbst)
SYNUVIVA	*Synuchus vivalis* (Illiger)
TRECMICR	*Trechoblemus micros* (Herbst)
TRECOBTU	*Trechus obtusus* Erichson
TRECQUAD	*Trechus quadristriatus* (Schrank)
TRICPLAC	*Trichocellus placidus* (Gyllenhal)

STAPHYLINIDAE

PAEDRIPA	*Paederus riparius* (Linnaeus)

OPILIONES

LACIEPHI	*Lacinius ephippiatus* (C.L. Koch)
MITOMORI	*Mitopus morio* (Fabricius)
NEMALUGU	*Nemastoma lugubre* (Müller)
OLIGTRID	*Oligolophus tridens* (C.L. Koch)
PAROAGRE	*Paroligolophus agrestis* (Meade)
RILATRIA	*Rilaena triangularis* (Herbst)

ARANEAE

AGROPROX	*Agroeca proxima* (O.P.-Cambridge)
AGYNDECO	*Agyneta decora* (O.P.-Cambridge)
AGYNRURE	*Agyneta rurestris* (C.L. Koch)
AGYNSUBT	*Agyneta subtilis* (O.P.-Cambridge)
ALLOSCOP	*Allomengea scopigera* (Grube)
ALLOVIDU	*Allomengea vidua* (C.L. Koch)
ALOPPULV	*Alopecosa pulverulenta* (Clerck)
ANTIELEG	*Antistea elegans* (Blackwall)
APHIMISE	*Aphileta misera* (O.P.-Cambridge)
ARCTLEOP	*Arctosa leopardus* (Sundevall)
ARGEPATU	*Argenna patula* (Simon)
ASTHPAGA	*Asthenargus paganus* (Simon)
BATHAPPR	*Bathyphantes approximatus* (O.P.-Cambridge)
BATHGRAC	*Bathyphantes gracilis* (Blackwall)
BATHPARV	*Bathyphantes parvulus* (Westring)
CENTBICO	*Centromerita bicolor* (Blackwall)
CENTDILU	*Centromerus dilutus* (O.P.-Cambridge)
CENTSYLV	*Centromerus sylvaticus* (Blackwall)
CERABREV	*Ceratinella brevipes* (Westring)
CLUBPHRA	*Clubiona phragmitis* C.L. Koch
CLUBRECL	*Clubiona reclusa* O.P.-Cambridge
CLUBSTAG	*Clubiona stagnatilis* Kulczynski
CLUBTERR	*Clubiona terrestris* Westring
CNEPOBSC	*Cnephalocotes obscurus* (Blackwall)
CRUSGUTT	*Crustulina guttata* (Wider)
DICYNIGR	*Dicymbium nigrum nigrum* (Blackwall)
DIPLCONC	*Diplostyla concolor* (Wider)
DIPLOCRIS	*Diplocephalus cristatus* (Blackwall)
DIPLPERM	*Diplocephalus permixtus* (O.P.-Cambridge)
DISMBIFR	*Dismodicus bifrons* (Blackwall)
DRASPUSI	*Drassyllus pusillus* (C.L. Koch)
ENOPMORD	*Enoplognatha mordax* (Thorell)
ENOPTHOR	*Enoplognatha thoracica* (Hahn)
ERIGARCT	*Erigone arctica* (White)
ERIGATRA	*Erigone atra* Blackwall
ERIGDENT	*Erigone dentipalpis* (Wider)
ERIGLONG	*Erigone longipalpis* (Sundevall)
ERO CAMB	*Ero cambridgei* Kulczynski
ERO FURC	*Ero furcata* (Villers)
ERO TUBE	*Ero tuberculata* (De Geer)
EUOPFRON	*Euophrys frontalis* (Walckenaer)
GONGVIVU	*Gongylidiellum vivum* (O.P.-Cambridge)
HAHNMONT	*Hahnia montana* (Blackwall)
HYPOBITU	*Hypomma bituberculatum* (Wider)
KAESPULL	*Kaestneria pullata* (O.P.-Cambridge)
LARICORN	*Larinioides cornutus* (Clerck)
LEPTROBU	*Leptorhoptrum robustum* (Westring)
LOPHPUNC	*Lophomma punctatum* (Blackwall)
MASOSUND	*Maso sundvalli* (Westring)
MEIORURE	*Meioneta rurestris* (C.L. Koch)
MICAPULI	*Micaria pulicaria* (Sundevall)
MICRHERB	*Micrargus herbigradus* (Blackwall)
MICRIMPI	*Microlinyphia impigra* (O.P.-Cambridge)
MICRPUSI	*Microlinyphia pusilla* (Sundevall)
MICRSUBA	*Micrargus subaequalis* (Westring)
MICRVIAR	*Microneta viaria* (Blackwall)
MIOXBLAN	*Mioxena blanda* (Simon)
OEDOAPIC	*Oedothorax apicatus* (Blackwall)
OEDOFUSC	*Oedothorax fuscus* (Blackwall)
OEDORETU	*Oedothorax retusus* (Westring)
OZYPTRUX	*Ozyptila trux* (Blackwall)
OZYPWEST	*Ozyptila westringi* (Thorell)
PACHCLER	*Pachygnatha clercki* Sundevall
PACHDEGE	*Pachygnatha degeeri* Sundevall
PALLERIC	*Palliduphantes ericaeus* (Blackwall)
PALLINSI	*Palliduphantes insignis* (O.P.-Cambridge)
PALLPALL	*Palliduphantes pallidus* (O.P.-Cambridge)
PARDAMEN	*Pardosa amentata* (Clerck)
PARDNIGR	*Pardosa nigriceps* (Thorell)
PARDPULL	*Pardosa pullata* (Clerck)
PARDPURB	*Pardosa purbeckensis* O.P.-Cambridge
PIRAHYGR	*Pirata hygrophilus* Thorell

PIRAPIRA	*Pirata piraticus* (Clerck)
POCAPUMI	*Pocadicnemis pumila* (Blackwall)
PORRMICR	*Porrhomma microphthalmum* (O.P.-Cambridge)
PRAEDUFF	*Praestigia duffeyi* Millidge
PRINVAGA	*Prinerigone vagans* (Audouin)
ROBEARUN	*Robertus arundineti* (O.P.-Cambridge)
ROBELIVI	*Robertus lividus* (Blackwall)
SAARABNO	*Saaristoa abnormis* (Blackwall)
SATIBRIT	*Satilatlas britteni* (Jackson)
SILOCURT	*Silometopus curtus* (Simon)
SILOELEG	*Silometopus elegans* (O.P.-Cambridge)
SILOREUS	*Silometopus reussi* (Thorell)
STEMLINE	*Stemonyphantes lineatus* (Linnaeus)
TALLEXPE	*Tallusia experta* (O.P.-Cambridge)
TARASETO	*Taranucnus setosus* (O.P.-Cambridge)
TENUTENU	*Tenuiphantes tenuis* (Blackwall)
TETREXTE	*Tetragnatha extensa* (Linnaeus)
THANSTRI	*Thanatus striatus* C.L. Koch
TISOVAGA	*Tiso vagans* (Blackwall)
TROCRURI	*Trochosa ruricola* (De Geer)
TROXSCAB	*Troxochrus scabriculus* (Westring)
WALCACUM	*Walckenaeria acuminata* Blackwall
WALCATRO	*Walckenaeria atrotibialis* (O.P.-Cambridge)
WALCKOCH	*Walckenaeria kochi* (O.P.-Cambridge)
WALCNUDI	*Walckenaeria nudipalpis* (Westring)
WALCUNIC	*Walckenaeria unicornis* O.P.-Cambridge
XYSTCRIS	*Xysticus cristatus* (Clerck)
ZELOELEC	*Zelotes electus* (C.L. Koch)
ZELOLATR	*Zelotes latreilli* (Simon)
ZELOLONG	*Zelotes longipes* (L. Koch)
ZELOSUBT	*Zelotes subterraneus* (C.L. Koch)
ZORASPIN	*Zora spinimana* (Sundevall)
ISOPODA	
TRACRATH	*Trachelipus rathkii* (Brandt)
TRICPUSI	*Trichoniscus pusillus* Brandt
DIPLOPODA	
CRASRAWL	*Craspedosoma rawlinsii* Leach

Spiders

In all 122,134 specimens of 103 species were caught during the 40 years. The data on the captures of spiders in the four sublocations of traps (table 4) are presented in the same way as those of carabids. The pattern is fully comparable too. During the first ten years, there are a number of pioneers that disappear soon, but another group of pioneers maintain for twenty years. After 1975 a group of spiders arrive that disappear after twenty years and after 1985 many species settle that remain till 2008; during the last years a number of species know to colonize too. Again, it is a continuum for species, however, now without special groups of less frequent species during some years.

The yearly numbers in specimens are illustrated in figure 22, with comparable results between the two locations. In the first fifteen years there are about 3000 specimens a year and this reduces to 500-1000 in the end of the research period. Different from the carabids, already in 1969 the spiders colonize the Lauwersmeer with 613 specimens, indicating an efficient dispersal. The higher peaks in the first years from figure 22 can again be explained by some species. In Sennerplaat in the first years are catches of 1400 specimens in *Eriogone longipalpis* (Sundevall) and 700 in *Pardosa purbeckensis* O.P-Cambridge; in 1983 were 1500 specimens *Pirata piraticus* (Clerck) and 1100 in *Pardosa purbeckensis*. Comparable, in Schildhoek the catch in 1971 was 2200 specimens of *Erigone longipalpis* and in 1982 1500 specimens of *Pardosa purbeckensis*. Next to these peaks in the graph, in both locations are many frequently caught species such as *Erigone arctica* (White), *E. atra* Blackwall, *Oedothorax apicatus* (Blackwall), *O. retusus* (Westring) and *Tenuiphantes tenuis* (Blackwall).

Data on spiders in detail

Evaluation of the represented spider species learns that five species (out of 103) are very scarce in the Netherlands with two to five known locations (P. van Helsdingen personal communication). These species are *Argenna patula* (Simon), *Allomengea scopigera* (Grube), *Praestigia duffei* Millidge, *Satilatlas britteni* (Jackson) and *Silometopus curtus* (Simon). With one exception, all locations where the species are found in the Netherlands are salt marshes along the Waddensea and in the province of Zeeland. See also Meijer (1975). All other species from the list are common to very common in the Netherlands, especially from salt marshes along the Waddensea or on Frisian islands, but also from inland locations.

The data on the spider catches (table 4) show the same general trends as in carabids: gradual replacement of species indicating a saline habitat by species of wet vegetation. But, contrary to carabids, a number of spiders already successful in 1969 is well known as ubiquists that are frequent aeronauts such as *Erigone atra*, *E. dentipalpis* and *Bathyphantes gracilis* (Blackwall) (Meijer 1977). Among the twelve species of spider caught in 1969 only two were halobionts: *E. longipalpis* and *E. arctica*. Some of the ubiquitous species are present during the full 40-year period, such as *Erigone atra*.

Other groups

The other minor groups were recorded if this was possible from the very first specimen of the group concerned. In this way myriapods (Diplopoda) with one species, woodlice (Isopoda, Oniscoidea) (14,811 specimens belonging to two species), harvestmen (Opilionidae) (9,342 specimens with six species) and one rove beetle species (Coleoptera, Staphylinidae) with 11,273 specimens of the easily identified *Paederus riparius* (Linnaeus) were added to the list of species studied. The catches for these minor groups are summarized in table 5.

The myriapod species *Craspedosoma rawlinsii* Leach invades Sennerplaat in 1992-'93, but this species is up to 2008 absent in Schildhoek. Around 1990 the two woodlice species (figure 23) reach Sennerplaat and from 1995 on they are frequently caught. However, Schildhoek is reached by woodlice only in 1995, with higher numbers in the year 2005. The harvestmen (figure 24) invade the two locations starting in 1985 and show as a whole group fluctuation in numbers. However, there is differentiation between the colonization of the species, with *Mitopus morio* (Fabricius) just in the period 1985-1992 and *Parologophus agrestis* (Meade) only in the period 2000-2008. Moreover, Sennerplaat always shows far higher numbers than Schildhoek, comparable with the myriapods and the woodlice. Finally, the rove beetle *Paederus riparius* invades Sennerplaat in 1986 with a peak with 1850 specimens in 1990-1991 and Schildhoek in 1991 with a small peak of 210 catches in 1997.

Dispersal of species

The occurrence of arthropods in the new polder Lauwersmeer depends in the first place on the dispersal power of the animals. All species have to immigrate the area and different ways of dispersal exist: walking, flying, drifting or swimming and passive dispersal by human activities and animals.

In carabids the flying of macropterous specimens is the fast

Table 3. Yearly total catches in carabids in period 1969-2008, summated for all locations. In second column is indicated the fly-capability for each species: brch = brachyptere (wingless), dimf = dimorphic without observed flight, DIMF = dimorphic with observed fight, poly = polymorphic without observed flight, POLY = polymorphic with observed flight, macr = macroptere without observed flight, MACR = macroptere (long wings) with observed flight. Each species value with a higher number than the median value is highlighted in the tables.
Table 3. Jaarlijkse totale vangsten van loopkevers in de periode 1969-2008 voor alle vangstlocaties. In de tweede kolom staat voor iedere soort het vliegvermogen: brch = brachypteer (vleugelloos), dimf = dimorf zonder vliegwaarneming, DIMF = dimorf met vliegwaarneming, poly = polymorf met vliegwaarneming, POLY = polymorf met vliegwaarneming, macr = macropteer zonder vliegwaarneming, MACR = macropteer (lange vleugels) met vliegwaarneming. Elk getal dat hoger is dan de mediaan is gemarkeerd.

species	wings	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986
Agonum muelleri	MACR	2		3										1			1		
Anchomenus dorsalis	MACR	2	1		1	2	2												
Bembidion varium	MACR		3139	4912	1287	284	208	398	6	2	3	1		1		1			
Amara convexiuscula	MACR			14	217	31	1	8	9	9									
Bembidion bruxellense	MACR		2	17	1	71	5												
Bembidion normannum	MACR		14	31	32	22	25	20			11	4	1			1	1		
Pogonus luridipennis	macr		1	4	16	44		1											
Amara familiaris	MACR				2		3		1	1			1						
Elaphrus riparius	MACR					3					1						2		
Bembidion tetracolum	DIMF			1		3	1			2			1				1		
Dyschirius obscurus	MACR						6	4	2	1									
Bembidion femoratum	MACR							7	1										
Amara bifrons	MACR					1	1	2	2	1	1			1					
Dicheirotrichus gustavii	MACR	3	97	4848	4577	13573	6273	548	3114	9014	8169	3061	743	33	2				
Pogonus chalceus	poly	1	22	32	351	921	527	202	428	743	896	181	66	4		2	2		
Agonum marginatum	MACR	3	2	7	48	23	5	1	4	8	4	18	12	43	4	4	3	2	
Bembidion aeneum	DIMF		23	119	418	29	50	88	129	39	74	227	198	340	349	231	504	141	79
Bembidion minimum	MACR		783	551	852	832	744	1630	886	110	214	870	389	179	315	460	326	3	2
Dyschirius salinus	MACR		3	89	154	1078	3315	5592	2614	1346	1720	397	93	21	24	15	10	3	
Bembidium bipunctatum	MACR					560	965	291	153	30	71	801	693	78	4	1		1	
Bembidion properans	DIMF	1			7	33	105	28	60	19	11	11	54	17	11	4	3		
Amara plebeja	MACR						3	8	11	9	5	28	6	1	1				
Bembidion iricolor	MACR			1				3	1	8		3	4	1	3	2		2	1
Harpalus rufipes	MACR			19	1	5		5	25	31	26	9	2		1				
Nebria brevicollis	MACR			1		2	2	1	7	6	1								
Dyschirius politus	MACR							1	5	1	3								
Harpalus affinis	MACR						1	1		4	21	3	4						
Pterostichus niger	MACR			1	1	3			1		5	4	1						
Amara spreta	MACR									2	1	1	3						
Anisodactylus binotatus	MACR								1		1	20	3	3	16	2	1		
Dyschirius tristis	MACR													301	345	168	16	3	
Panageus crux-major	macr												3	3	2	5	4	1	
Trechus quadristriatus	MACR	4	24	19	7	5		2	4	19	16	2		1	1	3		2	7
Clivina fossor	POLY		4	75	42	12	35	17	36	8	32	57	109	96	248	104	142	20	7
Blemus discus	MACR	1	1		3	4	1		1	1	3	2	1	2	2				2
Loricera pilicornis	MACR			2	83	20	23	24	2		34	516	51	7	2	1	3	6	6
Calathus melanocephalus	dimf			2					2	13		1	1	2			1		1
Bembidion lunulatum	MACR				3		3	6				1	3	9	4		20	4	2
Bembidion quadrimaculatum	MACR			1					3				1						
Bradycellus harpalinus	DIMF					2	3		5	10	2	3		2	2	3	2		
Pterostichus minor	DIMF															1	3		1
Badister bullatus	MACR														1	1			
Poecilus versicolor	MACR																		
Amara fulva	MACR		1						1										
Acupalpus parvulus	MACR			1	4	2	34	215	388	98	71	56	93	54	307	46	106	99	33
Amara communis	MACR						2	68	7	11	14	12	11	1	3	2	2		
Bembidion guttula	DIMF							2			2				1	1		1	
Amara aenea	MACR							5	13	11	1	1	1		1	1	1	4	
Pterostichus strenuus	POLY	4	1	2	124	54	63	47	47	34	99	118	367	299	446	97	116	96	227
Pterostichus vernalis	POLY			2	1	1	9	6	3		3	54	142	215	304	138	92	106	94
Dyschirius globosus	dimf										11	25	81	548	2112	5226	3314	2081	1480
Bembidion assimile	DIMF										1	15	19	248	1318	1018	2949	1993	196
Stenolophus mixtus	MACR													1	2	2	27	6	
Agonum emarginatum	DIMF												1		4		5	13	1
Agonum thoreyi	MACR								1		1		9	15	2	4	4	102	257
Odacantha melanura	macr												1				1	1	3
Trichocellus placidus	MACR												1						3
Pterostichus nigrita	POLY				2								5			1	4	4	
Leistus fulvibarbis	macr																		
Bembidion biguttatum	MACR																		
Acupalpus flavicollis	MACR																		
Badister sodalis	macr																	1	
Poecilus cupreus	MACR																		

1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	Total catch	
																1				1		9	AGONMUEL
												1	1									10	ANCHDORS
							1												1			10244	BEMBVARI
																						289	AMARCONV
																						96	BEMBBRUX
																						162	BEMBNORM
																						66	POGOLURI
			1																1	1		11	AMARFAMI
																						6	ELAPRIPA
																						9	BEMBTETR
1																						14	DYSCOBSC
																						8	BEMBFEMO
																						9	AMARBIFR
																						54055	DICHGUST
																						4378	POGOCHAL
1							1									1						194	AGONMARG
305	34	5				2	14	3	2	5		1				2		5		3	3	3422	BEMBAENE
1		2		1									1								1	9152	BEMBMINI
1				1	2	2		2	1		1											16484	DYSCSALI
1								1							1							3651	BEMBBIPU
1			1							1												367	BEMBPROP
							1				1											74	AMARPLEB
	1					1		11								1			1			44	BEMBIRIC
					1						1											126	HARPRUFI
			2		1										1	2	2	2				30	NEBRBREV
			1		1																	12	DYSCPOLI
			1						1													36	HARPAFFI
																						16	PTERNIGE
																						7	AMARSPRE
																			1			48	ANISBINO
					5																	838	DYSCTRIS
			1	2	3			1									1					26	PANACRUX
		2	3	1	13	9	5		1	1		2	1				1		1	1	1	158	TRECQUAD
11	7	5	34	11	23	65	26	36	40	25	27	7	15		6	4	8	8	7	20	7	1436	CLIVFOSS
1		2	5		1				4	1						2						40	BLEMDISC
17	8	1	5		1			1		4			2		3	1		3			1	827	LORIPILI
			1		2											1						27	CALAMELA
9	1	7	52	16	7	3			6		1				2		2	1		1		163	BEMBLUNU
										2						1						8	BEMBQUAD
	2			7		1	3													1	1	49	BRADHARP
				4	1	4		2		2			3		1	1						23	PTERMINO
				1	1	1		1		2						1			1	1		11	BADIBULL
					26						2					1	2					31	POECVERS
			1		1	2																6	AMARFULV
39	16	3	6	11		7	4	5	2	16	34	9	30		11	16	76	36	10	47	39	2024	ACUPPARV
2	4	5	21	4	12	14	1	3		4		1	1		1	8	5		3		2	224	AMARCOMM
								7	1				1				2	1	1	2	5	27	BEMBGUTT
	1				2				1	1						1	118	11	9	12	1	196	AMARAENE
345	94	46	148	86	179	193	109	130	44	52	47	36	27		60	30	96	51	86	80	52	4232	PTERSTRE
61	28	15	56	11	57	77	6	11	4	8	10	10	5		8	8	57	6	9	5	15	1637	PTERVERN
1151	1381	1500	2558	1167	2194	2259	947	1288	643	794	1433	1554	1101		1309	1945	1097	821	1022	1199	1075	43316	DYSCGLOB
820	413	129	2947	1120	1516	1106	289	537	311	599	472	190	618		441	64	155	46	137	227	61	19955	BEMBASSI
	1	6	10	42	23				2				1				11		1			135	STEMMIXT
6			31	4	2	6	3	7		4	4	2	4		15	2	17	5	17	7	1	161	AGONEMAR
536	973	499	926	645	450	719	568	662	252	874	524	562	465		213	510	191	108	106	86	139	10403	AGONTHOR
3	8	4	16	5	2	1	3	5	1	1	4	6	5		1	1	1		1		2	76	ODACMELA
8	9	5	6			125	22	23	22	29	3	5	3		10		3	2	8	3	2	292	TRICPLAC
3	5		20		1			11					3		2	5	9	4	10		1	90	PTERNIGR
						2	1		3										1			7	LEISFULV
		4		2	3	4	1	43	28	15	7		3		3	2	2	3	3	12	1	136	BEMBBIGU
			2	1	1			1			1							3		1		10	ACUPFLAV
1		2	29	107	117	81	10	5	9	27	57	22	24		12	10	67	22	47	87	67	804	BADISODA
	1					4			1			4	1				6		3			20	POECCUPR

Table 3. continuation / vervolg

species	wings	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986
Pterostichus diligens	DIMF														1		3	1	
Agonum fuliginosum	DIMF														1	3	2		
Carabus granulatus	brch																		
Leistus terminatus	macr																		
Philorhizus sigma	brch																		
Acupalus exiguus	MACR																		
Oodus helopioides	poly																		
Notiophilus aquaticus	DIMF	1																	
Bembidion obtusum	DIMF		1						1										
Trechoblemus micros	macr			1															
Bembidion lunatum	MACR			1															
Trechus obtusus	brch			1														1	
Pterostichus melanarius	DIMF				1														
Amara apricaria	MACR					1			1										
Bembidion lampros	DIMF					1													
Notiophilus palustris	DIMF					1													
Amara majuscula	MACR					1													
Agonum sexpunctatum	MACR						1		1										
Bradycellus caucasicus	dimf						2												
Amara lunicollis	MACR							1											
Notiophilus substriatus	MACR								2										
Amara famelica	MACR							1	2		1								
Amara quenseli	macr									2									
Synuchus vivalis	macr										1								
Paranchus albipes	macr										1								
Asaphidion flavipes	MACR												1		1				
Demetrias atricapillus	MACR																		
Badister lacertosis	macr																		
Badister unipustulatus	MACR																		
Philorhizus melanocephalus	MACR																		
Badister dilatatus	MACR																		
Harpalus latus	MACR																		
Notiophilus biguttatus	DIMF																		
Paradromius longiceps	MACR																		
Elaphrus cupreus	MACR																		
		1969	**1970**	**1971**	**1972**	**1973**	**1974**	**1975**	**1976**	**1977**	**1978**	**1979**	**1980**	**1981**	**1982**	**1983**	**1984**	**1985**	**1986**
n species		10	17	28	26	32	31	33	40	31	37	31	38	31	34	31	33	27	19
gain in spec.		10	10	15	7	10	8	10	13	4	13	3	10	7	8	5	7	4	4
loss of spec.		0	3	4	9	4	9	8	6	13	7	9	3	14	5	8	5	12	12
Year catch N		22	4119	10757	8235	17624	12418	9233	7980	11593	11531	6502	3175	2527	5840	7548	7671	4697	2402

way of dispersal over greater distances (Haeck 1971, Turin 2000). In table 3 the second column informs about the length of the wings in the species (cf. Boeken *et al.* 2002). From the 22 catches in 1969, nine species had long wings (macroptere or poly/dimorph with proof of flight capability) and one species that is polymorph without proven fly-activities, *Pogonus chalceus* (Marsham). However, the low numbers in carabids caught in the first year 1969 indicate that this behaviour is not a very common phenomenon all year long. One year later the high catches in the macroptere *Bembidion varium* and *B. minimum* (Fabricius) indicate the settlement of these species but the high numbers in other macroptere species arrive only in 1971. In that year *Trechus obtusus* Erichson is caught, remarkable because this species is known to be brachypterous (without wings). The next catches of carabids without wings are far later in 1988 and 1990, with *Carabus granulatus* and *Philorhizus sigma* (Rossi), but only after 2002 they are caught with higher numbers. The majority of the species in this ecosystem is during the whole research period macropterous, even after 40 years.

Spiders are well known for their capacity of aeronautic behaviour with ballooning. This is especially true for the small spiders from the Linyphiidae, but also from the far bigger Lycosidae in young instar phases (Richter 1971). This ballooning resulted already in a catch of more than 600 specimens in 1969. The difference in catches with the carabids is at least partly caused by differences in reproductive power in both groups. Spiders, especially pioneer species such as caught in high numbers in 1969 and 1970, are able to produce more generations a year (Meijer 1977, 1980), whereas the life cycle of carabids is more rigidly univoltine.

Opilions, isopods and diplopods are unable to fly and it is hardly likely that they reached the Schildhoek, let alone the Sennerplaat, on foot within a few years. The harvestmen invade after 16 years, the woodlice after 21 years and the myriapods after 24 years (however, the last not yet in Schildhoek). Along waterways such as the creeks in the Lauwersmeer, transportation on floating clumps of shore vegetation, or even washing away when the mudflats such as the Schildhoek are inundated, can be a way of dispersal. This would seem to be a way in which these animals can arrive in the polder. It concerns animals that

1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	Total catch	
40	34	172	356	245	398	503	486	663	593	558	444	543	516		410	681	893	760	487	510	655	9952	PTERDILI
34	18	17	18	24	32	85	139	85	109	408	241	263	231		81	124	177	182	174	136	197	2781	AGONFULI
	2		2		1	2				1	6	2	1		1	15	21	4	15	5	10	88	CARAGRAN
		1		1		1		1		1					2	1	10	7	5	2	9	41	LEISTERM
			2	1											3	4	5	10	3	6	3	37	PHILSIGM
									1	1		6	4		13	12	65	56	98	163	15	434	ACUPEXIG
																	1	1		3		5	OODEHELO
																						1	NOTIAQUA
1																						3	BEMBOBTU
																						1	TRECMICR
																						1	BEMBLUNA
																	1					3	TRECOBTU
			1				1						1									4	PTERMELA
																						2	AMARAPRI
						1						1										3	BEMBLAMP
																						1	NOTIPALU
																						1	AMARMAJU
																						2	AGONSEXP
																						2	BRADCAUC
																						1	AMARLUNI
											1											3	NOTISUBS
																						4	AMARFAME
																						2	AMARQUEN
																						1	SYNUVIVA
																						1	PARAALBI
																						2	ASAPFLAV
			1																			1	DEMEATRI
						1											1					2	BADILACE
						1																1	BADIUNIP
								2		1												3	PHILMELA
										1							1		1		1	4	BADIDILA
																1						1	HARPLATU
																	2	1				3	NOTIBIGU
																1	2				1	4	PARALONG
									1										2			3	ELAPCUPR
1987	**1988**	**1989**	**1990**	**1991**	**1992**	**1993**	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**		
26	22	22	33	26	33	31	23	28	26	29	22	21	27		25	34	35	27	33	28	29		
11	6	6	15	7	12	11	4	12	10	11	7	7	8		5	12	11	3	11	6	7		
4	10	6	4	14	5	13	12	7	12	8	14	8	2		7	3	10	11	5	11	6		
3399	3041	2432	7264	3520	5079	5282	2641	3547	2083	3438	3321	3227	3068		2610	3460	3108	2159	2272	2622	2368		

are common in inland shore vegetation and as a result of maintenance of the waterways in the hinterland floating clumps of reeds and other shore plants are often seen drifting into the polder.

Yearly species numbers

According to the theory in ecosystems (e.g. Odum 1971), the first phase in succession will be with a restricted number of pioneer species in high numbers, followed in time by other groups of species with less individuals that indicate more differentiation. After some/many years an optimum with many species will be reached, followed by a climax-phase with somewhat less species numbers (many times with a forest, not in Lauwersmeer). We observed from figure 18 and 22 the high specimen numbers in some pioneer specimens during the first decade in development, in line with theory. As an illustration, in figure 25 and 26 the yearly specimen numbers in the two locations is illustrated during the 40 years for the fifteen most frequent carabid species and the eighteen most frequent spider species.

Starting with the carabids, we took the total species number in all four sub-locations for the period 1969-2008. We also calculated the number of new species for Lauwersmeer (gain) and the species that disappeared (loss) in the samples for each year. All data are summarized in figure 27; not any real trend can be indicated in numbers, gain or loss. The linear regression of numbers has R^2=0.0005. Although the number of sample locations is restricted to four double traps, the high number of years make this result reliable. Because the different locations were taken together and local differences in carabids might be averaged, we repeated this calculation for the four locations separately (figure 28). Again, almost no difference can be indicated; only a higher number of species in the 1975-1978 in Sennerplaat B can be indicated. As a whole not any trend can be given in development in carabid species number during time.

As carabids behave ecologically different from the spiders, we expected other results from the same calculation in spider species per year at the four sub-locations (figure 29). Again, with the spider species the linear trend line is almost horizontal in the four sub-locations; only the first two years indicate some

Table 4. Yearly total catches in spiders in period 1969-2008 summated for all locations. Each species value with a higher number than the median value is highlighted in the tables.
Table 4. Jaarlijkse totale vangsten van spinnen in de periode 1969-2008 voor alle vangstlocaties. Elk getal dat hoger is dan de mediaan is gemarkeerd.

species	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988
Agyneta rurestris	17	13	7	1			1	2	1	1										
Praestigia duffeyi		16	2	1																
Erigone dentipalpis	57	58	70	5	17	12	11	10	25	22	2	2	1		6	4			2	1
Porrhoma microphthalmum	3	40	281	462	138	328	176	391	248	97	8	3	4	1	1	1		1		6
Prinerigone vagans			2	1	1	1			1											
Enoplognatha mordax		9	13	24	13	12	10	66	99	30	12	2				1				
Diplostyla concolor	6	4	432	321	111	49	41	101	48	20	2	1								
Palliduphantes insignis			18	10	5		1			2			1		1				1	
Tenuiphantes tenuis	5	23	639	529	1239	426	327	173	252	661	269	6	4		3			1		
Erigone longipalpis	129	981	4264	2409	3334	1766	2236	791	360	487	698	563	382	330	47	116	50	10		6
Micrargus subaequalis					1			2	1	1										
Silometopus elegans			8	3		1	3													
Erigone atra	162	168	148	64	62	56	92	74	50	68	64	64	27	4	98	97	24	41	13	37
Oedothorax apicatus	69	181	683	292	382	209	210	102	201	195	8	11	15	10	46	21	12	3		2
Bathyphantes gracilis	131	131	143	91	89	37	18	5	13	45	37	20	19	25	19	35	44	43	23	25
Clubiona stagnatilis		40	32	43	13	21	17	19	5	3	3	2	6	1	3	2			1	2
Oedothorax fuscus	30	94	131	44	142	166	212	747	418	572	105	30	2	2	36	21	7	1		3
Hypomma bituberculatum		174	21	30	87	101	85	206	166	68	38	19	38	34	12	57	23	12	27	23
Pachygnatha clercki		1	35	393	204	357	326	237	171	231	452	883	417	380	87	460	240	280	242	148
Pardosa purbeckensis		28	415	390	220	619	969	1779	410	403	623	1686	1465	2306	140	898	283	426	365	122
Oedothorax retusus	3	4	44	123	90	215	512	515	250	316	407	499	225	268	260	614	162	169	58	56
Larinioides cornutus					1		2		1			1								
Palliduphantes pallidus		2	2			1										2	1	1		
Walckenaeria kochi		4	11	47	16	8	6	2	9	4	52	180	97	51	7	31	29	86	58	11
Robertus arundineti		2	70	8	33	143	30	30	9	84	34	161	39	48	7	18	27	16	29	17
Centromerita bicolor			2	4	8	9	6	6	8	20	49	51	6	19	8	77	46	27	25	2
Argenna patula			2	3	11	43	90	220	210	158	52	58	11	10		55	20	24	3	
Silometopus curtus					1	1	9	81	41	74	101	41	3	4	1					
Micaria pulicaria								1	3			6	4	2		2	3			
Microlinyphia pusilla												4	7	4						
Zelotes longipes											1			1	18	1				
Walckenaeria unicomis															1	3	2			
Leptorhoptrum robustum			3	29	8	11	4	11	25	64	227	177	54	17	4	18	61	93	94	78
Pachygnatha degeeri	1	3	2	4	4	4	27	51	120	103	64	201	60	69	11	162	122	210	146	56
Trochosa ruricola				1		2	7	33	45	68	63	74	128	210	121	372	57	74	58	34
Agyneta decora									1	1	6	24	9	16	2	1	14	36	29	21
Pirata piraticus		1		1	2	10	37	23	264	468	1039	1417	2703	2455	2188	1521	1729	1550	793	1144
Bathyphantes approximatus						1	2		9	15	91	117	173	38	17	29	85	218	111	154
Pardosa amentata			6		1	1		4	8	14	151	274	296	411	28	205	74	212	156	130
Xysticus cristatus									1	1		9	4	23	1	13	1		1	
Drassyllus pusillus								2		1	2	2	2	2	1	5	2	2		
Zelopes latreilli									1			1						1	1	
Allomengea scopigera												11	25	30	4	16	43	60	10	10
Microlinyphia impigra											2		2	1	11	6	5	2		
Satilatlas britteni																3	22	19	14	15
Walckenaeria nudipalpis								1	1	1	1	11	11	10	5	13	14	30	19	22
Allomengea vidua																		3	2	4
Clubiona phragmites					1	3	2	6	3		3	10	5	1	2	7	5	3	3	
Gongylidiellum vivum		1									4	11	30	36	23	31	27	68	89	131
Walckenaeria atrotibialis												2	1	4	1	3	11	14	8	23
Alopecosa pulverulenta						1		1	3	2	3	2	3	26	1	11	2	14	1	4
Centromerus sylvaticus												1		1	1	6	1	29	14	24
Tallusia experta														1		4	4	39	27	22
Diplocephalus permixtus																		9	2	3
Lophomma punctatum				1								1					3	34	64	38
Robertus lividus		2			1							1								1
Palliduphantes ericaeus					3					1	1		1		1			2	8	1
Dismodicus bifrons														2		1	1		4	
Walckenaeria acuminata																				
Ero furcata																		2	1	
Kaestneria pullata																				
Ceratinella brevipes																				
Pardosa pullata																1		8		
Bathyphantes parvulus						1			2											
Ozyptila trux											1					1		1		
Agroeca proxima													1	1	1					
Pardosa nigriceps									1							1				
Microneta viaria																				

1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	total catch	species
																				43	AGYNRURE
																				19	PRAEDUFF
					1														1	307	ERIGDENT
																				2189	PORRMICR
1																			3	10	PRINVAGA
																				291	ENOPMORD
																				1136	DIPLCONC
			1							1										41	PALLINSI
																				4557	TENUTENU
2						2														18963	ERIGLONG
																				5	MICRSUBA
	2	4									1							2		24	SILOELEG
12	2	3	2	3	12	7	8	5	1	7				18	1	5	16	9	10	1534	ERIGATRA
17	27	5	4	1	4		3	3		1	2			3		3	1	8	1	2735	OEDOAPIC
46	41	18	19	2	19	8	45	24	39	24	21		14	14	1	24	4	6	7	1369	BATHGRAC
3	1	1	3	3	2		1	1	1		1		1	2			1	1		235	CLUBSTAG
	4	2				1			1									1	1	2773	OEDOFUSC
15	37	14	20	2	4	4	1	1					2	1	5			2	1	1330	HYPOBITU
106	195	45	61	84	69	120	45	73	71	45	79		73	71	54	21	25	26	39	6846	PACHCLER
264	287	98	164	148	48	14	17	5	22		4		1	2	9	1	1			14632	PARDPURB
23	19	42	17	9	10	5	4	2	3	5	5		3	5	1	1	1		1	4946	OEDORETU
																			1	6	LARICORN
	1					1	2	2		2	2				1					20	PALLPALL
6	12	4	2	1		4				1			3		2					744	WALCKOCH
2	7	21	5	7	2	5	1	3	2	3	4			1	2	1				871	ROBEARUN
	1	10	2	5	11	2		4						1					5	414	CENTBICO
				2		1														973	ARGEPATU
																				357	SILOCURT
				1																22	MICAPULI
2		2																		19	MICRPUSI
																			1	22	ZELOLONG
					1										1		1			9	WALCUNIC
11	7	4	1		4	7	8	7	16	14	8		14	7		2			2	1090	LEPTROBU
40	20	3	7	3	5	5	7	2		1	5			2						1520	PACHDEGE
20	34	20	54	43	36	24	27	32	27	9	4			4	13	2	1	3	1	1701	TROCRURI
7	14	8	9	3	3	4	1	4	4	1	1		1	1	2	2	4		5	234	AGYNDECO
1955	1435	654	814	925	1095	1266	679	1309	995	1090	1028		627	727	543	500	306	335	565	34193	PIRAPIRA
157	54	12	6	2	5	8	2		1	10	16		18	20	1	5	4		10	1391	BATHAPPR
172	412	81	64	54	19	58	10	25	61	4	6		1	1	8	1	3		2	2953	PARDAMEN
	4		7	6			8	3	8	1			1	1	4					97	XYSTCRIS
			5	4		2	3	4	7		1			1	4					52	DRASPUSI
1	1					1				1							1			9	ZELOLATR
102	16	51	6	3	32	27	71	11			1									529	ALLOSCOP
11	15		3		1															59	MICRIMPI
12	24	33	37	48	18	5	9			1				1					1	262	SATIBRIT
10	16	16	11	9	14	16	12	20	11	11	13		1	9	12	3	3	3	5	334	WALCNUDI
73	122	308	96	35	149	139	123	43	16	77	17		2	16		10	2		2	1239	ALLOVIDU
2	3		1		1	1				1	2		5	7	7	6		7	1	98	CLUBPHRA
83	109	77	26	22	11	16	15	40	41	57	32		62	38	83	34	45	56	75	1373	GONGVIVU
18	16	30	34	16	12	11	9	12	11	5	9		2	3	4	12			4	275	WALCATRO
5	13	7	36	90	19	24	33	25	34	2	4		4	7	47	7	6	4	4	445	ALOPPULV
20	9	53	2	90	48	36	34	175	3	33	4		45	46	30	59	13	29	27	833	CENTSYLV
12	23	44	27	12	23	47	40	27	12	27	4		19	13	13	28	2	4	7	481	TALLEXPE
1	1	1				11	8	2	1	6	1			2	3	2				53	DIPLPERM
7	25	26	28		9	8	20	35	16	24	32		36	89	62	12	2	24	20	616	LOPHPUNC
	18						1			2			4	4	12	5	2	6	7	66	ROBELIVI
1	4	6	3	3	2	7	7	6	7	2	5		1	2	3	17	8	5	1	108	PALLERIC
	7		2		7	2		5					1	3	2	2	10	9	1	59	DISMBIFR
	3	9	6	8	7	16	30	18	2	3	4		12	20	9	5	5	2		159	WALCACUM
	2	2	4		2		2	3		4				5	3		2	2	3	37	ERO FURC
2	2	3	3	8	4	3	3	2	8	5	1		1	4	1	4	6	5	6	71	KAESPULL
						11	3	3	2	7	2		6	12	4	1	1		1	53	CERABREV
1	2	5	7	26	20	45	44	155	128	25	34		50	43	156	31	35	41	60	917	PARDPULL
	1	1	2		4	9	22	15	11	7	18		7	9	12	2	11	13	14	161	BATHPARV
1				7	8	7	3	9	15	20	6		6	42	38	16	8	32	23	244	OZYPTRUX
5	4	2	5	2	6	1	17	15	2	22	6		6	32	13	20	14	14	3	192	AGROPROX
	2		2	2		15	6	6	7		1			24	7	4		1	2	81	PARDNIGR
	2								3					1				3	2	11	MICRVIAR

Table 4. continuation / vervolg

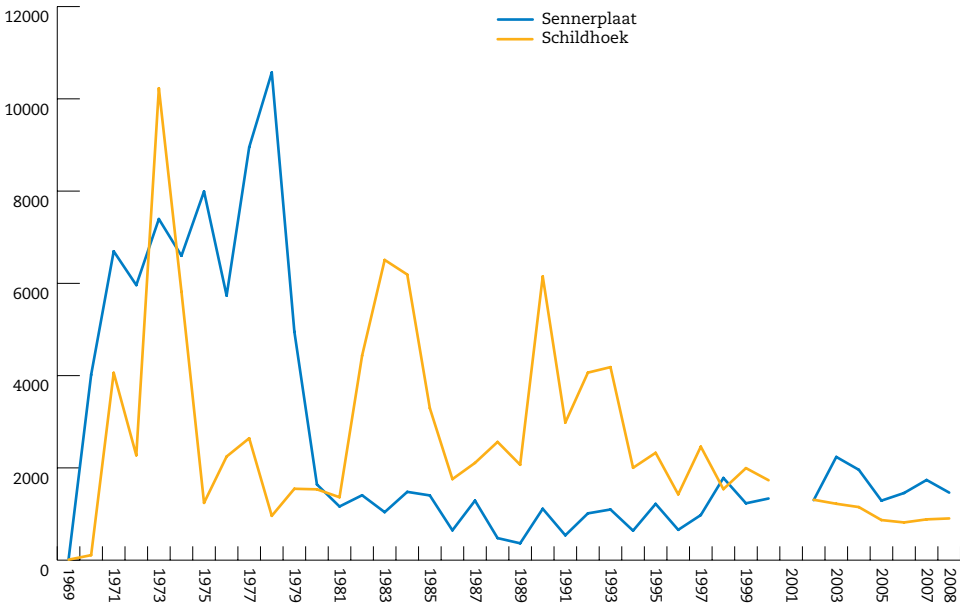
species	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988
Pocadicnemis pumila								1	1		1								2	
Saaristoa abnormis																				
Antistea elegans																				
Micrargus herbigradus							2													
Diplocephalus cristatus		1																		
Zora spinimana		1					1													
Pirata hygrophilus																				
Taranucnus setosus																				
Cnephalocotes obscurus																				
Agyneta subtilis																				
Clubiona reclusa		1																1		
Dicymbium nigrum nigrum		1																		
Tiso vagans			1					1												
Erigone arctica			2																	
Stemonyphanthes lineatus							1									1			1	
Hahnia montana							1													
Crustulina guttata									1											
Mioxena blanda										1										
Silometopus reussi										1		1								
Zelotes subterraneus													1							
Tetragnatha extensa														2						
Zelotes electus								1	1						2					
Asthenargus paganus																	1			
Ero cambridgei																		1		
Ozyptila westringi																				1
Ero tuberculata																				
Enoplognatha thoracica																				
Thanatus striatus																				
Clubione terrestris																				
Euophrys frontalis																				
Maso sundvalli																				
Centromerus dilutus																				
Troxochrus scabriculus																				
Aphileta misera																				
Arctosa leopardus																				
Year	**1969**	**1970**	**1971**	**1972**	**1973**	**1974**	**1975**	**1976**	**1977**	**1978**	**1979**	**1980**	**1981**	**1982**	**1983**	**1984**	**1985**	**1986**	**1987**	**1988**
n species	12	28	30	29	31	32	34	34	41	36	37	43	40	40	40	45	39	43	39	36
gain speies		16	9	3	7	6	7	8	9	5	6	10	5	6	7	10	2	10	8	5
loss species		0	7	4	5	5	5	8	2	10	6	5	7	4	6	6	9	5	11	9
Year catch N	613	1984	7489	5334	6238	4615	5474	5695	3487	4303	4676	6640	6282	6856	3226	4947	3257	3876	2505	2377

Table 5. Yearly total catches in other groups in period 1969-2008 summated for all locations. Each species value with a higher number than the median value is highlighted in the tables.
Table 5. Jaarlijkse totale vangsten uit de andere groepen in de periode 1969-2008 voor alle vangstlocaties. Elk getal dat hoger is dan de mediaan is gemarkeerd.

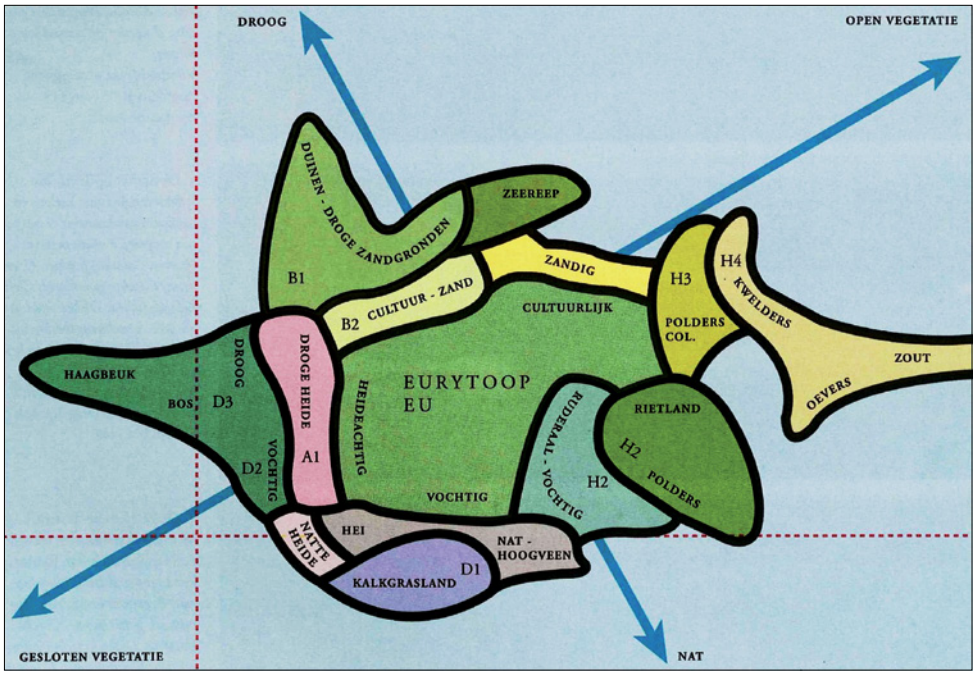
species	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988
Diplopoda																				
Craspedosoma rawlinsii																				
Isopoda																				
Trachelipus rathkii																				
Trichoniscus pusillus																				
Opiliones																				
Mitopus morio																	4	3	1	
Oligolophus tridens																	84	108	43	60
Nemastoma lugubre																			4	23
Paroligolophus agrestis																			1	2
Lacinius ephippiatus																				4
Rilaena triangularis																				
Staphylinidae																				
Paederus riparius																	2	48	186	328

1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	total catch	species
1				2			1				6		6	2	7	3	3	3	5	44	POCAPUMI
											1		2	2	1		2			8	SAARABNO
							1	1		25	26		156	376	163	153	196	117	167	1381	ANTIELEG
					1				4	2	3		22	12	9	14	12	19	14	114	MICRHERB
													4	1				4	2	12	DIPLOCRIS
							1							1	2	1		2	2	11	ZORASPIN
7				1					4	6	4		6	135	38	96	74	241	262	874	PIRAHYGR
										3			12	17	11	9	17	19	35	123	TARASETO
										1			1	3	41	20	6			72	CNEPOBSC
																	2	3		5	AGYNSUBT
																		1		3	CLUBRECL
																			1	2	DICYNIGR
																				2	TISOVAGA
																				2	ERIGARCT
																				3	STEMLINE
																				1	HAHNMONT
																				1	CRUSGUTT
	1																			2	MIOXBLAN
																				2	SILOREUS
																		1		1	ZELOSUBT
																				2	TETREXTE
																				4	ZELOELEC
																				1	ASTHPAGA
																				1	ERO CAMB
																				1	OZYPWEST
2																				2	ERO TUBE
			1						1											2	ENOPTHOR
								1	2									1		4	THANSTRI
									1											1	CLUBTERR
														1						1	EUOPFRON
															1					1	MASOSUND
																1	1	1		3	CENTDILU
																	1	2		3	TROXSCAB
																		2	1	3	APHIMISE
	1																	2		3	ARCTLEOP
1989	**1990**	**1991**	**1992**	**1993**	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**TOTAL**	**Year**
42	46	35	43	39	41	43	44	42	40	44	42		40	53	47	42	42	44	49		n species
11	13	1	8	5	9	9	8	4	8	13	8			13	3	4	7	12	15		gain
6	7	11	4	8	8	7	7	6	8	9	10			1	9	9	7	11	10		loss
3238	3058	1725	1609	1692	1748	2006	1387	2138	1601	1598	1424		1238	1864	1446	1145	858	1071	1414	122134	Year catch

1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	total catches
			3	8	7	8	32	32	10	13	27		16	27	53	15	19	54	23	347
57	114	66	294	397	323	481	743	1323	1034	1496	885		633	1460	1782	1130	658	499	621	13996
	6	38	1	14	30	7	76	74	53	38	9		89	45	43	81	173	20	18	815
	11	2	4							1	1			28	1	1	1			58
411	100	142	45	24	12	17	134	73	11	110	21		21	100	52	70	68	16	54	1776
30	174	359	914	278	278	289	367	903	180	681	254		232	275	498	386	400	172	432	7129
6		4		1			3	6		3	1		2	29		11	8		5	82
10	5	2	2	2		4	22	13		4			10	37	19	11	15	6	42	208
							1	4	2	0	5		1	17	13	7	2	4	33	89
1023	1863	1893	1324	833	342	511	680	746	218	262	119		94	163	272	100	109	67	90	11273



18. Year catches of carabids in the Sennerplaat (A + B) and the Schildhoek (A + B).
18. Jaarlijks aantal individuen loopkevers in Sennerplaat (A + B) en Schildhoek (A + B).



19. Diagram of 1616 Dutch carabid habitats with two major variation axes: dry-wet and closed to open (after Turin 2000).
19. Diagram van 1616 Nederlandse loopkever-habitats met de twee belangrijkste variatie assen: droog-nat en gesloten-open (naar Turin 2000).

lower values. This calculation was repeated with the four sub-locations merged (figure 30) and surprisingly this resulted in an increasing linear trend line with R^2=0.58, in line with the theory.

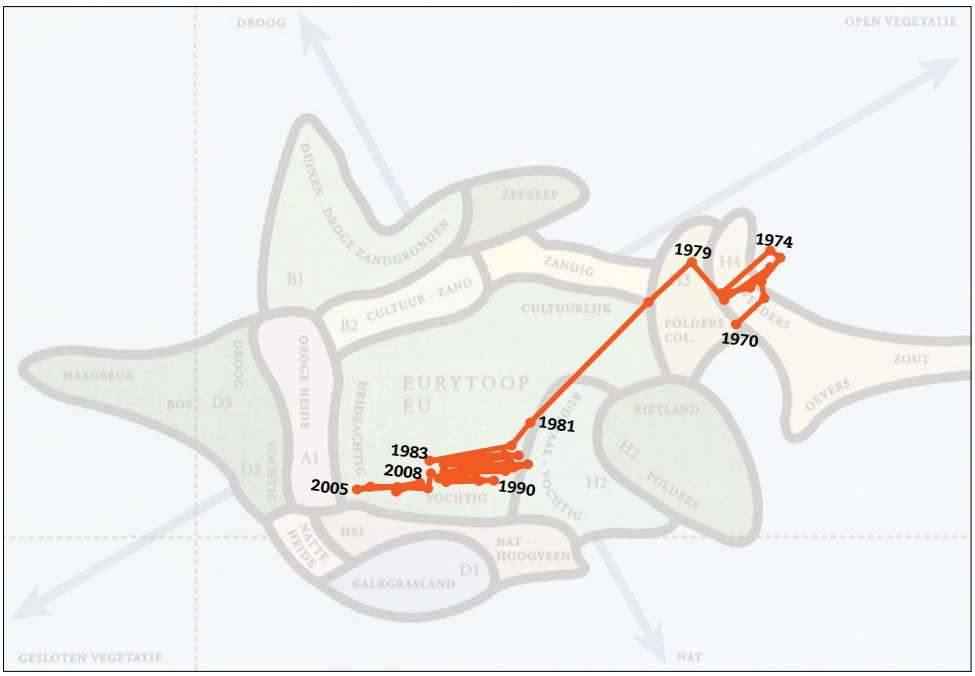
This information offers a conflicting result: in the carabids not any trend can be concluded, whereas in the spiders (only with merging data from four locations) an increasing number of species during the 40-year succession can be proved. It indicates first that carabids and spiders behave different in succession, and second that or space (more locations) or sample number has impact in this relation.

Salinity

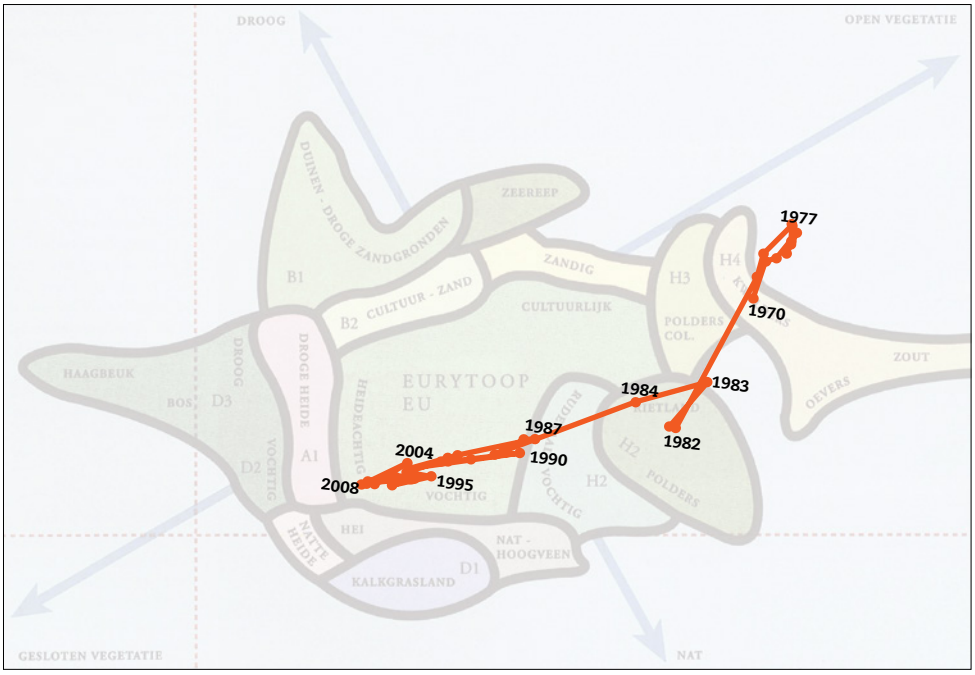
From 1969 on, the sand bar (Sennerplaat) and the mud flat (Schildhoek) were no longer influenced by tidal impact with saline water and precipitation started the desalinization in the soil. No measurements are available of this decrease in soil salinity and we will try to reconstruct this from the fauna.

During the first years, settlement of salt marsh plant species expanded and after a decade the settlement of grasses was the next succession phase. The typical fauna from salt marshes also disappeared, but general problem in the interpretation is that many frequent species in salt marshes are not connected to salinity, because most of them are only salt tolerant. They prefer permanent open space between a partly vegetated soil as an ecosystem structure. Many of these salt marsh species are also frequently found on mudflats and open shorelines of the tidal freshwater wetlands (Barendregt *et al.* 2009). For instance, the abundant spiders in salt marshes from the genera *Erigone*, *Oedothorax* and *Bathyphantes* are also well represented in this fresh dynamic system.

In the Lauwersmeer the initial increase of the carabid specimens is undoubtedly due to the successful reproduction of species that are halotolerant such as *Bembidion varium*, or halophilic (even halobiontic) ones such as *Dicheirotrichus gustavii*, *B. minimum* and *Dyschirius salinus* in the empty saline habitat.



20. Ordination in carabids per years for the Sennerplaat according to the calculated index (see text) based on data from figure 19.
20. Ordinatiediagram van alle loopkevervangsten per jaar voor de Sennerplaat, volgens de berekende index (zie tekst) gebaseerd op de gegevens uit figuur 19.



21. Ordination in carabids per years for de Schildhoek according to the calculated index (see text) based on data from figure 19.
21. Ordinatiediagram van alle loopkevervangsten per jaar voor de Schildhoek, volgens de berekende index (zie tekst) gebaseerd op de gegevens uit figuur 19.

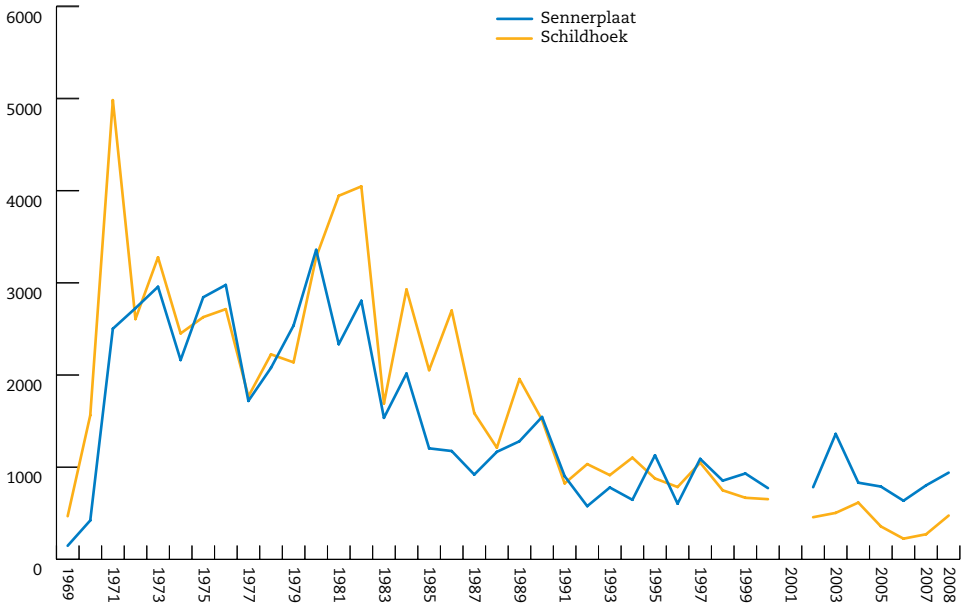
However, *Bembidion varium*, a species that is not halophilic, occurring in salt marshes as well as along fresh water (Turin 2000), was the most common carabid in the 1970 and 1971 captures. Gradually during the years the saline species were replaced by species typical for wet, non-saline conditions.

From literature (British Arachnological Society 2017, Harvey *et al.* 2002, Turin 1991, 2000) is known that a very restricted number of species really need saline conditions and according to these references the species *Dicheirotrichus gustavii*, *Dyschirius obscurus* (Gyllenhal), *D. salinus*, *Bembidion iricolor* Bedel, *B. normannum* Dejean, *B. minimum*, *Pogonus chalceus*, *P. luridipennis* (Germar), *Enoplognatha mordax* (Thorell), *Praestigia duffeyi*, *Pardosa purbeckensis* and *Silometopus curtus* have been selected as representatives of the halophilic species. The yearly total catches of these species are presented in table 6, for the locations Sennerplaat and Schildhoek separately; catches higher than the median value are highlighted.

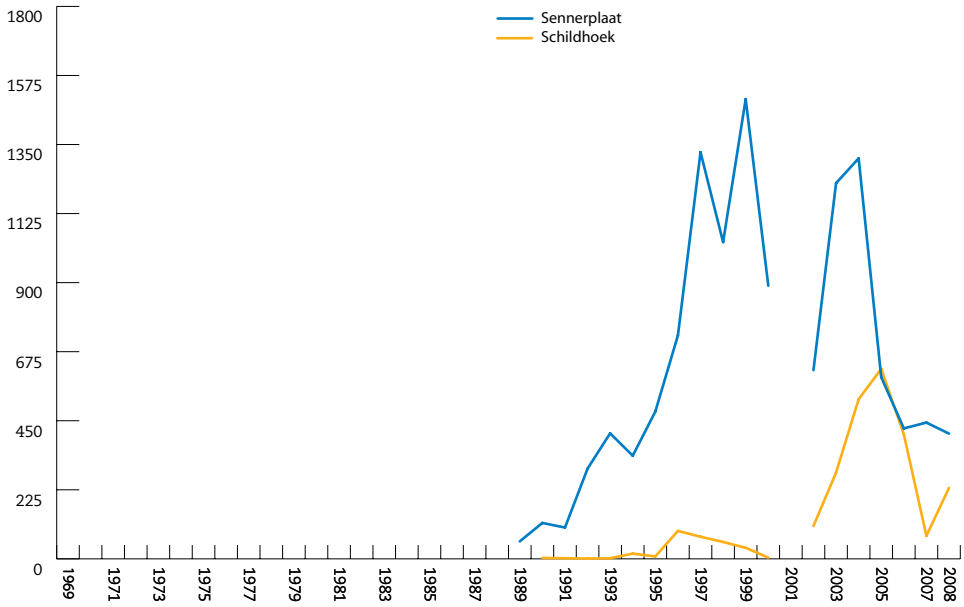
The presence of all twelve halophilic species is restricted to the period 1970-1980 and we conclude that after this decade the ecosystem will be changed from brackish to fresh. However, four species are present even ten to twenty years later, an indication that they are not strictly halophilic. Surprisingly, the differences between the sandy soil of Sennerplaat and the clay soil of Schildhoek, and linked to that also the characteristics in hydrology, are not reflected in the presence of halophilic species. Observing the number of catches, the species disappear from Sennerplaat only two years earlier than from Schildhoek. Soil does not dominate the effects of salinity.

Differences between Sennerplaat and Schildhoek

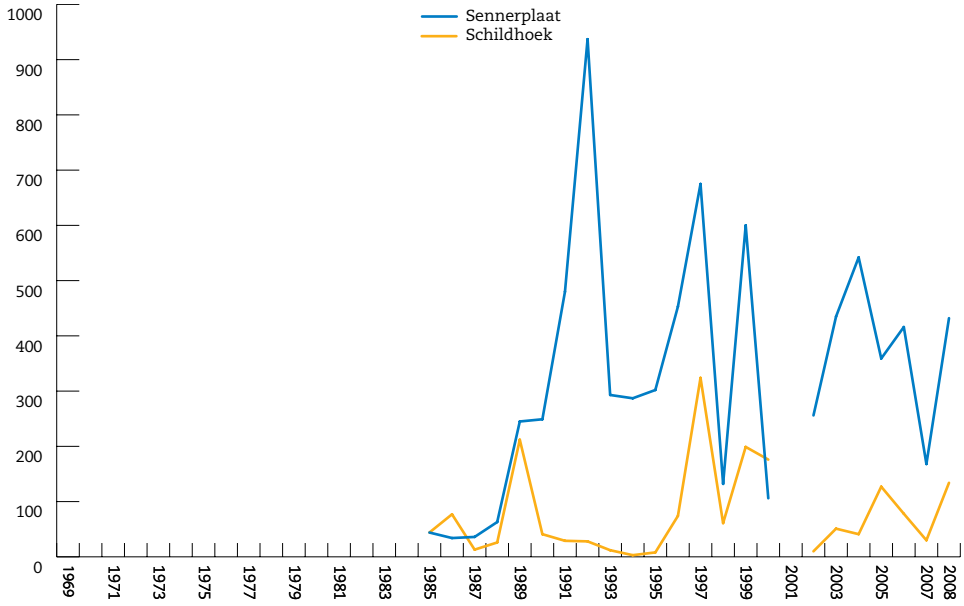
In 1969 the two locations started totally different as a more elevated sandbar and a lower mudflat. After a year a salt marsh vegetation started that at both locations, that within ten years changed into a grassy vegetation, already without salinity. Succession in vegetation continued and a reed marsh devel-



22. Year catches of spiders in the Sennerplaat (A + B) and the Schildhoek (A + B).
22. Jaarlijks aantal individuen spinnen in Sennerplaat (A + B) en Schildhoek (A + B).

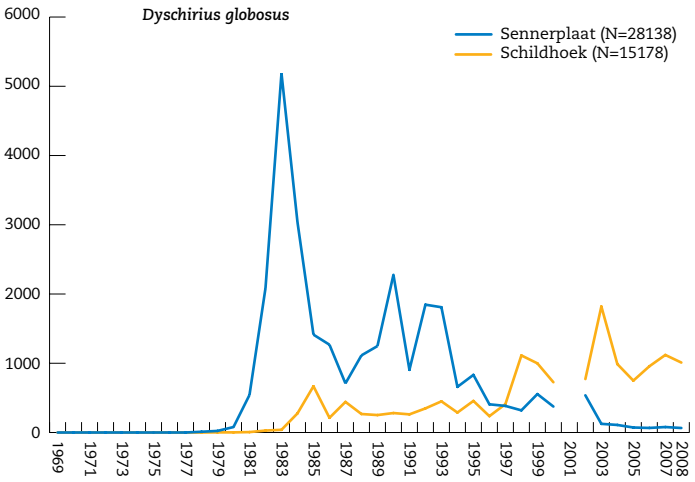


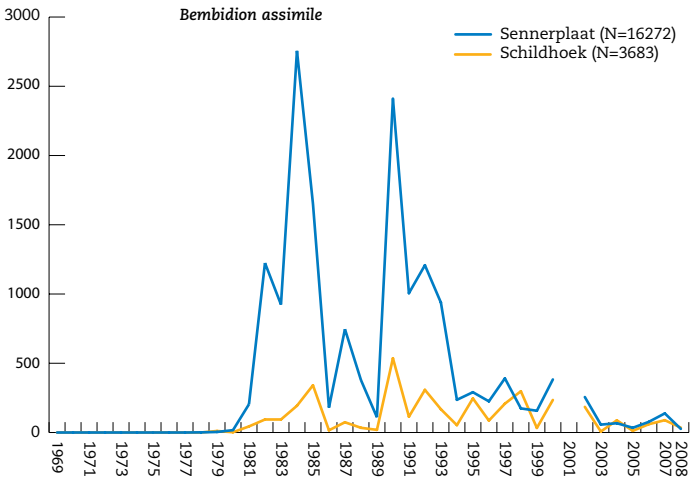
23. Year catches of woodlice in the Sennerplaat (A + B) and the Schildhoek (A + B).
23. Jaarlijks aantal individuen pissebedden in Sennerplaat (A + B) en Schildhoek (A + B).

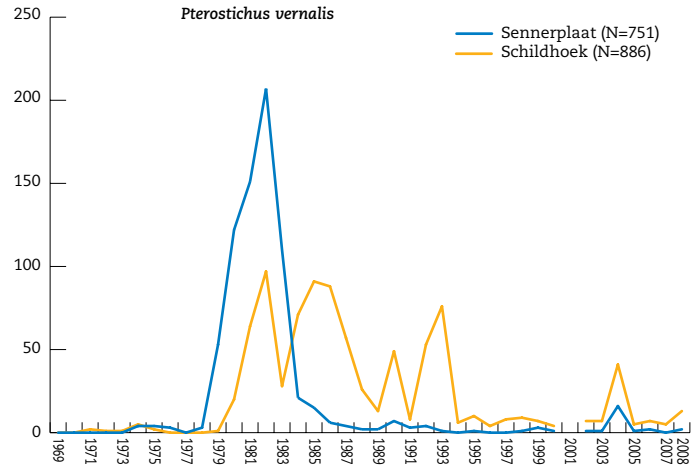


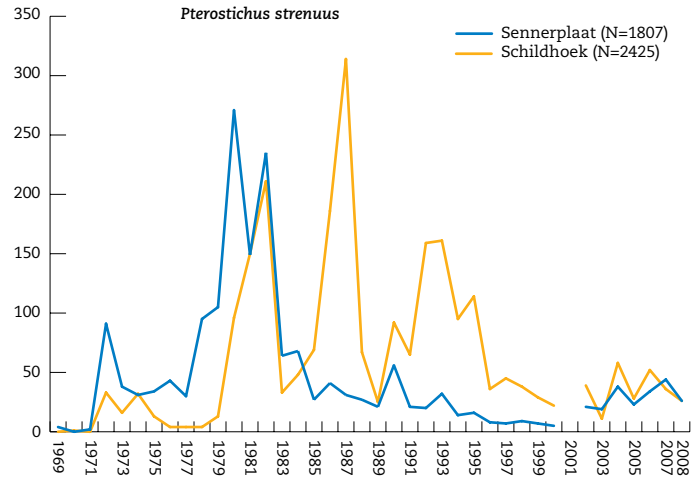
24. Year catches of harvestmen in the Sennerplaat (A + B) and the Schildhoek (A + B).
24. Jaarlijks aantal individuen hooiwagens in Sennerplaat (A + B) en Schildhoek (A + B).

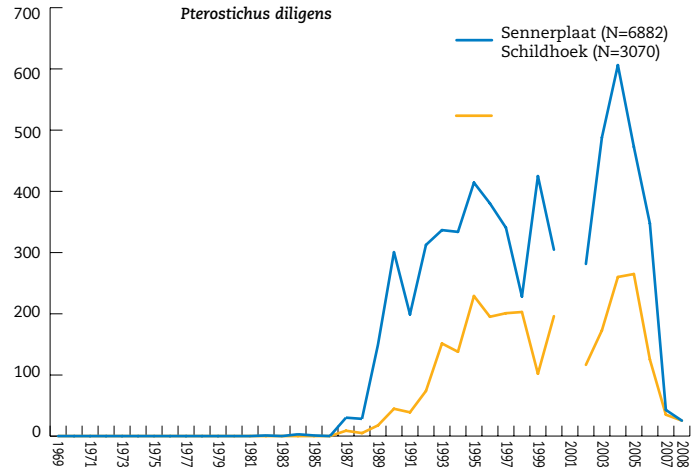
25. Yearly number of specimens in 15 carabid species for Sennerplaat and Schildhoek.
25. Jaarlijks aantal individuen van 15 loopkeversoorten op Sennerplaat en Schildhoek.

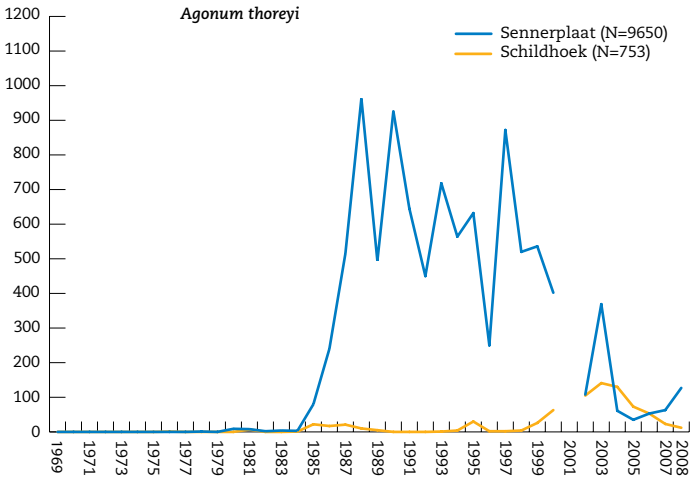

Dyschirius globosus
Sennerplaat (N=28138)
Schildhoek (N=15178)

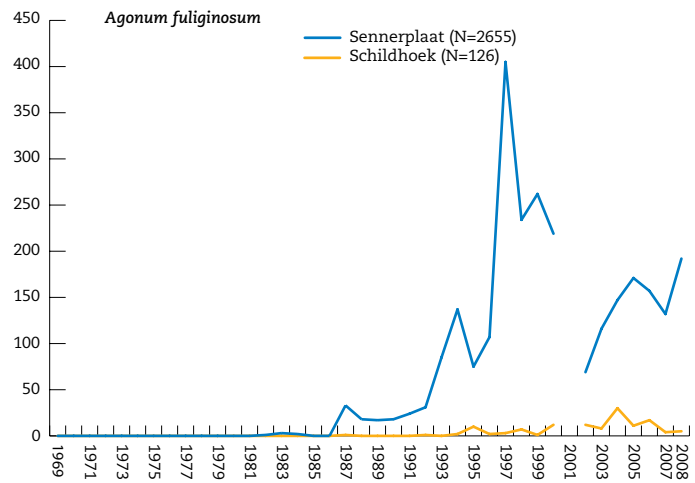

Bembidion assimile
Sennerplaat (N=16272)
Schildhoek (N=3683)


Pterostichus vernalis
Sennerplaat (N=751)
Schildhoek (N=886)

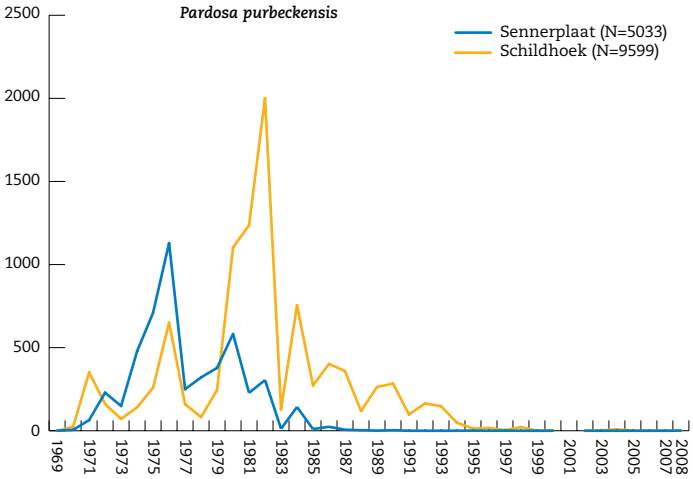

Pterostichus strenuus
Sennerplaat (N=1807)
Schildhoek (N=2425)

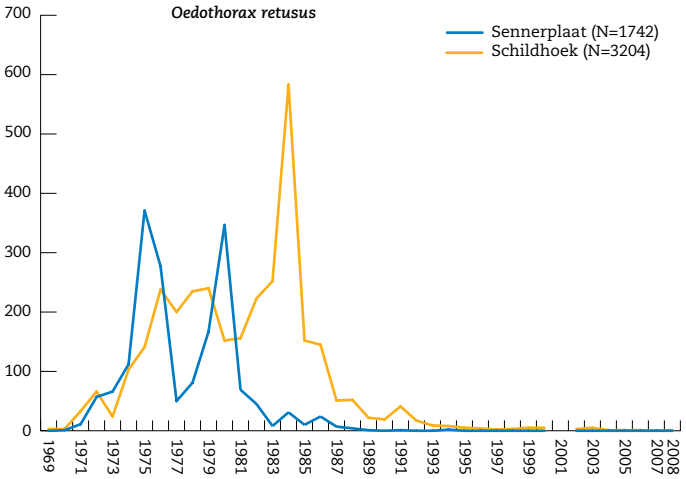

Pterostichus diligens
Sennerplaat (N=6882)
Schildhoek (N=3070)

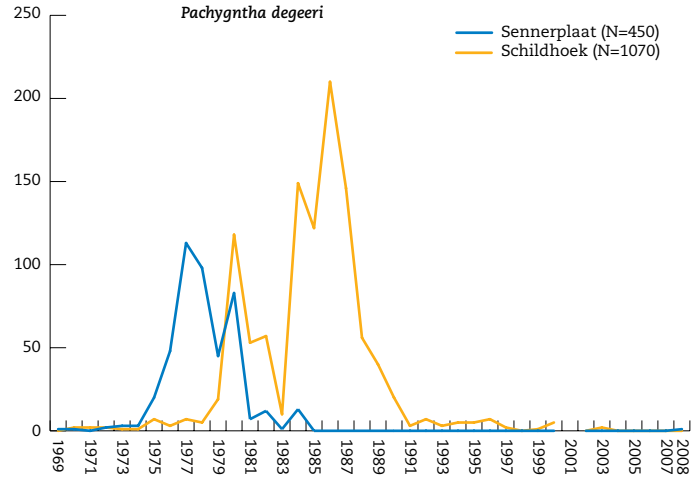

Agonum thoreyi
Sennerplaat (N=9650)
Schildhoek (N=753)

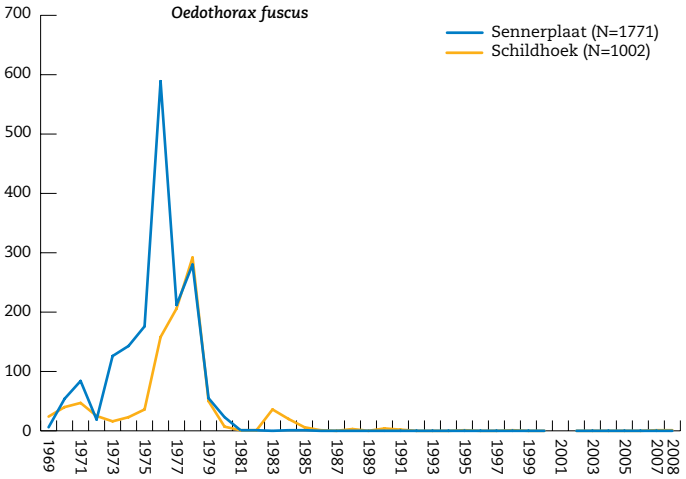

Agonum fuliginosum
Sennerplaat (N=2655)
Schildhoek (N=126)

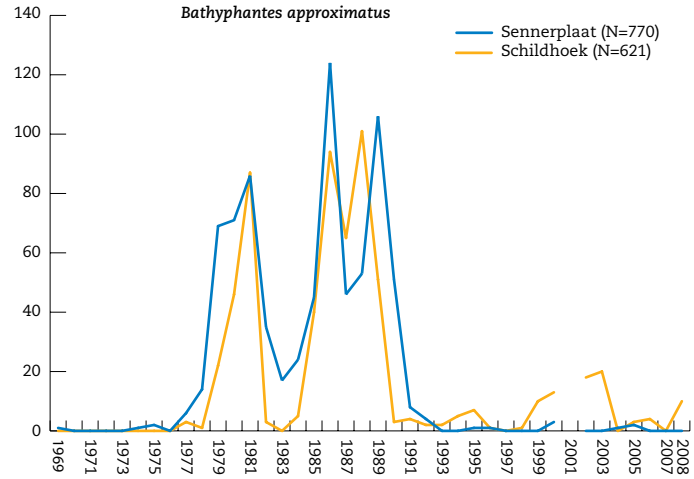
26. Yearly number of specimens in 18 spider species for Sennerplaat and Schildhoek.
26. Jaarlijks aantal individuen van 18 spinnensoorten op Sennerplaat en Schildhoek.

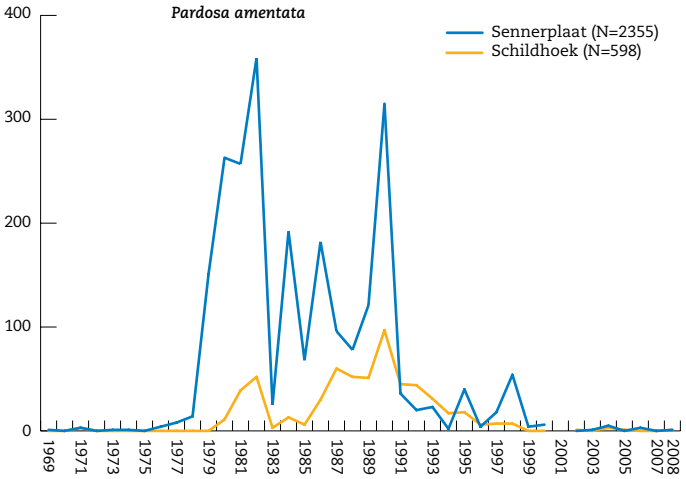

Pardosa purbeckensis
Sennerplaat (N=5033)
Schildhoek (N=9599)

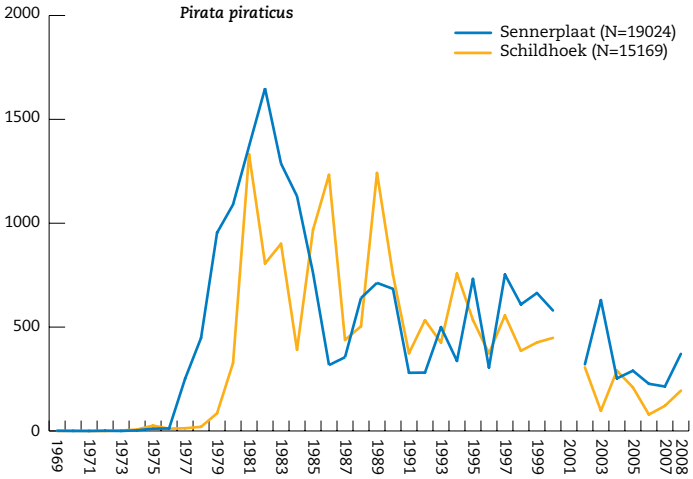

Oedothorax retusus
Sennerplaat (N=1742)
Schildhoek (N=3204)

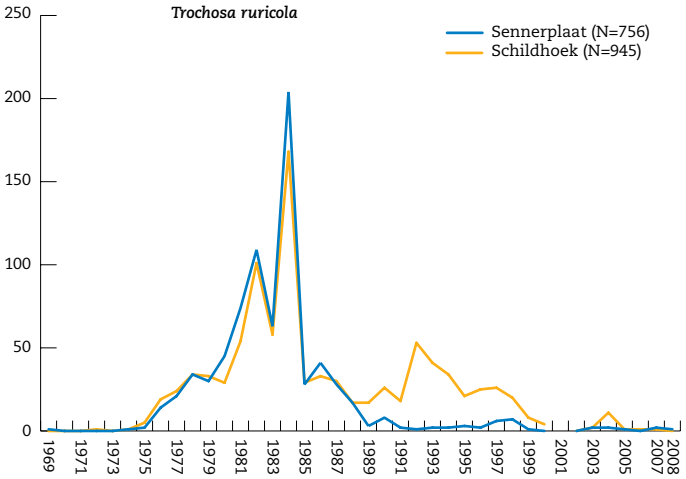

Pachygntha degeeri
Sennerplaat (N=450)
Schildhoek (N=1070)

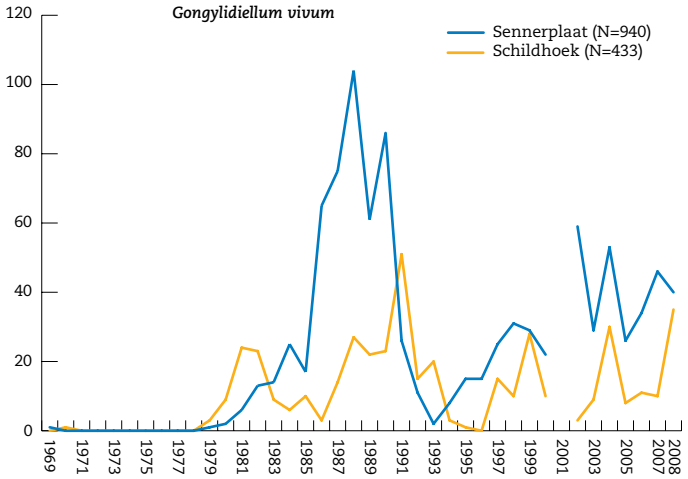

Oedothorax fuscus
Sennerplaat (N=1771)
Schildhoek (N=1002)

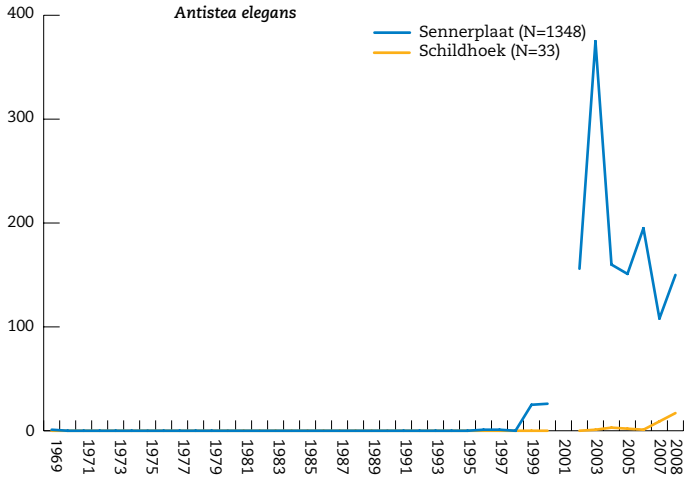

Bathyphantes approximatus
Sennerplaat (N=770)
Schildhoek (N=621)


Pardosa amentata
Sennerplaat (N=2355)
Schildhoek (N=598)


Pirata piraticus
Sennerplaat (N=19024)
Schildhoek (N=15169)


Trochosa ruricola
Sennerplaat (N=756)
Schildhoek (N=945)





oped at Sennerplaat in 1980 and at Schildhoek in 1990. What remained were the differences in soil and elevation after 1990. Due to the lower elevation at Schildhoek, higher water tables in winter in the lake cause flooding; figure 31 illustrates these conditions. However, the similarities in development of ground dwelling fauna in the two locations are prominent. The lists of represented species in both areas are almost identical and the total number of catches in the areas is almost the same in time for the spiders (figure 22); only in the carabids different peaks are present in time (figure 18), explained before with high numbers in some dominant species.

To search for the most prominent differences in the fauna of the locations, the species with less than 40 specimens in all years are removed, and from the remaining list only species are selected that differ more than five times in number of specimens between the two locations. The resulting 39 species are incorporated in table 7 with their total number of specimens in the two locations. Additionally, the decade of presence is indicated and finally the type of ecosystem in which the species is frequently present (according to British Arachnological Society 2017 and Turin 2000).

For the carabid group the sandy Sennerplaat and the muddy Schildhoek facilitate some different species during the first ten years. Two species in the genera *Bembidion* and *Amara* plus one *Anisodactylus* are more represented on Sennerplaat, in ecology known from open sandy areas and shore lines. More abundant in Schildhoek are typical salt marsh species from various genera: twice *Pogonus*, three times *Bembidion* and once *Dyschirius* (some years later another *Dyschirius* and *Bembidion*, known from shore lines). After circa 1985 in both subareas a number of new species colonize and they remain till the end of the research period. In Sennerplaat seven species are present that are known from vegetated wetlands (reed marsh or wood), in Schildhoek the last three species have only the wetlands in common. Moreover, from figure 18 we observe in Sennerplaat a peak in numbers during the years 1990-1993, with high numbers in *Agonum fuliginosum*, *A. thoreyi* and *Pterostichus diligens*. Just these three species invade Schildhoek later in time, without a peak in numbers. It is an indication that the succession in Schildhoek was less prominent or more gradual than in Sennerplaat.

For the other species groups no differentiation is present during the first years, because no specialized salt marsh species could be indicated. However, after circa 1990 a series in species from the spiders, harvestmen, a rove beetle, a woodlouse and a millipede establish on Sennerplaat and they are far less represented in Schildhoek. These species are known from grassland, wetlands and rough vegetation. The vegetation in both subareas was in succession and created a litter layer where the species can live, independent from the soil type. The development in height of the vegetation was faster in Sennerplaat, compare figure 8 and 9 from 1980 and figure 10 and 11 from 1984, with as a result also more litter production. Moreover, in Schildhoek the flooding in winter continued and flooding will remove the litter and might be lethal for spiders and harvestmen. This creates an explanation why the ground dwelling species in other groups from table 7 can only survive in Sennerplaat. The only exception is the presence of the spider *Allomengea scopigera* (Grube) in Schildhoek in the period 1980-2000, when salinity already disappeared. This halobiont species is known from some Frisian islands and the salt marshes of Friesland.

In conclusion, the muddy saltmarsh of Schildhoek offered optimal conditions for many carabids (*Pogonum*, *Bembidion*, *Dyschirius*, etc) during the first ten years, whereas most characteristic species in Sennerplaat indicate only sandy open soils (*Amara*). However, in a later phase just Sennerplaat facilitate many characteristic species. For sure this is true for the spiders and other groups, the arrears from the first years became an advance in later phases.

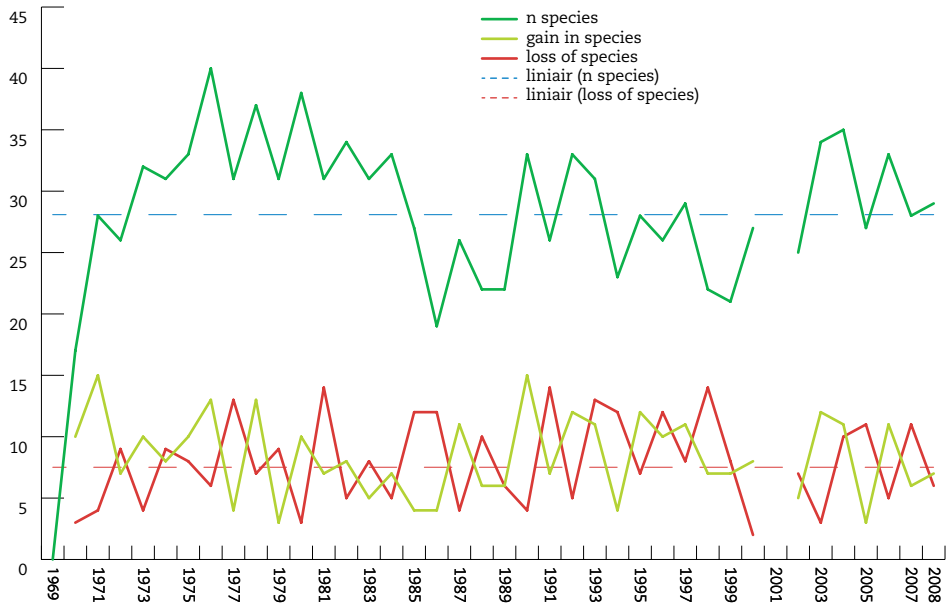
Methodological remarks on interpretation of data

As the data in the tables 3-5 concern catches, they do not necessarily reflect actual differences in population densities. An open vegetation structure during the first years will stimulate higher temperatures and more activity in the fauna with higher catches. Hence probably the decline in the catches due to increasingly dense vegetation and the development of a litter layer (*Raumwiederstand*, spatial resistance) are important, both factors increasingly reduce the movement of the fauna. This process might explain the high numbers in specimens during the first years, although this is a characteristic of the pioneer fauna with high reproduction. That during time permanently new species immigrate the area is an indication that at least the qualitative sampling is correct.

Focussing on the more frequent species entails the neglect of rare species. Smaller differences between the sets of traps are obscured and those species that in the long run could prove to be successful are not remarked. It stands to reasoning that species only rarely caught concern species that are accidental immigrants facing an uncertain future, but they may eventually prove to succeed in establishing large populations. For instance, if trapping had been stopped after ten years, the eventual success

Table 6. Number of catches of the twelve selected halophilic species for the two locations in the period 1969-2008. Each species value with a higher number than the median value is highlighted in the tables.
Tabel 6. Aantal vangsten van de twaalf geselecteerde halofiele soorten in de twee locaties gedurende de periode 1969-2008. Elk getal dat hoger is dan de mediaan is gemarkeerd.

species	location	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985
Dicheirotrichus gustavii	Sennerplaat		1	1633	1336	8653	3872	110	1174	2126	407	160	5		1			
Dicheirotrichus gustavii	Schildhoek	3	96	3215	3241	4920	2401	438	1940	6888	7762	2901	738	33	1			
Pogonus luridipennis	Schildhoek		1	4	16	44		1										
Pogonus chalceus	Sennerplaat					1		2	2	1	8	2	1			1	1	
Pogonus chalceus	Schildhoek	1	22	32	351	920	527	200	426	742	888	179	65	4		1	1	
Bembidion normannum	Sennerplaat		1	7		1	1	3								1		
Bembidion normannum	Schildhoek		13	24	32	21	24	17			11	4	1				1	
Dyschirius obscurus	Sennerplaat						6	4	2	1								
Praestigia duffeyi	Sennerplaat			2														
Praestigia duffeyi	Schildhoek		16		1													
Enoplognatha mordax	Sennerplaat			3	15	5	5	1	23	47	16							
Enoplognatha mordax	Schildhoek		9	10	9	8	7	9	43	52	14	12	2				1	
Silometopus curtus	Sennerplaat							7	66	8	5	8	31	2	3			
Silometopus curtus	Schildhoek					1	1	2	15	33	69	93	10	1	1	1		
Dyschirius obscurus	Schildhoek																	
Bembidion minimum	Sennerplaat		13	37	260	465	235	194	196	22	35	86	10	10	5	7	12	
Bembidion minimum	Schildhoek		419	326	563	699	567	960	593	77	111	670	221	75	142	302	167	1
Dyschirius salinus	Sennerplaat				3	285	528	233	188	218	135	55	15	9	6	5	6	
Dyschirius salinus	Schildhoek		3	89	151	793	2787	5359	2426	1128	1585	342	78	12	18	10	4	3
Bembidion iricolor	Sennerplaat			1				1		7		3	1		3	2		
Bembidion iricolor	Schildhoek							2	1	1			3	1				2
Pardosa purbeckensis	Sennerplaat		5	64	229	149	478	710	1129	250	321	378	583	228	305	12	143	10
Pardosa purbeckensis	Schildhoek	12	182	291	70	134	217	471	361	130	185	482	1506	1584	939	257	660	303



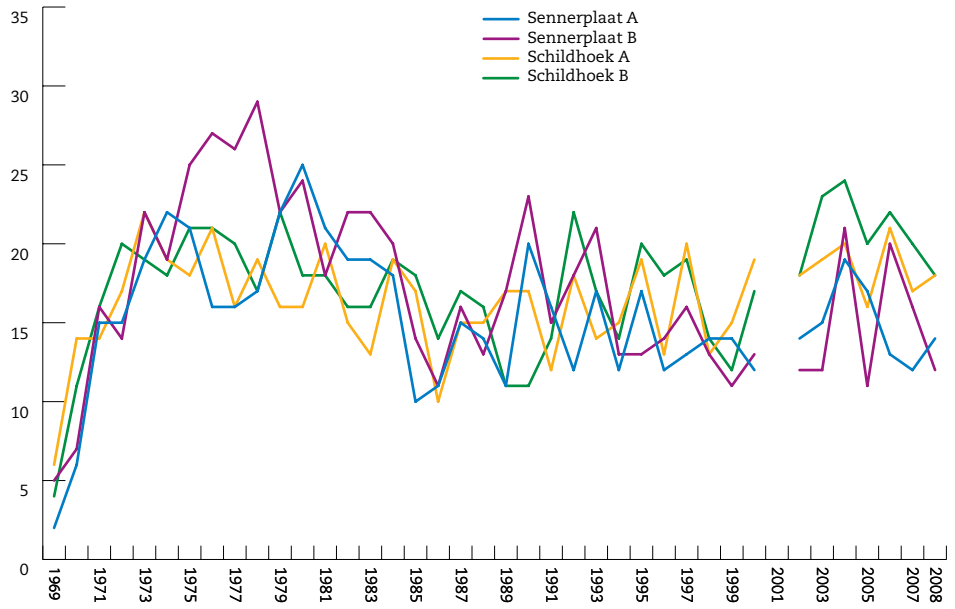
27. Total number of carabid species per year for all locations, including the gain and loss compared with the year before.
27. Jaarlijks aantal soorten loopkevers in Sennerplaat en Schildhoek gezamenlijk met winst en verlies in vergelijking tot voorgaand jaar.

of *Dyschirius globosus* would not have been observed (year catch > 5000 specimens in 1983). On the other hand, the ten specimens of *Anchomenus dorsalis* (Pontoppidan) caught from 1969 till 2000 evidently were unsuccessful immigrants or were only rare representatives of an intermediate phase in succession. Small catches can also indicate specialized resident species that occur only in very small numbers, for instance the spider *Praestigia duffeyi*, a species from grasslands in tidal habitats (British Arachnological Society 2017) of which 18 specimens were found in the catches in the early 1970's, or species that live in special niches (old reed stems) such as *Paradromius longiceps* (Dejean) and therefore are less readily caught in traps.

Final discussion

The encountered species in Lauwersmeer in the first years fit well to lists from comparable studies in other salt marshes in Europe (Finck *et al.* 2007, Petillon *et al.* 2008, Zijlstra 1973). However, most of this published research compares the presence of species in an elevation gradient and not in time with a succession. Petillon *et al.* (2008) compared the reaction of carabids and spiders in salt marshes and concluded that spiders are less related to salinity, whereas carabids were more connected to the edaphic environment such as open habitats. This can be confirmed by our results, because spiders and carabids responded different in species number and in relation to salinity; especially the first years in Schildhoek with open structure were optimal for the characteristic carabids for salt marshes.

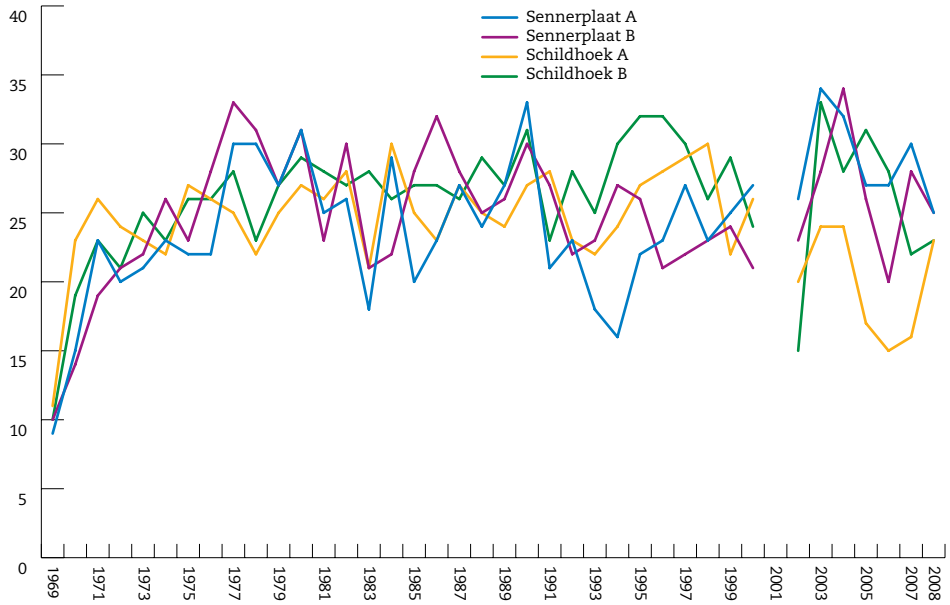
1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008
	1																					
2			1		1									1								
							1															
	1				1	1	2		2	1		1										
1		1					1		11								1			1		
24	6	3	1	3					1		1											
380	300	205	189	227	145	124	133	41	13	16	10	14	2	2		1	2	7	3	1		



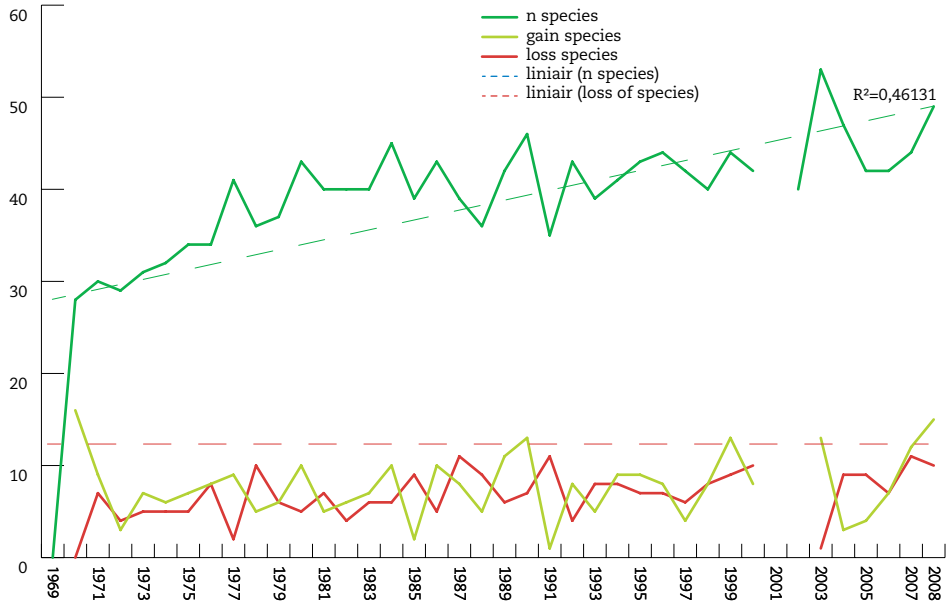
28. Total number of carabid species per year of the four sub-locations.
28. Totaal aantal loopkeversoorten per jaar voor de vier sub-gebieden.

A comparable research with Lauwersmeer derives from the Markiezaat salt marshes in the southwest of the Netherlands (Verschoor & Krebs 1995). In 1983 this marsh was blocked from the sea and the development in vegetation and carabids was followed in an elevation gradient for nine years. Also there a high diversity in carabids was present in the first three years, in represented species comparable with Lauwersmeer, but after that moment as well the number of individuals as the diversity went down. Verschoor & Krebs (1995) explain these peak values in the first years to open field stages in the start of the succession and after that the vegetation closes and does not facilitate high diversity in soil-dwelling fauna. The question remains if Lauwersmeer and Markiezaat are fully comparable. At least Lauwersmeer is much larger and with high water tables, and the number of years was higher, facilitating more species to invade. However, remarkable is that diversity in Lauwersmeer does not decrease after some years, contrary to Markiezaat.

The number of carabid individuals in Schildhoek is higher in the years 1971-1978 and the numbers stay on a lower level in other years; in Sennerplaat there are three peaks in 1973, 1983 and 1991. Higher numbers of individuals in spiders are in Schildhoek in the years 1971 and 1980-1981; in Sennerplaat the numbers are higher in the period 1971-1982. All these higher numbers are caused by a restricted number in populations of species. The yearly number of species, a measurement of diversity, remains on a constant level in carabids in Lauwersmeer for 40 years, at the locations and as a whole. However, diversity in spiders together from all locations gave a significant increase



29. Total number of spider species per year of the four sub-locations.
29. Totaal aantal spinnensoorten per jaar voor de vier sub-gebieden.



30. Total number of spider species per year for all locations, including the gain and loss compared with the year before.
30. Totaal aantal spinnensoorten per jaar voor alle locaties gezamenlijk met winst en verlies in vergelijking tot voorgaand jaar.

31. The Schildhoek inundated during a spell of bad weather in October 1998. Foto: Jan Meijer
31. De Schildhoek overspoeld bij slecht weer in oktober 1998.

Table 7. Main differences in the total number of individuals for the selected species in Sennerplaat and Schildhoek (see text), with additional the main period of presence in the succession and an indication of the ecosystem the species can be found elsewhere. With light blue an indication of the major difference between the areas; with green the species are indicated from the early phase.
Tabel 7. Belangrijkste verschillen in totale aantal individuen voor de geselecteerde soorten in Sennerplaat en Schildhoek (zie de tekst), met aanvullend de periode waarin de soorten aanwezig waren in de successie en een indicatie van het ecosysteem waarin de soort elders gevonden wordt. Met lichtblauw zijn de belangrijke verschillen tussen de gebieden aangegeven; met groen de soorten van de vroege successie stadia.

	species	Sennerplaat	Schildhoek	period	ecosystem
carabid					
	Bembidion bipunctatum	3,591	61	early	shore lines
	Bembidion properans	332	35	early	open shore lines
	Amara convexiuscula	268	21	early	open habitat
	Amara plebeja	64	10	early	indifferent
	Anisodactylus binotatus	46	2	early	open habitat
	Bembidion assimile	16,272	3,683	middle-end	shore lines
	Agonum thoreyi	9,651	753	middle-end	vegetated shores
	Agonum fuliginosum	2,655	126	middle-end	forest
	Odacantha melanura	72	4	middle-end	reed marsh
	Trichocellus placidus	221	71	middle-end	wetlands
	Leistus terminatus	38	3	middle-end	wood-wetlands
	Carabus granulatus	75	13	middle-end	wood-wetlands
	Pogonus luridipennis	0	66	early	salt marsh
	Pogonus chalceus	19	4,359	early	salt marsh
	Bembidion normannum	14	148	early	salt marsh
	Dyschirius salinus	1,687	14,797	early	salt marsh
	Bembidion minimum	1,587	7,565	early-middle	salt marsh
	Bembidion aeneum	284	3,138	early-middle	shore lines
	Dyschirius tristis	101	737	middle	shore lines
	Bembidion lunulatum	19	144	middle	shore - wetlands
	Bembidion biguttatum	11	125	middle-end	shore lines
	Acupalpus exiguus	7	427	end	wetlands
	Amara aenea	29	167	end	indifferent
spider					
	Microlinyphia impigra	56	3	middle	wetland
	Allomengea vidua	1,107	132	middle-end	wetland
	Centromerus sylvaticus	404	0	middle-end	grassland
	Agroeca proxima	181	11	middle-end	grassland
	Walckenaeria acuminata	143	16	middle-end	indifferent
	Antistea elegans	1,348	33	end	wetland
	Cnephalocotes obscurus	69	3	end	grasslands
	Micrargus herbigradus	105	9	end	wood-grassland
	Allomengea scopigera	17	512	middle	coastal wetland
harvestmen					
	Nemastoma lugubre	5,959	1,171	middle-end	rough
	Paroligolophus agrestis	82	0	middle-end	wood-wetland
	Lacinius ephippiatus	168	31	middle-end	rough
	Rilaena triangularis	83	6	end	wood-wetland
rove beetle					
	Paederus riparius	9,942	1,331	middle-end	shore-rough
woodlouse					
	Trachelipus rathkii	11,985	2,011	middle-end	wetland
millepede					
	Craspedosoma rawlinsii	347	0	middle-end	wood-wetland

during time, but not at the individual locations. The implication is that the spider fauna confirms that there is an increase in species diversity during 40 years of succession, whereas the carabid species still invade and leave the area and as a whole remain on one permanent level. This might be due to the dispersal of carabids: in Lauwersmeer high numbers in species is macropterous and most brachypterous species still have to reach the area, whereby 40 years is not yet enough. In dispersal the ballooning in spiders appeared to be a far more effective method compared to walking. In the other groups dispersal by feet is a slow process and they just started to invade with the first species in 1995. To document this succession correctly, another 40 years research is needed.

In conclusion, the development of the ground dwelling fauna of the sites in Lauwersmeer can be described as a succession of species encountering a favourable habitat (a phase in succession) with a constant arrival and disappearance of species that could not yet or no longer find favourable circumstances. Only in the spiders is some accumulation in species numbers. The overall impression of the catches is that there is a development from a pristine soil without terrestrial fauna to a fauna exploding in specimens, very characteristic for a saline habitat, to that of a

variable wet habitat with vegetation that still changes at a small scale. However, an ecosystem is dynamic and each year is different, with the consequence that populations numbers always fluctuate, as we can observe in this 40 year period. In this succession is a constant influx of new species in the marsh habitat (with extreme high catches after arrival), accompanied by a practically equal disappearance of species, and yearly fluctuations. Some species turn up and disappear very soon, while others turn up regularly and may be successful on the long term. Even after 40 years of ecosystem development there is little evidence of a stable community in the studied invertebrate groups. The succession is still active.

References

Bakker D 1957. Oostelijk Flevoland raakt begroeid. De Levende Natuur 60: 305-310.

Barendregt A, Ysebaert T & Wolff WJ 2009. Animal communities in European tidal freshwater wetlands. In: Tidal freshwater wetlands (Barendregt A, Whigham DF & Baldwin AH eds): 89-104. Backhuys Publishers.

Berg MP 2005. Naamlijst van de Nederlandse miljoenpoten (Myriapoda: Diplopoda). Nederlandse Faunistische Mededelingen 23: 1-12.

Berg MP & Wijnhoven H 1997. Landpissebedden. Een tabel voor de landpissebedden (Crustacea; Oniscoidae) van Nederland en België. Wetenschappelijke Mededeling KNNV nr 221. Stichting Uitgeverij van de KNNV, Utrecht.

Boeken M, Desender K, Drost B, Van Gijzen T, Koese B, Muilwijk J, Turin H & Vermeulen R 2002. De loopkevers van Nederland & Vlaanderen (Coleoptera, Carabidae). Jeugdbondsuitgeverij.

British Arachnological Society 2017. Spider and harvestman recording scheme website. Available at: http://srs.britishspiders.org.uk [accessed on 3-11-2017}.

Clevering A & Van der Toorn J 2000. Observations on the colonization of a young polder area in the Netherlands with special reference to the clonal expansion of *Phragmites australis*. Folia Geobotanica 35: 375-387.

Feekes W 1936. De ontwikkeling van de natuurlijke vegetatie in de Wieringermeerpolder - de eerste grote droogmakerij van de Zuiderzee. PhD thesis Landbouwhogeschool Wageningen.

Feekes W & Bakker D 1954. De ontwikkeling van de natuurlijke vegetatie in de Noordoost-polder. Van Zee tot Land 6: 1-92.

Finck O-D, Krummen H, Plaisier F & Schultz W 2007. Zonation of spiders (Araneae) and carabid beetles (Coleoptera: Carabidae) in island salt marshes at the North Sea coast. Wetlands Ecology and Management 15: 207-228.

Haeck J 1971. The migration and settlement of Carabids in the new IJsselmeerpolders. Miscellaneous papers Landbouwhogeschool Wageningen 8: 33-52.

Harvey PR, Nellist DR & Telfer MG (eds) 2002. Provisional atlas of British spiders (Arachnida, Araneae), Volumes 1 & 2. Biological Records Centre.

Joenje W 1974. Production and structure in the early stages of vegetation development in the Lauwerszee-polder. Vegetatio 29: 101-108.

Joenje W 1978. Plant colonization and succession on embanked sandflats. PhD thesis Groningen University.

Locher WP & H De Bakker 1987. Bodemkunde van Nederland Dl. 1, Algemene bodemkunde. Malmberg.

Meijer J 1971. Immigration of arthropods into the new Lauwerszeepolder. Miscellaneous papers Landbouwhogeschool Wageningen 8: 53-64.

Meijer J 1973. Die Besiedlung des neuen Lauwerszeepolders durch Laufkäfer (Carabidae) und Spinnen (Araneae). Faunistisch-Ökologischen Mitteilungen 4: 169-184.

Meijer J 1974. A comparative study of the immigration of Carabids (Coleoptera, Carabidae) into a new polder. Oecologia (Berl.) 16: 185-208.

Meijer J 1975. Some data on Argenna patula (Simon), Perimones arenarius (Emerton) and other spiders new to the Dutch spider fauna (Arachnida, Araneida). Entomologische Berichten 35: 135-140.

Meijer J 1977. The immigration of spiders (Araneida) into a new polder. Ecological Entomology 2: 81-90.

Meijer J 1980. Colonization of the Lauwerszeepolder by some elements of the arthropod fauna. PhD thesis Vrije Universiteit, Amsterdam.

Mook JH 1971. Observations on the colonization of the new IJsselmeerpolders by animals. Miscellaneous papers Landbouwhogeschool Wageningen 8: 13-31.

Muilwijk J, Felix R, Dekoninck W & Bleich O 2015. De loopkevers van Nederland en Belgie (Carabidae). Entomologische Tabellen 9: 1-215.

Odum EP 1971. Fundamentals of ecology. W.B. Saundres Company.

Petillon J, Geoges A, Canard A, Lefeuvre J-C, Bakker JP & Ysnel F 2008. Influence of abiotic factors on spider and ground beetle communities in different saltmarsh systems. Basic and Applied Ecology 9: 743-751.

Richter CJJ 1971. Some aspects of aerial dispersal in different populations of wolf spiders, with particular reference to *Pardosa amentata* (Araneae, Lycosidae). Miscellaneous papers Landbouwhogeschool Wageningen 8: 77-88.

Ter Heerdt GNJ 1994. Potential for the development of marsh vegetation from the seed bank after a drawdown. Biological Conservation 67: 1-11.

Turin H 1991. De loopkevers van de Nederlandse Waddeneilanden (Coleoptera: Carabidae). Entomologische Berichten 51: 69-78.

Turin H 2000. De Nederlandse loopkevers, verspreiding en oecologie (Coleoptera: Carabidae). Nederlanse Fauna 3. Nationaal Natuurhistorisch Museum Naturalis, KNNV Uitgeverij & EIS-Nederland.

Turin H, Alders A, den Boer PJ, van Essen S, Heijerman Th, Laane W & Penterman E 1991. Ecological characterization of carabid species (Coleoptera, Carabidae) in the Netherlands from thirty years of pitfall sampling. Tijdschrift voor Entomologie 134: 279-304.

Van der Toorn J, Brandsma M, Bates WB & Penny MG 1969. De vegetatie van Zuidelijk Flevoland in 1968. De Levende Natuur 72: 56-62.

Van Helsdingen PJ 2012. Naamlijst Nederlandse spinnen. Versie 2012.1. Beschikbaar op: www.eis-nederland.nl/spinnen.

Van Klink R & Van Schrojenstein Lantman IM 2015. Effecten van kwelderbeweiding op spinnen en insecten. Entomologische Berichten 75: 188-199.

Van Rooij SAM & Drost HJ 1996. Het Lauwersmeergebied - 25 jaar onderzoek ten dienste van natuurontwikkeling en beheer. Flevobericht nr. 387. Directoraat-Generaal Rijkswaterstaat Directie IJsselmeer.

Verschoor BC & Krebs BPM 1995. Diversity changes in a plant and carabid community during early succession in an embanked saltmarsh area. Pedobiologia 39: 405-416.

Wijnhoven H 2009. De Nederlandse hooiwagens (Opiliones). Entomologische Tabellen 3: 1-120.

Zijlstra M 1973. De loopkevers van de Slikken van Flakkee in 1972. Nota 73-13 Rijksdienst voor de IJsselmeerpolders, Wetenschappelijke Afdeling Lelystad. Bijlage bij het Interim-rapport Landschaps-Oecologisch Onderzoek Slikken van Flakkee.

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Samenvatting

Veertig jaren ongestoorde ontwikkeling van de bodemfauna in het Lauwersmeer, een afgesloten getijdegebied van de Nederlandse Waddenzee

Na de indijking van de Lauwerszee in 1969 bleef een gebied van 9000 ha met kreken, zandplaten en kwelders liggen met een vast waterpeil. Op twee locaties in dit gebied (Sennerplaat en Schildhoek) is in de periode 1969-2008 jaarlijks van maart tot in oktober onderzoek verricht naar de aanwezige loopkevers, spinnen, hooiwagens, pissebedden en miljoenpoten met vier dubbele vaste potvallen. Gedurende die jaren veranderde het ecosysteem door natuurlijke successie van een kale zandplaat of slibvlakte naar een zoutvegetatie, gevolgd door grasvegetatie en na twintig jaar een rietvegetatie. Tegelijkertijd ontstond er een strooisellaag op de bodem. Gedurende de 40 jaar onderzoek zijn meer dan 350.000 dieren gevangen, die op soortsniveau gedetermineerd zijn. Alle basisgegevens per jaar worden in dit artikel gepubliceerd en geanalyseerd. Het aantal individuen in loopkevers en spinnen is hoog in de eerste jaren na afdamming, echter er zijn ook hoge aantallen in tussenliggende jaren, veroorzaakt door enkele soorten die domineren. Na circa twintig jaar blijft het aantal op een constant niveau tot in 2008. Voor de andere diergroepen geldt dat ze pas na ca. twintig jaar de onderzoeklocaties bereiken. De analyse van het aantal aangetroffen soorten per jaar levert op dat na enkele jaren het soortenaantal op de locaties op een bijna stabiel niveau blijft (circa 15 soorten loopkevers en 25 soorten spinnen), echter dat de vertegenwoordigde soorten sterk wisselen gedurende de tijd. Slechts bij de sommatie van alle locaties in Lauwersmeer blijkt er een toename in het aantal aangetroffen spinnen gedurende de tijd aanwezig te zijn. De karakteristieke zoutsoorten voor kevers en spinnen in het gebied zijn na ruim een decennium verdwenen. Er zijn grote overeenkomsten tussen de soortenfauna in de twee deelgebieden en een analyse van het totale aantal individuen voor de meest verschillende soorten levert op dat de zandige Sennerplaat meer soorten van het ruderale milieu bevat terwijl de slikrijke en nattere Schildhoek vooral soorten van kwelders en oevers bevat. Voor de loopkevers en de spinnen wordt geanalyseerd welke aangetroffen soorten zeldzaam te vinden zijn in Nederland; voor de loopkevers wordt tevens een ordinatie uitgevoerd, waaruit duidelijk wordt dat er in de tijd een verloop aanwezig is van soorten kenmerkend voor een kwelder naar die van een gesloten vegetatie. In de discussie wordt kort vergeleken met andere onderzoeken op kwelders: het soortenspectrum blijkt goed overeen te komen met elders, echter over het gevolg van indijking en van langdurige successie blijken nauwelijks vergelijkbare onderzoeken te zijn. Uit het onderzoek naar de bodemfauna van het Lauwersmeer blijkt vooral dat er een constante immigratie van soorten gedurende de tijd is, maar ook een constant verdwijnen. De eerste jaren worden gekenmerkt door hoge aantallen in individuen die spoedig tot een lager niveau terug zakken. Door de verandering van een initieel zout milieu naar een hogere gesloten zoete vegetatie zijn wel duidelijke verschillen aan te geven in de bodemfauna, maar zelfs na 40 jaar blijken de soorten nog geen stabiel ecosysteem aan te duiden.

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