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Submerged macrophytes in the recently freshened lake system Volkerak-Zoom (The Netherlands), 1987–1991

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Abstract

Extensive biological research has been carried out during the first four years after isolation and freshening of Lake Volkerak-Zoom, a former part of the marine-tidal Oosterschelde. Freshening took place in 8 months. Research on submerged macrophytes has been an important part of the investigation because the aim of the water management was to establish a clear and stable freshwater ecosystem, despite high nutrient loading.

In the first year after closure the marine *Zostera noltii* vanished. and the brackish water *Ruppia maritima* colonized the lake. In subsequent years, several freshwater species colonized the lake (e.g. *Potamogeton pusillus*, *P. pectinatus*, *Zannichellia palustris*, *Callitriche sp.* and *Chara sp.*). The total area in the shallow zone (0.5–5.0 m) covered by submerged macrophytes, increased from less than 1% in 1987 to 22.5% in 1991.

Characteristics (height, flowering and fruiting) of the main species (*P. pusillus*, *P. pectinatus*, *Z. palustris*, *R. maritima*) were closely related to water temperature and secchi depth.

Waterfowl consumed about half of the production of the submerged macrophytes.

Introduction

In April 1987, the last dike was closed to create a 61 km^2 lake-system from part of the former Oosterschelde estuary (SW Netherlands). Freshening took place in just 8 months. The lake system forms an important inland shipping route between the ports of Rotterdam and Antwerp. At the same time water management aims at optimizing the natural values of this lake system by creating and maintaining a stable and clear freshwater ecosystem.

Besides chemical, physical and many biological parameters (e.g. birds, fish, benthic macrofauna, zoo- and phytoplankton), the colonisation of the system by submerged macrophytes has been monitored thoroughly. Submerged macrophytes perform a key function in stabilizing freshwater ecosystems (Scheffer, 1990). Macrophytes act as a refuge for spawning fish and zooplankton (Shapiro, 1990), stabilize the sediment (Moss, 1990), and act as a sink for nutrients (Ozimek *et al.*, 1990). This functional role of the macrophytes increases when the growing season is long and when plants fill the water column.

This paper presents results of the colonisation of the lake by submerged macrophytes in the first four years after freshening. The colonisation process is related to salinity and dispersion of macrophytes. The characteristics of the four main species during 1990 are also presented. Furthermore, the development of macrophyte consumption by herbivore and omnivore waterfowl is related to the standing crop of the submerged macrophytes.

Study area

The Lake system Volkerak-Zoom, is a stagnant freshwater system in the south-west of the Netherlands (Fig. 1). It was created in 1987 by closing part of tidal marine area Oosterschelde, and a subsequent freshening of the water in 8 months by flushing the system with Rhine and Meuse water and water from some small lowland streams (e.g. Dintel).

Lake Volkerak-Zoom consists of two Lakes, Lake Volkerak (45.7 km^2), Lake Zoom (15.8 km^2) and the connecting Eendracht canal. The system has a maximum depth of 20 m and a mean depth of 5.1 m. About half of the area of the lake system has a depth of less than 5 m.

The retention time of the water in the system is 2.5 to 5 months. The main water sources are the Hollandsch diep (water from Rhine and Meuse) and the river Dintel. Small reinforced dams were constructed at the 1 m depth contours, to protect the banks from waves, and to create calm shallow water zones. Sluice management was optimized to minimize the amount of incoming eutrophicated and polluted water of the rivers Rhine and Meuse. Also the loss of freshwater and incoming marine water of the Oosterschelde and Westerschelde due to sluicing is minimized.

Extensive research was carried out to monitor chemical, physical and biological changes (Gulati, 1990; Van Nes & Marteijn, 1991; Frantzen *et al*, 1994). A summary of physical and chemical data (Table 1) illustrates that a rapid freshening was followed by a gradual decrease in phosphate and chlorophyll-*a* concentrations, and an increase in the mean summer secchi depth to 1990.

Methods

Macrophyte distribution

Vegetation was mapped using a small boat (depth 0.4 m) provided with an orientation system with high accuracy (1 m). The – vertical projected bottom – coverage of all macrophyte species was estimated in a 10 by 2 m area. Mapping took place in the depth zone from 0.5 m to 5 m. Mapping sites were chosen, based on aerial views (1987, 1988), or on distribution information of previous years (1989–1991). In the years 1989, 1990 and 1991 the numbers of mapped plots were 285, 1960 and 361, respectively. In 1990, the plots uniformly covered the whole surface of the lake with a depth less than 5 m, and in 1989 and 1991 a representative part of it.

The distribution of the submerged macrophytes is related to a salinity index and to dispersion type (Table 2). The salinity index is based on the water salinity in which species were found in the Netherlands, during a survey of 600 waters by the Catholic University Nijmegen (De Lyon & Roelofs, 1986; Van Katwijk & Roelofs, 1988). Five categories are distinguished which are based on occurrence in: 1. marine water (always above 850 mmol l^{-1}); 2. brackish water (normally above 15 mmol l^{-1}, but often above 50 mmol l^{-1}); 3. ion very rich water (normally above 10 mmol l^{-1}, often above 15 mmol l^{-1}, seldom above 50 mmol l^{-1}); 4. ion rich water (seldom below 4 mmol l^{-1}, often above 15 mmol l^{-1}, not above 50 mmol l^{-1}) and 5. ion moderately rich water (seldom below 4, normally between 10 and 15 mmol l^{-1}). We consider the plants of category 1 as marine species, category 2 as brackish species and categories 3 to 5 as fresh water species.

The dispersion type is based on literature data (Ridley, 1930; Pijl, 1980) and for *Potamogeton pusillus* L. and *Elodea nuttallii* Planchon also on unpublished field information. Macrophytes can be dispersed by: 1. water flow (A: in the water; B: on the water); 2. birds (seeds or vegetative parts clinging to feathers or feet) and 3. wind (mainly seeds). When the dispersion is expected to be mainly vegetative a 'v' is added.

Skin divers harvested the above ground biomass from triplicate 0.02 m^2 bottom areas. All samples were washed in the laboratory, dried at 105 °C for 48 h (dry weight, DW), and combusted at 520 °C for 2 h (ash weight, AW). The ashfree

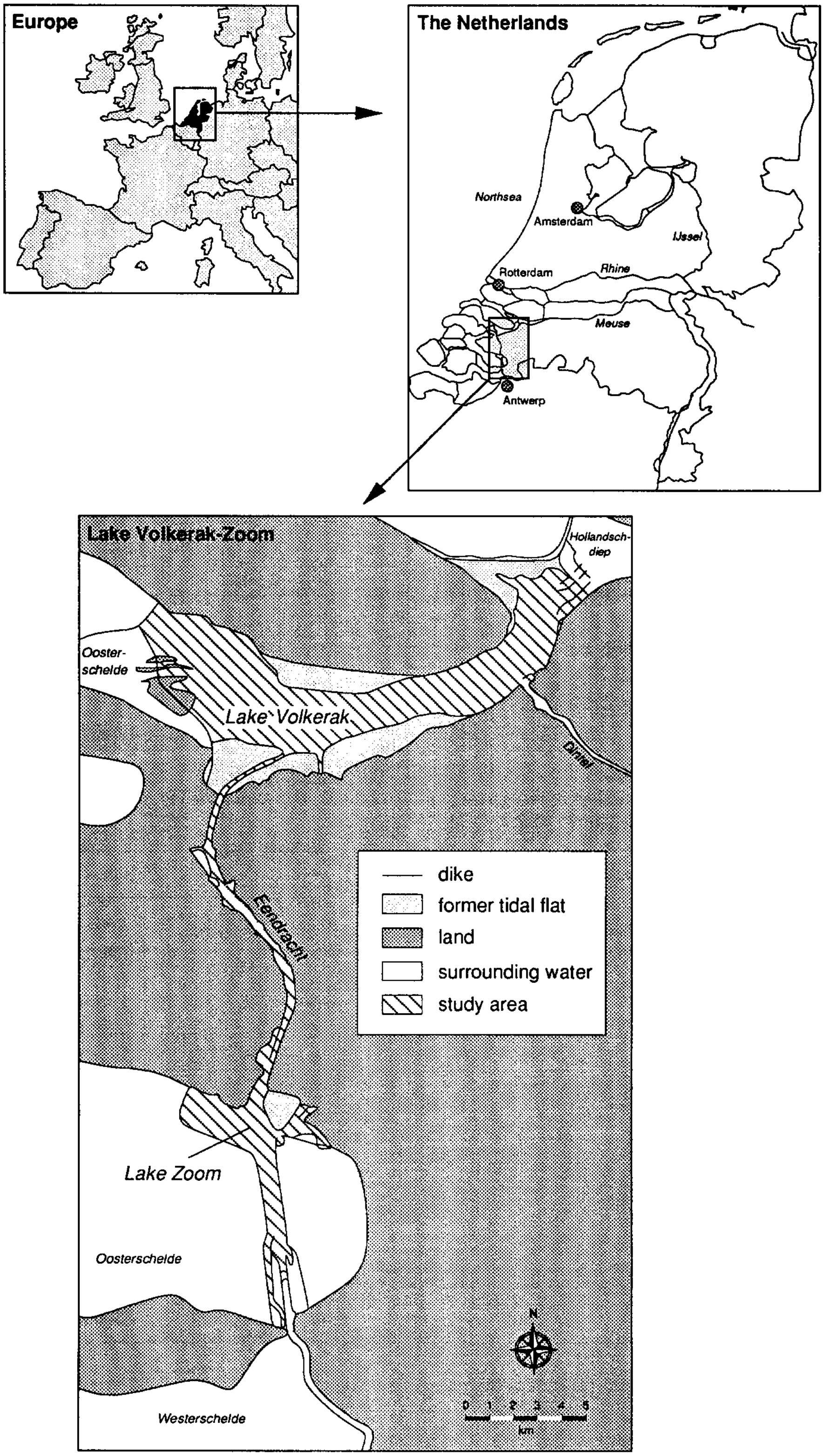

Fig. 1. The lake system Volkerak-Zoom.

Table 1. Mean summer values of chemical and physical parameters of Lake Volkerak-Zoom, indicating freshening and nutritional state. Data were collected bimonthly at two stations. The data between brackets indicate the range (data from the Rijkswaterstaat RIZA monitoring database, WORSRO).

Year	Tide	Secchi depth (m)	Euph. depth (m)	Cl^- ($mmol\,l^{-1}$)	Chlorophyll ($\mu g\,l^{-1}$)	Phosphate ($\mu mol\,l^{-1}$)	Nitrogen ($\mu mol\,l^{-1}$)	HCO_3^- ($mmol\,l^{-1}$)
1986	yes	–	–	328	15.8	5.2	11	–
				(220–384)	(1–28)	(1.7–8.1)	(4–41)	–
1987	no	–	–	102	55.2	5.2	26	–
				(13.1–286)	(4–226)	(0.0–11.6)	(19–36)	–
1988	no	2.2	4.9	5.8	18.1	3.2	34	2.7
		(0.6–3.6)	(2.3–6.8)	(3.9–7.4)	(2–89)	(0.6–6.5)	(21–63)	(2.0–3.1)
1989	no	2.8	5.1	7.8	9.6	4.2	41	2.7
		(1.7–3.9)	(3.9–7.3)	(5.9–16.0)	(1–31)	(1.0–3.2)	(17–41)	(1.5–3.6)
1990	no	3.3	6.5	9.0	6.8	1.3	34	2.6
		(1.2–5.6)	(3.1–8.1)	(7.2–12.0)	(1–17)	(0.3–2.6)	(16–47)	(2.4–3.0)
1991	no	2.6	6.0	9.0	8.6	1.3	31	2.7
		(1.4–4.9)	(3.8–7.6)	(8.3–10.0)	(1–17)	(0.3–2.6)	(19–55)	(2.3–3.0)

Legend:
- \- = not measured.
- Euph. depth = euphotic depth: penetration depth of 1% of the surface irradiance.
- Cl^- = chloride concentration.
- Chlorophyll = chlorophyll-*a* concentration.
- Phosphate = ortho-phosphate concentration (O-PO4).
- Nitrogen = N-Kjeldahl + NO_3 + NO_2 concentration as mmol $N \cdot l^{-1}$.
- HCO_3^- = bicarbonate concentration.

Table 2. Submerged macrophyte distribution in Lake Volkerak-Zoom from 1986 to 1991. Presence, coverage (in %) and total biomass in the shallow area of the lake (0.5–5 m) are presented. The dispersion type (Ridley, 1930; Pijl, 1982) and salinity index (de Lyon & Roelofs, 1986; Katwijk & Roelofs, 1988) are also shown.

Species	Year						Disp. type	Sal. index.
	1986	1987	1988	1989	1990	1991		
Zostera noltii Horneman	*	*	–	–	–	–	2 v	1
Ruppia maritima L.	*	*	*	0.8	1.0	0.6	2 3 v	2
Potamogeton pusillus L.	–	–	*	2.7	6.4	11.3	1B v 2 v	4
Elodea nuttallii Planchon	–	–	*	0.2	0.2	*	1A v 2 v	4
Zannichellia palustris L.	–	–	–	0.8	2.2	6.4	2 v	2
Potamogeton pectinatus L.	–	–	–	0.6	1.0	2.6	2 v	3
Myriophyllum spicatum L.	–	–	–	*	*	*	1A	3
Potamogeton perfoliatus L.	–	–	–	*	*	*	1A 2	5
Potamogeton crispus L.	–	–	–	*	*	*	1A 2	5
Callitriche spec.	–	–	–	–	*	1.6	1B 2 v	4/5
Ranunculus baudotii Godron	–	–	–	–	*	–	2 v	2
Chara spec.	–	–	–	–	*	0.2	1A 2 v	4
Total biomass (10^3 kg AFDW)	–	5.0	14.9	141.2	205.0	320.8		

Legend:
- Disp. type = dispersion type of the macrophyte (see Methods) (1A = water flow, in the water; 1B = water flow, on the water; 2 = birds; 3 = wind; v = mainly vegetative).
- Sal. index = salinity index (see Methods) (1 = marine; 2 = brackish; 3–5 = fresh).
- – = not found.
- * = present but density <0.1%.

dry weight (AFDW = DW-AW) reflects the organic content of the plants.

Characteristics of macrophytes

During 1990, the development over the growth season of the four dominant species (*P. pusillus*, *Potamogeton pectinatus* L., *Zannichellia palustris* L. and *Ruppia maritima* L.) was followed in quadrats (5 by 5 m) at a water depth of 2 m.

Every month, from March to November (except twice in May) the following parameters were determined in the stands: phenological state (vegetative state, flowering, fruiting), height and biomass. The biomass was determined as described above.

Macrophytes related to waterfowl

From 1987 on, the waterfowl were counted monthly from a ship and from the shore (Van Nes & Marteijn, 1991). The food consumption of the birds was estimated using number of bird days (mean number of birds per species counted, multiplied by the length of the interval between two counting events). The estimated food consumption was calculated using a formula which is based on existence energy and daily consumption, according to Kiørboe (1980). In this calculation the mean bird weights and fractions of plant material in the food according to Glutz v. Blotzheim & Bauer (1966–1985) and Cramp & Simouns (1977, 1980) were used. The food consumption of herbivore and omnivore waterfowl (in the growing period, July until mid October) was related to the cover and biomass of the submerged macrophytes by calculating Pearson's correlation coefficient.

Results

Macrophyte distribution

Before embankment the marine species *Zostera noltii* Horneman was present in very low densities (unpubl. data). On the tidal flats *R. maritima*, a brackish species, was locally abundant (Smit *et al.*, 1989).

In August 1987, four months after closure, *Z. noltii* was still found in very low densities, and *R. maritima* had colonised the shallow area near the former tidal flats. By 1988 *Z. noltii* had vanished, *R. maritima* was found frequently in the shallow area and the first freshwater species, *P. pusillus* and *E. nuttallii*, had colonised the lake. In 1989, 5.1% of the shallow area of the lake was covered with submerged vegetation in which *P. pusillus* dominated. Five new freshwater species had colonised the lake. In 1990 the submerged macrophytes covered 10.8% of the shallow area. The total number of species was 11 (see Table 2), and *P. pusillus* was still dominant. In 1990 the lake was colonised by two species (*Callitriche sp.*, *Chara sp.*) which normally occur

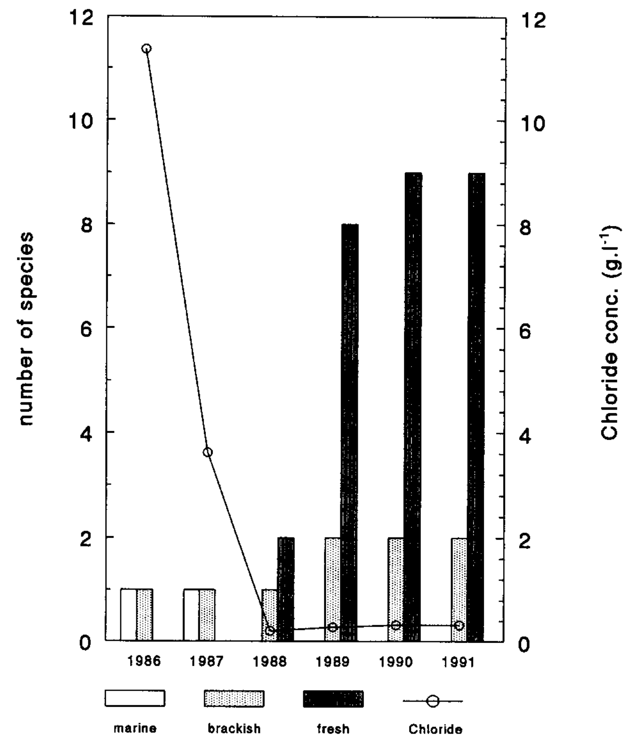

Fig. 2. Development of the number of macrophyte species in Lake Volkerak-Zoom (1986–1991), split into three groups (marine, brackish, fresh) according to a salinity index (see Methods). Also shown is the mean summer chloride concentration during the years.

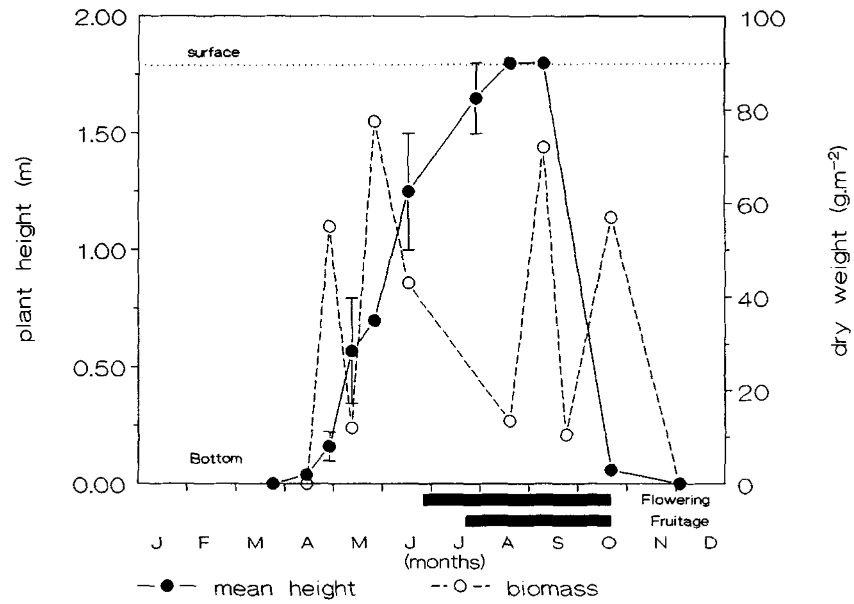

Fig. 3. Characteristics of *Potamogeton pusillus* L. in 1990 in Lake Volkerak-Zoom. Shown are the parameters mean plant height (with standard deviations), biomass and the period of flowering and fruiting.

in clear water. Also a new brackish species (*Ranunculus baudotii* Godron) was found in one place. In 1991 the area covered by submerged macrophytes doubled to 22.9%, and *P. pusillus* was still the dominant species. The number of species remained at 11, though the area covered

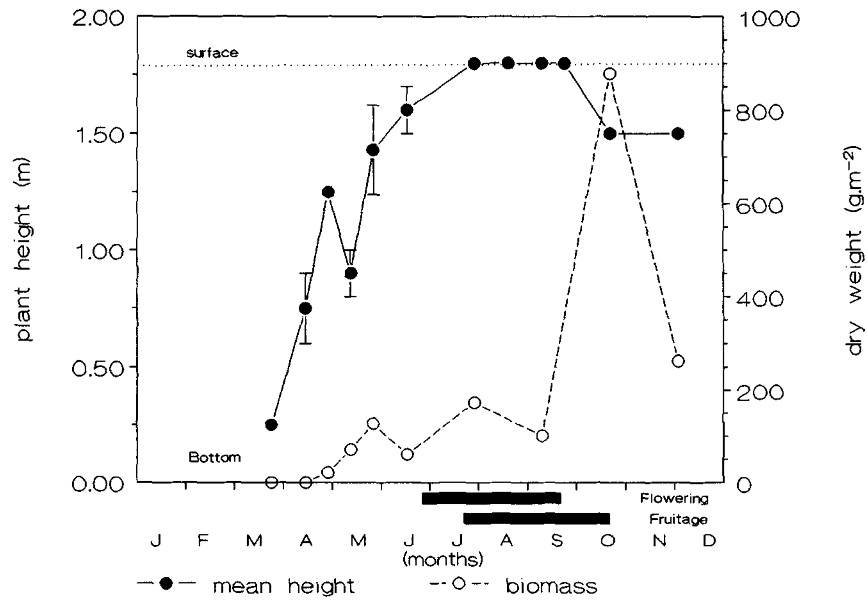

Fig. 4. Characteristics of *Potamogeton pectinatus* L. in 1990 in Lake Volkerak-Zoom. Shown are the parameters mean plant height (with standard deviations), biomass and the period of flowering and fruiting.

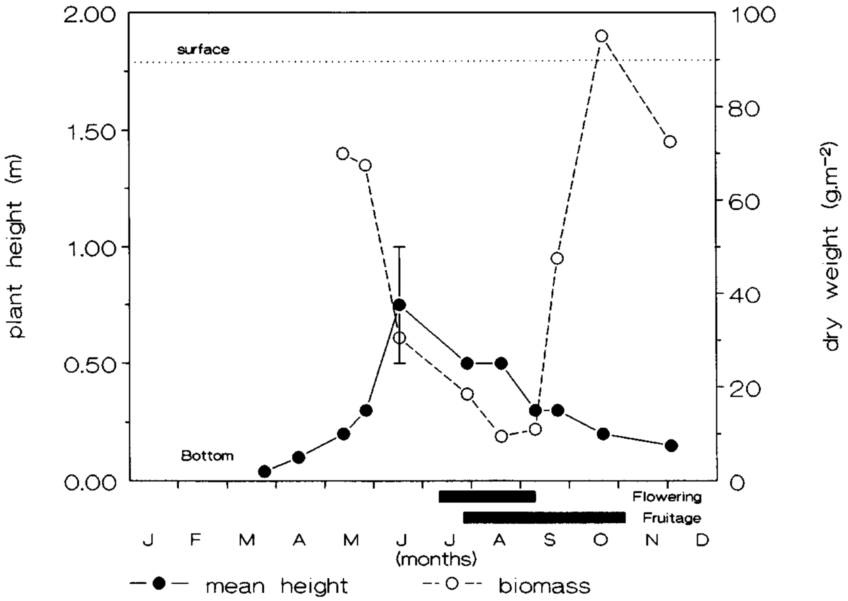

Fig. 5. Characteristics of *Zannichellia palustris* L. in 1990 in Lake Volkerak-Zoom. Shown are the parameters mean plant height (with standard deviations), biomass and the period of flowering and fruiting.

by *Callitriche sp.* and *Chara sp.* increased (Table 2). In Fig. 2 changes in the number of macrophyte species in Lake Volkerak-Zoom are related to chloride concentrations.

Due to the small number of samples, only an estimate of the biomass development of the macrophytes can be made (Table 2).

Characteristics of the macrophytes

In the Figs 3 to 6 the characteristics of four species in Lake Volkerak-Zoom are presented. All studied submerged macrophytes, besides *P. pectinatus*, started growing when the secchi depth (Fig. 7) equalled the water depth. *P. pectinatus* started the exponential growth phase before the other three species and reached the surface two weeks before *P. pusillus*. *Z. palustris* and *R. maritima* did not reach the water surface. *P. pusillus* and *P. pectinatus* remained at the surface until senescence at mid september. Vegetative remnants (see Fig. 4) of *P. pectinatus* were observed during the winter, which can be used by spawning fish in early spring.

Flowering was observed from mid June until the end of October. Flowering of the two *Potamogeton* species started before the plants had reached the water surface. Fruiting was observed from the end of July to the end of October. Fruiting of the two *Potamogeton* species (Figs 3 & 4) only took place after the plants had reached the water surface. *Z. palustris*, and *R. maritima* showed flowering and fruiting below the water surface.

P. pectinatus produced a high biomass compared with the other species. *R. maritima* showed a steady biomass growth during the season, followed by a steep decline. The biomass curves of the other two species, *P. pusillus* and *Z. palustris*, showed major fluctuations.

For the *Potamogeton* species the growing season lasted 6 (*P. pusillus*) or even 7 months (*P.pectinatus*). For the smaller species, *Z. palustris* and *R. maritima* the growing season lasted about 5 months.

Macrophytes related to waterfowl

In Table 3, the presence and calculated consumptions of herbivore and omnivore waterfowl are given. In Fig. 8, the development of macrophyte

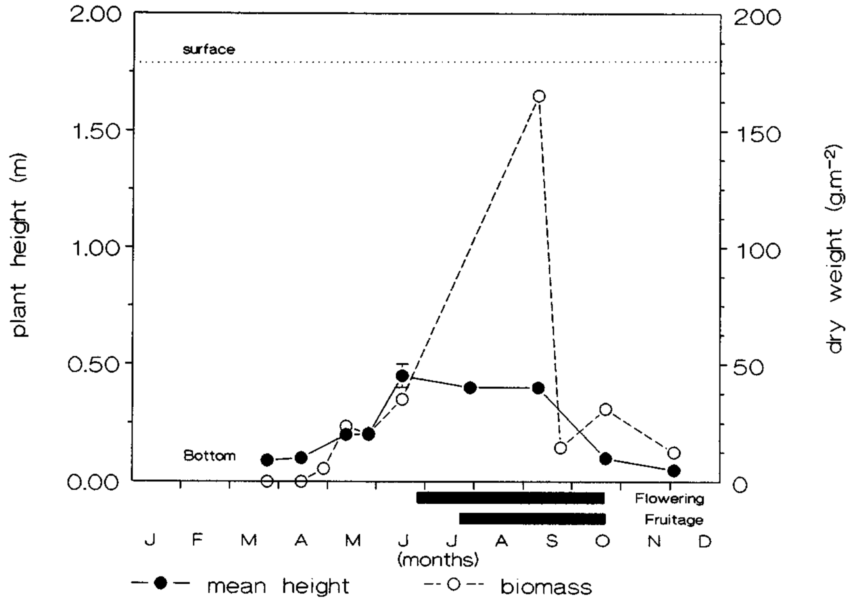

Fig. 6. Characteristics of *Ruppia maritima* L. in 1990 in Lake Volkerak-Zoom. Shown are the parameters mean plant height (with standard deviations), biomass and the period of flowering and fruiting.

consumption by herbivore and omnivore birds is compared to the development (cover and biomass) of the submerged macrophytes.

A significant Pearson's correlation, between standing crop of the submerged macrophytes and the calculated cumulative consumption of waterfowl, per growing season was found (Pearson's corr. coeff.: 0.96, $P<0.01$).

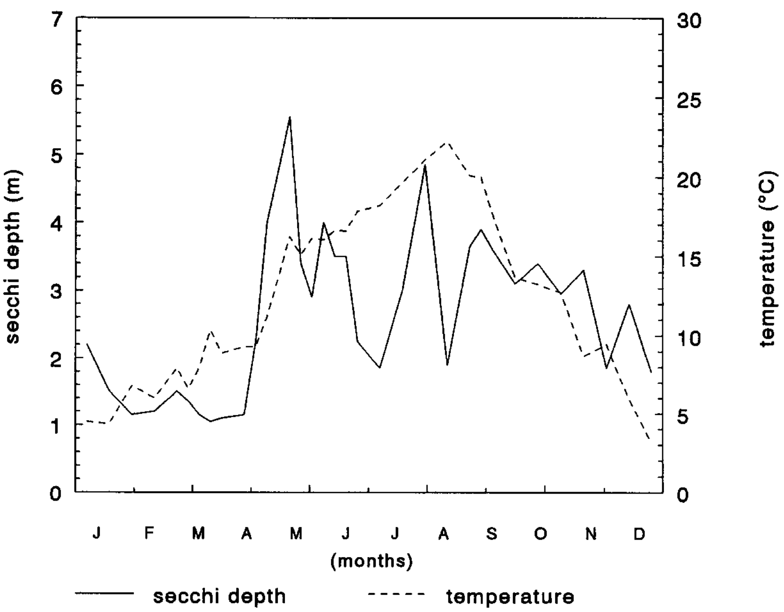

Fig. 7. Temperature and secchi depth during 1990 in Lake Volkerak-Zoom.

Table 3. Development of herbivore and omnivore waterfowl from 1987 to 1991, related to submerged macrophyte development, Lake Volkerak-Zoom. The calculated consumption is based on number of bird-days, percentage of plant food (% PL) according to Glutz v. Blotzheim & Bauer (1966–1985), and average food consumption according to Kiørboe (1980).

Waterfowl species	Number of bird-days (* 10^3)						Consumption (* 10^3 kg AFDW)				
	1987	1988	1989	1990	1991	% PL	1987	1988	1989	1990	1991
Cygnus olor L.	7	17	110	185	234	100	2.0	5.2	33.5	56.2	71.3
Anas penelope L.	209	522	628	955	905	50	4.2	10.5	12.6	19.1	18.1
Anas strepera L.	8	11	52	71	79	100	0.4	0.6	2.6	3.6	4.0
Anas crecca L.	41	94	246	253	360	100	1.0	2.3	6.0	6.1	8.8
Anas platyrhynchos L.	905	1561	1858	2022	1879	33	17.3	29.8	35.5	38.6	35.9
Anas acuta L.	20	31	77	143	159	90	0.8	1.3	3.0	5.6	6.3
Anas clypeata L.	5	21	103	231	326	100	0.2	0.8	3.9	8.7	12.2
Fulica atra L.	12	367	1350	2149	2110	100	0.6	16.9	62.4	99.3	97.5
Total	1206	2623	4424	6009	6048		26.4	67.3	159.5	237.2	254.0

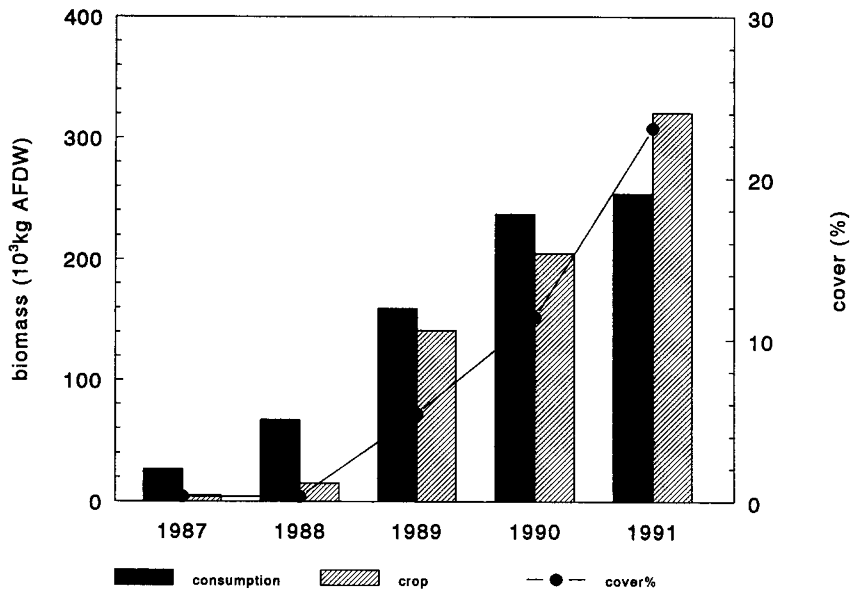

Fig. 8. Development of biomass and cover of submerged macrophytes in the zone between 0.5 and 5 m, and the calculated consumption of submerged macrophytes by herbivore and omnivore waterfowl, in Lake Volkerak-Zoom during the years 1987 to 1991.

Discussion

Macrophyte distribution

After the change in 1987, from a tidal marine area to a freshwater stagnant lake, colonisation by freshwater species began in 1988 and proceeded very rapidly in 1989. As expected the chemical and physical properties of the new system determined what species potentially could grow in the lake. During freshening, species with a high salinity tolerance (salinity index 1 & 2) colonised the lake. After freshening freshwater species (salinity index 3 to 5) invaded the lake (see Fig. 2).

All species present in 1991 were typical for larger waters with a relative high salinity and nutrient concentration, and mineral or slightly organic sediments (De Lyon & Roelofs, 1986). Contrasted with this was the presence of *Chara sp.* in 1990 and 1991, according to Krause (1981) normally indicating low nutrient concentrations. Probably water transparency and not the normally closely related nutrient concentration is the limiting factor for *Chara sp.* in eutrophic lakes.

In 1989 and 1990, speed of dispersion controlled the colonisation of the lake. In surrounding small water-systems (unpubl. data), all the species present in the Lake Volkerak-Zoom were found. In the rivers Rhine and Meuse, by which the system was flushed during freshening, only *P. pectinatus* and *Potamogeton perfoliatus* L. were found. Besides water coming from Rhine and Meuse, all surrounding water systems drained via pumping stations equipped with barriers for macrophytes. Thus only *P. pectinatus* and *P. perfoliatus* could have colonised Lake Volkerak-Zoom by water movement. All other species are probably transported by waterfowl. This is possible, considering the dispersion mode of the submerged macrophyte species now present (see Table 2).

The maximum colonisation depth is closely linked to the Secchi depth (Duarte & Kalff, 1989). The area of the euphotic zone (zone to which 1% of the surface irradiance penetrates) in a clear lake is much larger than in the same lake with shallower secchi depth. The zone of 0–5 m, the mean euphotic zone in Lake Volkerak-Zoom, has an area of 33 km^2. Thus potentially about 50% of the area of the lake system can be covered by submerged macrophytes. However when secchi depth drops from 2.5 to 1 m, only 18.4 km^2 can be covered with macrophytes.

Although the number of species found in the zone of 0.5 to 5 m water depth did not increase from 1990 up to 1991, the area covered doubled and may not yet have stabilized.

By creating more shallow waters (< 1 m), protected from wind induced waves by reinforced dams, new habitats may develop. Species less resistant to exposure such as broad-leaved *Potamogeton* species may settle in these areas. *Nymphaeids* may find a good habitat in the organic enriched muddy sediments in the system, such as in the former creeks.

Submerged macrophyte development during the period of this study was mainly influenced by environmental parameters and by dispersion. In future, competition of the submerged macrophytes may play a pivotal role in development and distribution.

Characteristics of the macrophytes

P. pectinatus propagates from tubers (van Wijk, 1989) before sunlight reaches the bottom (Figs 4 & 7). *P. pusillus*, *Z. palustris* and *R. maritima* hibernate as seeds or rhizomes and have to grow by means of newly assimilated energy. These species germinated after the sunlight had reached the bottom (secchi depth = water depth). The rapid growth phase seemed to start when the water temperature (Fig. 7) exceeded 10 °C.

The dry weight curves with time are not regular. This may be due to low sample numbers, a small sample area and/or a large differences in biomass between the oldest parts of the plant and the newly grown sides of the stand (Verhoeven, 1980). The biomass curve of *P. pectinatus* is more regular, though the plant reached the surface in July, the biomass (above the sediment) increased strongly during September. Energy assimilated in early summer is transported to the tubers (Van Dijk *et al.*, 1992). Later in the year generative production gained importance. This will probably occur only in water-systems with a long growing season for *P. pectinatus*.

The growing season in Lake Volkerak-Zoom is longer than in turbid lakes in the Netherlands. In Lake Volkerak-Zoom the growing season lasted five (*Z. palustris* & *R. maritima*) to seven months (*P. pectinatus*), whereas in the turbid Lake Veluwe the growing season of *P. pectinatus* lasted only two to three months (Van Dijk *et al.*, 1992). Doef *et al.* (1991) found a lengthening of the growing season of *P. pectinatus* from 3 to 4 months in Lake Wolderwijd after increasing the water transparency by biomanipulation.

Our data indicate that a higher water transparency benefits submerged macrophytes by enlarging both the potential area for plant growth and increasing the growing season. Several secondary effects on the macrophytes may be assumed. With increasing depth, the submerged macrophytes are less affected by wind-induced wave action and are less susceptible to predation by waterfowl either because they do not reach the surface (*Z. palustris* and *R. maritima*) or because only the upper part of the plants are consumed (*P. pectinatus* and *P. pusillus*). Furthermore, lengthening of the growing season enables the macrophytes to store more energy in vegetative structures like tubers (*P. pectinatus*) and enlarges the possibilities for flowering and seed production. All these processes increase the chance of macrophytes maintaining themselves in a water body.

Macrophytes related to waterfowl

Waterfowl can play an important role in the distribution of submerged macrophytes. Seeds and vegetative parts have been observed clinging to their feathers or feet, and in their faeces (Ridley, 1930; Pijl, 1980). Submerged macrophytes in their turn can act as an important food source for the herbivore and omnivore waterfowl.

In the years 1987 to 1990, the calculated consumption of the waterfowl exceeded the standing crop of submerged macrophytes. In 1991 the standing crop exceeded the consumption (Fig. 8). Naturally these high consumption rates have to be compared with production instead of standing crop (Kiørboe, 1980). Normally annual production is about two times the maximum standing crop (van Katwijk & Roelofs, 1988). Furthermore, waterfowl were also observed foraging on surrounding former tidal flats.

It is obvious that the submerged macrophytes are important as a food source for the waterfowl in Lake Volkerak-Zoom. An increase in submerged macrophytes may result in an increase in the number of waterfowl. The waterfowl, mainly coot (*Fulica atra* L.), mute swan (*Cygnus olor* L.) and mallard (*Anas platyrhynchos* L.) probably consumed about half of the annual production of submerged macrophytes in the lake. This is a high, but not abnormal (Kiørboe, 1980) percentage.

References

Cramp, S. & K. E. L. Simouns, 1977. Handbook of the birds of Europe the Middle East and North Africa. The birds of the western Palaearctic, vol 1: Ostrich to ducks. Oxford University Press, Oxford, UK.

Cramp, S. & K. E. L. Simouns, 1980. Handbook of the birds of Europe the Middle East and North Africa. The birds of the western Palaearctic, vol 2: Hawks to buzzards. Oxford University Press, Oxford, UK.

De Lyon, M. J. H. & J. G. M. Roelofs, 1986. Waterplanten in relatie tot waterkwaliteit en bodemgesteldheid. Parts 1 & 2. Catholic University Nijmegen, The Netherlands.

Doef, R. W., A. J. M. Smits & F. C. M. Kerkum, 1991. Water- en oeverplanten in het IJsselmeergebied (1987–1989). RIZA Report 90.015, Lelystad, The Netherlands (with English summary).

Duarte, C. M. & J. Kalff, 1989. Patterns in the submerged macrophyte biomass of lakes and the importance of the scale of analysis in the interpretation. Can. J. Fish. aquat. Sci. 47: 357–363

Frantzen, N. M. L. H. F., J. de Visser & E. H. van Nes, 1994. Colonization and succession of macroinvertebrates in recently freshened Lake Volkerak-Zoom (The Netherlands). Hydrobiologia 275–276/Dev. Hydrobiol. 94: 323–334.

Glutz v. Blotzheim, U. N. & K. Bauer, 1966–1985. Handbuch der Vögel Mitteleuropas, vol. 1–10 Wiesbaden, Germany.

Gulati, R. D., 1990. Structural and grazing responses of zooplankton community to biomanipulation of some Dutch water bodies. Hydrobiologia 200–201/Dev. Hydrobiol. 61: 99–118.

Kiørboe, T., 1980. Distribution and production of submerged macrophytes in Tipper Grund (Ringkøbing Fjord, Denmark), and the impact of waterfowl grazing. J. appl. Ecol. 17: 675–687.

Krause, W., 1981. Characeen als bioindikatoren für den Gewässerzustand. Limnologica 13: 399–418.

Moss, B., 1990. Engineering and biological approaches to the restoration from eutrophication of shallow lakes in which aquatic plant communities are important components. Hydrobiologia 200–201/Dev. Hydrobiol. 61: 367–378.

Ozimek, T., R. D. Gulati & E. van Donk, 1990. Can macrophytes be useful in biomanipulation of lakes? The lake zwemlust example. Hydrobiologia 200–201/Dev. Hydrobiol. 61: 399–407.

Pijl, L. van der, 1980. Principles of dispersal in higher plants. 3rd edition. Springer Verlag, Berlin, Germany.

Ridley, H. N., 1930. The dispersal of plants throughout the world. L. Reeve & co. Kent, UK.

Scheffer, M., 1990. Multiplicity of stable states in freshwater systems. Hydrobiologia 200–201/Dev. Hydrobiol. 61: 475–486.

Shapiro, J., 1990. Biomanipulation: the next phase – making it stable. Hydrobiologia 200–201/Dev. Hydrobiol. 61: 13–27.

Smit, H., Dirksen, S. & M. Snoek, 1989. *Ruppia maritima* on the 'Hellegatsplaten': growth and consumption by Mallards and Widgeons. De levende Natuur 90: 72–78 (in Dutch with English summary).

Van Dijk, A., W. Breukelaar & R. Gijlstra, 1992. Impact of light climate history and seasonal dynamics of a field population of *Potamogeton pectinatus L.* during a three year period (1986–1988). Aquat. Bot. 43: 17–41.

Van Katwijk, M. M. & J. G. M. Roelofs, 1988. Vegetaties van waterplanten in relatie tot het milieu. Catholic University Nijmegen, The Netherlands.

Van Nes, E. H. & E. C. L. Marteijn, 1991. Waterbirds in a new freshwater lake in the S-W Netherlands; developments in the first two years after embankment (1987–89). Limosa 64: 155–164 (in Dutch).

Van Wijk, R. J., 1989. Ecological studies on *Potamogeton pectinatus* L. I. General characteristics, biomass production and life cycles under field conditions. Aquat. Bot. 31: 211–258.

Verhoeven, J. T. A., 1980. The ecology of Ruppia-dominated communities in Western Europe. III. Aspects of production, consumption and decomposition. Aquat. Bot. 8: 209–253.