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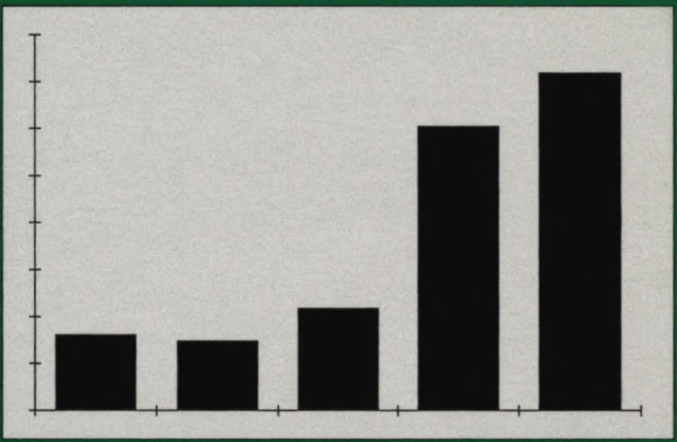
Esa Koskenniemi

The Ecological Succession and Characteristics in Small Finnish Polyhumic Reservoirs



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Esitetään Jyväskylän yliopiston matemaattis-luonnontieteellisen tiedekunnan suostumuksella julkisesti tarkastettavaksi yliopiston Musica-rakennuksen salissa (M103) joulukuun 8. päivänä 1995 kello 12.

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To my sons - Jan, Tom and Dan.

ABSTRACT

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In this work, the ecological succession and characteristics of Finnish reservoirs were studied. Bottom characteristics, water quality, macrozoobenthos and fish communities were studied in over ten reservoirs, whereas succession studies were concentrated on a typical Finnish reservoir, Lake Kyrkösjärvi (A=6.4 km^2 at summer HW, z_{mean}=2.5 m), since its filling up in 1981. Special attention was paid to macrozoobenthos, which - due to specific reservoir conditions - called for extraordinary work in sampling and taxonomic analysis.

Most of the Finnish reservoirs are constructed since the 60's in Western Finland for flood control and hydro power purposes. Their bottom areas are nearly totally terrestrial consisting of woodland and peatland, and the winter draw-down affects drying and/or freezing of the bottom. The woodland shorelines erode rapidly in reservoirs, but elsewhere the bottoms remain rather unchanged, due to low decomposition and sedimentation rates. In winter, severe oxygen depletion is detected in these polyhumic waters, where seasonal variations in water quality exceed well the long-term changes.

Vegetation and macrozoobenthos colonization is a rapid process, favored by species with high dispersal activity and rapid growth rate. In succession, the changes in species composition of biotic communities are clear and very few dominant species indicate different phases. In the most acidic reservoirs (pH 5 - 5.5) the overgrowth of water mosses is often observed, and many zoobenthic groups are poorly represented. The descriptive models of ecological succession in reservoirs fit Finnish conditions rather well, and general succession theory contributes to the understanding of these processes.

Despite the differences in water level regime and bottom characteristics, the biota of Finnish reservoirs are quite similar to those of natural forest lakes. The reservoir zoobenthos is characterized by a dominance of insects and community composition places reservoirs as somewhat intermediate between pools and lakes. Harsh environmental conditions restrict the diversity of biotic communities. In the most acidic reservoirs, fisheries management possibilities are very limited.

Key words: Succession; colonization; macrozoobenthos; polyhumic waters; reservoirs; *Chironomus*; Finland

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List of original papers

This thesis is based on the following papers, which will be referred to in the text by their Roman numerals:

I Paasivirta, L. & Koskenniemi, E. 1980: The Chironomidae (Diptera) in two polyhumic reservoirs in western Finland. - In: Murray, D.A. (ed.), Chironomidae: Ecology, systematics, cytology and physiology: 233-238. Pergamon Press, Oxford & New York.

II Koskenniemi, E. & Paasivirta, L. 1987: The chironomid (Diptera) fauna in a Finnish reservoir during its first four years. - Ent. Scand. Suppl. 29: 239-246.

III Koskenniemi, E. 1987: Development of floating peat and macrophyte vegetation in a newly created, polyhumic reservoir, western Finland. - Aqua Fennica 17: 165-173.

IV Koskenniemi, E. , Ranta, E.K., Palomäki, R., & Sevola, P. 1990: On the natural and introduced fish fauna in Finnish inland reservoirs. - In: W.L.T. Densen, B. Steinmetz and R.H. Hughes (eds), Management of freshwater fisheries: 74-81. Proc. Symp. EIFAC, Göteborg, Sweden, 31 May-3 June 1988. Pudoc, Wageningen.

V Koskenniemi, E. 1992: The role of chironomids (Diptera) in the profundal macrozoobenthos in Finnish reservoirs. - Neth. J. Aq. Ecol. 26: 503-508.

VI Koskenniemi, E. 1994: Colonization, succession and environmental conditions of the macrozoobenthos in a regulated, polyhumic reservoir, Western Finland. - Int. Revue ges. Hydrobiol. 79: 521-555.

In addition, some unpublished data are presented.

CONTENTS

1 INTRODUCTION

Finnish reservoirs are generally shallow and small polyhumic waters created on peatland and coniferous woodland. Most have been constructed in Western Finland for flood control and hydro power purposes, and the oldest reservoirs are now reaching an age of 30 years. Early studies of Finnish reservoirs addressed problems of regulation and water quality (Heinonen & Airaksinen 1974, Vogt 1978, Perttunen & Alasaarela 1981), while more recent attention is placed on monitoring the high mercury content in reservoir fish (Verta et al. 1986). Furthermore, the possible greenhouse gas emissions from reservoirs have recently become a popular topic - a debate started by Canadian researchers (Rudd et al. 1993).

Reservoir research is a multidisciplinary activity and a biologist will, besides scientific questions, face concrete social and economic problems caused by the construction of reservoirs. Odum (1969) has stated that "water impoundments have proved to be very useful additions to the landscape, but obviously we don't want the whole country inundated", whereas Vogt (1978) used expressions like "almost beautiful" to "very unaesthetic" or "terrible" when describing the shorelines of Finnish reservoirs. In Finland, the general debates of reservoirs has been periodically very intensive - especially in connection with the Vuotos reservoir, planned in the drainage area of the Kemijoki river.

The reservoir itself constitutes a new resource for the invading aquatic biota. The development of the biota - i.e. ecological succession - has been intensively studied in reservoirs throughout the world, although the aims of the studies have varied from practical purposes (introduction of fish, recreational use) to more theoretical and specific. Rapid changes in the biota at the beginning and the exceptional conditions (bottom structure, water level fluctuations) provide remarkable challenges for studying ecological succession in reservoirs. Further, monitoring the continuous changes will take years or even decades (Mordukhai-Boltovskoi 1979, Krzyzanek & Kownacki 1986, Zimbalevskaya et al. 1989). Vogt (1978) hypothesized, that it may take even hundreds of years for Finnish reservoir ecosystems to reach a stable state. These difficulties might partly explain, why succession studies of terrestrial vegetation (autotrophic succession) and heterotrophic succession in ephemeral habitats have contributed more to the succession theory (Gray et al. 1987, Schoenly & Reid 1987, Glenn-Lewin et al. 1992) than studies of aquatic ecosystems.

My first studies of the Finnish reservoirs showed many intriguing characteristics of these particular ecosystems (Koskenniemi 1985, I), but these early studies also lead to many interesting questions of the biotic communities and their development in these 'huge bog pools'. The next step was the study of the early succession of the Kyrkösjärvi reservoir, a typical Finnish reservoir filled-up in 1981 (Koskenniemi 1987, II, III). Because the construction of new reservoirs has practically been halted since then, this study was started really at the last moment. In 1986, a 3-year project, "The ecological succession in Finnish reservoirs", facilitated the continuation of the reservoir studies. As a result, profundal macrozoobenthos and fish fauna were studied in Finnish reservoirs varying in their environmental characteristics (IV, V). The sampling programme of the macrozoobenthos in the Kyrkösjärvi reservoir was continued up to the year of 1989, and this material was used in the summarizing paper on the macrozoobenthos colonization-succession (VI).

The main objectives of this work are:

1. Description of the structure of the Finnish reservoir ecosystems, with special emphasis on macrozoobenthos.
2. The identification of the role of environmental conditions in structuring the biotic communities in reservoirs.
3. Description of the ecological succession in Finnish reservoirs and identification of the main factors controlling these succession processes.
4. How do Finnish reservoirs resemble natural water bodies, especially regarding macrozoobenthos?

The term macrozoobenthos is here understood as "organisms that inhabit the bottom substrates (sediments, debris, logs, macrophytes, filamentous algae, etc.), for at least part of their life cycle and are retained by mesh sizes $\geq$200 to 500 um" (Rosenberg & Resh 1993 and references therein). Occasionally, also some actively swimming and surface-dwelling invertebrates are caught and included in the macrozoobenthos.

2 DESCRIPTIONS OF THE RESERVOIRS STUDIED

Twelve, of the altogether 13 studied reservoirs are situated in a restricted geographical area in the upper or middle reaches of the coastal rivers in Western Finland (Fig. 1). Created on flat landscape depressions and with a high proportion of peatlands and other terrestrial habitats on their inundated bottoms, the Finnish reservoirs (Table 1) represent a special aquatic environment (Vogt 1978). The proportion of pre-impoundment natural waters is only 1 % or less, except in the Kalajärvi reservoir (23 %) due to an inundated lake complex (Vogt 1976, National Board of Waters and the Environment - hereafter NBWE, unpubl.). The reservoirs are strongly regulated, with a relatively constant summer water level (amplitude < 1m), but in late winter, when the water level reaches its annual minimum (Table 1), the reservoir water volume is usually ≤ 10 % and the area ≤ 50 % of the summer values (Vogt 1978).

TABLE 1 General characteristics of the reservoirs studied.

Reservoir	Age in 1994	Area at HW	Mean depth	Theo-retical resi-dence time	Mean regula-tion effi-ciency	Peat soils of the bot-tom area	Proportion of different shoreline types (%) of the natural shoreline length			
							Minero genic	Organogenic		
								higher veget.	water moss	without veget.
	years	km^2	m	days		%				
1. Vissavesi	29	3.7	1.8	260	1.27	52	40	0	30	30
2. Liikapuro	27	3.1	1.5	296	0.97	75	50	0	50	0
3. Kivi- ja Levälampi	17	9.7	1.7	140	1.25	62	30	0	0	70
4. Venetjärvi	29	17.5	1.6	200	1.81	58	35	1	60	4
5 . Hirvijärvi	21	15.5	2.6	120	1.32	33	65	5	10	20
6. Kalajärvi	17	11.3	3.8	110	1.36	20	75	5	10	10
7. Kyrkösjärvi	14	6.4	2.4	23	0.62	50	40	22	33	5
8. Patana	27	11.0	4.8	190	1.26	32	80	0	5	15
9. Uljua	24	28.0	5.4	150	1.31	48	90	0	0	10
10. Pitkämö	23	1.0	7.0	4	0.99	0	80	20	0	0
11. Hautaperä	19	7.6	6.7	71	1.50	10	90	0	0	10
12. Kuona	26	5.4	1.9	60	1.05	0	80	20	0	0

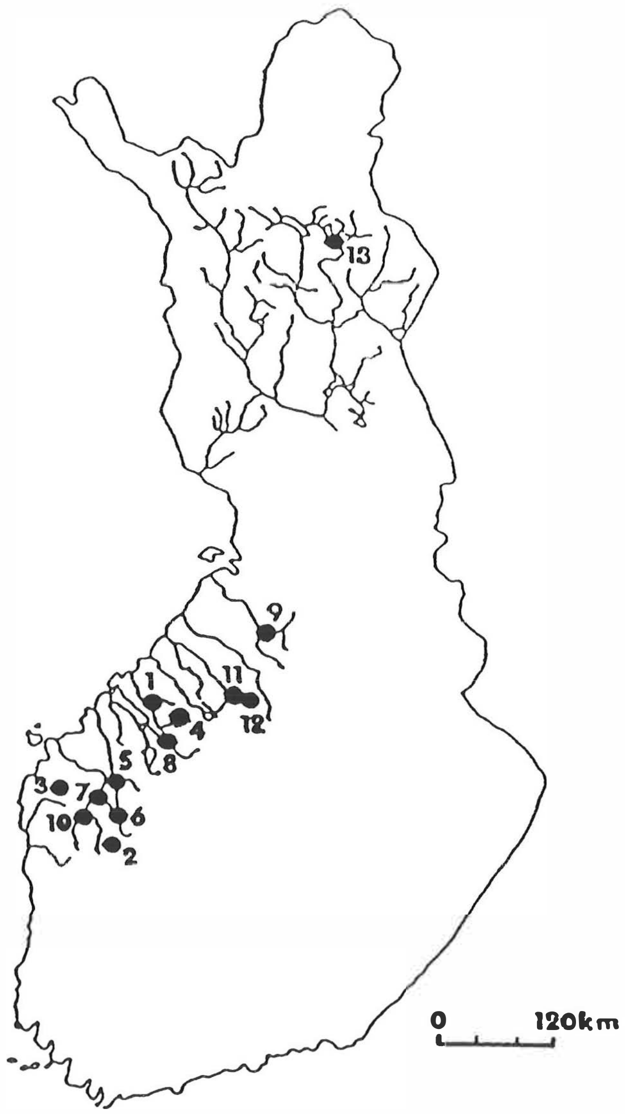

FIGURE 1 Study area. For description of reservoirs (1-13), see Table 1.

3 MATERIAL AND METHODS

3.1 Bottom characteristics

The general classification of the shorelines in reservoirs was based on the field observations taken by boat and by using maps included in the construction plans of reservoirs (IV, NBWE, unpubl.). The sediment structure was examined through visual observations of the bottom fauna samples and sedimentation rate in the Kyrkösjärvi reservoir was evaluated also visually from bottom samples taken by a peat borer in 1990 (VI). Both aerial photographs and field observations were used to evaluate the amount of floating peat in the Kyrkösjärvi reservoir (III).

3.2 Water quality

The water analyses were carried out using the standard methods of the NBWE and the data was collected from the water quality data register of the NBWE. In this work, a statistical package of Cluis et al. (1989) was used for the trend analyses of four main parameters (oxygen, pH, phosphorus, color) measured at the permanent water quality monitoring site in the 'epilimnion' (1 m) and in the 'hypolimnion' water (2h-1m=4-6m depending on the season) of the Kyrkösjärvi reservoir. The parameters above are also included in the Finnish general lake water quality index developed by Malin (1984).

3.3 Vegetation

The occurrence of vegetation (vascular plants and water mosses) is included in the general classification of the shorelines (see 3.1). A study of vegetational development along the whole shoreline length (21 km) of the Kyrkösjärvi reservoir was performed in late summer of 1981-83 and in 1985-86 (III). The aquatic macrophyte stands (species composition, site, size, occurrence depth) were mapped by boat. Dry mass per square meter (80 °C, 24 h, high ventilation drying case) of the dominant plants was measured from sample quadrats taken in 1986. The artificial plexiglass method (Eloranta & Kunnas 1976) was used in 1981 to study the depth distribution and summer development of periphytic algae (III).

3.4 Macrozoobenthos

Quantitative soft-bottom samplers (Ekman grab) only could be used on the soft-bottom substrates of inundated lakes and bog ponds and in older reservoirs also in areas of new sediments (I, II, V). On shallower bottoms (0.5-2 m) of the Kyrkösjärvi reservoir, a modified, manually operated hydraulic suction sampler (sampling area 82 cm^2, Boulton 1985) was used for quantitative studies (II, VI). This gear was easy to use and was effective in collecting samples from minerogenic, woodland and peatland bottoms. Suction sampling has later been used successfully also in Finnish regulated lakes (Tikkanen et al. 1989, Palomäki & Koskenniemi 1993). A plastic box (236 cm^2), pressed tightly onto the substrate was used in the shallowest ($\leq$0.5 m) areas (I, VI; woodland and water moss bottoms).

Qualitative bottom samples were taken with a standard hand net at $\leq$2 m depths (SFS 1989) and with a triangular dredge on deeper bottoms. This form of sampling could be used on all bottom types and allowed a rapid collection of a large number of samples and was therefore used when monitoring the colonization-succession (II, VI). According to biomass ranking of the species, the results of the qualitative sampling were comparable with the quantitative analyses (VI).

Winter samples were taken during draw-down by using a small shovel through an ice hole (regulated zone) or with the pump method (submerged zone) (VI). The condition of the animals sorted was checked in the laboratory one day after sampling.

A mesh size of 0.4 mm (excluding funnel traps) was used throughout the whole study. Sorting of the animals was mostly performed on fresh samples, which minimized the sorting time and allowed the use of larvae for karyological analysis (VI). Subsampling was used to save time in sorting samples, which often included a large amount of detritus (VI).

Hand netting and emergence trapping of adults were used parallel with bottom sampling (I, II). Adults were collected from swarms and among the near-shore vegetation (15-30 min sweep netting/occasion) during the open-water season at two sites situated near the inundated peatland and woodland areas in the Kyrkösjärvi reservoir (II, fig. 1). The funnel trap used was a submerged model placed on the bottom with a sampling area of 0.5 m^2 (I, 0.5 mm stainless mesh cone) or 0.25 m^2 (II, 0.5 mm nylon mesh cone supported by a metal frame).

Sampling was done in spring, summer and autumn to obtain more comprehensive information on the faunal composition in the habitats (I, II and VI). To avoid the risk of emergence loss, spring bottom sampling occurred shortly after the ice-out (I, II, VI). A sampling interval of once every three weeks was used to cover the possibly rapid faunal changes expected to occur in the first summer colonization period of the Kyrkösjärvi reservoir (VI).

The animal material collected is presented separately in each study. New literature has appeared since the first study on identification of many insect groups (VI). The three identification books (Wiederholm 1983, the first book) on Holarctic chironomid genera were, for example, important contributions to the taxonomy of this species-rich family common in all kinds of freshwater habitats. The material collected from these reservoirs has also been used in many taxonomical papers (Wülker 1987, 1991a, 1991b and several manuscripts in preparation, Langton 1991). The biomass (AFDM) for the majority of species was calculated according to a length-mass regression developed by I.J. Holopainen and L. Paasivirta (unpubl., the Finnish Pääjärvi Project). For some oligochaete and insect taxa, the calculations of Meyer (1989) and my own measurements were used (VI).

Statistical tests were used to compare the different sampling methods, spatial distribution and temporal differences in the fauna (VI). In addition, DCA ordination (Hill 1979) of sites of the profundal and colonization-succession data (V, VI) was related to associated environmental data by the product-moment correlation.

3.5 Fish

The data on the natural fish stocks and their diet was obtained from the reports published by the relevant local authorities (the District Offices of the NBWE). Standard gill net series and fyke nets were used in fish studies. The latter method was widely used in some reservoirs, because the terrestrial bottom quality restricted fishing attempts and even damaged the nets due to snagging on large twigs and stumps. The available data on the fish stocks and fisheries management was complemented by interviews with local fishermen and authorities. Fish stocking data was collected from official statistics and the successfulness of stocking was studied from the literature data and interviewing local fishing guilds and authorities.

4 RESULTS

4.1 Bottom characteristics

Initially the natural shorelines in reservoirs are generally organogenic, but the proportion of the minerogenic content increases during succession and that type frequently dominates the majority of reservoirs (III, IV, table 1). The organogenic shoreline was divided into three parts, of which the water moss shorelines were very common in the small, acidic reservoirs.

Former terrestrial bottom areas were usually found in nearly pre-impoundment condition after several decades, and the occurrence of new sediments was observed to be restricted on deeper bottoms (I, II, V, VI). The maximum sedimentation rate in the Kyrkösjärvi reservoir was estimated as 1 cm x a^{-1}, decreasing rapidly towards the central part of the reservoir (VI).

Floating peat is a common, special phenomenon in Finnish reservoirs (III). The peat is lifted up from the bottom by microbial decomposition gases with the annual maximum occurrence in late summer. Two types of floating peat were found: the d r i f t i n g type which usually consisted of small pieces of floating peat, with no living vegetation. The a t t a c h e d type, which was similar to a submerged 'hill' with its top above the surface. This latter type was rapidly colonized by vegetation (grasses, sedges), and could be separated from the drifting type by using aerial photos. The maximum amount of floating peat in the Kyrkösjärvi reservoir occurred during the 4th year after the filling-up, when the coverage was ca. 11 % of the total reservoir area (III, fig. 2).

It is difficult to divide reservoir bottoms into different zones (V). One possibility is to simply divide the bottoms into regulated and permanently submerged zones, i.e. a 'littoral' and a 'profundal' (Fig. 2). The regulated zone of the Kyrkösjärvi reservoir was divided into three types (VI):

type A: m i n e r o g e n i c bottoms, which freeze solid in winter up to 10-15 cm below the surface;

type B: o r g a n o g e n i c woodland bottoms, which freeze only at the surface (2-3 cm), but which are capable of keeping the substrate below moist throughout the draw-down period. Only the water edge of the organic shorelines is frozen and should be classified in the former group in terms of freezing effects.

type C: o r g a n o g e n i c peatland bottoms, which do not freeze but, where the interstitial water is often anoxic and rich in H_2S.

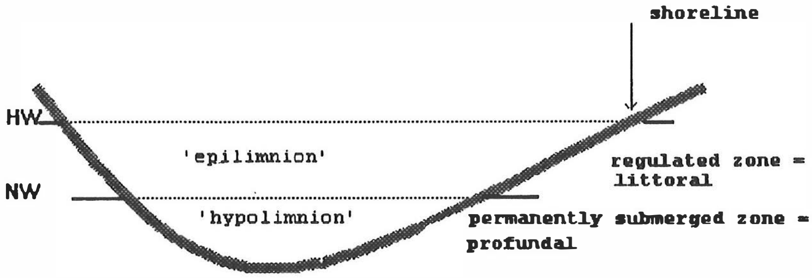

FIGURE 2 A schematic cross section of a Finnish reservoir.

4.2 Water quality

The upper-reach reservoirs have the poorest water quality with a low pH (IV, V), and even the whole water column may become oxygen-free during the winter draw-down affecting high nutrient and iron concentrations and color values especially in the bottom-near water (I, II). Deeper, moderately acidic reservoirs have, in contrast, frequently low oxygen content in the 'hypolimnion' water during their summer stagnation, but are not totally oxygen-free in winter.

The long-term water quality development in the Kyrkösjärvi reservoir shows a slight trend for nearly all parameters (Table 2).

TABLE 2 The trend analysis on some water quality parameters from 1981 upto 1994 in the Kyrkösjärvi reservoir ('epilimnion' and 'hypolimnion') and the Jouttikoski monitoring station in the river Seinäjoki, 15 kms upstreams from the reservoir. Seas.=seasonality. Trend tests: HS=Hirsch and Slack, KS=Kendall seasonality and SL=Spearman-Lettenmaier test. + = seasonality or increasing trend exists and - = decreasing trend exists ($p<0.05$). Level values are shown only when trends were detected.

	n	Seas.	Trend	Test	1981 level	1994 level
'epilimnion':						
oxygen (%)	116	+	+	HS	69	79
pH	117	+	+	HS	5.7	5.9
tot P (µg/l)	117	+	-	KS	72	61
color (Pt mg/l)	117	no	no	SL		

(continued)

TABLE 2 (continued)

'hypolimnion':						
oxygen	116	+	+	KS	36	46
pH	117	+	+	KS	5.6	6.0
tot P	117	+	-	HS	341	67
color	117	+	no	HS		
Jouttikoski:						
oxygen	122	+	no	HS		
pH	138	+	no	HS		
tot P	137	+	no	KS		
color	130	+	no	HS		

'Epilimnion' and 'hypolimnion' water showed similar trends. The river control station didn't show any trend, but had seasonality characteristics as the reservoir.

4.3 Vegetation

Higher vegetation is usually very sparse in reservoirs (IV, table 1), whereas water mosses (*Drepanocladus/Warnstorfia*) reach a mass occurrence on the gently sloping peatland shores in some acidic reservoirs (I).

The vegetation succession of the Kyrkösjärvi reservoir was divided into three phases (III):

1) The first phase had a mass occurrence of filamentous green algae (*Ulothrix, Spirogyra*) during the first summer (1981) on the shallows (0.1-0.5 m). Their maximum biomass (ca. 5 mg x cm^{-2} as a dry weigth) was reached in late summer at a depth of 0.2-0.3 m, and decreased to 0 mg x cm^{-2} at 1 m (III, fig. 5). Higher macrophytes occurred extremely sparsely, altogether only 29 small stands (< 1 m^2) belonging to four species were found along the whole reservoir shoreline (III, table 2).

2) During the second phase (1982-83), the floating *Callitriche palustris* L. stands occurred in vast areas near the shoreline and on the shallows rooted plants, esp. *Sparganium emersum* Rehman, began to invade the shores (III, fig. 4a).

3) After the *Callitriche* phase there was a rapid, synchronous growth of *Drepanocladus* (*D. procerus* (Renn. H.Arn) Warnst.) mosses along the natural shoreline, and they formed dense mats along sheltered shores (III, fig. 4b). Along a stretch of 4 km, they grew as a uniform belt along the shoreline to at least a depth of 0.1 m and within a width of at least 1 m. Similarly, stands of higher plants grew larger in size and increased in density and spatial distribution. The *Sparganium* stands became very common in exposed areas, where mosses did not occur (III, fig. 4b). The number of plant species increased to 12, a value which remained unchanged at the end of the study (III, table 2). In most cases, species colonized inlet areas first. The block dam shores remained uninhabited during the study period, excluding the patchy and sparse occurrence of filamentous algae.

The occurrence of the aquatic plant species was restricted to shallow water, and the depths of maximal density never exceeded 0.7 m (*Nuphar luteum* L.), and was usually 0.3 m or less (III, table 3). The *Drepanocladus/Warnstorfia* water mosses were found in a good condition and continued their growth after the ice-out in the reservoirs (I, III). Similarly, the seeds of *Sparganium* began to germinate in the laboratory for samples taken from the frozen sandy littoral (III).

4.4 Macrozoobenthos

4.4.1 Colonization and succession in the Kyrkösjärvi reservoir

Colonization (the first summer period)

The first summer period showed a clear temporal change in the fauna (VI, fig. 3 and table 4), and was divided into two phases (VI, fig. 2). In early summer, large insects, with actively moving larval or aquatic adult stages (Ephemeroptera, Heteroptera) were important (VI, table 5). In addition, *Asellus* was abundant near the inundated water areas after the first summer month (VI, fig. 5). Later in summer, high densities were noted, when chironomid colonizers (esp. *Chironomus*) produced their first generation (II, fig. 3, VI, tables 5 and 8). The total species number remained rather stabile during the whole summer, with a clear dominance of insects or animals attached to them (water mites), i.e. winged species (VI, table 2).

Succession (long-term changes)

Macroinvertebrate community composition changed continuously up to the last study year (VI, fig. 2). Spatial (bathymetric) distribution seemed to be more important than temporal changes when all study years were analysed together (VI, table 4). The total number of winged species did not change during the succession phase (II, table 3 and VI, table 3), but the number of non-winged species (e.g. molluscs, oligochaetes and leeches) increased towards the end of the study (VI, table 3, app. 1) and some predatory insects became more common (*Cyrnus*, *Procladius* sp. b; VI, table 6).

The faunal composition of different habitats showed a change in dominant species composition during the succession phase (VI, table 7). The proportion of *Chironomus* species decreased from 30 % in 1981 to 20 % in 1989 of the total macrozoobenthos biomass, and this decrease was observed in nearly all habitats. The distribution pattern of *Chironomus* spp. was more patchy in the 9th year compared with the first year (VI, figs. 6g and h). New habitats appeared in the Kyrkösjärvi reservoir, which clearly contributed to the species composition and diversity during the succession phase (VI).

4.4.2 Related environmental conditions

4.4.2.1 Bottom characteristics

In the spring, several macrozoobenthic metrics were poorest on the bottoms, which froze solid in winter (type A, water edge of type B, see 4.1, I, VI). These areas were generally inhabited by actively moving fauna (lumbriculids, leeches, adult beetles). In the organogenic regulated zone (the rest of type B, type C), 80 % of the zoobenthos density (dominated by chironomids) was alive during the winter draw-down (VI). These areas showed high abundance and biomass values in the spring, and soon after the ice-out, intensive emergence appeared from these bottoms (I, II, VI). The abundance and biomass values of the regulation zone did not differ significantly from the values of the permanently submerged zone in the spring or autumn (VI, table 8).

The number of lacustrine species (VI, p. 534) and their proportion in the profundal biomass increased continuously during the succession phase (VI, fig. 6). After six years of inundation, the tubificid oligochaetes (*Limnodrilus*, *Potamothrix*) began to predominate on the profundal soft-bottom, whereas on coarse bottoms the chironomids were more common. In older reservoirs (ranging from 9 to 21 years) lacustrine species were common in the profundal (V), but species composition varied markedly among reservoirs. In the eroded littoral, lacustrine species slowly became more common (VI, table 10). Of these species, the chironomids *Glyptotendipes gripekoveni* Kieff., *Stictochironomus sticticus* (Fabr.), *Tribelos intextus* (Walk.) and the mayfly *Heptagenia fuscogrisea* (Retz.) did not dominate at other sites.

4.4.2.2 Water quality

The reservoirs were grouped as acid, upper reach reservoirs and as moderately acidity and low summer oxygen content in the hypolimnion (mostly larger reservoirs) according to their profundal fauna (V). The species of *Chironomus* were especially common in the profundal of the most acidic reservoirs, and molluscs were totally absent (I, V). Of the molluscs, small clams (*Pisidium* and *Sphaerium* spp.) were only found in reservoirs with pH > 5.5 (I, V). *Stylodrilus heringianus* Clap. was the only common oligochaete species in reservoirs with pH < 5, whereas the tubificids *Limnodrilus hoffmeisteri* Clap. and *Potamothrix hammoniensis* (Mich.) occurred commonly in lakes with pH > 5.5 and the latter species were also found in reservoirs with a low hypolimnetic summer oxygen content. *Asellus aquaticus* L. was the only macrocrustacean species found in the reservoirs, and this species was also noted in very acid conditions (I). However, *Asellus* appeared to be intolerant to low winter and/or summer oxygen stress in the profundal (VI).

4.4.3 Special characteristics

The reservoirs studied had a high diversity of *Chironomus* species (I, V). During the succession of the Kyrkösjärvi reservoir, over 30 species (!), belonging to all four subgenera of the genus, were found (II, table 2, VI, app. 1). The freshwater sponge *Spongilla lacustris* L., occurred in Kyrkösjärvi reservoir, occupying nearly the whole bottom area and building colonies especially on submerged branches, twigs and ericaceous plants (VI).

The bathymetric distribution of several macroinvertebrate taxa showed reservoir-characteristic features. Littoral species - like naidid oligochaetes, *Asellus*, and many chironomids (*Endochironomus*, *Glyptotendipes*, *Microtendipes*) - occurred commonly in the profundal area of the reservoirs (I, V, VI).

Insect emergence from organic bottoms (water moss, woodland, peatland) had a strong spring maximum, with a dominance of large-sized detritus-feeding species (I, II). The strength of spring maxima was not exceeded later in summer, and this reservoir-specific emergence pattern was reached already after the first winter (II, figs. 4 and 5).

4.5 Fish

The fish fauna of the studied reservoirs usually originated from bog ponds and/or small forest lakes present in the area before impoundment. Pike, perch, roach, ruffe and burbot were the most common species. The number of fish species was particularly low in the most acidic reservoirs, where pike was often the only dominant species (IV, table 3). The critical pH level for the occurrence of cyprinids and the burbot seemed to be ca. 5.5. The reservoir bottom fauna plays an important role in providing fish food, even for predatory (pike) and semi-predatory fish (burbot, perch). During the mass emergence of the chironomids in spring, their pupae were readily consumed by these fish. *Asellus* is also an important food item during the whole open-water period.

Introduction of species (IV, table 3) able to reproduce in the reservoirs is mainly achieved with spawning bream from nearby waters. Coregonids (*Coregonus lavaretus*, *C. muksun*, *C. peled*) have been introduced in most reservoirs, but with less success than introductions of bream or pike. Several salmonid species and grayling also have been introduced as game fish, with varying success. The introduction activity seemed to have been more dependent on social factors than on site-specific conditions of each reservoir.

5 DISCUSSION

5.1 Bottom characteristics

Wave action and the loosening of the bottom surface layers by freezing rapidly erodes the exposed woodland shores of Finnish reservoirs (III, IV, table 1). Erosion processes can continue for decades even in very large reservoirs (Mordukhai-Boltovskoi 1979, pp. 270, 295), forest areas left uncut before the filling-up may dampen these processes.

Decomposition of organic matter is relatively slow in Finnish reservoirs. Sundbäck (1976) reported that the inundated peaty bottoms are nearly in initial condition after five years of impoundment. Also, Vogt (1978) found the terrestrial vegetation to be easily identifiable after 15 years' inundation. These results agree with my own observations (I, V).

Butorin (1979) has evaluated the average sedimentation rate in the upper reach Volga reservoirs as 0.2 cm x a^{-1} , a value of the maximum rate in Finnish conditions near the outlet dam regions (Vogt 1978). The relatively high sedimentation rate found for the Kyrkösjärvi reservoir is evidently due to higher river input (IV, table 1, theoretical residence time) of allochthonous matter, a feature observed also by Fillion (1967).

High water temperatures enhance the lifting-up of peat by microbial decomposition gases, as indicated by the maximum occurrence of floating peat in autumn. The disappearance of drifting type in the Kyrkösjärvi reservoir has continued in later years (Koskenniemi 1989), a similar observation was made for the Lokka reservoir (Ruuhijärvi et al. 1976). If not totally removed from the bottom before inundation, covering by e.g. a moraine layer prevents rising-up of peat (Koskenniemi 1989).

5.2 Water quality

The Finnish reservoirs are classified as having "poor" or "passing" water quality (NBWE 1988). Only the northern Lokka-Porttipahta reservoir complex belongs to "satisfactory" waters - the middle group in a total of five classes. Vogt (1978) called Finnish reservoirs "super-polyhumic" due to the high amounts of humic matter in their water.

Seasonal variations in water quality of Finnish reservoirs often well exceed the magnitude of the long-term changes (Vogt 1978, Koskenniemi 1987). The easily degraded detrital matter left after inundation caused very severe oxygen conditions during the first years, referred to as "a biological bomb" by (Vogt 1978). In the Kyrkösjärvi reservoir, only a slight improving trend in the water quality was detected (Table 2). Regulation and the relatively low retention time result in winter oxygen depletion in Finnish reservoirs (Heinonen & Airaksinen 1974, Perttunen & Alasaarela 1981, Koskenniemi 1987).

5.3 Vegetation

Vegetation succession of the Kyrkösjärvi reservoir agreed with the model of Ekzertzev (1979) on winter-regulated Volga reservoirs, and characteristics of maturing ecosystems (higher species diversity, higher spatial heterogeneity, and an increase in the number of species with lower dispersal ability, Odum (1969)) were characteristic of later succession phases. The succession of the water mosses could be better understood using models of Connell & Slatyer (1977). Mosses make the habitat unsuitable for settlement of new invader species (inhibition model) and being resistant to environmental conditions (tolerance) they are a relatively stable element. In the Lawton's (1994) classification, the water mosses can be regarded as "autogenic engineers" in the reservoir ecosystem. The Connell-Slatyer models were inadequate for use in eroding woodland shores, due to changes in physical conditions.

Tolerance to freezing and low pH in water facilitates the overgrowth of mosses in some reservoirs (I, III). In the Venetjärvi reservoir, the mosses covered nearly half of the reservoir bottom area (Koskenniemi 1985). Poor establishment of higher vegetation in reservoirs may arise from several factors (III, Vogt 1978):
1) the regulation and minerogenisation of the littoral increases the freezing risk of the substrate, killing the stands and making the substate poor in nutrients;
2) the bottom quality (the lack of soft, silty bottoms) can be unfavorable for many species and;
3) the low transparency restricts the growth of submerged species.

The species composition of the Kyrkösjärvi reservoir was similar to that of the shallow Veittijärvi reservoir in northern Sweden, where the bottom was frozen in winter (Danell & Sjöberg 1982). Similarities were found regarding the dominant species in the natural humic lakes (*Equisetum fluviatile*, *Sparganium emersum*, *Potamogeton natans*, *Nuphar luteum*, see Ilmavirta & Toivonen 1986), but their occurrence seems to be more patchy and poorer in reservoir conditions.

5.4 Macrozoobenthos

The dispersal ability of the species and the nearness to their natural habitats determine the colonizative faunal composition in the Kyrkösjärvi reservoir. The rapidly developing fish fauna of the Kyrkösjärvi reservoir seems to be vulnerable to the occurrence of many large-sized, actively moving colonizators (VI, p. 538; see Brittain 1982, Oscarson 1987). The invasion of the chironomids, especially species of *Chironomus*, by oviposition over the whole bottom area (VI, table 5, fig. 6g) is in good agreement with observations made by Mordukhai-Boltovskoi (1961): " ... was den Eindruck einer biologischen Explosion hervorruft. ... der ganze Boden des Stausees mit einer einförmigen '*Tendipes*-Hülle' bedeckt wird."

The global importance of the genus *Chironomus* as a rapid invader in newly created waters is a combination of several factors (Mordukhai-Boltovskoi 1961, Lellak 1966, Paterson & Fernando 1969a, McLachlan 1970, Cantrell & McLachlan 1977, Brown & Oldham 1984, Matena 1990):

- the world-wide distribution of genus,
- the rich food resources of dctritus for larvac over the bottom area,
- the tolerance of the larvae to harsh environmental conditions,
- the high reproductive capacity and
- the rapid growth of larvae, which reach a relatively large size, i.e. due to the high space competition ability on the bottom.

For non-winged species, several years are often necessary for dense population development in reservoirs to occur. They may be early invaders only, when they can colonize from the pre-impoundment aquatic areas (Paterson & Fernando 1969a, Mordukhai-Boltovskoi 1979). These differences in the colonization rate could clearly be seen for *Asellus* and, on the other hand, for molluscs and tubificid oligochaetes, which had to invade via rivers upstream in the catchment.

In the succession phase, the zoobenthos of reservoirs shows characteristics similar to that expected during maturing process of an ecosystem (sensu Odum 1969). The fauna is increasingly controlled by habitat development. This is indicated by a pronounced bathymetric distribution (VI, table 4), the specific fauna in the habitats appeared during the ageing (e.g. lacustrine profundal species, IV, p. 534) and the increased faunal distance of the habitats studied (Fig. 3a). Similarly, predatory species increased in later years, but had a short peak after the filling-up in 1981, when hemipteran corixids and Coleoptera were more common (VI, table 6, Fig. 3b). Odum's attribute for species with a longer life-cycle is difficult to show in Finnish reservoirs, although well documented in Central Europe, as the increase in the occurrence of unionid mussels (Krzyzanek et al. 1986).

An impoverished community of the regulated zone is frequently observed in strongly regulated lakes, where the littoral area freezes solid during the winter draw-down (Grimås 1961, Kaster & Jakobi 1978) . In Finnish reservoirs, the same negative effects on the fauna are evident in littoral areas washed to a minerogenic state (I, tables 2 and 3; VI, subarea E in table 8), and only fauna capable of moving to this region actively after the thaw are found here in the spring. The regulated organic shores, not so sensitive to freezing and rich food in resources do, however, contribute to high macrozoobenthic abundance and biomass throughout the year. Many species inhabiting these bottoms are known to be tolerant to harsh regulation conditions (Paterson & Fernando 1969b, Danell 1981, Koskenniemi & Sevola 1989). Notably, these conditions have similarities with the seasonality (drying-up/ freezing) and the substrate structure (coarse detritus) of natural pools.

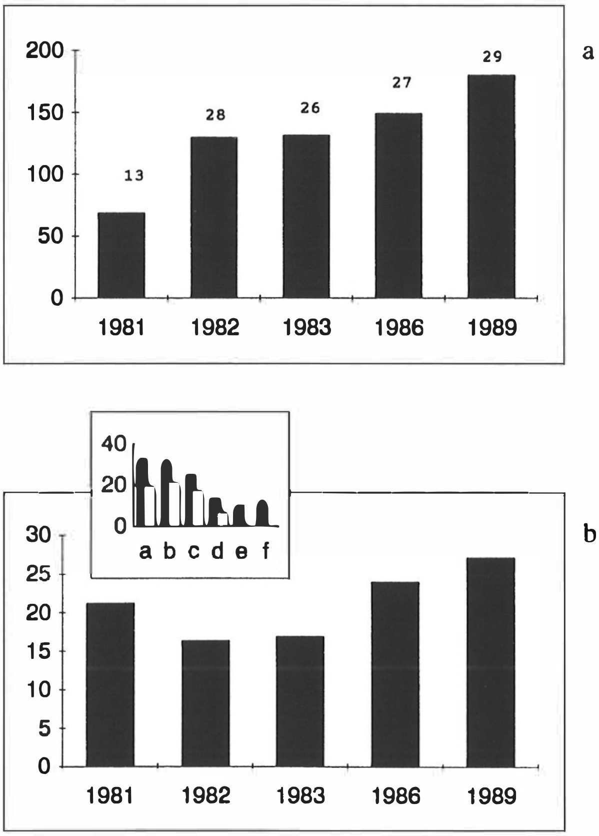

FIGURE 3 a: Mean Euclidean distances between the pairs of sites at different depth zones (source: VI, fig. 3b). Standard errors (n=9) marked above the bars. b: The proportion (%) of predatory species of total macrozoobenthic biomass in 1981-1989 (Source: VI, app. 1, exact numerical values). The year of 1981 is shown for different study periods. White bars: Hemiptera + Coleoptera.

Pisidium casertanum seems to be the most tolerant mollusc species to low pH in Finnish reservoirs (I, V). That species also was shown to be as acid-tolerant in river and lake conditions (Meriläinen 1984, Meriläinen & Hynynen 1990). As in Finnish reservoirs, the oligochaete *Stylodrilus heringianus* is acid-tolerant in river conditions (Braukmann 1994). Meriläinen & Hynynen found this particular species occurring in acidic lakes, but pointed out the importance of other environmental factors influencing their occurrence. The paucity of these slowly invading species in reservoirs may also be due to invasion barriers (V). As in Finnish reservoirs, species of *Chironomus* tend to be dominant in acidic lakes (Mossberg & Nyberg 1979). Poor oxygen conditions evidently favor the *Chironomus* dominance in reservoir profundals (Brundin 1956).

Rosenberg et al. (1984) attempted to show specific faunal characteristics of littoral communities of Holarctic reservoirs (impounded lakes included). No true reservoir species were found, but the dominance ranking of the macrozoobenthos can be drastically changed in reservoir conditions. In contrast, Prat (1980) succeeded in developing a modification of Brundin's (1956) profundal fauna typology adapted to Spanish reservoirs. Finnish reservoirs belong to the category of polyhumic waters, which, on the other hand, are difficult to classify typologically (Saether 1979, Johnson & Wiederholm 1989) and cannot be included in models created for clear-water conditions (see Palomäki 1994).

A special feature of profundal macrozoobenthic communities of reservoirs is the occurrence of the species which do not belong to the list of Brundin. For example, *Chironomus* sp. 16 (=*C.* sp. a in V, *C. esai*, sp.n. in Wülker, manuscr.) is very common in the profundal of reservoirs, but this species is also found in a natural lake in Central Finland (Wülker, manuscr.). Other difficulties which occur when attempting to use typological classifications are the common occurrence of littoral species in the profundal and the initially organic-rich bottom, which makes the Finnish reservoirs 'too eutrophic' when applying lake typology system.

The rich fauna of *Chironomus* is undoubtedly due to the large amount of specific habitats (water mosses) and conditions varying from lacustrine (soft sediments in deeper regions) to pool-like conditions (temporally flooded, organic rich littorals). By karyological analysis it was possible to identify a number of species, which otherwise would have remained as uncertain or genus-level determinations using traditional morphological characters (Webb & Scholl 1985).

The wide occurrence of coarse bottom types in deeper regions provide favorable food conditions for littoral species in deeper areas, and results in a peculiar bathymetric species-specific distribution patterns. Johnson & Wiederholm (1989) also stressed, that food availability is important for understanding the zoobenthic community structure of profundal regions. The coarse bottom type also serves as suitable attachment substrata, for e.g. *Spongilla* in Finnish reservoirs (Vogt 1978) .

A pronounced spring emergence peak was observed in Kyrkösjärvi reservoir. Wiederholm et al. (1977) also showed a similar emergence pattern for a shallow, small reservoir in northern Sweden. One reason for the seasonal emergence synchronization, is the tendency for the species to overwinter in their most resistant larval stage, which usually is the last one (Wiederholm et al. 1977). Wiggins et al. (1980, p. 181) pointed out that detritus-feeding species can utilize the food resources rich in pool conditions immediately after the winter, which favors the early emergence. Both of these ideas support the emergence pattern observed for Finnish reservoirs.

The coarse, 'three-dimensional' bottom quality and favorable food conditions seem to allow a freely living habit for some tube-building chironomid larvae (*Chironomus*, *Glyptotendipes*). Sediment development has been shown to influence the tube structure of *Chironomus plumosus* L. larvae (McLachlan & Cantrell 1976), but little is known of the tube-building behavior of this genus. Moss habitats in Finnish reservoirs show a rich and special fauna, a part of which can inhabit the decomposition layers below the greenish parts of the moss growths (e.g. *Stylodrilus*, several *Chironomus* species) (Wülker 1987, Koskenniemi 1989). This fauna might often be overlooked due to ineffective sampling methods and the difficulty to penetrate deep enough into the moss growths in sampling.

5.5 Fish

The species composition of the reservoirs resembles that of natural Finnish forest lakes and - similarly to results obtained from natural lakes - pike and perch were the most tolerant species to acidity (Rask & Tuunainen 1990, Rask et al. 1992).

The predatory and semi-predatory fish (pike, burbot, perch) switch more their diet to benthic macroinvertebrates in reservoirs compared to larger natural lakes (see Viljanen 1974). Diets are, however, rather similar to that of small forest lakes, evidently due to rich benthic food resources and lack of fish food in the most acidic reservoirs (Rask & Tuunainen 1990). In forest lakes perch is, however, forced to eat more zooplankton due to relatively low benthic food resources in summer (Nyberg 1979, Rask 1986).

Due to invasion barriers, bream is lacking in many reservoirs. As in many reservoirs, bream introductions have also been successfull in natural forest lakes (Rask et al. 1992). But the introduction of whitefish has not been so successfull as expected, because of the poor water quality and the extreme winter conditions. The future fisheries management activity should be concentrated to reservoirs with better environmental conditions, or alternatively attempts should be made to improve the reservoir conditions by e.g. decreasing the regulation regime. A well considered, long term planning is needed in each case to guarantee successfull results of management procedures.

6 CONCLUSIONS

1) Water level regulation, the terrestrial coarse bottom and polyhumic water quality combine to create a 'typical' Finnish reservoir, where very few dominating species characterize the structure of the various ecosystem levels. Freezing of the bottom, low pH and oxygen levels contrain community development, but may favor the mass occurrence of organisms tolerant to these conditions, such as water mosses and many chironomid species.

2) The descriptive models of ecological succession in reservoirs (Mordukhai-Boltovskoi 1961, Ekzertzev 1979, Krzyzanek et al. 1986) fit rather well for Finnish conditions, where the dominant species are, however, different. High dispersal ability and a rapid growth rate are attributes which favor species-specific colonization behaviors, but large-scale habitat changes may control the vegetation and zoobenthos development during the succession phase. The models of Odum (1969) and Connell & Slatyer (1977) help to better understand these processes. The development of biotic communities to that of a more stable state seems to take 5-10 years in Finnish reservoirs (VI, fig. 8), reflecting the deacceleration of processes changing environmental conditions. Interestingly, water mosses create a self-controlling habitat, evidently a very stable element in our conditions and a sign of the development of these areas to a terrestrial environment (see Kairesalo et al. 1992).

3) Despite quite marked changes, and differences in water level regime and bottom characteristics, the biota of Finnish reservoirs are quite similar to that of natural forest lakes. Reservoir macrozoobenthos shows, however, many specific features, being a mixture of species with different kinds of natural waters as source habitats. Finnish reservoirs may be scaled or ranked as intermediate waters between pools and lakes (V, VI). Many zoobenthic species, some of them newly described, reveal our poor knowledge of the biota, especially that of bog pool and wetland areas (Paasivirta et al. 1988). The very severe winter conditions during the draw-down can act as a 'guillotine' to the biota, hampering especially fisheries management of Finnish reservoirs.

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YHTEENVETO

Suomen polyhumoosisten tekojärvien ekologinen kehitys ja luonteenpiirteet

Tässä väitöskirjassa tutkittiin suomalaisten tekojärvien eliöyhteisöjen ja niiden elinympäristöjen kehitystä ja luonteenpiirteitä. Pohjan ominaisuuksia, veden laatua, syvännepohjaeläimistöä ja kalastoa kuvattiin ja vertailtiin yli kymmenessä tekojärvessä. Kehitystutkimukset suoritettiin keskitetysti Etelä-Pohjanmaan Kyrkösjärven tekojärvessä (pinta-ala 6.4 km^2 kesävedenpinnan tason mukaan, keskisyvyys 2.5 m) sen täyttövuodesta (1981) lähtien. Kyrkösjärvi on tyypillinen suomalainen tekojärvi, jonka ominaisuuksia ovat mataluus, metsien ja soiden suuri osuus allejääneillä pohja-alueilla, voimakas talviaikainen säännöstely, ruskeavetisyys, veden happamuus ja varsinkin talvisaikaan ilmenevät hapettomuusongelmat. Työssä keskityttiin erityisesti pohjaeläimistöön, minkä tutkiminen vaati tekojärvien erityisolojen vuoksi varsin paljon lisätyötä näytteenotossa ja aineiston määrityksessä.

Pääosa Suomen tekojärvistä on rakennettu 1960-luvulta lähtien Pohjanmaalle tulvansuojelu- ja voimatalouskäyttöön. Niiden kesänaikaisen vesipinnan taso pidetään varsin vakaana, mutta lopputalvella vesipintaa lasketaan voimakkaasti. Tämän seurauksena tavallisesti suurin osa tekojärvien vesivarastosta tyhjennetään ja laajat ranta-alueet jäävät laskeutuvan jääpeitteen alle. Mineraalipitoiset alueet jäätyvät tällöin helposti pintaosistaan, kun taas erityisesti suoalueiden pohjat pysyvät sulina pidättäen runsaasti vettä, joka on lopputalven säännöstelyn aikaan kuitenkin hapetonta. Aiemmilla metsämailla, joissa on ohut humuskerros, tekojärvien ranta-alueet kuluvat muutamassa vuodessa karuiksi mineraalimaiksi. Erityisesti, avoimet, suuret ulapat karuunnuttavat rantoja tehokkaasti voimakkaan aallokon vuoksi. Sensijaan loivasti veteen laskeutuvien suoalueiden rannat kestävät hyvin aallokon kuluttavaa vaikutusta. Kuitenkin pohja-aineksen hajotus ja uusien hienojakoisten pohjasedimenttien muodostuminen näyttää tapahtuvan tekojärvissämme hitaasti, ja vielä vuosikymmentenkin kuluttua voidaan laajoilla pohja-alueilla edelleen tunnistaa aiemman maakasvillisuuden jäänteet. Veden laadun vuodenaikaisvaihtelut ovat tekojärvissämme suuria, ja mitattujen suureiden (hapen pitoisuus, happamuus, kokonaisfosforipitoisuus, kokonaisväri) vuotuiset vaihtelut ovat tavallisesti huomattavasti suurempia kuin pitkäaikaisseurannassa havaitut keskimääräiset muutokset.

Tekojärvissämme kasvillisuus ja pohjaeläimistö kehittyy nopeasti ja alkuvaiheen kolonisaatiolajit ovat tyypillisesti nopealevintäisiä ja -kasvuisia. Kyrkösjärvessä rihmalevien ensimmäisen vuoden massaesiintymisen jälkeen, kasvillisuuden kehitys jatkui kahtena seuraavana vuonna kelluvien kasvien (pikkuvesitähti) voimakkaana esiintymisenä. Pohjaeläimistön kehitys oli ensimmäisen kesän aikana kaksivaiheinen, ja eläimistön massaesiintyminen saavutettiin loppukesällä, kun surviaissääsket ja vesisiira olivat valloittaneet tekojärven pohja-alueen. Pitkäaikaiskehityksessä (6-9 vuotta) eliöyhteisöjen muutokset olivat selviä, ja yhteisöjä luonnehti muutaman harvan lajin vallitsevuus tekojärveä kokonaisuutena tarkasteltaessa. Happamimmissa tekojärvissä (veden pH 5-5.5) havaittiin usein vesisammalten massaesiintyminen, ja pohjaeläimistön jotkut ryhmät (esimerkiksi kotilot ja simpukat) olivat niissä harvalukuisia. Ekosysteemin sukkessiota kuvailevat mallit soveltuvat varsin hyvin suomalaisiiin tekojärviin, ja sukkessioteoriat auttavat ymmärtämään tekojärviemme kehitystä.

Suomalaiset tekojärvet muistuttavat vesipinnan vaihtelun ja pohjan ominaisuuksien eroista huolimatta varsin paljon eliöyhteisöiltään omia metsäjärviämme. Kuitenkin tekojärvemme ovat esimerkiksi pohjaeläimistönsä perusteella järvien ja lammikkojen välimaastossa. Ankarat ympäristöolot, erityisesti talvisin, rajoittavat monien eliöryhmien esiintymistä. Tästä syystä varsinkin happamimmissa tekojärvissä kalastonhoitotoimet ovat hyvin rajoitettuja.

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V

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VI

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