Temporal variation in the wetland waterfowl communities of the Finnish lake district

Jukka Kauppinen

Kauppinen, J., Närevaara, FIN-77600 Suonenjoki, Finland
Present adress: Kuopio Museum of Natural History, Myhkyrinkatu 22, FIN-70100 Kuopio, Finland

Variation in the waterfowl community structures of wetland habitat types were studied in the northern part of the Finnish lake district during two decades (1970–1990). Mixotrophic and eutrophic lake types were identified on the basis of DCA ordinations of waterfowl assemblages. The community gradients of these lake types were distinguished also on an annual scale. The communities were found to be fairly stable across time. Total waterfowl densities fluctuated most (CV% 13–14), and the number of species (CV% 5–7) and species diversity (CV% 1–3) the least. The between-year component for total diversities was only 1–2% and the number of species 12–13%. The two lake types showed different dynamics of species populations. CV% of pair numbers of the three most abundant species were 12–29% in mixotrophic lakes and 30–36% in eutrophic ones. Gradients of community structure and long-term dynamics seem to be primarily connected with habitat, indicating that the lakes are in different phases of ecological succession.

1. Introduction

The structure and dynamics of bird communities may be affected by interspecific interactions and species-specific responses — e.g., morphology, physiology, behavior, habitat selection, dispersal and intraspecific interactions — to environmental features, such as climate, habitat, food, and area (Wiens 1989a, b; see also Fretwell 1972, Järvinen 1979, Cody 1985). Further more, the dynamics of communities may display long-term trends,often directional developments (ecological succession), and short-term or only stochastic fluctuations (e.g., Głowaciński 1981, Helle & Mönkkönen 1986, Wiens 1989b).

It is well-known that some waterfowl species are ecologically specialized with respect to the use of food and habitat (e.g., Szijj 1965, Sugden 1973, Lack 1974, Siegfried 1976, Eadie et al. 1979, Toft et al. 1982, Nudds 1982, Nudds & Bowlby 1984, Pöysä 1983, 1987, Kauppinen 1993a). This specialization could lead to the structuring of specific species assemblages of the lakes and lake types (see Kauppinen & Väisänen 1993). Certain environmental factors affecting community structure may remain fairly stable, such as lake size, while others can be seen to be slowly changing, such as lake depth and vegetation. On the other hand, temporal changes in breeding habitats can sometimes

be abrupt and extreme. Indeed, many North American studies have shown that populations and community structure may vary dramatically in certain unstable wetland habitats due to fluctuations in water level (e.g. Stoudt 1971, Stewart & Kantrud 1974, Boyd 1981, Nudds 1983, Burger 1985). Patterns of waterfowl community stability in North America may be related to emigration and immigration in response to variability of climatic conditions in the southern prairies (Bethke 1993).

Although, changes in the breeding waterfowl populations of European boreal lakes may be affected by weather conditions during the breeding, migratory and wintering season, as well as by hunting pressure (Kauppinen & Väänänen 1995, and references therein), little is yet known about the dynamics of entire waterfowl communities. Pöysä (1989) has studied geographical gradients in the stability of waterfowl communities in Finland and found that community stability decreased as one moved northward.

In a study describing ornithological lake types, Kauppinen and Väisänen (1993) examined the gradients of waterfowl community structure in boreal lakes and found that the gradients were explained by the quantity of emergent vegetation, and the size and depth of the lake. They classified wetlands into two types: shallow mixotrophic lakes surrounded by forests and boggy soils, and eutrophic lakes surrounded by arable land. The present study investigates more closely the waterfowl community patterns in these two different wetland types. It is assumed here that waterfowl communities of these wetland types differ from each other also on a temporal scale. Furthermore, it is assumed that waterfowl communities in the boreal wetlands of northern Europe are more stable than in variable conditions in North America. Habitat factors may primarily affect the main gradients of community structure, as well as the long-term dynamics of the community, but have relatively little effect on the short-term dynamics.

2. Material and methods

The data for this study of breeding waterfowl were collected in northern Savo, within the northern part of the Finnish lake district, in an area of about 20 000 km^2, comprising 32 lakes. Most of the lakes

(85%) were 20–400 ha, consisting of mixotrophic ($\bar{x}$ = 82.2 ha) and eutrophic lakes ($\bar{x}$ = 85.1 ha). Of these lakes, 26 lakes (22.4 km^2) were investigated once at the beginning of the 1970s (1972–75) yielding 651 breeding pairs and then again at the beginning of the 1980s (1983–85) providing 937 pairs. In addition, 11 lakes (10.5 km^2) had also been monitored yearly during the period between 1984 and 1993. The environmental parameters of these monitored lakes are presented in Table 1 (for measurements, see Kauppinen & Väisänen 1993).

Over half of the area of lakes was covered by emergent vegetation. These wetland habitats were created by the lowering of lake water levels. Lakes in this study were previously included in a study analysing ornithological lake types by Kauppinen and Väisänen (1993) and were divided into mixotrophic and eutrophic lake types. Mixotrophic lakes were very shallow, dys-eutrophic lakes characterized by shallow emergent vegetation (generally *Equisetum* and *Carex*) with shores surrounded by forests and bogs. Eutrophic lakes were surrounded by arable land; emergent vegetation was taller (*Phragmites*), and the lakes were situated on less acidic, fertile loamy clay soil near eskers. Mixotrophic lakes were shallower and more acidic than eutrophic ones and also had poorer water transparency (Table 1; for further information, see also Kauppinen & Väisänen 1993).

The waterfowl data consisted of the census results of all breeding waterfowl species (*Gaviiformes, Podicipediformes, Anseriformes* and the Coot *Fulica atra* in *Rallidae*). A census of all breeding waterfowl pairs was conducted twice during the breeding season using the census criteria of Kauppinen (1980, 1983) and field work as recommended by Kaup-

Table 1. Features of the lakes monitored (mixotrophic lakes, n = 5; eutrophic lakes, n = 6).

Parameter	Mixotrophic		Eutrophic	
	$\bar{x}$	SD	$\bar{x}$	SD
Area, ha	83.8	87.8	106.5	67.9
Vegetation coverage, %	55.6	22.5	51.0	23.9
Maximum depth, m	1.4	0.5	4.6	2.6
Transparency of water, m	0.6	0.1	1.4	0.6
Acidity, pH	5.8	0.6	6.8	0.8

pinen et al. (1991). The criteria for determining breeding pairs have been previously outlined in Kauppinen and Väisänen (1993). The data were collected by the author and supplemented by one other reseacher during the period between 1984 and 1993. Each lake census was conducted by the same person.

Waterfowl community structure was analysed with the detrended correspondence analysis (DCA) of Hill and Gauch (1980) as described by Kauppinen and Väisänen (1993). Scores for each community were calculated using the species-specific scores on the first two axes (the DCA1 and DCA2 scores of Kauppinen & Väisänen 1993) and the number of breeding pairs from each species. The DCA scores for species were calculated on a matrix of densities (pairs/km², overall surface area of the lake) of waterfowl species (see Kauppinen & Väisänen 1993). For example, taking a hypothetical community sample of only two species, three pairs of the Mallard *Anas platyrhynchos* and two of Teal *Anas crecca*, given frequencies 3/5 = 0.6 and 2/5 = 0.4. When a species-specific DCA1 is given 1.28 for Mallard and 1.33 for Teal, the score of the first axis for the community of this sample is DCA1 = 0.6 × 1.28 + 0.4 × 1.33 = 1.30. The first gradient (DCA1 axis) ordered the lakes from oligotrophic to eutrophic; the second axis (DCA2) ordered oligotrophic lakes as large and small lakes, and wetlands as mixotrophic and eutrophic lakes (Kauppinen & Väisänen 1993). Scores of communities in mixotrophic and eutrophic lake types were calculated using pooled data of lakes at each lake type: i) at the beginning of the 1970s, ii) at the beginning of the 1980s, iii) in each year during the period between 1984 and 1993.

The community parameters used included the number of species (S), density in pairs/km² (D), species diversity (H'), and evenness of species-abundance distribution (J' = H'/ln S). Community parameters between lake types during the period between 1984 and 1993 were tested with the Mann-Whitney U-test.

The between-year component for total diversity of the community was measured by DIVdiff: DIVdiff = H'Tot–H', where H'Tot = diversity in the whole period, and H' = average annual diversity (Järvinen & Väisänen 1976). The between-year component for the number of species (S) was calculated analogously.

Average species turnover, T, was measured as the arithmetic mean of T = (I + E)/(S1 + S2), where I and E represent the number of species which were observed between season 1 and 2 to have immigrated and disappeared, respectively; S1 and S2 are the total of species in the years 1 and 2, respectively (Järvinen 1979). T-values were calculated for successive years.

The stability of the community is expressed by coefficients of variation (CV%) for community parameters (see, e.g., Järvinen 1979, Noon et al. 1985). The following stability indices were used: coefficient of variation (CV%) for bird density (D), for number of species (S), for species diversity (H'), and for evenness (J'). Coefficients of variation for DCA scores (DCA1 and DCA2) were also used to indicate the stability of community structure.

3. Results

3.1. Structure and annual variation of waterfowl communities

Mixotrophic and eutrophic lake types were found to be composed of particular species assemblages, more distinct in the beginning of the 1980s than in the beginning of the 1970s (ordinations in Fig. 1). Annual examination of species assemblages also revealed clear community differences between these two lake types (Fig. 1). Mean community indices for 1984–93 are presented in Table 2. The lake types differed most with respect to the species assemblages, indicated by DCA1 and DCA2 scores, and evenness (Mann-Whitney U-test, P = 0.0001), followed by density and diversity (P < 0.005). Number of species did not differ significantly between lake types (P > 0.5). Among the 13 species observed in mixotrophic lakes, the six most abundant core species accounted for 83% of all pairs and were in declining order of importance: Tufted Duck *Aythya fuligula*, Teal, Wigeon *Anas penelope*, Mallard, Goldeneye *Bucephala clangula*, and Pintail *Anas acuta*. Six core species, among the 12 species observed in eutrophic lakes, accounted for 73% of all pairs: Teal, Coot, Tufted Duck, Great Crested Grebe *Podiceps cristatus*, Wigeon, and Mallard.

Community structure of the eutrophic lake type shows more "eutrophic characteristics" dominated by southern species than mixotrophic lakes, par-
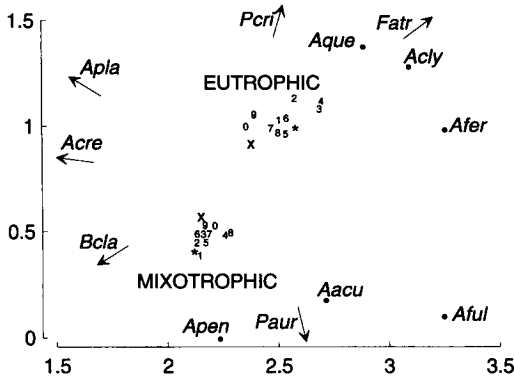
Fig. 1. DCA ordination for waterfowl communities in mixotrophic and eutrophic lake types. x denotes scores for waterfowl communities in the 1970s; * denotes scores for waterfowl communities in the 1980s. Numbers (0–9) indicate annual community scores for 1984–93 (e.g., 4 = year 1984,... 0 = year 1990, etc.). The locations of waterfowl species (acronyms of scientific names) on the DCA ordination are also illustrated (in details, see methods). Arrows describe species scores located outside the scale of figure.

could be detected in any of the community parameters. At that time the total waterfowl populations fluctuated rather greatly (see Kauppinen & Väänänen 1995). In general, density fluctuated the most, and the number of species and especially the diversity showed only slight fluctuations (Table 2). The between-year component (%) for total diversities of both lake types was only 1–2%, and for number of species 12–13%. The average species turnover (T) was low, 0.02 (variation 0–0.04) in the mixotrophic lake type and 0.04 (0–0.08) in the eutrophic lake type. The number of species varied from 11 to 13 in the mixotrophic and from 11 to 12 in the eutrophic lake type.

3.2. Annual variation of waterfowl populations

The abundances and population variations of species in both lake types are presented in Table 3. These species are divided into three groups according to habitat distribution (Kauppinen 1993a; see also species relations in Fig. 1). Typical species of eutrophic lakes with southern distribution accounted for 41.7% of total pairs in eutrophic lakes and 14.2% in mixotrophic lakes.

Coefficients of variation indicating pair fluctuations of species have earlier been shown to be dependent on sample size and the density of species (e.g., Svensson 1978, Helle & Mönkkönen 1986, Solonen 1986). In my data, the densities of the most abundant species were generally of the same order of magnitude in the two different lake types, and populations of many abundant species were found to fluctuate considerably (Table 3). In eutrophic lakes, the CV% (D) of species

ticularly in the 1980s and 1990s, indicated also by scores of DCA in communities of lake types (Fig. 1). In the yearly data from 1984 to 1993, two typical species — Coot and Great Crested Grebe — accounted for over 25% of all pairs, with the proportion of these species in mixotrophic lakes totalling only 4.5%.

During the ten-year period (1984–93), mixotrophic lakes showed a decreasing trend in the number of species (Spearman rank correlation, $r_s = -0.70$, $P < 0.05$) and an increase in evenness ($r_s = 0.62$, $P < 0.1$); whereas, in eutrophic lakes no consistent trends

Table 2. Parameters (means of years) of the waterfowl communities in mixotrophic and eutrophic lake types for 1984–93. $\bar{x}$, SD, and coefficients of variation (CV%) are given for each parameter.

	Mixotrophic lake type			Eutrophic lake type		
	$\bar{x}$	SD	CV %	$\bar{x}$	SD	CV %
Density, pairs/km^2	42.4	5.58	13.2	55.6	7.56	13.6
Number of species	12.3	0.82	6.7	11.5	0.53	4.6
Diversity (H')	2.13	0.06	2.9	2.26	0.03	1.3
Evenness (J')	0.85	0.03	3.5	0.92	0.02	2.2
DCA1-score	2.17	0.06	2.8	2.51	0.12	4.7
DCA2-score	0.48	0.04	8.3	1.01	0.06	5.9

showed no correlation with the number of pairs (Spearman rank correlation, $r_s = -0.05$). Among the abundant species, Coot and Tufted Duck were the most unstable. In mixotrophic lakes, the CV% (D) of species correlated negatively with the number of pairs ($r_s = -0.63$, $P > 0.05$). Species that were few in numbers were less stable and consisted typically of southern species, where as abundant species were stable and consisted of generalists. Both irregularly breeding species and those species of very low population densities, i.e., the Slavonian Grebe *Podiceps auritus* and the Whooper Swan *Cygnus cygnus*, were omitted from analysis in both lake types, as well as the Coot in mixotrophic lakes.

In mixotrophic lakes, the coefficients of variation of the three most abundant species (Tufted Duck, Teal, and Wigeon) were 12–29%.In eutrophic lakes, the coefficients of the three most abundant species (Teal, Coot, and Tufted Duck) were 30–36%. The densities of all these species were at least 4 pairs/km², with dominancies exceeding 10%. Generalists and typical species of mixotrophic lakes (see Table 3) had more stability in mixotrophic lakes than in eutrophic ones.

4. Discussion

4.1. Structure and stability of communities in different wetland types

The ornithological lake types concerned clearly reflected specific species assemblages. Eutrophic lakes included abundantsouthern species, such as the Great Crested Grebe and the Coot. The abundant species observed in mixotrophic lakes consisted mainly of generalists and of typical boreal species, such as the Wigeon and the Goldeneye. In addition to species assemblages, the lake types differed also in the most community parameters.

The number of species found in communities, and especially the diversity, was more stable than the density, as has earlier been reported in other Finnish waterfowl communities studied by Pöysä (1984, 1989) and in most land bird communities (e.g., Järvinen & Väisänen 1976, Järvinen 1979, Głowaciński 1981, Noon et al. 1985, Helle & Mönkkönen 1986). The communities in my study area were fairly stable also with respect to densities (CV% 13.2 and 13.6). The corresponding values

Table 3. Waterfowl populations (range, mean, dominance-%, and coefficient of variation, CV%) of the lakes monitored between 1984 and 1993.

Species group/ species	Pairs in mixotrophic lakes				Pairs in eutrophic lakes			
	range	mean	dom.	CV%	range	mean	dom.	CV%
1. Generalists								
Anas crecca	25–40	32.4	18.2	20.6	41–98	62.4	17.6	29.5
A.platyrhynchos	15–25	18.0	10.1	19.6	18–37	30.3	8.5	22.6
Bucephala clangula	12–22	16.1	9.0	17.4	10–24	16.1	4.5	31.7
2. Typical species of mixotrophic lakes								
Podiceps auritus	1–5	2.1	1.2		0–1	0.3	0.1	
Cygnus cygnus	2–4	2.7	1.5		0–1	0.1		
Anas penelope	22–37	30.2	17.0	12.5	18–43	31.5	8.9	22.9
A.acuta	5–10	8.9	5.0	25.6	15–40	26.7	7.5	32.4
Aythya fuligula	23–58	42.4	23.8	28.8	24–62	39.9	11.2	32.8
3. Typical species of eutrophic lakes								
Podiceps cristatus	5–10	7.3	4.1	23.3	33–48	38.4	10.9	13.8
Anas querquedula	2–7	3.9	2.2	44.3	8–19	13.2	3.7	29.4
A.clypeata	4–9	6.0	3.4	27.2	20–36	29.4	8.3	17.9
Aythya ferina	3–10	7.3	4.1	29.6	7–16	11.5	3.2	29.0
Fulica atra	0–2		0.4		34–85	55.5	15.6	35.8

observed earlier were 17.2 for southern Finnish wetland waterfowl communities, and 36.2 for northern one (Pöysä 1989).

Waterfowl communities of eutrophic lakes may be generally more dynamic than those of mixotrophic. Populations of some core species,such as Coot with southern distribution, are not as well established as the basic "boreal" species in mixotrophic lakes. Furthermore, Pintail, Goldeneye and Tufted Duck, i.e. species with more or less boreal distribution, were almost equally unstable in eutrophic lakes. In general, higher annual fluctuations in bird populations are more likely to be found in sub-optimal or marginal habitats than in the most favourable or most "suitable" ones (e.g. Svärdson 1949, Fretwell & Lucas 1970, v. Haartman 1971). Communities of the shallow mixotrophic lakes surrounded by forested and bog shores are mainly composed of species with northern distribution favouring shallow open vegetation with sedge and horsetail stands (Kauppinen 1993a). This habitat may be optimal for these boreal species with stable populations.

Species assemblages of the two lake types concerned seem to include different species components with respect to habitat distribution, biogeography and population dynamics of species (see also Kauppinen 1993). According to the stability hypothesis of Järvinen (1979), the productivity of the habitat and environmental (climatic) unpredictability may be important causes for geographical differences in land bird community stability in northern Europe. The specific structure and long-term trends of communities in the lake types in this study area may be primarily connected with the habitat, whereas short-term dynamics may be affected more by non-habitat factors (Kauppinen & Väänänen 1995). The wetland areas in this study were created by the lowering of the water level in the nineteenth century and the first half of the twentieth century. The lakes appear to represent different phases in the ecological succession of water bodies and the development of vegetation. Eutrophic lakes surrounded by arable land are deeper and less dystrophic than mixotrophic ones (Kauppinen & Väisänen 1993, see also Table 1). They are characterized by taller vegetation (reed stands). Farming has increased their eutrophication. Community development follows the succession trend of *Phragmites*-lakes as illustrated by Kauppinen and Väisänen

(1993); in the eutrophic phase, the proportion of southern species (e.g., Great Crested Grebe and Coot) may rise considerably.

In general, the physical environment determines the pattern and the rate of change in ecological succession (e.g., Odum 1969). In North America, breeding waterfowl communities are characteristically unstable. Annual changes in populations are dramatic and may be caused mainly by alterations in habitat, due to variation in precipitation (e.g., Stoudt 1971, Stewart & Kantrud 1974, Trauger & Stoudt 1978, Boyd 1981, Leitch & Kaminski 1985). Also, geographical patterns of stability in communities may be connected with regional environmental conditions (Bethke 1993). In contrast, the communities are rather stable in the boreal lakes of northern Europe (this study, Nordic data analysed by the author (unpublished); see also Pöysä 1989). Changes in waterfowl communities are slow in the terminal phases of lake succession, especially in mixotrophic lakes. The periodicity of visible changes in succession may often occur on a scale of decades or even centuries. Many waterfowl species may also show flexibility in their habitat use (Kauppinen 1993a and references therein), indicating that changes in habitat may not always be immediately reflected in the community structure.

4.2. General population trends in community dynamics

The waterfowl communities represent different stages of postglacial succession of lakes. The basic species assemblages of waterfowl communities in Finnish inland wetlands has, however, developed over the course of a century. It was accelerated by the lowering of the lake water levels, the eutrophication of waters, and expansion of certain species (e.g., Great Crested Grebe, Pochard, Coot). All the present wetland species, except the Whooper Swan, were already to be found in the Finnish inland lake district in the 1930s (old local ornithological publications, see Kauppinen 1993b). Total waterfowl populations in Finnish wetlands have, in the long-term, increased (e.g., Lehikoinen 1977, Helminen & Eriksson 1978, Siira & Eskelinen 1983, Helminen & Walls 1984, Pöysä 1984). The population increase of many species may be due to an expansion in distribution and population pressures.

Most southern and southeastern wetland species have increased and expanded their distribution in central and northern Europe during this century (e.g., Kalela 1946, Onno 1965, Yarker & Atkinson-Willes 1971, v. Haartman 1973).

Southern or southeastern wetland species, such as the Slavonian Grebe, Garganey, Pochard, and the Coot represent populations which have decreased or undergone great fluctuations in recent times, either in my study area or more widely in northern Europe. My study area corresponds to the northernmost edge of their distribution. Population pressure and the expansion of these species from the centre of their distribution area may decrease or periodically fluctuate.

5. Concluding remarks

Although, the species assemblages of two lake types concerned fluctuated to some extent, recent community structures of these lake types have, however, remained very typical; the ornithological wetland types presented by Kauppinen and Väisänen (1993) also remained valid on a temporal scale.

The spatial scale is, however, crucial considering the annual variations in the communities (e.g., Wiens 1981, 1989b). Communities may be more stable regionally than locally with random "noise". An individual lake is, in spite of the local small sampling plot, a relevant unit with natural borders reflecting its own specific habitat factors and intracommunity relations. But, are the communities of separate lakes hardly distinguishable from each other on the basis of species assemblages? A preliminary analysis of recent community dynamics (1982–93) in some of the lakes in this study (Fig. 2) shows that each lake has a fairly specific waterfowl community structure almost without overlaps in ordinations. The species assemblage of each lake on a temporal scale fluctuated only to such an extent which would enable us to identify the communities of these lakes individually. The community structure of single, small lakes fluctuates, however, with a wider amplitude than communities on a regional scale (Kauppinen unpubl.).

Acknowledgements. I am grateful to Veli-Matti Väänänen for providing his census data for many eutrophic lakes.
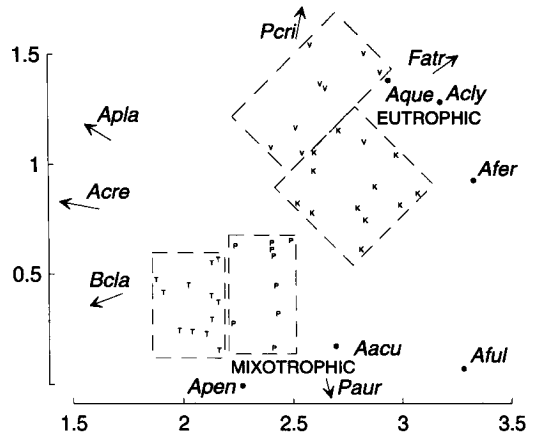

Fig. 2. DCA ordination for waterfowl communities in four lakes during 1982–93. T = Lake Tuomiojärvi (area 226 ha), P = Lake Pitkäjärvi (34 ha), K = Lake Keskimmäinen (58 ha), V = Lake Valkeinen (77 ha). Locations of waterfowl species (acronyms of scientific names) on the DCA ordination are also illustrated (in details, see methods). Arrows describe species scores located outside the scale of figure.

Selostus: **Runsaskasvustoisten järvien vesilintuyhteisöt ja niiden vaihtelut**

Vesilintuyhteisöjen rakennetta ja dynamiikkaa tutkittiin Pohjois-Savon matalilla ja runsaskasvustoisilla järvillä 1970–90-luvuilla. Kahden kosteikkotyypin, metsä- ja suorantaisten miksotrofisten (dyseutrofisten) järvien sekä viljelyseutujen eutrofisten järvien, vesilintuyhteisöjen rakenne erosi toisistaan DCA-ordinaatio-analyysissä. Miksotrofisia järviä luonnehtivat runsaat generalistit sekä boreaalisten järvien tyyppilajit, kuten haapana ja telkkä. Eutrofisilla järvillä eteläisen lajistoaineksen — mm. nokikana ja silkkiuikku — osuus kokonaisparimäärästäoli huomattava. Ajallisessa mittakaavassa tutkittujen järvityyppien vesilinnustot erosivat toisistaan linnuston koostumuksen lisäksi mm. tiheydeltään ja diversiteetiltään.

Järvityyppien yhteisöt olivat ajallisesti melko vakaita. Eniten vaihteli vesilinnuston kokonaistiheys (CV% 13–14), vähiten vaihtelivat lajimäärä (CV% 5–7) ja diversiteetti (CV% 1–3).

Eutrofisilla järvillä yhteisöt lienevät yleensä dynaamisempia kuin miksotrofisilla järvillä. Monilla eutrofisten järvien lajeilla, kuten eteläisellä nokikanalla, populaatiot eivät ole niin vakaita kuin miksotrofisten järvien peruslajeilla. Kolmen runsaimman lajin parimäärien vaihtelukertoimet (CV%) olivat miksotrofisilla järvillä 12–29 ja eutrofisilla järvillä 30–36.

Yhteisörakenteen erot ja pitkäaikaisdynamiikka lienevät ensisijaisesti habitaatin säätelemiä. Miksotrofiset järvet ovat matalampia, happamampia ja ruskeavetisempiä kuin eutrofiset järvet; niiden suurkasvillisuus on matalaa korteikkoa ja saraikkoa — eutrofisilla järvillä on myös ruokokasvustoja. Yhteisörakenne heijastelee järvien ekologisen sukkession eri vaiheita.

References

Bethke, R. W. 1993: Geographical patterns of persistence in duck guilds. — Oecologia 93: 102–108.

Boyd, H. 1981: Prairie dabbling ducks, 1941–1990. — Can. Wildl. Serv. Prog. Notes 119: 1–9.

Burger, J. 1985: Habitat selection in temperate marsh-nesting birds. — In: Cody, M. L. (ed.), Habitat selection in birds. Academic Press, Orlando, pp. 253–281.

Cody, M. L. 1985: An introduction to habitat selection in birds. — In: Cody, M. L. (ed.), Habitat selection in birds. Academic Press, Orlando, pp. 3–58.

Eadie, J. McA., Nudds, T. D. & Ankney, C. D. 1979: Quantifying interspecific variation in foraging bahaviour of syntopic Anas (Anatidae). — Can. J. Zool. 57: 412–415.

Fretwell, S. D. 1972: Populations in a seasonal environment. — Princeton Univ. Press, Princeton.

Fretwell, S. D. & Lucas, H. L. 1970: On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. — Acta Biotheor. 19: 16–36.

Głovaciński, Z. 1981: Stability in bird communities during the secondary succession of a forest ecosystem. — Ekol. Polska 29: 73–95.

Haartman, L. von 1971: Population dynamics. — In: Farner, D. S. & King, J. R. (eds.), Avian biology 1. — Academic Press, New York, pp. 391–459.

— 1973: Changes in the breeding bird fauna of North Europe. — In: Farner, D. S. (ed.), Breeding biology of birds, pp. 448–481.

Helle, P. & Mönkkönen, M. 1986: Annual fluctuations of land bird communities in different successional stages of boreal forest. — Ann. Zool. Fennici 23: 269–280.

Helminen, O. & Eriksson, J. 1978: Changes in the bird fauna of lakes on Åland during 50 years. — Ornis Fennica 55: 110–119 (in Swedish with English summary).

Helminen, O. & Walls, S. 1984: Changes in the bird fauna of lakes in the surroundings of Karis, S. Finland, during 40 years. — Lintumies 19: 94–101 (in Swedish with English summary).

Hill, M. O. & Gauch, H. G., Jr. 1980: Detrended correspondence analysis: an improved ordination technique. — Vegetatio 42: 47–58.

Järvinen, O. 1979: Geographical gradients of stability in European land bird communities. — Oecologia (Berl.) 38: 51–69.

Järvinen, O. & Väisänen, R. A. 1976: Between-year component of diversity in communities of breeding land birds. — Oikos 27: 34–39.

Kalela, O. 1946: Zur Ausbreitungsgeschichte der Vogel vegetationsreicher Seen. — Ann. Acad. Sci. Fenn., Ser. A, IV. Biol. 12: 1–81.

Kauppinen, J. 1980: Sources of error in estimation methods of breeding waterfowl populations. — Lintumies 15: 74–82 (in Finnish with English summary).

— 1983: Methods used in the census of breeding ducks in northern Savo (Finland) at the beginning of the breeding season. — Finnish Game Res. 40: 49–81.

— 1993a: Densities and habitat distribution of breeding waterfowl in boreal lakes in Finland. — Finnish Game Res. 48: 24–45.

— 1993b: Keskimmäinen. Riistaveden lintujärvien linnusto ja sen kehitys. — Manuscript (in Finnish).

Kauppinen, J., Koskimies, P. & Väisänen, R. A. 1991: Waterfowl round count. In: Koskimies, P. & Väisänen, R. A., Monitoring bird populations. — Zoological Museum, Finnish Museum of Natural History, Helsinki, pp. 45–53.

Kauppinen, J. & Väisänen, R. A. 1993: Ordination and classification of waterfowl communities in south boreal lakes. — Finnish Game Res. 48: 3–23.

Kauppinen, J.& Väänänen, V.-M. 1995: Factors affecting changes of waterfowl populations in the eutrophic wetlands in the Finnish lake district. — Manuscript.

Lack, D. 1974: Evolution illustrated by waterfowl. — Blackwell, Oxford.

Lehikoinen, E. 1977: Kokemäenjoen Puurijärven kasvillisuus ja linnusto. — Vesihallitus, Tiedotus 127. Helsinki (in Finnish with English summary).

Leitch, W. G. & Kaminski, R. M. 1985: Long-term wetland-waterfowl trends in Saskatchewan grassland. — J. Wildl. Manage. 49: 212–222.

Noon, B. R., Dawson, D. K. & Kelly, J. P. 1985: A search for stability gradients in North American breeding bird communities. — Auk 102: 64–81.

Nudds, T. D. 1982: Ecological separation of grebes and coots: interference competition or microhabitat selection? — Wilson Bull. 94: 505–514.

— 1983: Niche dynamics and organization of waterfowl

guilds in variable environments. — Ecology 64: 319–330.

Nudds, T. D. & Bowlby, J. N. 1984: Predator-prey size relations in North American dabbling ducks. — Can. J. Zool. 62: 2002–2008.

Odum, E. P. 1969: The strategy of ecosystem development. — Science 164: 262–270.

Onno, S. 1965: The numbers of waterfowl in Estonia. — Wildl. Trust Ann. Rep. 16: 110–114.

Pöysä, H. 1983: Resource utilization pattern and guild structure in a waterfowl community. — Oikos 40: 295–307.

— 1984: Temporal and spatial dynamics of waterfowl populatons in a wetland area — a community ecological approach. — Ornis Fennica 61: 99–108.

— 1987: Ecology of foraging behaviour in dabbling ducks *Anas* spp. — Univ. Joensuu Publ. Sci. 10: 1–19.

— 1989: Geographical gradients in the stability of waterfowl communities in Finland. — Suomen Riista 35: 7–16 (in Finnish with English summary).

Siegfried, W. R. 1976: Segregation in feeding behaviour of four diving ducks in southern Manitoba. — Can. J. Zool. 54: 730–736.

Siira, J. & Eskelinen, O. 1983: Changes in the abundance of breeding waterfowl in the Liminka bay in 1954–81. — Finnish Game Res. 40: 105–121.

Solonen, T. 1986: Stability of a bird community in southern Finland. — Ornis Scand. 17: 106–116.

Stewart, R. E. & Kantrud, H. A. 1974: Breeding waterfowl populations in the prairie pothole region of north Dakota. — Condor 76: 70–79.

Stoudt, J. H. 1971: Ecological factors affecting waterfowl production in the Saskatchewan parklands. — U. S. Fish Wildl. Serv. Resource Publ. 99: 1–58.

Svensson, S. E. 1978: Efficiency of two methods for monitoring bird population levels: Breeding bird censuses contra counts of migrating birds. — Oikos 30: 373–386.

Svärdson, G. 1949: Competition and habitat selection in birds. — Oikos 1: 157–174.

Sugden, L. G. 1973: Feeding ecology of pintail, gadwall, american wigeon and lesser scaup ducklings. — Can. Wildl. Serv. Rep. Ser. 24: 1–43.

Szijj, J. 1965: Ökologische Untersuchungen an Entenvögeln (Anatidae) des Ermatinger Beckens (Bodensee) — Vogelwarte 23: 24–71.

Toft, C. A., Trauger, D. L. & Murphy, H. W. 1982: Tests for species interactions: breeding phenology and habitat use in subarctic ducks. — Am. Nat. 120: 586–613.

Trauger, D. L. & Stoudt, J. H. 1978: Trends in waterfowl populations and habitats on study areas in Canadian parklands. — Trans. North Am. Wildl. Nat. Resour. Conf. 43: 187–205.

Wiens, J. A. 1981: Scale problems in avian censusing. — Stud. Avian Biol. 6: 513–521.

— 1989a: The ecology of bird communities. Vol. 1. — Cambridge University Press, Cambridge.

— 1989b: The ecology of bird communities. Vol. 2. — Cambridge University Press, Cambridge.

Yarker, B. & Atkinson-Willes, G. L. 1971: The numerical distribution of some British breeding ducks. — Wildfowl 22: 63–70.