Ann. Zool. Fennici 31:397–404
Helsinki 21 December 1994
ISSN 0003-455X

Acidification and ecological interactions at higher trophic levels in small forest lakes: the perch and the common goldeneye

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Received 5 July 1994, accepted 8 September 1994

The disappearance of acid sensitive fish species that usually are the most important top predators in freshwater ecosystems is an important ecological consequence of lake acidification. This may have beneficial consequences for insectivorous waterbirds that may compete for food with fish. We studied the response of common goldeneye (*Bucephala clangula*) pairs and broods to pH, perch (*Perca fluviatilis*) density and invertebrate abundance in small forest lakes in southern Finland. Neither the density of breeding pairs nor that of broods showed an overall trend with lake acidity but both of them increased with invertebrate abundance. Among three lakes studied in more detail for several years both pair density and brood density were highest in the lake with lowest pH and perch density and highest invertebrate abundance. Goldeneye brood density, but not pair density, increased after a sudden perch death in an experimental lake. Our results indicate that both breeding pairs and broods of goldeneyes may benefit of acidity-induced release in food competition after the disappearance of fish competitors.

1. Introduction

Acidification of lakes modifies the structure and function of freshwater ecosystems in many direct and indirect ways (for a recent review, see Appelberg et al. 1993). An important ecological consequence of acidification is the loss of acid sensitive fishes that usually are the most important top predators in freshwater ecosystems (e.g. McNicol et al. 1987a, Blancher et al. 1992, Rask 1992). Disappearance of fish is often coupled with an increase of the abundance of macroinvertebrates previously regulated by fish predation (Eriksson et al. 1980, Bendell 1986, Bendell & McNicol 1987). These changes may have twofold consequences for waterbirds:

piscivorous birds suffer from the disappearance of fish but, on the other hand, insectivorous birds may benefit of the increased availability of macroinvertebrates as food.

Fish-waterbird interactions induced by lake acidity have been studied extensively in Canada and Sweden (reviews in Eriksson 1984, Blancher & McAuley 1987, McNicol et al. 1987b). One of the most intensively studied interaction is that between fish and the common goldeneye, *Bucephala clangula*. Basis for this was provided by Eriksson (1979) and Eadie & Keast (1982) who examined competitive interactions between fish (especially the perch, *Perca fluviatilis*, and the yellow perch, *P. flavescens*) and goldeneyes. The perch is quite tolerant to acidification, but at pH levels 5.0–4.5 the populations decrease. Usually the reason is impaired reproduction but sometimes increased adult mortality also takes place due to acid-aluminium stress (Rask 1984, 1992). Due to high diet overlap food competition between the perch and common goldeneye may exist (Eadie & Keast 1982; see also Table 1). Both Eriksson (1979) and Eadie & Keast (1982) concluded that food competition by fish affects habitat use of common goldeneyes. Based on this conclusion recent studies demonstrating a positive association between lake acidity and lake preference by common goldeneyes have considered the acidity-mediated release in food competition as one explanation for the association (DesGranges & Darveau 1985, McNicol et al. 1987a, Blancher et al. 1992, McNicol & Wayland 1992, Mallory et al. 1993, Pöysä & Virtanen 1994).

Earlier studies have rather promisingly indicated that acidification of lakes may affect goldeneyes positively by reducing or eliminating food competition by fish. However, the evidence is very sporadic because earlier studies have analysed only some of the important elements of the complex interaction network pH-fish density-invertebrate abundance-goldeneye density. All the important elements of the network have not been considered in one study (but see McNicol & Wayland 1992). Moreover, from the goldeneye's point of view the effects of acidification on the reproductive success, of course, are of primary importance and, thus, we consider it important to study simultaneously the response of both breeding pairs and broods to lake acidity, fish density and invertebrate abundance. This is especially because goldeneye females frequently use different lakes for nesting and brood rearing (Eriksson 1978, Pöysä & Virtanen 1994).

In this paper we take a more comprehensive approach by answering the following questions: 1) Is there an overall increase in goldeneye pair and brood density with increasing lake acidity? 2) Does goldeneye pair and brood density increase with decreasing perch density and increasing invertebrate abundance? 3) Does the use of a lake by breeding individuals and broods of goldeneyes increase after elimination of the perch?

2. Study area

The study area is a barren forested watershed (Evo State Forest) in southern Finland (61°10′N, 25°05′E) and contains 53 small lakes and ponds (from 0.1 to 49.5 ha). The shore types of the lakes vary from oligotrophic bog and forest without emergent plants to more eutrophic ones with relatively lush stands of *Equisetum* and *Typha* (Nummi & Pöysä 1993). In a representative sample of 22 lakes the pH varied from 4.3 to 6.7 (measurements are from surface water (0.5 m) samples taken through the ice in late March 1989–91; Rask et al., unpublished). More specific information of the trophic status of lakes in the area is given by Arvola et al. (1990).

3. Material and methods

3.1. Perch populations

The population density of perch was estimated by marking and recapturing in three lakes each at different stage of acidification: Lake Vähä Valkjärvi (2.2 ha, pH 4.3), L. Iso Valkjärvi (3.9 ha, pH 5.4 in 1990) and L. Iso Mustajärvi (2.7 ha, pH 6.3). The density of perch > 8.5 cm (total length) was 148 fish/ha in L. Vähä Valkjärvi and 1432/ha in L. Iso Mustajärvi in spring 1986 (Lappalainen et al. 1988). In L. Iso Valkjärvi the marking and recapturing of perch in 1990 gave a density estimate of 2900/ha (Rask et al., unpublished).

L. Vähä Valkjärvi experienced a rapid acidification due to air pollutants during the 1980's.

The perch population of the lake has been monitored regularly and its density has decreased recently to levels of < 50 fish/ha (Rask 1992).

In L. Iso Valkjärvi, which is less acidified than the neighbouring L. Vähä Valkjärvi, a liming experiment was started in 1991. The lake was divided in two parts of equal size with a plastic curtain. One side of the lake was neutralized and the other served as a control (Rask 1991). The size of perch population has been measured since then from both sides of the lake. The density of perch was at levels 1700–2200 in both sides of the lake in 1991 and 1992. During the autumn turnover of 1992 almost all the fish in the control side of the lake died suddenly. The density of perch in spring was not more than 50/ha whereas in the limed side the perch density was 1850/ha at the same time (Rask et al., unpublished).

3.2. Invertebrates

Aquatic invertebrates were sampled in 12 lakes in 1989–92 using methods described in detail in Nummi & Pöysä (1993, 1995). In brief, free-swimming invertebrates were trapped with an activity trap, a four liter glass jar equipped with a white plastic funnel with openings of 140 mm at the large end and 20 mm at the narrow end. Activity traps were suspended horizontally in the water column 20–40 cm from the surface at a water depth of 50–100 cm deep close to the shore line. Four activity traps were used per lake and trapping was continuous over the breeding season from the late May to late July each year. The length of trapping periods varied somewhat between years but all trapping procedures were identical between lakes in each year.

The traps were usually emptied at weekly intervals. Animals in catches were identified and their size was assigned following the taxon list and six length categories given by Nudds & Bowlby (1984, table 2). For calculations of the invertebrate abundance index, the number of individuals within each taxon was multiplied by the mean size of its length category. The abundance index of free-swimming invertebrates is given per 100 trap days (see also Nummi & Pöysä 1993, 1995). The taxon composition of activity trap catches corresponds reasonably well with the diet of goldeneyes and perch (Table 1).

3.3. Goldeneye

Goldeneye data are from the breeding seasons 1989–93. Since 1989 we have made routine censuses of breeding pairs (two censuses in May each year) and broods (six censuses in June–August each year) in all lakes using the standard point count and round count methods (Nummi & Pöysä 1993, 1995; for census methods and the interpretation of observations as pair numbers see Koskimies & Väisänen 1991). Censuses were made every second week between early May and mid August each year.

Table 1. The percentage of individuals of different invertebrate taxa in activity trap catches (pooled data from 12 lakes and 4 years) and the occurrence of invertebrate taxa in the diet of goldeneye adults and downy ducklings and perch. Invertebrate taxon list corresponds to Nudds & Bowlby (1984, table 2) completed with Notonectidae, Sialidae, Aranea and Turbellaria. The occurrence of different prey taxon in the diet of goldeneyes and perch are according to the following sources: goldeneye adults, Cramp & Simmons (1977); goldeneye ducklings, Eriksson (1976), Cramp & Simmons (1977); perch, Rask (1983, 1984, 1986), Rask & Arvola (1985).

Taxon	Activity traps (%)	Goldeneye Adults	Goldeneye Ducklings	Perch
Cladocera	26.9			x
Hydracarina	19.5	x	x	
Dytiscidae	13.0	x	x	
Corixidae	9.0	x	x	x
Oligochaeta	8.4			
Chironomidae	4.8	x	x	x
Ephemeroptera	4.6	x	x	x
Copepoda	3.0			
Odonata	2.9	x	x	x
Trichoptera	2.3	x	x	x
Isopoda	1.4	x	x	x
Gastropoda	1.0	x		
Notonectidae	0.8		x	x
Coleoptera	0.6	x	x	x
Diptera (other than Chironomidae)	0.4		x	x
Ceratopogonidae	0.4			
Valvatidae	0.3	x		
Lepidoptera	0.1			
Turbellaria	0.1			
Hirudinae	0.1			x
Hemiptera	0.1			
Pelecypoda	0.1			
Aranea	0.03	x		x
Sialidae	0.01	x		x

After the division of the L. Iso Valkjärvi in spring 1991 (see above) the occurrence of breeding individuals (May observations) and broods was recorded for both lake sides during each census. Additional observations from extra visits (invertebrate sampling, etc.) to the lake were coded similarly and included in the analyses. If the lake was visited more than once per day only one observation per day was included.

4. Results

4.1. Overall relationship between goldeneye density and pH

Neither the density of breeding pairs nor that of broods showed an overall increase with increasing lake acidity: average (1989–93; L. Iso Valkjärvi excluded) pair density vs. lake pH, Kendall's rank correlation $\tau = -0.249$, 1-tailed $P = 0.074$, $N = 22$; average brood density vs. pH, $\tau = -0.099$, 1-tailed $P = 0.422$, $N = 22$. Variation in lake size and habitat structure did not affect these correlations because goldeneye densities did not correlate with lake size (pair density vs. the length of shore line, $\tau = -0.135$, $P = 0.351$, $N = 22$; brood density vs. the length of shore line, $\tau = 0.049$, $P = 0.713$, $N = 22$) nor with lakes' position on a principal component axis describing the luxuriance of shore vegetation (habitat scores from Nummi & Pöysä 1993; pair density vs. habitat score, $\tau = 0.306$, $P = 0.069$, $N = 22$; brood density vs. habitat score, $\tau = 0.107$, $P = 0.419$, $N = 22$).

4.2. Goldeneye density, perch density and invertebrate abundance

In general, goldeneye pair density ($\tau = 0.769$, $P = 0.021$, $N = 12$) and brood density ($\tau = 0.851$, $P = 0.010$, $N = 12$) increased with invertebrate abundance (Fig. 1).

The three lakes studied in more detail differed drastically in pH, perch density and invertebrate abundance (see Fig. 2). These differences were reflected in goldeneye densities so that both pair density (Kruskal-Wallis test, $H = 8.65$, $P = 0.013$) and brood density ($H = 9.26$, $P = 0.010$) were highest in the lake with lowest pH and perch density and highest invertebrate abundance (Fig. 2). This result was consistent in all the four years studied.

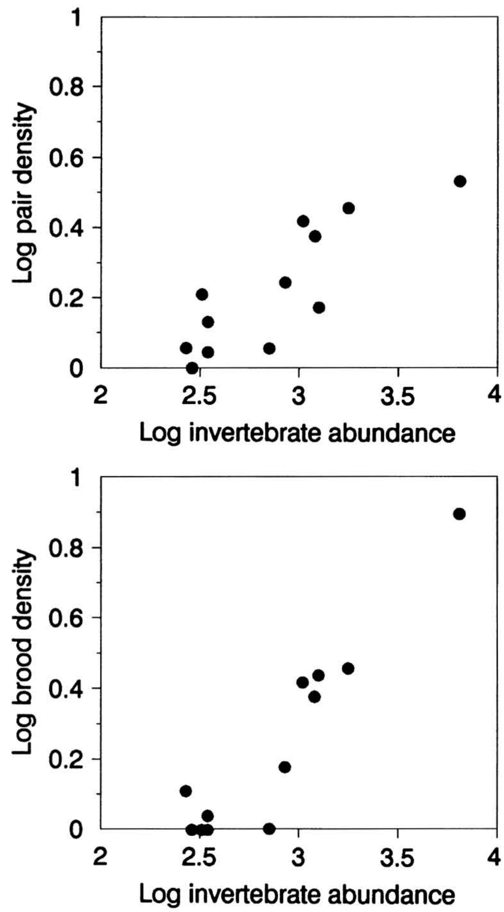

Fig. 1. Breeding pair density and brood density of goldeneyes in relation to invertebrate abundance in 12 lakes. Bird densities and invertebrate abundance indices are given as log-transformed average values from years 1989–92. Pair density is measured as the number of pairs per km of shore line and brood density as the number of broods per census per km of shore line. Invertebrate abundance is measured as the modified number of individuals per 100 trap days (see methods)

4.3. Response of goldeneyes to changes in perch density

In the control side of the L. Iso Valkjärvi the perch density crashed down from 1992 to 1993 (Fig. 3). Goldeneye pair density did not show

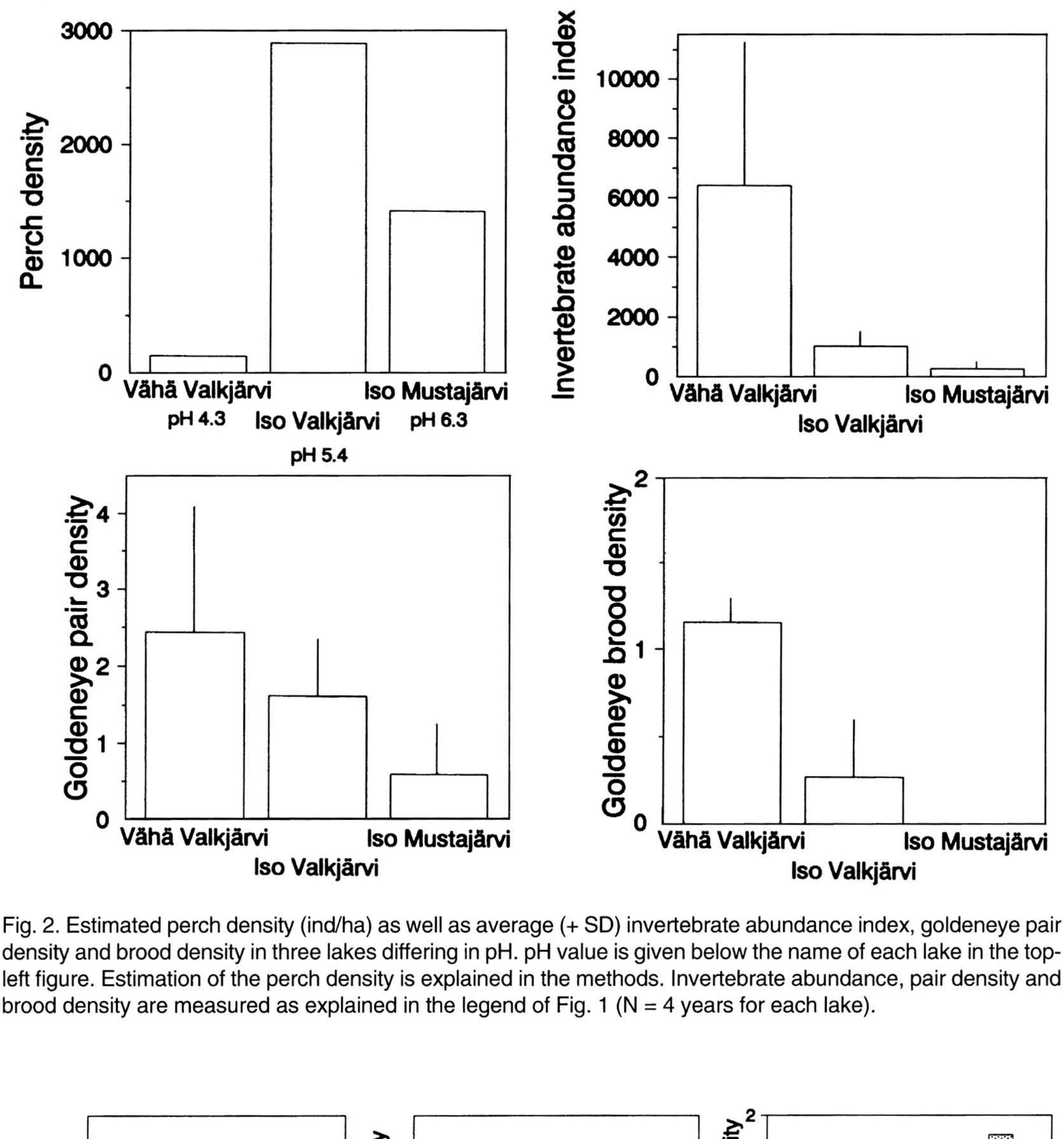

Fig. 2. Estimated perch density (ind/ha) as well as average (+ SD) invertebrate abundance index, goldeneye pair density and brood density in three lakes differing in pH. pH value is given below the name of each lake in the top-left figure. Estimation of the perch density is explained in the methods. Invertebrate abundance, pair density and brood density are measured as explained in the legend of Fig. 1 (N = 4 years for each lake).

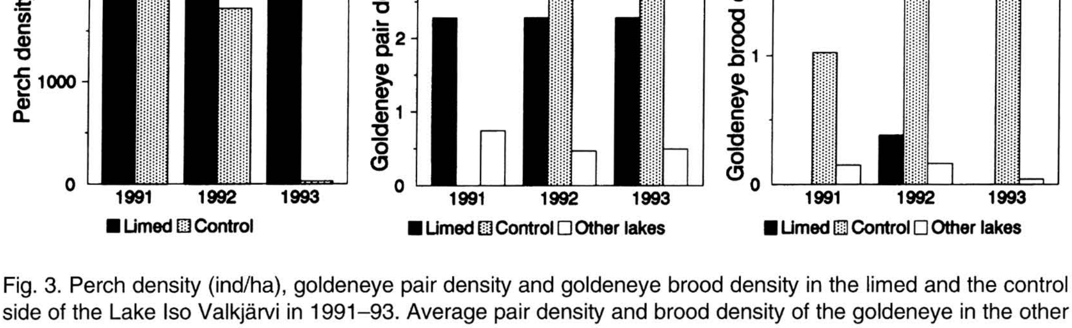

Fig. 3. Perch density (ind/ha), goldeneye pair density and goldeneye brood density in the limed and the control side of the Lake Iso Valkjärvi in 1991–93. Average pair density and brood density of the goldeneye in the other lakes (N = 52) of the study area in 1991–93 is also given. Pair and brood densities are measured as explained in the legend of Fig. 1.

any change associated with the crash in the perch density but brood density increased from 1992 to 1993 (Fig. 3). It is noteworthy that, at the same time, brood density in the limed side of the L. Iso Valkjärvi and also in other lakes in the area decreased (see Fig. 3).

We studied the effect of the perch crash on goldeneyes in more detail by considering the distribution of all observations of breeding individuals and broods between the two lake sides before and after the perch crash (Fig. 4). Also this analysis showed that breeding individuals did not respond to the perch crash (Fishers test, $P = 0.68$) whereas broods clearly increased the use of the control side after the perch crash while the use of the limed side decreased ($G = 6.40$, $P < 0.05$).

5. Discussion

We did not find a clear overall response of goldeneye pair and brood density to lake pH in pair-wise comparisons. However, when information of fish density and invertebrate abundance associated with lake pH was considered clear responses were found: goldeneye densities were consistently highest on the lake with lowest pH and perch density and highest invertebrate abundance. The lack of an overall association between goldeneye density and lake acidity agrees with our earlier findings based on the relative abundance of breeding goldeneyes in a pooled data from Finland and Sweden (Elmberg et al. 1994) but contradicts with results from Canada. Based on presence/absence data of single visits to lakes and pooled over breeding individuals and broods DesGrances & Darveau (1985) found in southern Quebec that the presence of goldeneyes was strongly associated with lakes of high acidity (pH ≤ 5.5). Similarly based on presence/absence data Blancher et al. (1992) found in central Ontario a negative pair-wise association between breeding goldeneye pairs and lake pH but not between broods and lake pH. Besides differences in the accuracy of the goldeneye data (density data vs. presence/absence data) there were differences in the distribution of pH values between our data and those from Canada: only 13.6% ($N = 22$) of our lakes had a pH ≤ 5.5

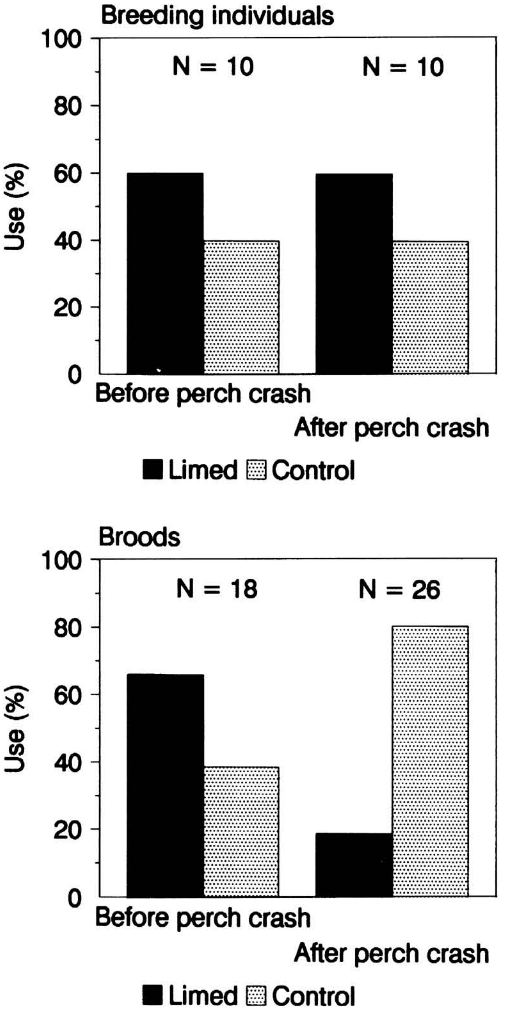

Fig. 4. The percentage use of the limed and the control side of the Lake Iso Valkjärvi by breeding individuals and broods of goldeneyes before and after the perch crash of the control side. N gives sample size (number of individuals or broods).

whereas 57.9% ($N = 126$) of those used by DesGrances & Darveau (1985) and about 30% ($N = 212$) of those used by Blancher et al. (1992) had a pH of that level. Accordingly, Canadian data may have included more fishless lakes with high invertebrate abundance than did our data and, as a consequence, the association between lake acidity and lake preference by goldeneyes was stronger. Also the possible impacts of different fish faunas in the two continents have to be kept in mind (see Tonn et al. 1990, McNicol & Wayland 1992).

Both breeding pairs and broods of goldeneyes showed a strong positive association with invertebrate abundance. This result was obtained with data pooled over four years but, especially in the broods the result is repeated year-after-year (see Nummi & Pöysä 1993, 1994). A study based on individually-marked goldeneye females has confirmed that invertebrate abundance is an important factor affecting lake selection of broods in our study area (Pöysä & Virtanen 1994). In Sweden Eriksson (1978) also found a correlation between invertebrate abundance and lake preference by goldeneye broods. In addition, in this study lakes with steadily low pH, low perch density and high invertebrate abundance were preferred by breeding pairs and broods. McNicol & Wayland (1992) concluded that goldeneye broods preferred lakes with species-poor and acid-tolerant benthic fauna over the equally abundant and species-rich but acid-sensitive fauna. These findings indicate that lake acidification mediated through changes in fish density and invertebrate abundance may be an important factor affecting habitat selection of goldeneyes.

The drastic decrease in perch density in the control half of L. Iso Valkjärvi was in fact associated with an increase in the abundance of some invertebrate prey even though, in general, the responses were not very strong just one year after the perch crash (Rask et al., unpublished, Nummi & Pöysä, unpublished). Considering the strong association between goldeneye densities, especially of broods and invertebrate abundance, some increase in the use of the control side after perch crash was to be expected. Indeed, broods clearly responded to the sudden decrease in perch density but breeding individuals did not. In our study area most goldeneye females breed in nest boxes and if there is no nesting failure females usually use the same nest box and nesting lake year-after-year. By contrast, females usually do not rear the brood in the nesting lake (Pöysä & Virtanen 1994) and they may also easily change the brood-rearing lake between successive years (Pöysä et al., unpublished). Breeding pairs may thus be more fixed in their selection of the breeding lake whereas lake selection during the brood rearing phase may be more easily adjusted to the prevailing environmental conditions each breeding season. This of course is not to say that pH is not an important factor affecting nest site selection of breeding pairs (see above and Mallory et al. 1993). However, it may explain why broods but not breeding pairs showed a rapid response to the sudden decrease in perch density. It is also possible that because goldeneye males aggressively defend the breeding territory there simply was no room for additional breeding individuals in the lake.

Our results of the competitive interaction between the perch and goldeneye agree with those of other studies. Eriksson (1979) found in Sweden that fledged goldeneyes used more fishless lakes than lakes with fish. Using experimental removal of fish he also demonstrated that some aquatic insects were sensitive to fish predation and that fledged goldeneyes increased the use of a lake after fish were removed. Eriksson (1983) also found a negative association between fish abundance and the occurrence of both adult and young common goldeneyes. In Canada Eadie & Keast (1982) demonstrated a high diet overlap between common goldeneye ducklings and yellow perch and a negative relationship between their abundances. They also showed that food resources actually were limited in some of the study sites and that the coexistence of goldeneye ducklings and yellow perch was associated with high resource abundance.

In conclusion, information of all elements in the interaction network pH-fish density-invertebrate abundance-goldeneye density in lakes is needed before conclusive analyses of the effects of lake acidity on the interactions at higher trophic levels can be made. Both breeding pairs and broods of goldeneyes do respond in habitat selection to invertebrate abundance and may thus benefit, although with a different readiness, of acidity-induced release in food competition after the disappearance of fish competitors.

Acknowledgements. We wish to express our thanks to numerous field assistants and to the staffs of Evo Game Research Station and Evo State Fisheries and Aquaculture Research Station for help in field work and to Ismo J. Holopainen and Jouko Sarvala for useful comments on the manuscript. Juha Virtanen kindly allowed us to use his common goldeneye brood observations from the L. Iso Valkjärvi.

References

Appelberg, M., Henrikson, B.-I., Henrikson, L. & Svedäng, M. 1993: Biotic interactions within the littoral community of Swedish forest lakes during acidification. — Ambio 22: 290–297.

Arvola, L., Metsälä, T.-R., Similä, A. & Rask, M. 1990: Seasonal fluctuations in the chemistry of small forest lakes in southern Finland with special reference to acidity. — Aqua Fennica 20: 71–79.

Bendell, B. E. 1986: The effects of fish and pH on the distribution and abundance of backswimmers (Hemiptera: Notonectidae). — Can. J. Zool. 64: 2696–2699.

Bendell, B. E. & McNicol, D. K. 1987: Fish predation, lake acidity and the composition of aquatic insect assemblages. — Hydrobiologia 150: 193–202.

Blancher, P. J. & McAuley, D. G. 1987: Influence of wetland acidity on avian breeding success. — Trans. N. Am. Wildl. & Nat. Res. Conf. 52: 628–635.

Blancher, P. J., McNicol, D. K., Ross, R. K., Wedeles, C. H. R. & Morrison, P. 1992: Towards a model of acidification effects on waterfowl in Eastern Canada. — Environ. Pollut. 78: 57–63.

Cramp, S. & Simmons, K. E. L. (eds) 1977: The birds of the western palearctic. Vol. 1. — Claredon Press, Oxford. 722 pp.

DesGranges, J.-L. & Darveau, M. 1985: Effect of lake acidity and morphometry on the distribution of aquatic birds in southern Quebec. — Holarct. Ecol. 8: 181–190.

Eadie, J. M. & Keast, A. 1982: Do goldeneye and perch compete for food? — Oecologia 55: 225–230.

Elmberg, J., Sjöberg, K., Nummi, P. & Pöysä, H. 1994: Patterns of lake acidity and waterfowl communities. — Hydrobiologia 279/280: 201–206.

Eriksson, M. O. G. 1976: Food and feeding habits of downy goldeneye Bucephala clangula (L.) ducklings. — Ornis Scand. 7: 159–169.

— 1978: Lake selection by Goldeneye ducklings in relation to the abundance of food. — Wildfowl 29: 81–85.

— 1979: Competition between freshwater fish and goldeneyes Bucephala clangula (L.) for common prey. — Oecologia 41: 99–107.

— 1983: The role of fish in the selection of lakes by nonpiscivorous ducks: mallard, teal and goldeneye. — Wildfowl 34: 27–32.

— 1984: Acidification of lakes: effects on waterbirds in Sweden. — Ambio 13: 260–262.

Eriksson, M. O. G., Henrikson, L., Nilsson, B.-I., Nyman, G., Oscarson, H. G., Stenson, A. E. & Larsson, K. 1980: Predator-prey relations important for the biotic changes in acidified lakes. — Ambio 9: 248–249.

Koskimies, P. & Väisänen, R. A. (eds.) 1991: Monitoring bird populations. — Zool. Mus., Finnish Mus. Nat. Hist., Univ. Helsinki, Helsinki. 144 pp.

Lappalainen, A., Rask, M. & Vuorinen, P. 1988: Acidification affects the perch, Perca fluviatilis L., populations in small lakes of southern Finland. — Env. Biol. Fish. 21: 231–239.

Mallory, M. L., Weatherhead, P. J., McNicol, D. K. & Wayland, M. E. 1993: Nest site selection by Common Goldeneyes in response to habitat features influenced by acid precipitation. — Ornis Scand. 24: 59–64.

McNicol, D. K., Bendell, B. E. & Ross, R. K. 1987: Studies of the effects of acidification on aquatic wildlife in Canada: waterfowl and trophic relationships in small lakes in northern Ontario. — Can. Wildl. Serv. Occas. Pap. 62.

McNicol, D. K. & Wayland, M. 1992: Distribution of waterfowl broods in Sudbury area lakes in relation to fish, macroinvertebrates, and water chemistry. — Can. J. Fish. Aquat. Sci. 49 (Suppl. 1): 122–133.

McNicol, D. K., Bendell, B. E. & McAuley, D. G. 1987: Avian trophic relationships and wetland acidity. — Trans. N. Am. Wildl. & Nat. Res. Conf. 52: 619–627.

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

Nummi, P. & Pöysä, H. 1993: Habitat association of ducks in different phases of the breeding season. — Ecography 16: 319–328.

— 1994: Habitat use of waterfowl during various stages of the breeding cycle (in Finnish with English summary). — Suomen Riista 40: 72–81.

— 1995: Breeding success of ducks in relation to different habitat factors. — Ibis (in press).

Pöysä, H. & Virtanen, J. 1994: Habitat selection and survival of Common Goldeneye (Bucephala clangula) broods - preliminary results. — Hydrobiologia 279/280: 289–296.

Rask, M. 1983: Differences in growth of perch (Perca fluviatilisa L.) in two small forest lakes. — Hydrobiologia 101: 139–144.

— 1984: The effect of low pH on perch, Perca fluviatilis L. III. The perch population in a small, acidic, extremely humic forest lake. — Ann. Zool. Fennici 21: 15–22.

— 1986: The diet and diel feeding activity of perch, Perca fluviatilis L., in a small lake in southern Finland. — Ann. Zool. Fennici 23: 49–56.

— 1991: Iso Valkjärvi research: an introduction to a multidisciplinary lake liming study. — Finnish Fish. Res. 12: 25–34.

— 1992: Changes in the density, population structure, growth and reproduction of perch, Perca fluviatilis L. in two acidic forest lakes in southern Finland. — Environ. Pollut. 78: 121–125.

Rask, M. & Arvola, L. 1985: The biomass and production of pike, perch and whitefish in two small lakes in southern Finland. — Ann. Zool. Fennici 22: 129–136.

Tonn, W. M., Magnuson, J. J., Rask, M. & Toivonen, J. 1990: Intercontinental comparison of small-lake fish assemblages: the balance between local and regional processes. — Amer. Nat. 136: 345–375.