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The biomass and production of pike, perch and whitefish in two small lakes in southern Finland

Martti Rask & Lauri Arvola

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In two small forest lakes total fish biomass was 73 kg/ha and 32 kg/ha, and fish production 30 and 16 kg/ha, respectively. The fish of the first lake were perch, pike and introduced whitefish, of the second perch and whitefish. The main reasons for the differences in fish biomass and production were probably light and oxygen conditions. The diet segregation between perch and whitefish, which reduced interspecific competition, and predation by pike on perch, which reduced intraspecific competition for food among perch, also resulted in improved fish production in the first lake.

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1. Introduction

Since 1979 intensive research on the ecology of small forest lakes has been performed at the Lammi Biological Station, Finland (Arvola 1983, 1984, Arvola & Rask 1984, Salonen et al. 1983, 1984, Rask 1983, 1984). Due to their relatively simple ecosystems, these lakes provide good opportunities to study the basic interactions between species and their environment as well as interspecific relations.

In this paper we measured biomass and production of fishes in two small forest lakes and compared them with studies from other countries (Holcik 1977, Craig et al. 1979, Ciepielewski 1973, Nyberg 1976, Mann 1980) and other lakes in Finland (Sumari 1971, Lind et al. 1974, Pruuki et al. 1982). Attention was given to several factors known to affect the fish production in lakes (LeCren 1972): general productivity measured as primary production, interspecific interactions among fishes, including the predator - prey relation between pike and perch and diet overlap between perch and whitefish, and population abundance measured as growth and density of the fish species. Differences in the physical and chemical properties of the lakes, especially light and oxygen conditions, are presented as reasons for the different productivities of the two lakes, causing differences in fish biomass and production.

2. The lakes

Alinen Mustajärvi is an autumn monomictic, oligo-mesohumic lake and Horkkajärvi a meromictic, polyhumic lake in the Evo region, Lammi, southern Finland (Fig. 1). The surface areas of the lakes are 0.7 and 1.1 ha and the maximum depths are 6.5 and 13 m, respectively. Alinen Mustajärvi is a groundwater lake with no inlets and only a small outlet that does not allow any immigration or emigration of fishes. A 3-4 meter surface layer warmed up to 10°C and remained oxygenated throughout the 1980 growing season (Fig. 2). Other physical and chemical properties are shown in Table 1. The amount of macrophytes in the lake is low, consisting of some *Carex* vegetation inshore and *Nuphar lutea* L. (Smith) slightly offshore. One third of the shoreline is surrounded by a floating *Sphagnum* mat. The original fish species in the lake were perch, *Perca fluviatilis* L., and pike, *Esox lucius* L. In the autumn of 1975 a small population of whitefish, *Coregonus muksun* Pallas was introduced into the lake.

Lake Horkkajärvi has two small inlets and one small outlet (Fig. 1). No migrations of fishes to or from the lake occurred during the 1979-1983 study period. The temperature and oxygen conditions of the lake differed clearly from those in Alinen Mustajärvi in 1980. Only a two meter water layer warmed up to 10°C and the oxygenated water layer decreased from 3 to 1.5 m during the summer (Fig. 2). This caused a decrease in the oxygenated littoral zone, from 2200 m^2 to 500 m^2, while this oxygenated area in Alinen Mustajärvi remained at 3100 m^2 throughout the summer. In autumn, due to partial circulation, the oxygenated littoral increased in Horkkajärvi to 3000 m^2. Excluding the temperature and oxygen conditions, which were mainly due to differences in water colour, other physical and chemical water properties of the lakes were rather similar (Table 1). The macrophytic vegetation of Horkkajärvi also was similar to that in Alinen Mustajärvi. Perch was the only initial

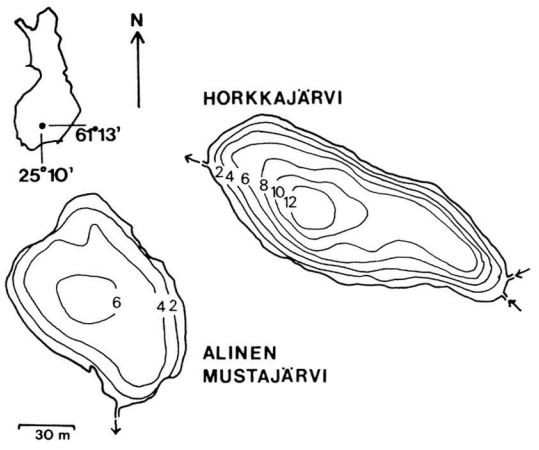

Fig. 1. The location and the bathymetric maps of the study lakes. The drainage areas are 0.5 ha for Alinen Mustajärvi and 70 ha for Horkkajärvi.

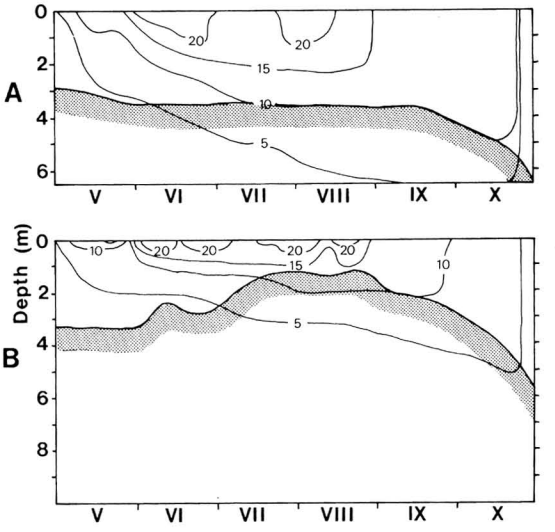

Fig. 2. (A) The distribution of temperature (°C) and the level of anoxis (shaded) in Alinen Mustajärvi and (B) in Horkkajärvi, during the growing season 1980.

species of fish, but in autumn 1978 200 individuals of whitefish, *Coregonus peled* Gmelin, were introduced. Whitefishes do not reproduce in either lake. The introductions of whitefish into both lakes were performed by Evo Inland Fisheries and Aquaculture Research Station.

3. Materials and methods

Perch were captured from both lakes with traps (1 cm square mesh). During 1979 and 1980 growing seasons sampling occurred at two weeks interval for age, growth and food determinations. The traps were in the lake overnight and emptied in the morning. During 1979–1983 daily samples were taken after ice-out for population estimation. Pikes from Alinen Mustajärvi were captured with larger traps of the same mesh size from May to September 1983. Whitefishes were caught from both lakes during 1979–1980 with gill nets. The mesh sizes used were 40, 45, and 60 mm in Alinen Mustajärvi and 20, 30, and 40 mm in Horkkajärvi.

The size of the perch population was estimated by mark and recapture (fin clipping) and calculating Schnabel estimates (Robson & Regier 1971). No removals of fish were made during this period. Total lengths of the marked perch were measured for length distributions. Mortality of perch was estimated according to the year class distribution and by re-marking the marked fishes after a year. The estimation of pike and whitefish populations in Alinen Mustajärvi was based on the catches from intensive capturing while in Horkkajärvi a natural annual mortality of 30 % was assumed for the 200 introduced whitefishes.

The age and growth of perch were determined from the opercular bone according to LeCren (1947). For small pike (<40 cm total length) age determination was based on the opercula and on the cleithra for larger pike (Casselman 1979).

The biomasses of perch were estimated from the population sizes and size distributions. For pike and whitefish the yields of intensive fishing were used for biomass estimates, being thus minimum values. The production of each species, defined as the potential increase in the amount of fish tissue during a year, was calculated using the population estimates and growth rates.

A volumetric points method was used for food analyses and the numbers given are percent of stomach contents. The stomach contents of 202 perch, 13 pike and 21 whitefish were analyzed from Alinen Mustajärvi. From Horkkajärvi sample sizes were 301 perch and 31 whitefish.

Samples of zooplankton were taken from both lakes with a Sormunen-type tube sampler, from one station in the middle of the lake. The samples were filtered through a net (mesh size 50 μm), and results are given as individuals per liter.

4. Results and discussion

4.1. The fish populations

During the 1979–1983 study period, perch population in Alinen Mustajärvi averaged 1900 ±340 (*SE*) individuals, while in Horkkajärvi the population averaged 1360 ±160. The mean densities of the populations were thus 2700 and 1240 individuals per hectare. Perch smaller than 8.5 cm (total length), which included age groups 0+ and 1+, were excluded from these numbers due to size selectivity of the traps. From the proportion of 2+ perch in the population of Alinen Mustajärvi in spring 1982 (Fig. 3) and

Table 1. Properties of water in the lakes Alinen Mustajärvi and Horkkajärvi during May - October in 1979-1980.

	Alinen Mustajärvi		Horkkajärvi	
Depth (m)	0.1	6.0	0.1	6.0
pH	5.3-5.8	5.7-6.2	4.6-6.0	5.6-6.4
Alkalinity (meq/l)	0.01-0.03	0.13-0.43	-0.01-0.07	0.34-0.64
Conductivity (μS/cm 20°C)	15-18	21-43	33-41	35-64
Colour (mg Pt/l)	44-83	160-250	200-430	300-420
Total P (μg/l)	6-36	44-71	18-110	120-210
Total N (μg/l)	260-900	1220-3800	440-910	620-1920
Na (mg/l)	0.5	0.6	1.4-2.7	1.7-2.0
Mg (mg/l)	0.4	0.5	0.9-1.1	0.9-1.5
K (mg/l)	0.4	0.4	0.9-1.7	1.2-1.7
Ca (mg/l)	1.8-2.0	3.3-4.4	3.1-4.1	5.4-8.2
Mn (mg/l)	0.03	0.04	0.01-0.04	0.04-0.09
Fe (mg/l)	0.1-0.2	1.1-1.7	0.2-0.6	1.7-2.4

using the mortality rate of 0.45 for 1+ perch given by Nyberg (1976), the number of perch from the 1980 year class present in spring 1981 was estimated to be 1000. Thus the real density of the perch population in spring 1981 was about 4000 individuals per hectare. Similar densities of perch from small forest lakes have been reported by Alm (1946), Lind et al. (1974) and Nyberg (1976).

The size of the perch populations in these lakes depended on the occurrence of strong year classes. In Horkkajärvi the catchable perch population decreased during 1980-1982 from 1950 (Rask 1983) to 1050 due to poor reproduction, whereas in Alinen Mustajärvi it remained at a high and constant level, 1800-1900 individuals, due to the growth of the strong 1980 year class to a catchable size. The total removal of perch by sampling during the study period 1979-1983 was 360 individuals in Alinen Mustajärvi and 780 in Horkkajärvi. From the length distributions of the populations (Fig. 3) it appears that strong year classes were brought off every three years in both lakes. Because perch appeared in the mark-recapture catches at the age of two years (length groups 8-9 cm), one can conclude that reproduction was successful in Alinen Mustajärvi in 1977 and 1980 and in Horkkajärvi during 1978 and 1981.

The populations of pike and whitefish in Alinen Mustajärvi were small, with densities of 20 individuals per hectare for pike and 30 per hectare for whitefish. In Horkkajärvi the density of whitefish was 120 individuals per hectare in 1979 and 60 per hectare in 1980.

The annual mortality of perch ≥2 years old in Alinen Mustajärvi was 0.6. This agrees with the mean total mortality of perch from six

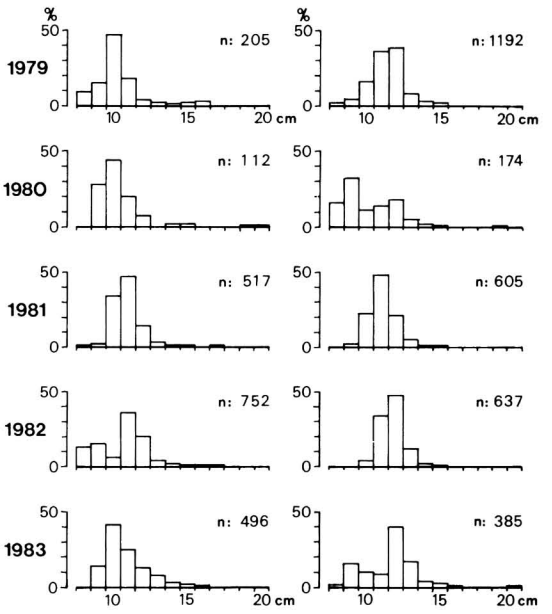

Fig. 3. The length distribution of perch in Alinen Mustajärvi (left) and in Horkkajärvi (right) during 1979-1983.

studies summarized by Thorpe (1977). The proportion of this mortality caused by pike predation was estimated to be 2/3, based on the relation of food consumed to production in pike (food coefficient). The food coefficient used, 5.2, was a mean value from studies by Kipling & Frost (1970), Backiel (1971), Mann (1976) and Białokoz & Krzywosz (1978). In Horkkajärvi the annual mortality of perch varied between 0.2 and 0.3, which is typical in lakes with no predatory fishes (Nyberg 1976).

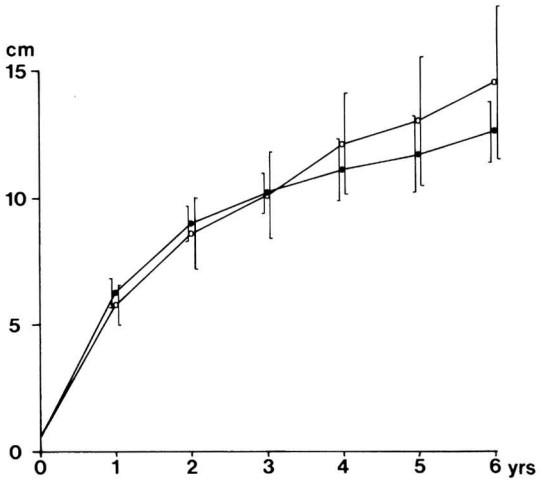

Fig. 4. The growth of perch in Alinen Mustajärvi (open circles, $n=202$) and in Horkkajärvi (closed circles, $n=300$). Vertical bars = *SD*.

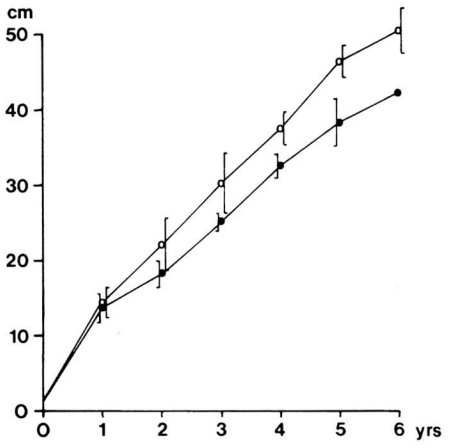

Fig. 5. The growth of pike in Alinen Mustajärvi, females (circles, $n=7$) and males (dots, $n=5$), vertical bars refer to *SD*.

4.2. Age and growth

In Alinen Mustajärvi the growth of perch during the first years of life was somewhat slower than in Horkkajärvi, but it turned higher after three years (Fig. 4). Neither difference was significant, however ($P>0.1$, *t*-test). In comparison to studies by Pihu (1964), Neuman (1976), and Craig (1980) perch grew slowly in our study lakes. Compared to perch populations in other small forest lakes, however, growth was similar (Alm 1946, Nyberg 1976, Tikka & Paasivirta 1979, Rask 1983, 1984). Female perch grew faster than males in both lakes, but the difference was significant only in Alinen Mustajärvi, for fish ≥4 years old ($P<0.01$, *t*-test).

The growth rate of pike in Alinen Mustajärvi (Fig. 5) was only slightly slower than in some other Finnish lakes (Järnefelt 1921, Viljanen et al. 1982), but there are clear differences in growth when compared, for example, to Windermere (Kipling 1983), where 3 years old pikes are larger than 6 year olds in Alinen Mustajärvi.

The whitefishes showed the following growth rates: mean total length of 39.6 cm and weight 620 g after four years in Alinen Mustajärvi and 32.0 cm and 280 g after three years in Horkkajärvi. These values exceed the mean growth rate of introduced whitefish populations in two other lakes of the same area (Pruuki et al. 1982).

4.3. Food

Because perch typically switch from planktonic to benthic food (Allen 1935, Popova & Sytina 1977, Guma'a 1978) the composition of the diet is presented for two length groups, <11 cm and 11-12 cm, separately (Fig. 6). Perch of both length groups in Alinen Mustajärvi foraged mostly on benthic food items whereas zooplankton formed >50 % from the diet of perch <11 cm in Horkkajärvi throughout the growing season. Zooplankton was also relatively more important for the 11-12 cm length group in Horkkajärvi. The planktonic food eaten by perch in both lakes was primarily cladocerans, 95 % in Alinen Mustajärvi and 89 % in Horkkajärvi. *Ceriodaphnia quadrangula* Müller was eaten most frequently in both lakes.

Perch was the main food item of pike in Alinen Mustajärvi. In only two cases had pike eaten something else, *Asellus aquaticus* L. (the pike was 13.0 cm) and a small rodent (a pike of 54.0 cm). Using a food coefficient of 5.2 we calculated that pike consumed about 9 kg perch per annum, which is 70-80 % of the annual production of perch ≥2 years old.

Whitefish in Alinen Mustajärvi fed on zooplankton (45 %), larvae of *Chaoborus flavicans* Meigen (40 %) and *Pisidium* mussels (15 %). In Horkkajärvi the diet of whitefish was dominated by zooplankton (94 %). The rest included *Pisidium* spp. and *Hydracarina*. In Alinen

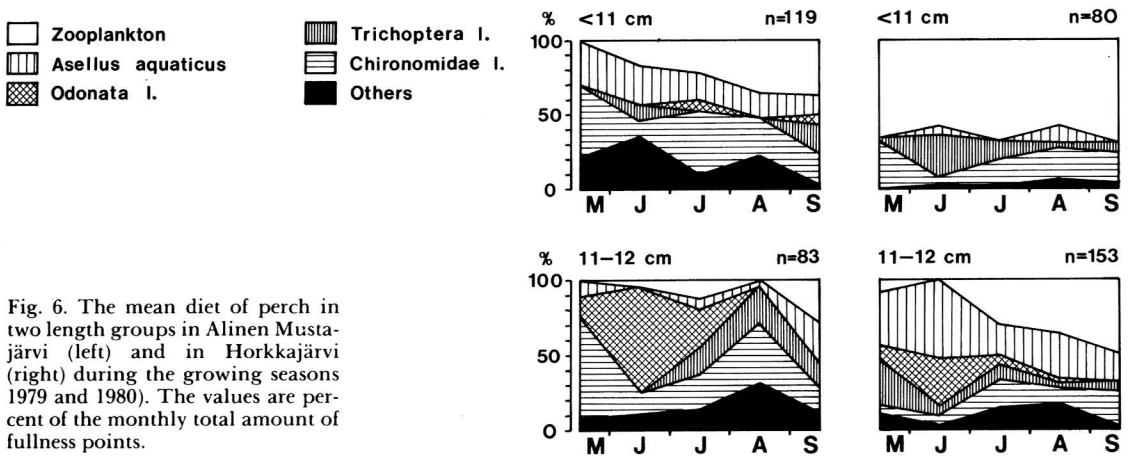

Fig. 6. The mean diet of perch in two length groups in Alinen Mustajärvi (left) and in Horkkajärvi (right) during the growing seasons 1979 and 1980). The values are percent of the monthly total amount of fullness points.

Table 2. The mean primary production, total respiration and density of zooplankton in the study lakes during May - September 1980. References: a = Arvola & Rask (1984), b = Arvola (1983), c = Salonen et al. (1983).

	Alinen Mustajärvi	Horkkajärvi
Primary production ($g\ C/m^2$/year)	7–8[a]	5–8[b]
Total respiration ($g\ C/m^2$/year)	17[a]	11[c]
Density of zooplankton (mean ± *SD*, ind/l, 0–5 m)		
Cladocera	64 ± 40	70 ± 51
Copepoda	108 ± 69	50 ± 32

Table 3. The mean production P (kg/ha/year) and biomass B (kg/ha) of fishes in the study lakes during 1979–1983.

	Alinen Mustajärvi			Horkkajärvi		
	P	B	P/B	P	B	P/B
Perch	15.9	37.0	0.4	5.3	21.0	0.3
Pike	2.6	6.9	0.4	-	-	-
Whitefish	11.8	29.1	0.4	10.2	11.2	0.9
Total	30.3	73.0		15.5	32.2	

Mustajärvi 89% of the zooplankton eaten by whitefish were copepods, especially *Cyclops scutifer* Sars., whereas in Horkkajärvi 78% of the zooplankton consumed by whitefish were cladocerans, mostly *Ceriodaphnia quadrangula*.

4.4. Biomass and production

The biomass of perch ≥2 years old in Alinen Mustajärvi varied between 36.0 and 38.0 kg/ha. In spring 1981 there was an additional 2.6 kg/ha from the 1980 year class, bringing the total biomass to 40.5 kg/ha. The production of perch ≥2 years old varied between 14.8–16.6 kg/ha in 1981–1983. In the 1981 growing season the 1+ age group could have produced 7.5 kg/ha, giving a potential total production for perch of 23.7 kg/ha. The turnover ratio (P/B) of perch ≥2 years old varied between 0.4–0.5 during the study period. The ratio was 0.6 in 1981 if the 1+ age group was taken into account. The biomass of pike in the lake was 6.9 kg/ha, production was 2.6 kg/ha and P/B was 0.4. Corresponding values for the whitefish were 29.1 kg/ha, 11.8 kg/ha and 0.4 respectively. The mean total fish biomass in Alinen Mustajärvi was thus 73 kg/ha and the production was 30 kg/ha (Table 3).

In Horkkajärvi the biomass of perch ≥2 years old varied between 19.0 and 22.9 kg/ha, production was 4.2–7.2 kg/ha and P/B varied between 0.2–0.3. The maximum values occurred in the 1979 growing season, P = 16.7 kg/ha, B = 26.0 kg/ha and P/B = 0.6, when the 1+ fish from the 1978 year class were taken into account. The mean values for whitefish were P = 10.2 kg/ha, B = 11.2 kg/ha and P/B = 0.9. The total fish biomass in Horkkajärvi was thus 32 kg/ha and production was 16 kg/ha. The different P/B values in whitefishes between the lakes were due to the different age of the fishes.

The biomass and production of perch in our study lakes were low in comparison to studies by Holcik (1977) and Craig et al. (1979). However in comparison to other small lakes in the Evo region, those in Alinen Mustajärvi

were higher (Tikka & Paasivirta 1979, Rask 1983, 1984), and also exceeded values given by Lind et al. (1974), Nyberg (1976) and Viljanen & Holopainen (1982). Sumari (1971) gave a mean perch biomass of 11.9 kg/ha from 32 rotenoned ponds. He found a negative correlation between the biomass of perch and number of fish species in the lake. The mean biomass of perch was 25 kg/ha in single species ponds, 14 kg/ha in those with two species, 9 kg/ha with three species and 8 kg/ha with four. Against this background the biomass and production of perch in Alinen Mustajärvi were high while those in Horkkajärvi were normal for small lakes (Table 3).

Although the biomass and production of pike in Alinen Mustajärvi were low in comparison to studies from other parts of Europe (Ciepielski 1973, Mann 1980), they may be close to the Finnish average (Lind & Kaukoranta 1975, Tuunainen et al. 1979). In comparison to other small forest lakes (Sumari 1971) the values for Alinen Mustajärvi were higher, which was probably due to stable food conditions, e.g. the dense population of perch. Pike did not need to feed on invertebrates after their first year of life, which often occurs in small lakes in Finland (Rask unpubl.).

Because of the low density of whitefishes in the lakes, their biomass and production were relatively low in comparison to other introduced populations in the Evo region (Pruuki et al. 1982), although the growth rates of whitefishes in both lakes were high.

The differences in fish biomass and production between the study lakes were partly due to better light and temperature conditions in Alinen Mustajärvi (Table 1, Fig. 2). The primary production in water column was similar in both lakes (Table 2), but better light conditions in Alinen Mustajärvi could make perch more effective in resource utilization, because it is a visual feeder. Due to different oxygen conditions in the lakes during the summer (Fig. 2) the littoral zone in Alinen Mustajärvi provided a better environment for a benthic community to develop into a sufficient resource base for the fishes. This suggestion is supported by the different proportions of benthic animals in the diet of perch in the lakes (Fig. 6). This difference is a sign of better feeding conditions in Alinen Mustajärvi which could be based on high productivity of benthic algae. Perch are adapted

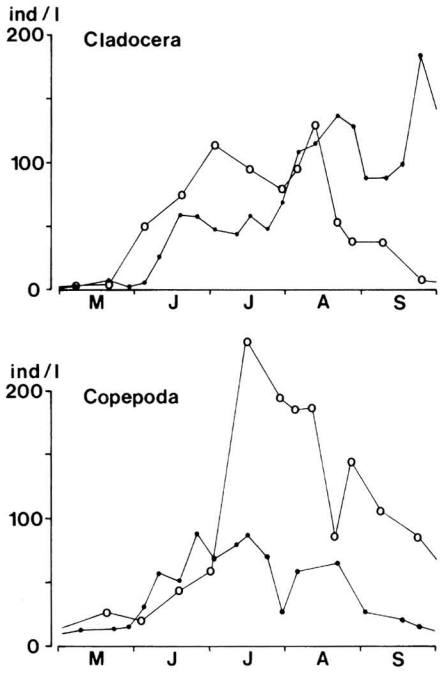

Fig. 7. The density of crustacean zooplankton in Alinen Mustajärvi (open circles) and in Horkkajärvi (closed circles) during the growing season 1980.

to feed on benthos after their first two years of life whereas continued feeding on zooplankton, the abundance of which was rather similar in both lakes (Table 2, Fig. 7), becomes less economical, in terms of energy, with increasing size of fish (Kerr 1971).

The relations among the fish species probably further emphasized the differences in fish biomass and production between the lakes. The predation by pike on perch in Alinen Mustajärvi prevented the density of perch to increase beyond the carrying capacity of the environment (potential food resources). Thus severe intraspecific competition for food was avoided and somewhat better growth (Fig. 4) and production (Table 3) resulted compared to Horkkajärvi, where pike were absent.

In Alinen Mustajärvi there was no dietary overlap between whitefish and perch. The only benthic food item of whitefish, *Pisidium*, was not taken by perch and the main planktonic food items of whitefish, *Cyclops scutifer* and *Chaoborus* larvae, were eaten seldom by perch. In Horkkajärvi the opposite situation was found: both perch and whitefish were

more dependent on zooplankton and both foraged intensively on *Ceriodaphnia quadrangula*. Thus, the possibility of interspecific competition existed, especially between the smaller perch that fed mostly on zooplankton, and whitefish.

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