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Intra-cohort variation in the individual size of juvenile pikeperch, *Stizostedion lucioperca*, and perch, *Perca fluviatilis*, in relation to the size spectrum of their food items

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Size distributions of cohorts of pikeperch and perch originating from three lakes in the Netherlands were compared to test the hypothesis that skewness or bimodality within cohorts of pikeperch and perch develops especially in environments with a discontinuous size distribution of their potential food items. In older, more eutrophic lake ecosystems like Tjeukemeer and IJsselmeer, where macro-invertebrates occur in low densities, 0-group pikeperch generally exhibit differential growth of fast-growing piscivores and slow-growing zooplanktivores. The size distributions of such cohorts become positively skewed during their first summer and often become bimodal at the end of the growing season with modes at ca. 10–15 cm and 6–8 cm, respectively. The size attained by zooplanktivorous 0-group perch in these systems is relatively small (6–9 cm) and is positively related to summer temperature. Cohorts of perch in these systems shift to piscivory, partially or totally, in their second or third summer. The differential growth of zooplanktivorous and piscivorous perch of the same cohort can cause a broadening and a positive skewness in the cohort size distribution, but never results in a bimodal size distribution. In the recently freshened, mesotrophic Volkerak ecosystem, the initial high availability of the macro-invertebrate *Neomysis integer*, in the first couple of years enabled 0-group pikeperch and perch to reach similar large sizes of 12–14 cm and to both switch to piscivory in their second summer. After ca. 5 years Volkerak became more eutrophic, the stock biomass of cyprinids increased, the size distribution of 0-group pikeperch became bimodal and the 0-group perch stayed small (< 10 cm), as in the older, more eutrophic systems. It is postulated that more productive systems with a higher fish biomass, but with lower biomasses of macro-invertebrates and less large-sized zooplankton probably have stronger selection mechanisms for recruiting percids.

1. Introduction

Differential growth in a cohort of fish, coincident with intense predation pressure, can cause the selective survival of only the largest individuals, which ultimately recruit to the adult population. Such differential growth has been observed for piscivores, especially largemouth bass, *Micropterus salmoides*, (Shelton *et al.* 1979, Timmons *et al.* 1980), walleye, *Stizostedion vitreum*, (McIntyre *et al.* 1987) and pikeperch, *Stizostedion lucioperca* (Van Densen 1985a, Buijse & Houthuijzen 1992). The 0-group pikeperch exemplifies this pattern with a zooplanktivorous group and a piscivorous group which differ in condition and survival rate (Van Densen 1985a, Buijse & Houthuijzen 1992). Because the largest individuals in the cohort become piscivorous first, and because of the positive effect of piscivory on growth rates, the initially symmetric size distribution of the 0-group fish develops into a positively skewed, and finally bimodal size distribution (Van Densen 1985a, Buijse & Houthuijzen 1992). This process, however, might be rather specific for the local assemblage of fish species and food organisms, for the trophic status of the lake ecosystem or for the climatological conditions under which this process is studied. A more general concept of the size differentiation within cohorts of piscivores would facilitate comparisons between situations.

It can be hypothesized that the differential growth within cohorts is more prominent in systems with a strong discontinuity in the size distribution of potential food items. Various authors have used size distributions of organisms to characterize and compare aquatic ecosystems (Sheldon *et al.* 1977, Sprules *et al.* 1991, Boudreau & Dickie 1992, Gaedke 1992, Sprules & Goyke 1994). In such cases, first the total biomass of all organisms per size (or energy) category was plotted against the size (or energy) category using a logarithmic scale. Marine systems seem to have more continuous size distributions of organisms than freshwater lakes (Boudreau & Dickie 1992), and mature systems more continuous distributions than immature systems (Gaedke 1992).

The discontinuity in the size distribution of food items in a particular lake could arise from trophic interactions between fish, macro-invertebrates and zooplankton. An example is the size-selective predation by zooplanktivorous fish, which has an impact on zooplankton community structure (Zaret 1980). This causes a discontinuity in the biomass size distribution for eutrophic systems occupied by medium- and large-sized zooplankton. Macro-invertebrates like mysids predate on the smaller sizes of cladocerans and, when present in abundance, could create a gap in the biomass size distribution of the zooplankton, potentially halting the recruitment of large cladocerans to mature sizes (Richards *et al.* 1975, Langeland 1981). Finally, the stock of macro-invertebrates, which are preferred by certain fish species, for example chironomid larvae selectively taken by bream, *Abramis abrama*, could be depleted by a high stock biomass of their predators (Lammens 1986).

The objective of this study was to develop a more general concept for the process of size differentiation within cohorts of piscivorous fish, so as to link the population dynamics of piscivores to characteristics of lake ecosystems. For this purpose we compared the growth and size distributions of juvenile pikeperch and perch, *Perca fluviatilis*, in three systems (Tjeukemeer, IJsselmeer and Volkerak) which differed with respect to age and trophic state using both published data and field observations. Tjeukemeer is a centuries-old polder reservoir, representative of most inland waters in the Netherlands. These lakes are eutrophic and have high standing stocks of fish, which exert a strong influence on the size structure of the zooplankton community, resulting in the dominance of small-sized zooplankton (Lammens *et al.* 1985). IJsselmeer is the largest lake in the Netherlands and is less eutrophic than Tjeukemeer. It originates from a brackish water area, and was freshened after the construction of a dam in 1932. Volkerak, which like IJsselmeer originates from a brackish water area, was freshened more recently (1987) and is mesotrophic. Initially, just after dam construction more oligotrophic lakes are characterized by the fast growth of colonizing freshwater fishes and by the high abundance of macro-invertebrates in the first period after dam construction (Willemsen 1977, Buijse *et al.* 1993).

2. Material and methods

2.1. Study area

Shallow, eutrophic Tjeukemeer is a polder reservoir and is part of the Friesian lake district (Table 1). The chloride content varies between 50 (winter) and 250 mg Cl/l (summer) (De Haan 1982). Summer values for Chlorophyll-*a* equal 200 µg/l (De Haan 1982). In the less eutrophic IJsselmeer, chlorophyll-*a* varied between 50 and 120 µg/l in the period 1975–1992 (Prins *et al.* 1995). The chloride content is currently around 200 mg Cl/l (Willemsen 1977). The recently-freshened Volkerak, created by embankment in April 1987, is mesotrophic. It is an unstable system in which water transparency initially (1988–1990) increased from 1.9 to 3.1 m but later steadily decreased to < 1.5 m in 1994 (Ligtvoet & de Jong 1995). In the same period, chlorophyll-*a* initially decreased from 25 to 8, but later increased to 27 µg/l (Ligtvoet & de Jong 1995). The water management for Volkerak aims at chloride concentrations of < 400 mg/l, and since early 1988 actual values ranged between 200–450 mg Cl/l (Behrens 1992). The lake is flushed with water from the lower Rhine-Meuse, which contains high quantities of nutrients, and which will cause further eutrophication of the lake (Frantzen *et al.* 1994).

Fish standing stock and community composition varies among the lakes. In Tjeukemeer, the standing stock of fishes which have remained unexploited since 1977 is 400–800 kg of fish per ha and is dominated by bream, pikeperch and smelt, *Osmerus eperlanus*, with smaller proportions of perch, roach, *Rutilus rutilus*, and ruffe, *Gymnocephalus cernuus* (Vijverberg & van Densen 1984, Lammens *et al.* 1990). In IJsselmeer, on the contrary, the stock biomass of perch (17.1 kg/ha) is larger than that of pikeperch (2.0 kg/ha), which is heavily exploited by gillnet fishery. Together, these percids form a minor portion of the total fish stock biomass of ca. 130 kg/ha, which is dominated by smelt and ruffe (Buijse *et al.* 1993). Perch in IJsselmeer switch from eating zooplankton towards eating fish at a size of ca. 12–16 cm (Buijse 1992). In this size range, macro-invertebrates (*Neomysis integer, Gammarus* spp.) are of some importance as prey but their frequency of occurrence in perch diets never reaches 100% (Buijse 1992). In Volkerak, where the fish stock is not exploited, perch and pikeperch together formed half of the total fish stock biomass of ca. 50–75 kg/ha in the early period 1989–1992, with the biomass of perch being twice as large as that of pikeperch (Ligtvoet & Grimm 1992). The stock size of perch and pikeperch (ca. 20–40 kg/ha) showed no trend over the years, but the portion of other species, mainly bream and roach, steadily increased from ca. 20 kg/ha in 1989 to over 100 kg/ha in 1994 (Ligtvoet & de Jong 1995). Smelt is absent from this lake. *Neomysis integer* and large *Daphnia* were dominant food items in the stomachs of perch in the lake during autumn 1988–1990 (Houthuijzen *et al.* 1993).

2.2. Fish size distribution

The 0-group and older fish were sampled with fine-meshed trawls in all three lakes. The trawl used in Tjeukemeer had a head rope of 8.5 m and a 3.3-mm bar meshed codend; in IJsselmeer the head rope was 15 m and the mesh of the codend was 5 or 10 mm, depending on summer or autumn sampling (Buijse 1992); in Volkerak the head rope was 14 m and the codend had a mesh size of 5-mm bar mesh (Ligtvoet 1995). Fish were measured to the nearest mm or 0.5 cm *FL* (Tjeukemeer, Volkerak) or *TL* (IJsselmeer); for pikeperch $TL(\text{cm}) = 1.054 \times FL(\text{cm}) + 0.35$; for perch $TL(\text{cm}) = 1.061 \times FL(\text{cm})$. The 0-group fish were easily distinguished from 1+ and older fish using modes in the length–frequency distributions (LF-distribution). Also, 2- and 3-year-old individuals of the exceptionally strong 1980 year-class of perch in Tjeukemeer could be aged from modes in the LF-distributions. Older pikeperch were aged using scales.

The skewness of the size distributions per cohort was calculated as the third central moment divided by the cube of the standard deviation:

$$\frac{1}{ns^3}\Sigma\left(Y - \bar{Y}\right)^3$$

with standard error (Sokal & Rohlf 1981, p. 139):

$$S.E. = \sqrt{\frac{6n(n-1)}{(n-2)(n+1)(n+3)}}$$

The significance of skewness was tested using one-tailed 5% and 1% percentage from the distribution of skewness (Snedecor & Cochran 1980, table A20).

2.3. Energy content of individual food items

The abundance and size composition of the zooplankton in the food of 0-group pikeperch in Tjeukemeer was scored and converted to energetic composition as described in Van Densen (1985b). Subsequently the energy content per mean plankter in the food was calculated (mCal). The size of *N. integer* in

Table 1. Physical and chemical characteristics of the study lakes.

	Tjeukemeer	IJsselmeer	Volkerak
Surface area (ha)	2 147	112 000	4 570
Mean depth (m)	1.5	4.5	5.0
Maximum depth (m)	2	8	24
Chloride content (mg/l)	50–200	200	200–450
Transparency (m)	0.3–0.5	0.1–2.0 (mean 0.65)	1.5–3.0
Chlorophyll-*a* (µg/l)	200 (summer)	50–120	8–27

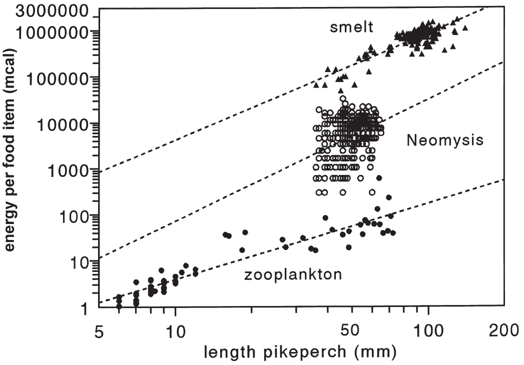

Fig. 1. Energy content of three food categories in the food of 0-group pikeperch in Tjeukemeer. Data for *Neomysis integer* and smelt are from mid-summer 1977 and summer 1976 respectively. Mean size of *N. integer* in the stomachs increased significantly from 8 to 12 mm in 35–65 mm pikeperch ($n = 330$, $r = 0.366$, $p < 0.05$).

the stomachs of 0-group pikeperch was measured in mm total length and converted to energy units using the relationship W (dry weight, mg) = $0.00391L^{2.48}$ (Bremer & Vijverberg 1982), and an energy density of 5 000 mCal per mg dry weight. The size of smelt in the stomachs of 0-group pikeperch was reconstructed from the shape and size of the otoliths using methods described in Van Densen (1985a). For 0-group smelt, length (L, mm) was converted to dry weight (W, mg) using: $\log W = 5.107\log L - 6.27$ (< 30 mm), $\log W = 3.734\log L - 4.17$ (> 29 mm). Energy density of smelt also was assumed to be 5 000 mCal per mg dry weight.

2.4. Food studies

The presence of major food categories (zooplankton, *Neomysis integer*, fish) in the food of 0-group pikeperch in Volkerak and of 1-group and older perch in Tjeukemeer was quantified using the frequency of occurrence method (Windell 1971). For previously published studies on the feeding behaviour of fish in Tjeukemeer and IJsselmeer, diet of zooplanktivores was quantified by numerical and energetic composition per species category (Van Densen 1985b, Buijse 1992). For all other fishes, diet was quantified by the frequency of occurrence method (Van Densen 1985b, Buijse 1992).

3. Results

3.1. Pikeperch

In Tjeukemeer, the onset of piscivory in 0-group pikeperch occurred in almost every year, resulting in positively skewed and ultimately bimodal size distributions. Fast-growing piscivores, eating mainly smelt, reached sizes between 10 and 15 cm, while zooplanktivores reached sizes of ca. 6–8 cm (Van Densen 1985ab). Depending on the success in the onset of piscivory the proportion of large piscivorous pikeperch varied strongly among years. Mean length attained by pikeperch in the period 1975–1987 ranged between 6 and 15 cm. Summer densities of 0-group smelt, which largely fluctuate among years, are the governing factor in the onset of piscivory of 0-group pikeperch in this lake. *Neomysis integer* occurred in the food of 0-group pikeperch only infrequently (Van Densen 1985b). Although *N. integer* is intermediate in caloric content between large zooplankton and smelt (Fig. 1), it does not bridge the gap in the prey spectrum of 10–40-mm pikeperch in Tjeukemeer because of the generally low density of *N. integer* in this lake. When *N. integer* became dominant in the food of 0-group pikeperch in late summer 1977, the size distribution became unimodal with a mean length of 81 ± 7 mm.

In IJsselmeer, the average size attained by 0-group pikeperch (8.2–17.3 cm) also was largest when they fully switched to piscivory (Buijse & Houthuijzen 1992). The faster growth of 0-group pikeperch in warm summers made more smelt available for these gape-limited, 0-group piscivores. The high correlation found by Buijse (1992) between mean length attained by 0-group pikeperch and summer temperature in IJsselmeer ($R^2 = 0.72$, $n = 24$, $p < 0.01$), was not observed in Tjeukemeer ($R^2 = 0.20$, $n = 11$, *N.S.*), where large inter-annual variation in densities of 0-group smelt probably played a more important role than lake temperature.

In Volkerak, the average size (13 cm) attained by 0-group pikeperch at the end of the summer was initially almost as large as that attained by piscivorous 0-group pikeperch in Tjeukemeer and IJsselmeer, but decreased over the years (Fig. 2). This decrease could not be attributed to a decrease in summer temperature ($R^2 = 0.01$). The size distribution at the end of the growing season, which was unimodal in the first couple of years, became significantly and strongly positively skewed (Fig. 3), and finally bimodal in later years. In the first 3–4 years the size distribution was probably unimodal throughout the season, as is concluded from the mid-summer situation in 1991 (Fig. 2). Food

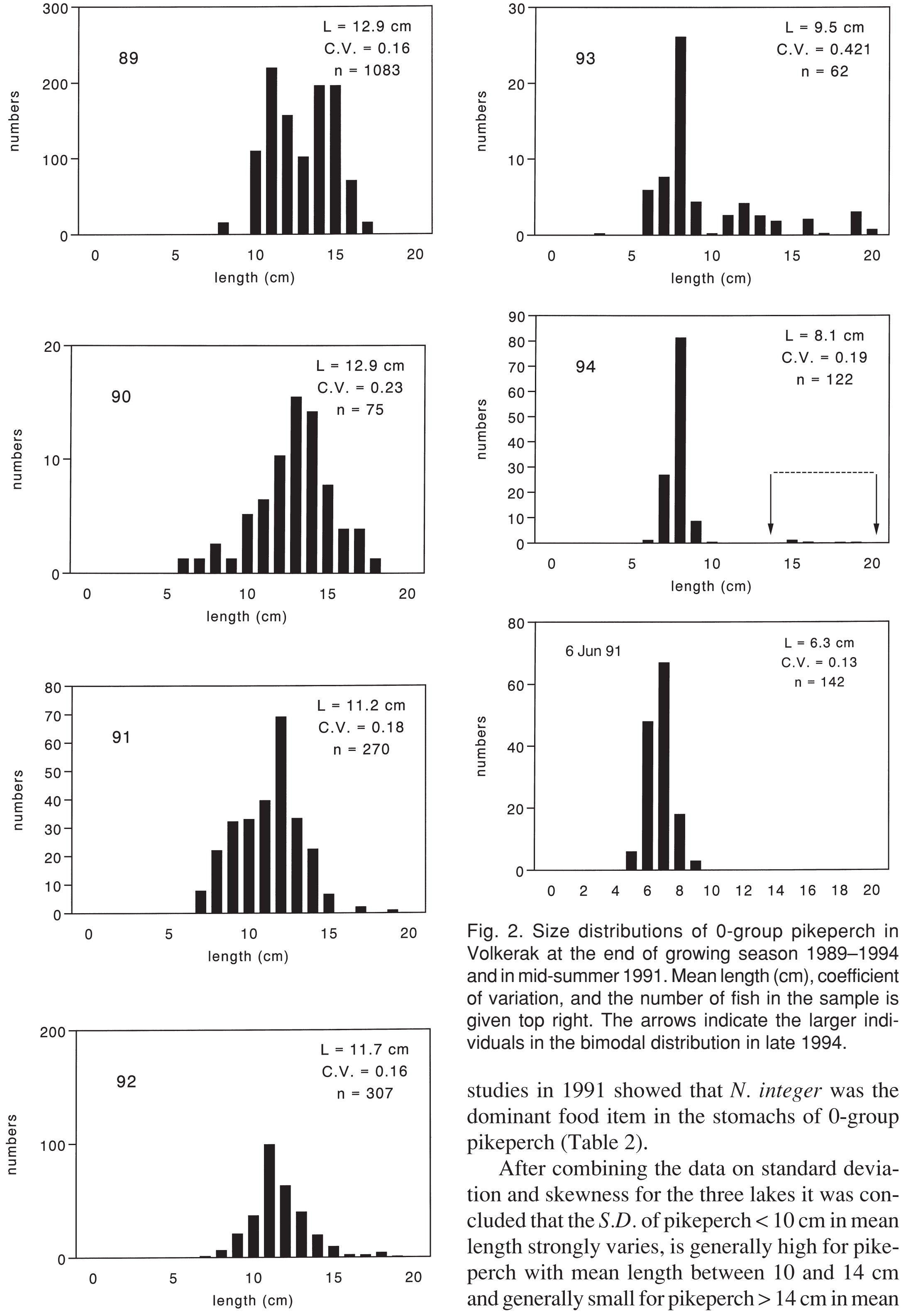

Fig. 2. Size distributions of 0-group pikeperch in Volkerak at the end of growing season 1989–1994 and in mid-summer 1991. Mean length (cm), coefficient of variation, and the number of fish in the sample is given top right. The arrows indicate the larger individuals in the bimodal distribution in late 1994.

studies in 1991 showed that *N. integer* was the dominant food item in the stomachs of 0-group pikeperch (Table 2).

After combining the data on standard deviation and skewness for the three lakes it was concluded that the *S.D.* of pikeperch < 10 cm in mean length strongly varies, is generally high for pikeperch with mean length between 10 and 14 cm and generally small for pikeperch > 14 cm in mean

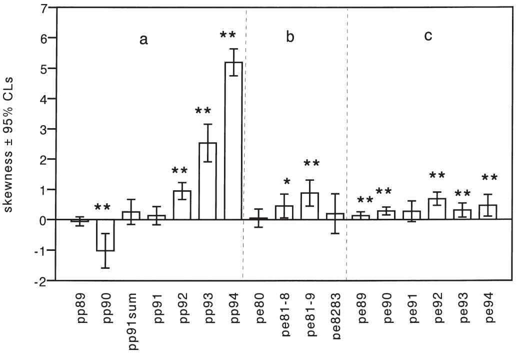

Fig. 3. Skewness of (a) 0-group pikeperch in Volkerak, (b) year-class 1980 of perch in Tjeukemeer in 1980 and 1981 and in winter 1982–1983, (c) 0-group perch in Volkerak. The asterisk indicates the significance of the skewness (* $p < 0.05$, ** $p < 0.01$).

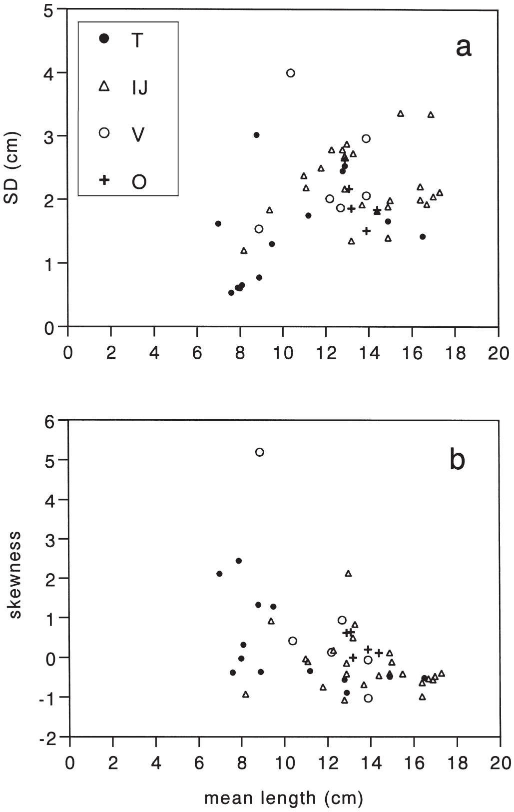

Fig. 4. Standard deviation (a) and skewness (b) in the size distribution of 0-group pikeperch and walleye at the end of the first growing season as a function of mean length (*TL*, cm) attained. T = Tjeukemeer, IJ = IJsselmeer, V = Volkerak, O = Oneida Lake.

length (Fig. 4). Skewness shows a decreasing trend over these size categories and is mostly negative for pikeperch > 14 cm in mean length. In Fig. 4 the data for walleye used for comparison refer to the 1960–1964 situation in Oneida Lake and were read from graphs in Forney (1966). The size distribution of 0-group walleye in years with a somewhat slower growth had a slight positive skewness. In the period 1956–1975 mean length attained by 0-group walleye only varied between 12 and 17 cm (Forney 1966, 1976).

3.2. Perch

In Tjeukemeer, 0-group perch are mainly zooplanktivorous (Van Densen 1985b) and reaches sizes of ca. 6–8 cm. The earliest onset of piscivory was observed for 1-group perch in summer 1981 (Fig. 5), when 0-group smelt densities were consistently high (10/m^2). The onset of piscivory, determined by the length at which the frequency of occurrence of fish prey in stomachs containing food was 50%, increased from 9.5 to 11 cm, between early August and late September 1981. Although the LF-distribution of these 1-group perch became significantly and positively skewed at the end of this summer (Fig. 3) it did not become bimodal (Fig. 5). After three summers even the skewness had become insignificant.

In IJsselmeer, the size of perch at the onset of piscivory varied between 11 and 15 cm (1- or 2-group fish), and was smaller in situations with high 0-group smelt densities or a large *Daphnia* size in the lake (Buijse 1992). Here, as in Tjeukemeer, size bimodality was never observed, but in years when only the large perch were piscivorous the size distribution of the cohort became positively skewed, with maximum coefficient of variation of 11.1% and maximum skewness of 1.54 in the cohort size distribution of females (Buijse 1992).

Table 2. Frequency of occurrence (%) of the food items in the food of 0-group pikeperch in Volkerak.

Date	*n*	Full	Frequency of occurrence (%)			
			Zoopl.	Neomysis	Fish	Others
5 Aug 91	116	95	7.7	83.0	–	9.3
5 Nov 91	133	128	–	97.7	–	2.3

In Volkerak, the LF-distribution for 0-group perch was always unimodal and, with the exception of 1991, was always significantly and positively skewed (Figs. 3 and 6). The sizes attained by 0-group perch in the period 1989–1994 were not correlated with temperature ($R^2 = 0.03$). In the first three years, the average size of 0-group perch (11.6–12.2 cm) was as large as that of 1-group perch in Tjeukemeer, but in the three succeeding years they fell into the size range (5–9 cm) for 0-group perch in Tjeukemeer (1976–1988) (Mooij *et al.* 1994) and IJsselmeer (1966–1989) (Buijse 1992), which are mainly zooplanktivorous (Van Densen 1985b, Buijse 1992).

3.3. Variance in the size distribution of cohorts of pikeperch and perch

At the end of the growing season, the coefficient of variation (*C.V.*) in the size distribution of 0-group pikeperch (max 0.42) was generally larger than for perch (max 0.16) (Fig. 7a and b). In Tjeukemeer and IJsselmeer, the *C.V.* was small when either the 0-group pikeperch was < 8 cm and unable to become piscivorous, or when most of the pikeperch were > 12 cm and had successfully switched to piscivory (Fig. 7a). Between 8- and 12-cm average length the *C.V.* was relatively large. As pikeperch age, the variance in their cohort size distribution decreases: *C.V.* 0.07, 0.08, 0.05 and 0.06 after 2, 3, 4 and 5 years, when pikeperch in Tjeukemeer had attained sizes of 29, 41, 48 and 53 cm respectively. This implies that the standard deviation in the cohort size distribution stayed relatively constant (2–3 cm).

The intra-cohort variance in perch lengths in Tjeukemeer and IJsselmeer was small after their first summer (*C.V.* = 0.05–0.10), but increased when perch switched to piscivory in their second (Tjeukemeer) or third summer (IJsselmeer) (Fig. 7b).

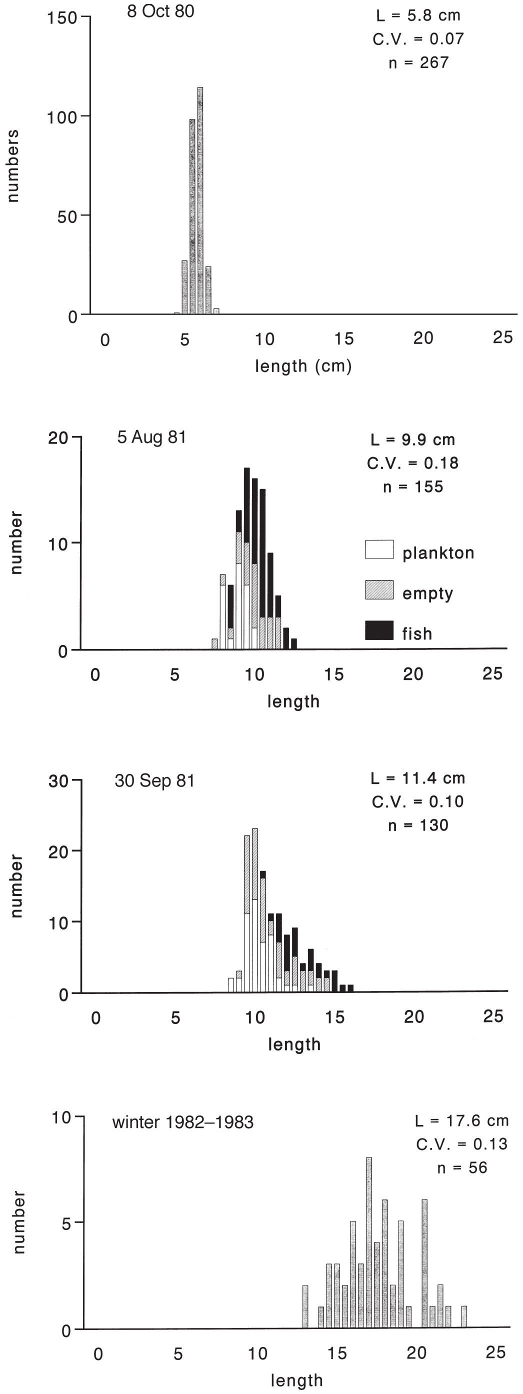

Fig. 5. Size distributions of the [1980] cohort of perch in Tjeukemeer after the first summer, in middle and at the end of the second summer, and at the end of the third summer. Mean length (cm), coefficient of variation (*C.V.*), sample size are shown. It is assumed that 0-group perch with empty stomachs were piscivorous.

4. Discussion

High densities of macro-invertebrates like *N. integer* seem to enhance the growth and recruitment of pikeperch and perch in Dutch inland waters. In the first years after the freshening of Volkerak, the 0-group pikeperch ate mainly *N. integer* and

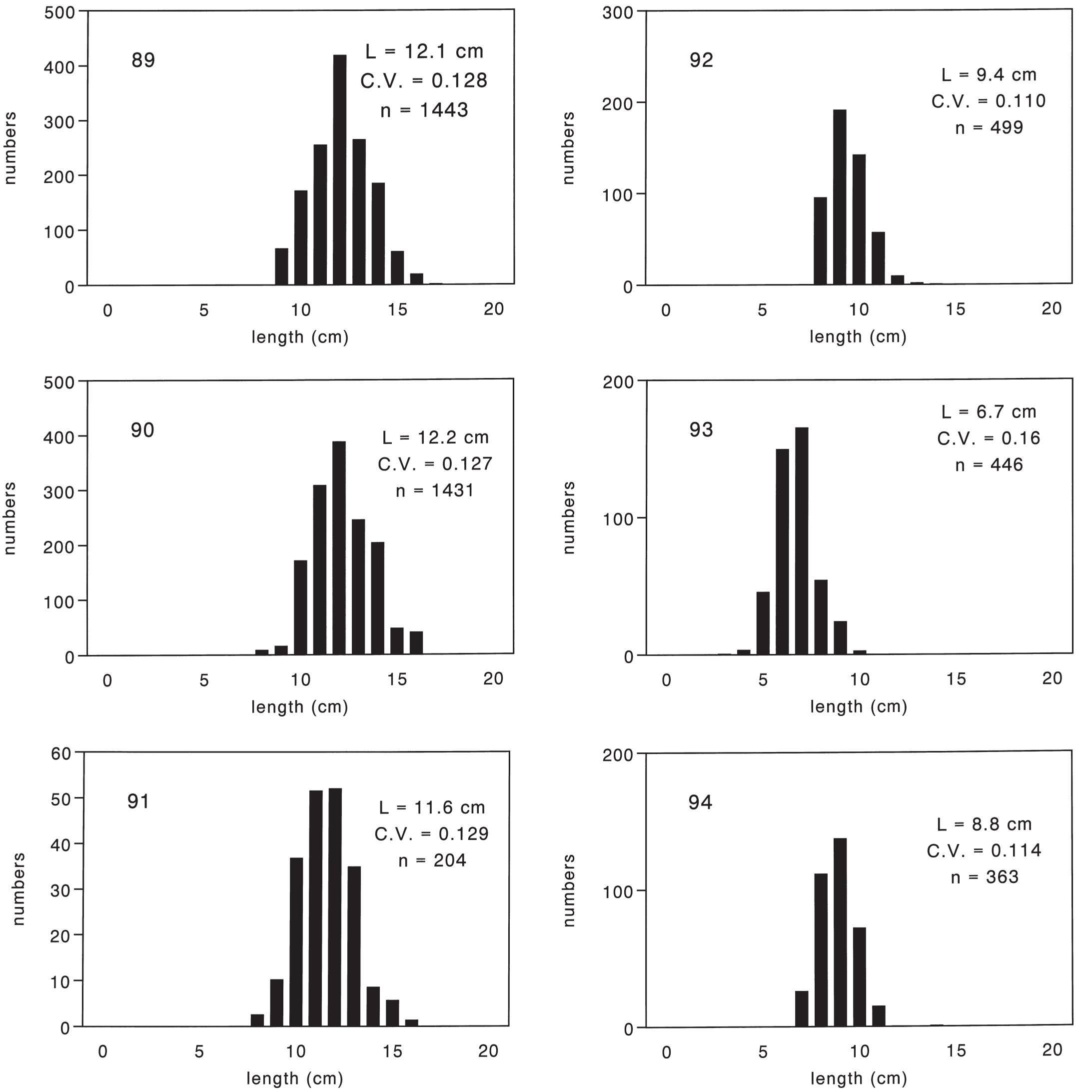

Fig. 6. Size distributions of 0-group perch in Volkerak at the end of growing season 1989–1994. Mean length (cm), coefficient of variation (*C.V.*), and sample size are shown.

grew to an average size of > 10 cm without intracohort size differentiation as is evidenced from the 1991 data. Also, food studies in Volkerak in late 1992 indicated that *N. integer* was prevalent in the diet of 5–15-cm pikeperch (Ligtvoet 1995). Most pikeperch in the 15–25-cm size range (1-group pikeperch) had already made the shift to piscivory with a dominance of ruffe and roach in the diet and a low incidence of cannibalism (Ligtvoet 1995). The growth pattern of older pikeperch in Volkerak is very similar to that in IJsselmeer. Length at age for 2-, 3-, 4- and 5-year-old pikeperch in Volkerak was (1992): 30.2–42.3–49.3–54.3 cm (Ligtvoet 1995), and in IJsselmeer 28.1–39.5–47.1–53.8 cm (Willemsen 1977). The successful switch of yearling piscivorous pikeperch in Volkerak to a non-smelt fish diet, as deduced from its fast growth in later years, shows that the absence of smelt from this reservoir was of less importance in the early years of this freshened ecosystem.

In later years, lower densities of *N. integer* in Volkerak may have caused 0-group pikeperch growth to vary. In 1994, juvenile roach may have become available as fish prey for relatively few 0-group pikeperch because of the expanded stocks of cyprinids. Variance in the size distribution of 0-group pikeperch at the end of the 1994 growing season was large with a second mode of probably piscivorous pikeperch of ca. 15–20 cm. High variance in pikeperch size may be associated with low pikeperch recruitment in Volkerak, given the lower survival rates of < 10 cm pikeperch observed in Tjeukemeer and IJsselmeer (Van Densen 1985a, Buijse & Houthuijzen 1992).

In IJsselmeer and Tjeukemeer, the availability of smelt as an alternative to small-sized zooplankton governs the process of cohort splitting for 0-group pikeperch. In these lakes, it is mainly smelt which guarantees an ultimate size of over 10 cm at the end of the first growing season and a higher survival rate for the large-sized piscivores in the cohort.

Inter-annual variance of mean length and standard deviation of 0-group walleye in Oneida Lake was small in comparison with the variance observed for 0-group pikeperch in the three Dutch lakes. Still, variance in mean length of walleye could be explained from the annual variation in lake temperature and in the growth of 0-group yellow perch, *Perca flavescens*, its principal prey item (Forney 1966). The probability of a complete mismatch between predator and principal prey fish, as observed for 0-group pikeperch and smelt in cold summers in Tjeukemeer, seems to be small in Oneida Lake. Fast-growing 0-group yellow perch, however, can outgrow gape-limited predation by 0-group walleye at the end of the summer and this explains part of the small variance in walleye growth (Forney 1966). The relatively small differences in walleye growth still have consequences for subsequent cohort survival, because adult walleyes select smaller individuals in a cohort (Chevalier 1973).

Cohorts of 0-group perch in Volkerak did not show differential growth. The 0-group perch fed both on zooplankton and *N. integer* in the early years (Houthuijzen *et al.* 1993), and most probably on zooplankton only in later years, when length attained was in the same range as observed for the mainly zooplanktivorous 0-group perch in IJsselmeer and Tjeukemeer. The size attained by perch after 2 summers was considerably higher in Volkerak in the early years than in IJsselmeer: mean lengths ranged from 19.9 to 23.1 cm in Volkerak in the period 1989–1992 (Ligtvoet 1995), as compared with 14.2 cm on average in IJsselmeer (Willemsen 1977). After 3 years, all perch in IJsselmeer had become piscivorous and reached an average size of 19.8 cm.

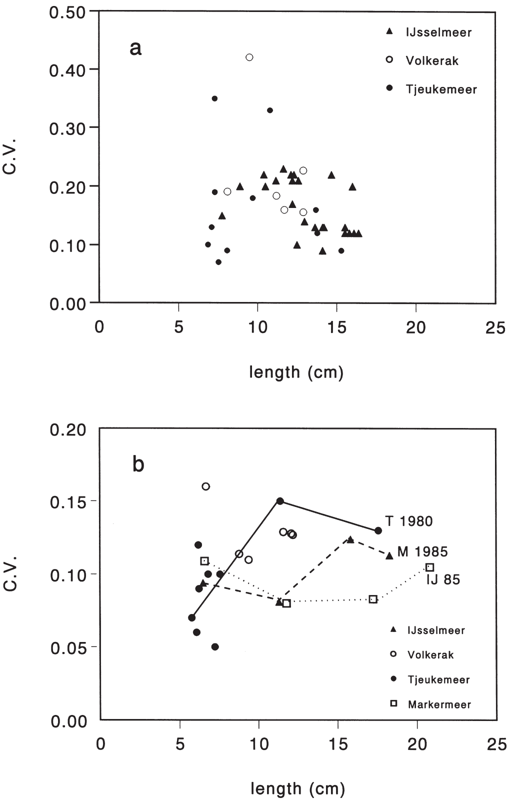

Fig. 7. (a) Coefficient of variation in size distribution of 0-group pikeperch at the end of the growing season in IJsselmeer, Volkerak and Tjeukemeer. *C.V.*s for IJsselmeer were based on data in Buijse and Houthuijzen (1992). (b) Coefficient of variation in size distribution of 0-group perch at the end of the growing season in Tjeukemeer and Volkerak, and coefficient of variation of perch of year-class 1980 in Tjeukemeer, year-class 1985 in IJsselmeer and year-class 1985 in Markermeer, the isolated southern part of IJsselmeer. Data for IJsselmeer and Markermeer are from Buijse (1992).

The onset of piscivory in perch was advanced in the developing Volkerak ecosystem. In late 1990, the food of up to 30-cm perch in Volkerak was still dominated by large-sized zooplankton and *N. integer* (Houthuijzen *et al.* 1993). But, in late 1992, 15–25-cm perch had switched to piscivory with a dominance of ruffe and roach in the diet and a low incidence of cannibalism (Ligtvoet 1995). Although perch in IJsselmeer utilize macro-invertebrates, especially *Gammarus* spp. and to a much lesser extent *N. integer* and chironomids (Buijse 1992), the densities of these food organisms are apparently never high enough to enable 0-group perch to reach sizes larger than 9 cm. The onset of piscivory in 10–15-cm perch in IJsselmeer and Tjeukemeer, at high smelt densities, did not provide for a growth advantage in comparison with Volkerak perch, which in the early years continued to feed on invertebrates at that length. The absence of bimodality in the size distribution of the 1980 perch cohort in Tjeukemeer in 1981, when they did not use macro-invertebrates as transition food between the zooplanktivorous and the piscivorous feeding stage, also proves the limited gain of a shift to piscivory for 10–20-cm perch. It is concluded that the high abundance of large-sized zooplankton, and of *N. integer* in particular, guarantees sustained growth of perch in Volkerak. Faster growth shortens the life stage in which perch are vulnerable to predators and assures higher survival rates and rates of recruitment to the adult population (Nielsen 1980).

It is not yet clear to what extent physiological factors like chloride content, fish predation pressure and other biotic factors related to the eutrophication process explain the variance in the stocks of *N. integer* in inland waters (Bremer & Vijverberg 1982). As chloride content in Volkerak was more or less stable during the study period, we assume that predation by an increasing fish stock biomass of cyprinids and ruffe depressed the densities of *N. integer*. When the average size of the zooplankton in Volkerak is lowered from increased predation pressure by small zooplanktivorous cyprinids and ruffe, the initially small gap in the size (energy) distribution at ca. 100 000 mCal, in the absence of smelt, will become wider at its lower end (100–10 000 mCal).

The largest discontinuity in the size (energy) distribution may be found in eutrophic freshwater ecosystems with a high density of zooplanktivores, depressing medium- and large-sized cladocerans, and with *N. integer* and smelt absent or present in low densities. Here the onset of piscivory of pikeperch is based on cannibalism or on the consumption of the relatively slender roach, *Rutilus rutilus*, in the littoral zone (Van Densen 1986 *et al.*, Frankiewicz *et al.* 1996). Although medium- and large-sized prey fish might be abundant in such systems, recruitment to the stocks of piscivores might still be hampered both in the case of pikeperch and perch.

Certainly density-dependent processes in the freshwater fish community intensify with increasing trophic state of the ecosystem, especially because of the increasing stocks of cyprinids and of benthivorous ruffe. Juvenile competitive bottlenecks, which are described for piscivores like perch competing with roach at the zooplankton feeding stage (Persson 1988), also might occur in the fish communities described here, although the interactions seem to be more complex. Intensive competition for macro-invertebrates between juvenile pikeperch (or perch) and ruffe, an efficient benthivore (Bergman 1991), could be the mechanism for a juvenile competitive bottleneck for the recruiting pikeperch. Still, in the absence of *N. integer* but at high summer temperatures, and with smelt present in abundance, recruitment of 0-group pikeperch to the piscivorous stage could be almost complete and thus non size-selective, as was occasionally found in Tjeukemeer and IJsselmeer (Van Densen 1985a, Buijse & Houthuijzen 1992). In the absence of smelt, cannibalism or predation on roach could enable some pikeperch to become piscivorous.

Predation may be less size-selective within cohorts of perch than of pikeperch, because of the smaller variance in individual size in perch cohorts. In systems like Tjeukemeer and IJsselmeer, size differentiation in perch cohorts develops in the second or third summer, depending on whether prey fish densities are high during the second or during the third growing season. Theoretically, size differentiation does even not necessarily have to occur if all perch are large enough to switch fully to piscivory. But the switch is seldom absolute, and in early summer of the following years, a temporary return to zooplanktivory is possible.

Size differentiation within cohorts of pikeperch and perch can be related to species and system characteristics. Bowker (1995) suggested that most short-lived species or r-strategists show a rapid decline in the *C.V.* in length with age, whereas K-strategists still have a large *C.V.* in length at a higher age, possibly because of strong competition for food or space. Pikeperch might belong to the first category, but perch is difficult to categorize with a more system-related development in the variance over the years, increasing after 2 or 3 years as in Tjeukemeer and IJsselmeer, or with a monotonous decrease in the *C.V.* like in Volkerak in the early years.

A system approach to understanding size differentiation in fish cohorts based on the size distributions of food items available seems promising, as there is a growing understanding of how system characteristics influence size distributions of organisms, for example macro-invertebrates (Rasmussen 1993, Rodriguez & Magnan 1993). The availability of medium-sized prey (*Hexagenia* spp., trichopterans, amphipods) preferred by yellow perch decreased during the process of eutrophication in Western Lake Erie and caused the stunting of yellow perch (Hayward & Margraf 1987). This finding suggests that a lake characteristic like trophic status may very well affect the biomass size distribution of potential food organisms, macro-invertebrates in particular, and in this way also the growth of amongst others percid fish. In Oneida Lake, the macro-invertebrate *Hexagenia limbata* was important in the diet of walleyes in early summer, but was replaced by chironomids and fish when *H. limbata* declined in the 1960s, and subsequently more predation pressure was exerted on recruiting 0-group fish, including young walleye (Forney 1980).

Further study is needed of Volkerak and other lakes to test our hypotheses on size differentiation. In this study, only three lakes were compared, although the time series for Tjeukemeer (13 years) and IJsselmeer (24 years) were of considerable length. Fish stocks in Volkerak should be monitored as the lake becomes more eutrophic to assess the persistence of growth variability of 0-group pikeperch and growth retardation of 0-group perch, and their consequences for year-class success. More lakes should be sampled to test hypotheses which could explain the high or low availability of macro-invertebrates. In brackish or lightly brackish waters, salinity could possibly be as important as low fish predation pressure in explaining the relatively high abundance of these medium-sized prey organisms. Also, lakes which have different temperature regimes should be studied. At a much higher latitude, where growth may be limited by cooler temperatures (Lehtonen 1979), pikeperch will shift to piscivory at a later age, and this will probably limit the variance in the size distribution of 0-group pikeperch.

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