Zonation of a lentic ecotone and its correspondence to life history strategies in fish

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Abstract

A drainage channel network southeast of lake Neusiedl was investigated for fish species distribution. The network consists of relatively large and permanent channels providing a stable habitat for fish and smaller unstable channels drying up approximately once every five years. A consistent pattern of fish species distribution was found which could be interpreted with the help of a new triangular model of life history adaptations. In permanent channels so-called periodic and equilibrium species prevail whereas temporary channels are inhabited by opportunistic species exclusively. In the drainage channel network a number of locally endangered fish species which have disappeared from the adjacent lake during the last decades were found suggesting that the channel network functions as a refuge for these fishes.

Introduction

Ecotonial habitats have great temporal and spatial heterogeneity and often display gradients in ecological factors within a relatively narrow area. Therefore they offer good opportunities to test ecological concepts (Wiens *et al.*, 1985; Pieczynska, 1990). In aquatic-terrestrial boundary zones, ecotone size and configuration depend on shore slope and water level fluctuation as well as depositional and erosional processes. Water level fluctuation creates shifting boundaries and causes changes in the proportion of aquatic and terrestrial species of animals and plants (Pieczynska, 1990). These fluctuations create changing water and moisture gradients which exhibit regular patterns in aquatic-terrestrial ecotones and are ecologically of great significance (Cowardin *et al.*, 1979). With increasing distance from a permanent water body, aquatic habitats become less stable. Near permanent bodies of water, seasonally flooded areas are often found which have a more or less predictable wet-and-dry cycle. Further away, aquatic habitats are created only by periodic flooding and have a higher probability of drying up (Cowardin *et al.*, 1979). Thus, water bodies distant from the main water body are less stable and less predictable in providing habitat for aquatic life.

The idea that stability of ecological factors correlates with life history strategies of organisms has been formulated by various authors (McArthur & Wilson, 1967; Murphy, 1968; Pianka, 1970; Schaffer, 1974; Stearns, 1976; Winemiller, 1992). Older models of life history strategies were unidimensional: r-K continuum (McArthur & Wilson, 1967; Pianka, 1970) as well as the 'bet-hedging' model (Murphy, 1968; Schaffer, 1974). Winemiller recently (1992) developed a triangular life history model. He distin-
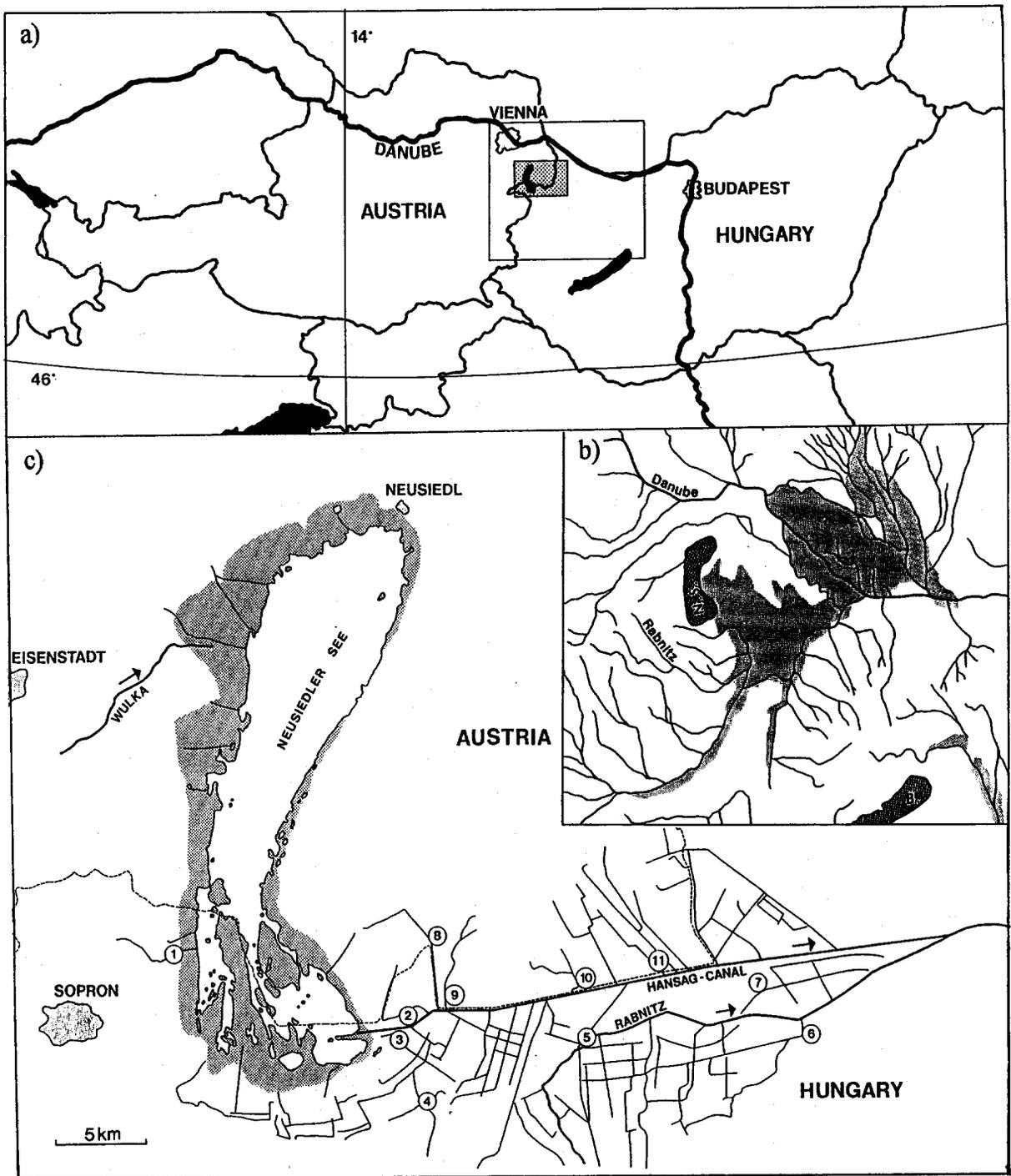
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Fig. 1. Location of lake Neusiedl at the Austrian-Hungarian border (a), the regularly inundated areas in the vicinity of the lake before water control measures (drawn after a map in the Hungarian National Atlas) (b), and the location of eleven sampling stations within the current drainage channel network of the Hansag region (c).

guished three endpoints on the adaptive surface of life-history strategies based on trade-offs between three fundamental demographic axes (age at maturity, fecundity, and juvenile survivorship), despite reservations concerning the use of dimensions in defining life history strategies (Southwood, 1988; Stearns, 1992). The endpoints are represented by an 'opportunistic strategy', maximizing colonization capabilities in environments that change frequently or stochastically, a 'periodic strategy', which is favored in environments with large-scale cyclic or spatial (seasonal) variation, and an 'equilibrium strategy', which is favored in environments with low variation in habitat quality and strong biotic interactions. The model has been developed for fish but explains also life history adaptations of many other animal groups such as amphibians, reptiles, birds, mammals, insects, and many other invertebrates (Winemiller, 1992). The interaction of habitat type and stability, especially of terrestrial-aquatic transition zones, and fish species distribution has been the focus of a number of investigations in stream ecology (see Schlosser, (1991) for a review, and other articles in this volume). Lentic systems have received less attention up to now.

This study examines the extent to which Winemillers life history model can explain fish species composition in habitats of different stability within a lentic ecotone. A second aspect of the study was to evaluate the role of the ecotone as a refuge for locally endangered fish species that disappeared from the adjacent lake during the last decades.

Material and methods

Lake Neusiedl is situated on the Austrian-Hungarian border 50 km south-east of Vienna (Fig. 1a). The area south-east of lake Neusiedl, the so-called Hansag, was a huge swampland (about 300 km^2) connecting the shallow lake (mean $z = 1$ m) with the floodplains of the Danube and the Rabnitz and Raab rivers (Fig. 1b). In 1911 an artificial outlet of the lake, the Hansag-canal, was finished and since then the area was successively drained and converted to farmland. Figure 1c shows the locations of 11 sampling stations within this drainage channel network where fish populations were studied during a one-year period. Sampling stations were located at 9 drainage ditches of different sizes and distance from the lake and at two little brooks. At each sampling point a stretch of 100 m was electrofished with a 7.5 kW direct current electrofishing device four times during the study period. Fish larger than 10 cm were identified, weighed and measured in the field and then released. Smaller fish were subsampled, fixed with formalin, and brought to the laboratory for further analysis. Indigenous fish species were categorized according to Winemiller's life-history model based on literature data on age at maturity, fecundity and parental investment (a correlate of juvenile survivorship, see also Winemiller (1989)) (Deelder & Willemsen, 1964; Backiel & Zawisza, 1968; Thorpe, 1977; Kizina, 1987; Lelek, 1987; Terofal, 1984; Muus & Dahlström, 1981; Toner & Lawler, 1969; Ladiges & Vogt, 1965). Fish species in which females usually reach sexual maturity after two years, fecundity is more than 100000 eggs per average female spawning once per breeding season, and can be classified as nonguarders and open substrate egg-scatterers (sensu Balon, 1984) were considered relative periodic species (Table 1) (with one exception: Stizostedion lucioperca which is a guarder and nest spawner but was also considered a periodic species because of its late maturation and high fecundity). Species with essentially the same features but displaying fractional spawning and in some cases lower fecundities were placed between the periodic and the opportunistic endpoints. These were further divided between those tending more toward the periodic strategy because of lower individual growth rates and maturation after three years versus those tending more to the opportunistic strategy because of higher growth and sexual maturation after two years (species indicated with an asterix in Table 1). Misgurnus fossilis was classified as an opportunistic species because females can reach sexual maturity after one year, fecundity is low (Käfel, 1991) and it is a non-guarder

Table 1. Fish species found in the larger, permanent channels (2,6,7) and in the smaller, temporary channels (4,9,10) respectively, and their life-history category after Winemiller, 1991.

Species	Channel no.	Life history category
Permanent channels		
Esox lucius	2,6	periodic
Stizostedion lucioperca	2	periodic
Perca fluviatilis	2,6,7	periodic
Gymnocephalus cernua	2	periodic
Abramis brama	2,6,7	periodic
Ambramis ballerus	2	periodic
Rutilus rutilus	2,6	periodic
Scardinius erythrophthalmus	2,6,7	periodic
Blicca bjoerkna	6	periodic
Pelecus cultratus	2	periodic
Alburnus alburnus	2,6,7	periodic-opportunistic
Tinca tinca *	2,6,7	periodic-opportunistic
Carassius carassius *	6,7	periodic-opportunistic
Carassius auratus gibelio *	2,6,7	periodic-opportunistic
Misgurnus fossilis *	2,6,7	opportunistic
Leucaspius delineatus *	2,6,7	opportunistic-equilibrium
Proterorhinus marmoratus *	6	opportunistic-equilibrium
Rhodeus sericeus amarus	6,7	opportunistic-equilibrium
Temporary channels		
Carassius carassius *	9	periodic-opportunistic
Carassius auratus gibelio *	4,9,10	periodic-opportunistic
Leucaspius delineatus *	9	opportunistic-equilibrium

(*sensu* Balon, 1984). The other species in Table 1 have similar features but display territoriality and egg guarding. They were therefore placed between the opportunistic and the equilibrium endpoints of the adaptive surface of life history strategies. This group was further divided into a group tending more to the equilibrium strategy (one species, the bitterling *Rhodeus sericeus amarus* which has very high juvenile survival due to hiding eggs in freshwater mussels) and the rest with comparably higher juvenile mortality tending more to the opportunistic strategy (species indicated with an asterix in Table 1). To substantiate this grouping we performed a cluster analysis using the literature data mentioned above. To elucidate the relationship between life history groups and habitat characteristics a redundancy analysis was made using the computer program CANOCO (Ter Braak, 1989). Habitat characteristics used in this analysis were channel size (area of cross-section) and the nominal variable 'permanent' *vs* 'temporary'.

Results

Table 2 gives an overview of our catches at the 11 sampling points. Twenty six fish species were found during the study. At sampling points close to the lake (sites 1, 2, 3) a fish community very similar to the one in the lake was found. In the channels further away the fish community changes and a number of small sized, locally endangered fishes were found. Figure 2 shows the development of the fish community in lake Neusiedl during the last decades (after Herzig-Straschil, 1989) in comparison to the species found during our study. Several of the locally endangered fish species that disappeared from the lake were found in the drainage channel network of the Hansag region. The sampling point at the Rabnitz brook (site 5) shows a quite distinct fish community with many rheophilic fish species found only in this place.

To address the question of channels with different stability, we compared three larger, deeper, and relatively permanent channels (sites 2, 6, 7) with three smaller, temporary channels (sites 4, 9, 10) which had completely dried up in the summer of 1990 and were filled again during our study. According to long term water level measurements of the lake, the smaller channels dry up approximately once every five years. Table 1 shows the fish species caught in the permanent and the temporary channels respectively and their classification according to Winemiller's life-history model. The result of the cluster analysis, which produced species groups identical to our main groups, is shown in Fig. 3. The majority of fish species caught in the permanent channels belong to a group characterized by a relative periodic life-history strategy or can be placed between the periodic and the opportunistic endpoints (15 species out of 20). The four species placed between the periodic and the opportunistic endpoints were further divided as outlined above: one species tending more to the periodic strategy and three species tending more to the opportunistic strategy (marked by an asterix in Table 1). Only one species was classified as opportunistic and four species were placed between the opportunistic and

Table 2. Numbers of individual fish caught at 11 different sampling stations located in the drainage channel network of the Hansag region (for sampling station numbers refer to Fig. 1c).

Species	Sampling stations										
	1	2	3	4	5	6	7	8	9	10	11
Anguilla anguilla	5	8	1	0	0	0	0	0	0	0	0
Esox lucius	0	2	0	0	0	18	0	0	0	0	2
Stizostedion lucioperca	0	9	0	0	0	0	0	0	0	0	0
Perca fluviatilis	0	1	0	0	0	17	3	0	0	0	0
Pelecus cultratus	0	4	0	0	0	0	0	0	0	0	0
Alburnus alburnus	0	156	12	0	44	1	1	0	0	0	0
Abramis brama	0	74	11	0	5	16	1	0	0	0	0
Blicca bjoerkna	0	0	0	0	0	1	0	0	0	0	0
Rutilus rutilus	15	60	90	0	86	21	0	0	0	0	0
Tinca tinca	0	2	3	0	2	23	26	0	0	0	0
Scardinius erythrophthalmus	2	13	14	0	10	66	7	3	0	0	0
Gymnocephalus cernua	0	8	0	0	1	0	0	0	0	0	0
Abramis ballerus	0	1	0	0	0	0	0	0	0	0	0
Carassius auratus gibelio	8	39	105	55	2	88	101	104	3	3	0
Carassius carassius	0	0	0	0	0	26	76	0	0	0	0
Misgurnus fossilis	0	1	0	0	5	26	7	0	0	0	0
Leucaspius delineatus	0	4	0	0	1	3	1	0	1	0	0
Rhodeus sericeus amarus	0	0	6	0	91	145	117	0	0	0	0
Proterorhinus marmoratus	0	0	0	0	8	1	0	0	0	0	0
Pseudorasbora parva	0	2	5	0	15	14	6	0	0	0	0
Leuciscus cephalus	0	0	0	0	104	0	0	0	0	0	0
Leuciscus leuciscus	0	0	0	0	10	0	0	0	0	0	0
Gobio gobio	0	0	0	0	22	0	0	0	0	0	0
Gobio albipinnatus	0	0	0	0	94	0	0	0	0	0	0
Chondrostoma nasus	0	0	0	0	2	0	0	0	0	0	0
Barbus barbus	0	0	0	0	1	0	0	0	0	0	0
Total	30	384	247	55	503	466	346	107	4	3	2
Grand Total	2147										

the equilibrium endpoints. The latter were further divided into species nearer to an opportunistic strategy (three species) and those nearer to an equilibrium strategy (one species, the bitterling *Rhodeus sericeus amarus*). In this way, two main groups were distinguished: a relative opportunistic group of species (marked with an asterix in Table 1) and a periodic-equilibrium group. In the permanent channels, species of the periodic-equilibrium group outnumber the opportunistic group (13:7). However in the temporary channels only three species were found, all of which belong to the opportunistic group. This pattern is repeated on the level of individuals. Figure 4 shows percentages of individuals belonging to the periodic-equilibrium or the opportunistic group of

species respectively. In the permanent channels 66% of the individuals belong to species categorized as either periodic or equilibrium whereas 33% of the individuals were assigned to species of the opportunistic group. In the temporary channels all the fishes caught belong to opportunistic species.

The redundancy analysis of life history groups and habitat characteristics revealed a highly significant relationship. The eigenvalues of the ordination axes are 0.46, 0.35, and 0.03 respectively, the 'species-environment' correlation coefficients being 0.85 and 0.26. A Monte Carlo permutation test showed significance of the first ordination axis ($p < 0.05$).
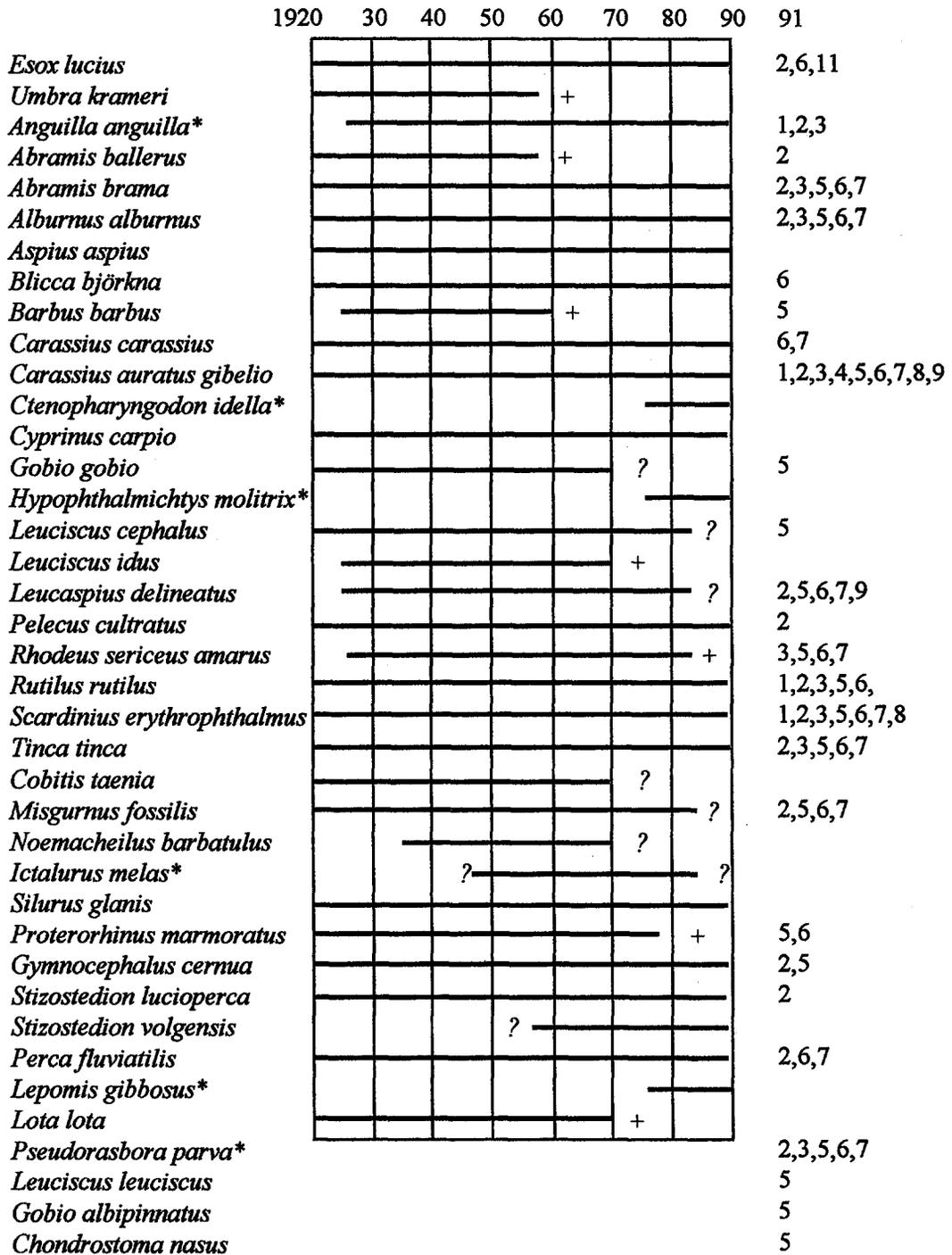
	1920	30	40	50	60	70	80	90	91
Esox lucius									2,6,11
Umbra krameri					+				
Anguilla anguilla*									1,2,3
Abramis ballerus					+				2
Abramis brama									2,3,5,6,7
Alburnus alburnus									2,3,5,6,7
Aspius aspius									
Blicca björkna									6
Barbus barbus					+				5
Carassius carassius									6,7
Carassius auratus gibelio									1,2,3,4,5,6,7,8,9
Ctenopharyngodon idella*									
Cyprinus carpio									
Gobio gobio						?			5
Hypophthalmichtys molitrix*									
Leuciscus cephalus							?		5
Leuciscus idus					+				
Leucaspius delineatus							?		2,5,6,7,9
Pelecus cultratus									2
Rhodeus sericeus amarus							+		3,5,6,7
Rutilus rutilus									1,2,3,5,6,
Scardinius erythrophthalmus									1,2,3,5,6,7,8
Tinca tinca									2,3,5,6,7
Cobitis taenia						?			
Misgurnus fossilis							?		2,5,6,7
Noemacheilus barbatulus						?			
Ictalurus melas*			?					?	
Silurus glanis									
Proterorhinus marmoratus							+		5,6
Gymnocephalus cernua									2,5
Stizostedion lucioperca									2
Stizostedion volgensis			?						
Perca fluviatilis									2,6,7
Lepomis gibbosus*									
Lota lota						+			
Pseudorasbora parva*									2,3,5,6,7
Leuciscus leuciscus									5
Gobio albipinnatus									5
Chondrostoma nasus									5

Fig. 2. The development of the fish community of the lake since 1920 (after Herzig-Straschil 1989) in comparison to the species caught in the drainage channel network in 1991 (numbers on the right side refer to station numbers in Fig. 1c). —— occurrence confirmed, ? occurrence uncertain, + species extinct, * introduced species.
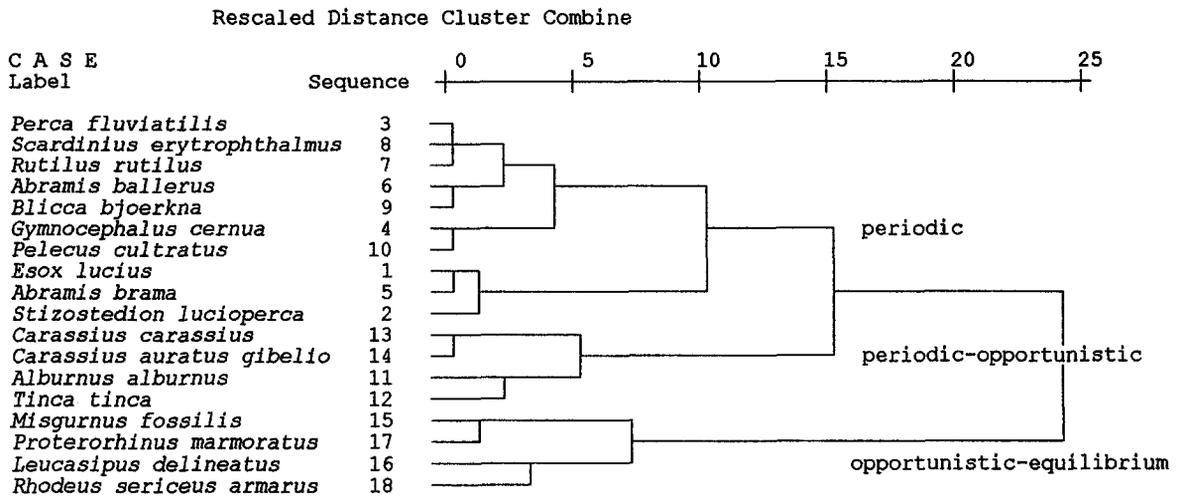
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                              Rescaled Distance Cluster Combine

  C A S E                                    0        5        10        15        20        25
  Label                       Sequence       +--------+--------+---------+---------+---------+

  Perca fluviatilis               3
  Scardinius erytrophthalmus      8
  Rutilus rutilus                 7
  Abramis ballerus                6
  Blicca bjoerkna                 9
  Gymnocephalus cernua            4                                              periodic
  Pelecus cultratus              10
  Esox lucius                     1
  Abramis brama                   5
  Stizostedion lucioperca         2
  Carassius carassius            13
  Carassius auratus gibelio      14                                   periodic-opportunistic
  Alburnus alburnus              11
  Tinca tinca                    12
  Misgurnus fossilis             15
  Proterorhinus marmoratus       17
  Leucasipus delineatus          16                                   opportunistic-equilibrium
  Rhodeus sericeus armarus       18
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Fig. 3. Dendrogramm showing the result of a cluster analysis of the native fish species based on life history characteristics.

Discussion

The finding of most of the locally endangered fish species in the drainage channel network of the
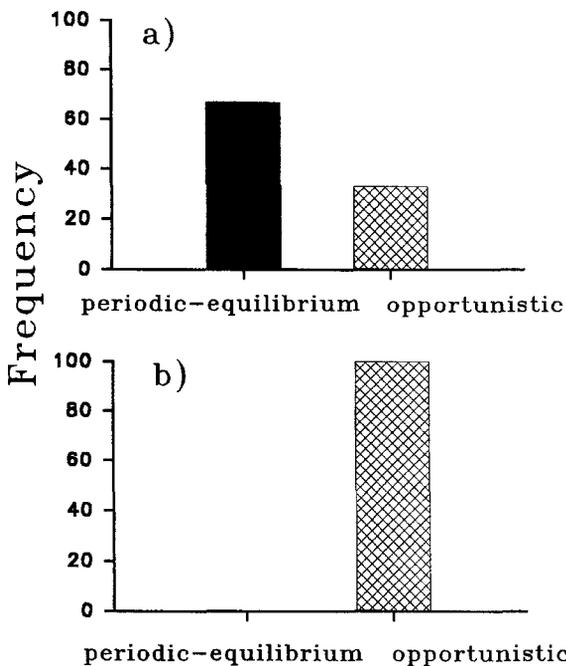
Fig. 4. Relative frequency (% of all individuals sampled) of individual fish belonging to the periodic or equilibrium groups of species or to the opportunistic group in (a) permanent channels and in (b) temporary channels.

Hansag region confirms the idea that this ecotone functions as a refuge for these fish species. The disappearance of these fishes from the lake has been attributed to the heavy stocking of non-native eel (*Anguilla anguilla*) (Waidbacher, 1985; Herzig-Straschil, 1989), a predator of small fishes (Lelek & Pelz, 1986; Tesch, 1991). In the drainage channels, eels are either absent or found in low numbers (maximum was four eels per 100 m) compared to the lake (where on average 100 eels per 100 m shoreline are found, Mikschi pers. comm.). However, other factors like eutrophication of the lake as well as the loss of natural water level fluctuations might influence the observed distribution of locally endangered fish species.

A clear trend was found with regard to the correlation of life history features of fish species and their distribution in habitats of different size and stability. Species classified as periodic or equilibrium dominate in relatively large and permanent channels, whereas relatively small and temporary channels were inhabited by opportunistic species exclusively. Channel size might be one factor influencing fish species distribution. However, two brooks (# 1 and 5) were comparable in size with the smaller channels but provide a more stable habitat for fishes. In these brooks, fish species of both groups, opportunistic as well as periodic-equilibrium species, were found.

The small channels were dried up in the summer of 1990, an incidence happening approximately once every five years. This situation leads to a complete destruction of the fish community in these habitats, which are recolonized from larger, deeper channels with rising water levels. Opportunistic species are supposed to have relatively high colonization abilities (Winemiller, 1992) due to their low age at maturity, small clutch size, and low parental investment per progeny (allowing several spawnings per year) leading to their prevalence in the smaller channels. Especially wild goldfish (*Carassius auratus gibelio*) dominated in newly flooded channels. This species has many of the opportunistic characters already mentioned and is known to reproduce gynogenetically leading to extremely low parental investment and consequently superior colonization abilities. In fact this species colonized large parts of the Danube system within the last three decades (Holcik, 1980).

In general, the observed pattern in fish species distribution corresponds well with the life history model proposed by Winemiller (1992). Nevertheless, the results appear unidimensional along a 'bet-hedging' axis, which is indicated in this model running from the opportunistic endpoint to a line connecting the periodic and equilibrium endpoints. However, in this study only two types of habitats were distinguished: relatively permanent and relatively temporary drainage channels. Since also the permanent channels show strong seasonal variation in many important ecological factors (e.g. temperature, water level, vegetation) relatively periodic species are expected in these habitats according to the triangular life history model. Habitats lacking seasonal variation in which 'true' equilibrium species in Winemiller's sense are expected, were not present and they might be rare in temperate regions. There, the scarcity of suitable habitats corresponds with the scarcity of species which can be classified as equilibrium species according to life-history features. This is expected to be more pronounced in Europe than in North America when differences in recolonization processes after the last ice age, *i.e.* reduced recolonization by southern species due

to the barrier of the Alps, are taken into account. Most of the families of teleost fishes exemplified in Winemiller (1992, Table 1) as having many equilibrium species are predominantly tropical or subtropical. *Cyprinidae*, either 'large minnows' or 'small minnows', which are categorized as relatively periodic and opportunistic strategists respectively represent the majority of species dealt with in the present study (Table 1). In fact we placed only one species, the bitterling (*Rhodeus sericeus amarus*), near an equilibrium life history strategy and it was only found in the permanent channels. Altogether a distinction between fish communities, dominated by periodic species on the one hand, and equilibrium species on the other hand, was neither possible nor was it expected according to habitat features. Insofar the studied ecotone provides a special case in Winemiller's triangular life-history model because of the absence of very stable habitats in which equilibrium species are expected. However, the usefulness of new models might be tested just as much if applied to special cases as if applied to general cases. The triangular life history model was found most useful for assigning fish species to different life history strategies because it provides a relatively objective system with measurable characters. The resulting scheme of life histories of the fish species caught was helpful in interpreting distribution patterns in the studied aquatic-terrestrial, lentic ecotone. In general life-history adaptations to habitats of different stability are important factors influencing species distribution in addition to other factors already investigated (Weinstein *et al.*, 1980; De Nie, 1987; Townsend & Peirson, 1988; Leslie & Timmins, 1990; Tonn, 1990; Winemiller & Leslie, 1992).

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