

TEMPORAL AND SPATIAL DYNAMICS OF 0+ *CHONDROSTOMA NASUS*, AT THE INSHORE ZONE OF A LARGE RIVER

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Received April 17, 1997
Accepted November 19, 1997

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Abstract

This paper focuses on the temporal and spatial distribution patterns of the "key species" *Chondrostoma nasus* during the first months of life. "Point abundance samples" were taken from May to August at weekly to monthly intervals and environmental variables (water velocity, water depth, substrate, structure, temperature) were recorded at each of the 1508 points. Habitat preferences of larvae and juveniles did not change significantly during ontogeny. Suitable habitat was defined as water velocity < 10 cm.s⁻¹. Short-term fluctuations of abundance, as a result of individuals immigrating from upstream spawning areas and emigrating individuals were observed. We present evidence that hydrology and the structural properties of inshore nursery zones are significant for the abiotic microhabitat conditions and the dynamics of temporal and spatial abundance of 0+ *C. nasus*. Our results suggest that the population of 0+ fish present in a nursery zone is not a stable unit, but a dynamic assemblage, structured by imports from upstream and downstream exports.

Key words: Larval fish, habitat preferences, niche shift, suitable habitat modelling, nursery zones

Introduction

Chondrostoma nasus is a characteristic fish species of the epipotamal zone of European rivers and their populations have declined drastically during the last few decades (L e l e k 1987, L u s k 1995, L u s k & H a l a č k a 1995). Therefore, the species has become a major research target, in order to analyse the causes of decline and to develop a means of habitat revitalisation. S c h i e m e r et al. (in press) proposed that the success of this riverine fish species will be determined primarily by the reproductive success and mortality during early development.

K e c k e i s et al. (1996) demonstrated that shoals of nase spawn in numerous sections of the main channel of the Austrian Danube. Thus they underlined the importance of the main channel for reproduction and recruitment of the nase. This finding is in contrast with the assumption that reproduction takes place only in shallow water tributaries. It remained unclear whether spawning in the main channel is part of a new behaviour pattern, induced by river channelisation and excision of side arms, or whether spawning in the main channel is a common reproductive strategy in a large river. They concluded, that the presence of appropriate river bed structures for spawning did not limit recruitment, but the connectivity and proximity of the spawning sites to high quality nursery zones was important. The availability of adequate nursery zones for 0+ fish in a river

channel gains additional significance, since the disintegration of the river and its floodplains has increased drastically in many river systems owing to regulation schemes. Recent studies have targeted the marginal habitats of river channels (Schiemer et al. 1991, Peňáz et al. 1991, 1992, Jurajda 1994, Persat et al. 1995, Scheidegger & Bain 1995, Schiemer et al. in press a and b, Baras et al. 1996, Wintersberger 1996) intensively, and it is argued that the nearshore areas with low current velocity may be the primary nursery zones, when substantial backwater and off-channel habitats are lacking.

The analysis of habitat use in the main channel of rivers showed that larval *C. nasus* are bound to sheltered lentic bays with low water velocities. With increasing body size in summer to autumn, they migrate to adjacent shallow gravel banks with water velocities of $< 50 \text{ cm.s}^{-1}$ (Schiemer et al. 1991, Baras et al. 1996, Wintersberger 1996). These habitat shifts are in accordance with the findings of studies within the floodplain (Copp et al. 1991, 1994, Kurmayer et al. 1996) where the abundance and relative frequency of the nase is low and restricted to lotic refuges in late summer.

Fish distribution, abundance and habitat shifts are known to be associated with physical features of the environment such as, water velocity (Schlosser 1985, Facey & Grossman 1990), water depth (Harvey & Stewart 1991, Wintersberger 1996), substrate type (Dolloff & Reeves 1990), food availability (Naesje et al. 1991, Greenberg 1991) and accompanied by ontogenetic changes in bioenergetic performance (Govoni et al. 1986, Wieser et al. 1988, Houde & Scheckter 1983, Houde 1988, Kaufmann 1990, Keckeis & Schiemer 1990, 1992) and foraging ecology (Brodeur 1991, Mills et al. 1985, Wanzenböck 1992). On the other hand, habitat is not rigid and the availability of habitat features changes at daily, seasonal, and yearly scales. The habitat characteristics are dynamically controlled by hydrology, especially patterns of current velocity and temperature depend on the inshore relief and the water level (Baras et al. 1996, Keckeis et al. 1997).

Drift migrations and downstream displacements are another important phenomenon affecting the abundance and distribution of riverine 0+ fish. Drift represents an important link in the migratory circle of fishes which favours the dispersion of fish (Mantifel et al. 1978) and the exploitation of high quality nursery areas (Prokeš & Peňáz 1979, Pavlov 1994). Downstream migrations are known to be influenced by behavioural mechanisms and hydrological factors such as water discharge, water level, water velocity, turbulence and water turbidity (Ottaway & Forrest 1985, Heggenes & Traaen 1988, Pavlov 1994, Persat et al. 1995). However, the consequences of these movements on population dynamics and in which way they influence growth, survival and recruitment still remains open (Pepin et al. 1995, Persat et al. 1995, Dew 1995, Mason et al. 1995).

The present paper will concentrate on the dynamics of temporal and spatial distribution patterns of the "key species" *C. nasus* at inshore nursery zones in a large river during their first months of life. The ultimate goal was to link population dynamics with autecological requirements, structural properties of the inshore zone and hydrological dynamics. Specific questions were addressed: (1)

How long is the hatching period? (2) Are there any ontogenetic niche shifts? (3) Does fish abundance change over time at one sampling location? (3) Are there any differences in fish abundance among sampling locations? (4) Is there a relationship between fish distribution, environmental measures and hydrology?

Study Site

The shoreline of the Danube downstream from Vienna to the Slovakian border can be characterised by richly structured zones with large gravel banks and small littoral bays and, on the other hand, by steep straightened artificial embankments (rip-rap). The annual average discharge is $1890 \text{ m}^3 \text{ s}^{-1}$ with seasonal fluctuations from 800 to $6000 \text{ m}^3 \text{ s}^{-1}$. At mean water conditions, the current velocity in the channel is approximately 2.5 m s^{-1} . Both the connectivity with the floodplain and the shoreline configuration strongly depend on water level fluctuations. There are seven side-arm-systems, connected on 10 to 20 days per year at mean water level plus 1.5 m of water and three tributaries. At this 50 km long section of the Danube, only 18 large gravel bars can be found (S c h i e m e r et al. 1991). They are the main nursery areas for riverine 0+ fish within the main channel. Three inshore stretches of 100 m length at one of the 18 gravel bars were studied in detail (bay = "Bay", gravel bar 1 = GB1, gravel bar 2 = GB2, Fig. 1) from May to August, 1994. The "Bay" can be characterised by low water currents, smaller grain sizes, higher temperatures, when compared with the gravel banks. The "Bay" dried out at low water. The "GB1" showed the highest water currents and lowest water depths over a broad range of different water levels. At the "GB2" water velocities decreased with increasing water level, whereas mean water depth increased (see in K e c k e i s et al. 1997).

Material and Methods

The inshore bathymetry of three nursery stretches was surveyed and a relief map in 10 cm steps constructed (Fig. 2). The data set from the survey and the detailed contour maps of the sampling stretches ($100 \times 100 \text{ m}$ each stretch) ensured the exact location of each sampling point throughout the investigation period. This data set formed the basis for further analysis with a Geographical Information System ("GIS"). Inshore morphology was combined with hydrological data for modelling the influence of water level fluctuations on the area of different water depth classes (1 = 0-20, 2 = 20-40, 3 = 40-60, 4 = > 60 cm). Sampling started at the appearance of the first *C. nasus* larvae (visual observations) at the beginning of May, in weekly (May - July) to monthly (July - August) intervals. A systematic sampling design based on a grid-design, was chosen for the investigations. The 100 m stretches were divided in 21 transects with 5 m distance between them. Three sampling points along each transect were taken at different distance from the shoreline. Overall, 1508 points were analysed. At each of the 63 points per sampling site and date, the water velocity was measured using a propeller current meter (Ott C2). With the "GIS" (ARC/INFO Software) we interpolated between these 63 points and determined the area of different water velocity classes (1 = 0-10, 2 = 10-15, 3 = 15-20, 4 = > 20 $\text{cm}\cdot\text{s}^{-1}$). The influence of water level fluctuations on the area of each velocity classes was modelled. Temperature was measured at each of the 63 points. Additionally, a data logger (testo 170)

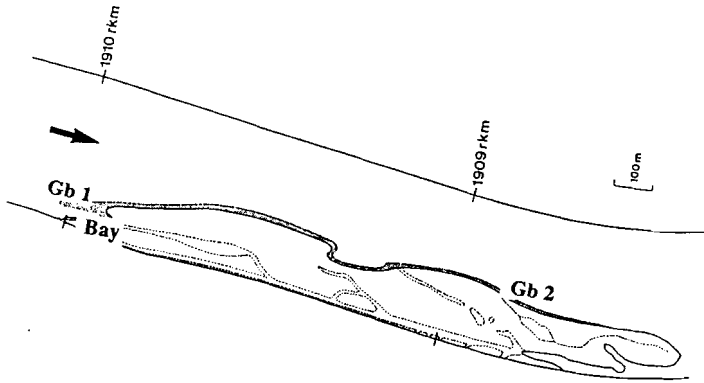
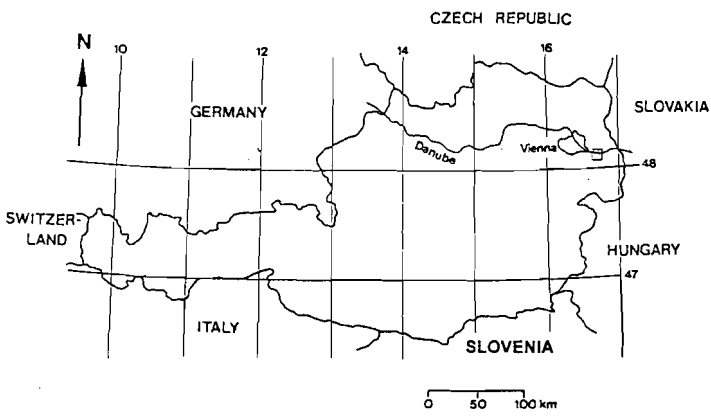


Fig. 1. Study site in the Austrian part of the Danube River. Sampling stretches are located at river-kilometre 1910: a = "Bay", b = "GB1", and river-kilometre 1909: c = "GB2".

measured water temperature in hourly intervals. Water level and water temperature from the main channel were provided by the Austrian River Authority. Distribution patterns of structural parameters (substrate type, type and density of vegetation and woody debris) were visual estimated and recorded.

Fish were sampled with electrofishing equipment adapted for juvenile fish (8.5 kW generator, 400-500 V, approx. 8 A). The anode diameter was 30 cm. It was fixed on a 4 m long pole, to minimise disturbing effects. The sphere of action was empirically tested and determined (approx. 0.5 m² area). A few seconds after immersing the activated anode, a dip-net was put into the water to collect the fish. Small unit samples (n=63 on each date) were taken according to the grid-sampling-design described above. Species determination and length measurements of fish were carried out in the laboratory. *Leuciscus leuciscus* and *Rutilus rutilus* data were pooled, due to difficulties in species determination during early development. The 0+ *C. nasus* were grouped into the size classes 0-12.5, 12.5-17.5, 17.5-30, and > 30 mm. Potential spawning time was designated as the time period where the temperature reached 8° C and do not exceed 12° C (referring to P e ě á z 1974, 1984, K e c k e i s et al. 1996). Freshly hatched fish

were defined as fish of the last embryonic and first larval step (according to Peňáz 1974) with a total length below 12.5 mm. The portion (relative fish number in %) of freshly hatched fish was calculated from the pooled data of all fish captured and a logistic curve was fitted. Relative densities of each fish size class in water depth and water velocity classes were calculated from the 63 sampling points on each date and site. The mean value \pm S.E. was calculated from these relative densities at the 26 sampling events and Kruskal-Wallis one-way analysis of variance was applied to detect significant differences between the size classes. From the determined habitat preferences and laboratory derived maximum sustainable water velocities (Flöre & Keckeis, in press.), we defined suitable habitat as the zone where water velocity remains under $10 \text{ cm}\cdot\text{s}^{-1}$ and habitat available, as the area of this zone. The number of *C. nasus* at the investigated stretches (presented in Table 5 and Fig. 7) was calculated by multiplying the mean fish density (mean value + S.E. of 63 samples at each stretch) with the given area of suitable habitat. Differences in fish numbers between sampling dates and sampling stretches were analysed with Kruskal-Wallis one-way analysis of variance and Mann-Whitney-U-Test for two-independent-samples.

Results

Duration of the Hatching Period

Freshly hatched *C. nasus* embryos and larvae were caught from the 10th May to the 21st June, a period of 42 days. The relative portion of freshly hatched fish ranged between 85% on the 10th of May to 0.25% on the 21st June (Fig. 3) and a logistic regression model was fitted to this data. The curve estimation was highly significant ($p < 0,001$, $r^2 = 0,904$) and revealed that on the 23rd may 50% and on the 26th May 25% of all fish captured were freshly hatched.

Habitat Preferences during Ontogenetic Development

Water Depth

There were no significant differences in relative fish density between the depth classes and between the size classes shown in Fig. 4 (Kruskal-Wallis, $p > 0.05$). Then the fish data of the water depth classes 0-20 and 20-40 cm were pooled and relative density in these depth classes ranged from >72% for the smaller sized fish, to 100% for the fish >30 mm. Relative density of all fish sizeclasses was significant higher in the depth class 0-40 cm than in the class >40 cm (Mann-Whitney-U-Test, $p < 0.002$).

Water Velocity

Relative densities of all *C. nasus* size classes were higher than 75% in the water velocity class of 0-10 $\text{cm}\cdot\text{s}^{-1}$ (Fig. 5). The relative density of all fish size classes was in the velocity class 0-10 $\text{cm}\cdot\text{s}^{-1}$ significant higher, than in other classes (Kruskal-Wallis, $p < 0.01$). No significant differences could be detected between size classes ($p > 0.05$).

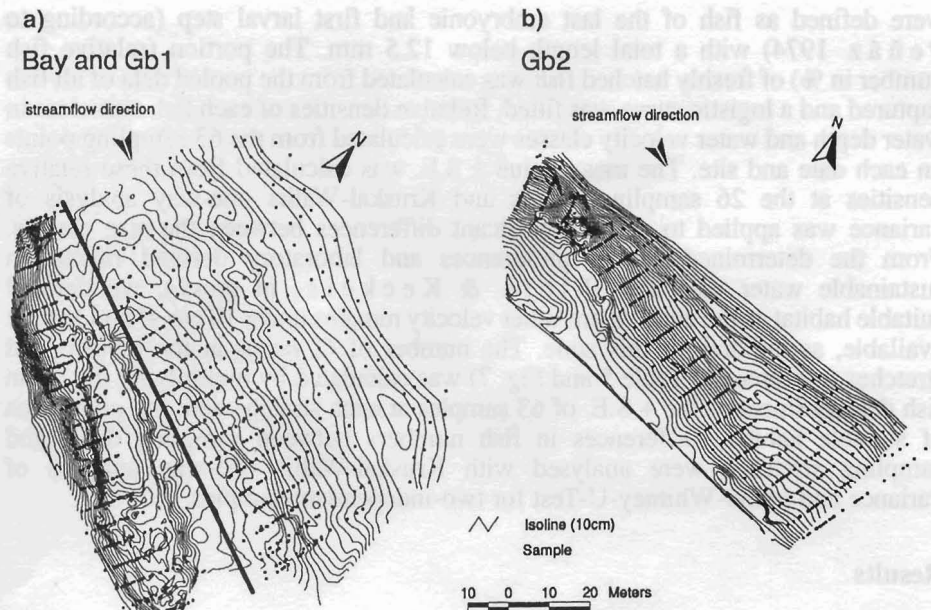


Fig. 2 a. Contour plots of the nursery habitats “Bay” and “Gb1”. The black dots indicate all sampling points throughout the investigation. (Fish abundance, water depth, water velocity, temperature, and substrate type were recorded at each point).
b. Contour plots of the nursery habitat “Gb2”. The black dots indicate all sampling points throughout the investigation. (Fish abundance, water depth, water velocity, temperature, and substrate- type were recorded at each point).

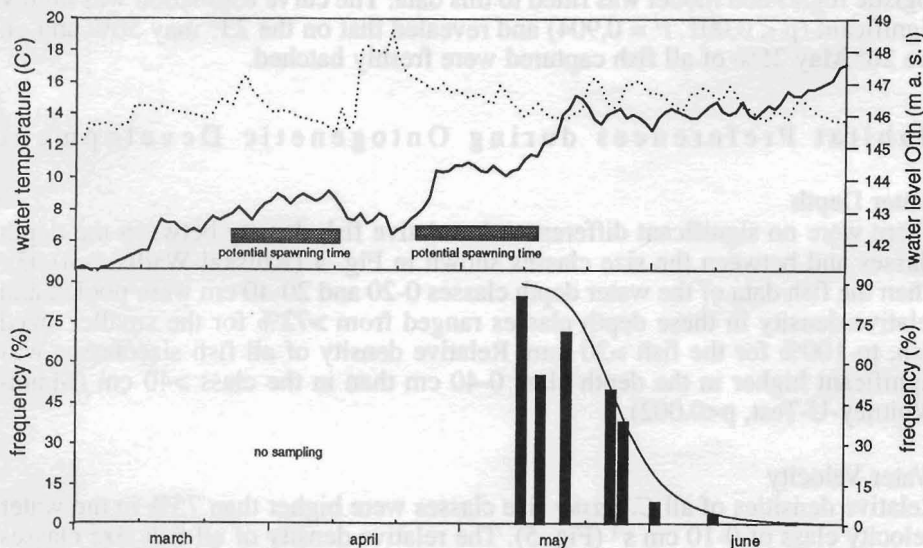


Fig. 3. The portion of freshly hatched fish (in %, from the pooled data of all fish captured; Sigmoid curve: $y = \frac{\max - \min}{1 + (x/IP)^{\text{SLOPE} + \min}}$; $\max = 90$, $\min = 0$, $IP = 25$, $\text{SLOPE} = 6.231$, $r^2 = 0.904$). Water level (dashed line) water temperature (solid line) of the main channel.

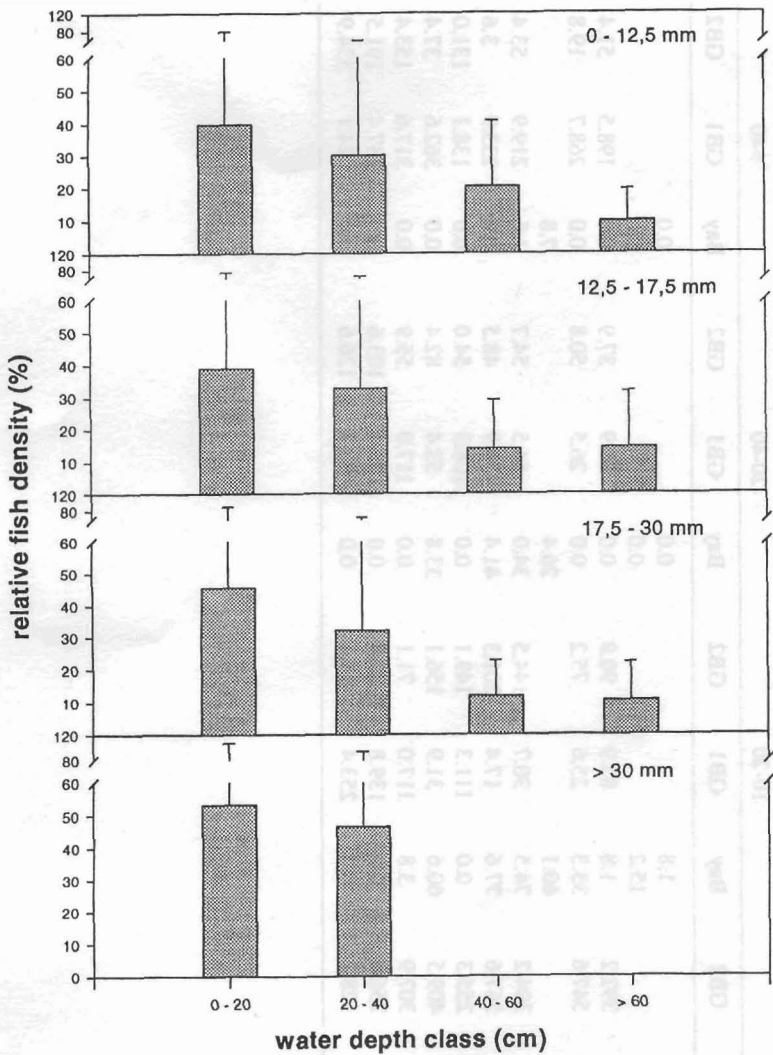


Fig. 4. Habitat preferences of *Chondrostoma nasus* during ontogenetic development concerning water depth (relative fish density in mean \pm S. E.).

Habitat Availability and Hydrology

The relationship between water level and suitable habitat area (water velocity class 0-10 $\text{cm}\cdot\text{s}^{-1}$) differed between the three stretches (Fig. 6). "GB1" showed highest habitat availability at low water in late summer (Table 4), and the area decreased with increasing water level (linear regression, $p < 0.01$, $r^2 = 0.83$) down to zero on the 9th June (Table 1). In contrast, habitat availability was highest for "GB2" at high water level and decreased with decreasing water level (linear regression, $p < 0.01$, $r^2 = 0.84$). The "Bay" area felt dry below mean water. Habitat

Table 1. Temporal and spatial change in habitat (m²). Suitable habitat was defined as the area where water velocity did not exceed 10 cm.s⁻¹. Areas of different water velocity classes are given in m². 0-10 = 0-10 cm.s⁻¹, 10-20 = 10-20 cm.s⁻¹, 20-40 = 20-40 cm.s⁻¹, >40 = >40 cm.s⁻¹, w. l. = water level, in meters above sea level.

	0-10			10-20			20-40			>40			
	w. l.	Bay	GB1	GB2	Bay	GB1	GB2	Bay	GB1	GB2	Bay	GB1	GB2
10. May	145.9	590.3			1.8			0.0			0.0		
13. May	146.1	597.2			15.2			0.0			0.0		
17. May	145.9	590.3	222.8	392.2	1.8	83.9	90.9	0.0	62.9	37.9	0.0	198.5	51.4
24. May	146.2	600.2	32.1	547.6	33.3	25.6	75.2	0.0	26.5	50.8	0.0	268.7	19.8
26. May	147.0	269.8			60.1			26.4			7.8		
31. May	146.7	418.6	74.7	394.2	74.5	30.7	144.5	34.0	64.5	54.7	1.6	219.9	53.4
09. June	146.5	446.3	0.0	567.6	77.6	17.4	201.3	41.4	20.9	48.5	0.0	233.9	3.6
15. June	146.0	592.9	159.2	255.3	0.0	111.3	149.1	0.0	108.3	54.0	0.0	138.1	131.0
21. June	146.3	424.6	73.9	409.5	60.6	31.9	156.1	33.8	53.4	82.4	0.0	362.6	37.4
29. June	145.9	591.1	419.6	307.9	3.8	117.0	71.1	0.0	117.0	55.9	0.0	317.6	153.4
12. July	145.4	0.0	263.4	256.8	0.0	139.8	107.9	0.0	129.4	103.6	0.0	287.4	191.5
16. Aug.	144.6	0.0	536.9	128.2	0.0	253.4	119.1	0.0	130.7	126.6	0.0	24.1	334.9

Table 2. 0+ fish association and the most abundant fish species caught at the three sites. Given are absolute numbers (n), and percentages (%).

	bay		GB1		GB2	
number of species	16		8		10	
endangered species	8		5		5	
diversity index H'	1.42		0.92		0.83	
sample points	482		459		567	
	(n)	(%)	(n)	(%)	(n)	(%)
<i>Chondrostoma nasus</i>	3106	49.3	508	46.6	1300	76.9
<i>Barbus barbus</i>	546	8.7	646	48.7	179	10.6
<i>Alburnus alburnus</i>	301	4.8	20	1.5	87	5.1
<i>L. leuciscus</i> + <i>R. rutilus</i>	1784	28.7	27	3.6	102	6.0
<i>Leuciscus cephalus</i>	216	3.4	0	0	1	0.1
Total fish sampled	6317	100	1223	100	1698	100

Table 3. Temporal and spatial change in absolute fish numbers of the most abundant fish species (total numbers of fishes caught). *Cn* = *Chondrostoma nasus*, *Bb* = *Barbus barbus*, *Aa* = *Alburnus alburnus*, *Ll* + *Rr* = *Leuciscus leuciscus* and *Rutilus rutilus*.

	<i>Cn</i>			<i>Bb</i>			<i>Aa</i>			<i>Ll</i> + <i>Rr</i>		
	Bay	GB1	GB2	Bay	GB1	GB2	Bay	GB1	GB2	Bay	GB1	GB2
10. May	20			0			0			0		
13. May	223			0			0			7		
17. May		11	21	0	0	0	0	0	0	0	0	0
24. May	895	89	64	0	0	1	4	0	0	35	2	0
26. May	135			0			0			13		
31. May	149	20	485	11	1	1	26	0	0	62	1	5
09. June	152	7	102	10	1	3	49	0	0	245		5
15. June	166	84	329	34	3	8	29	0	0	484	4	38
21. June	871	210	276	74	8	18	111	1	1	502	14	35
29. June	446	34	22	218	11	36	71	0	13	431	2	2
12. July		22	0		78	30		1	40		4	17
16. Aug		31	1		544	82		18	33		0	0

availability increased steeply with increasing water level (polynomial regression, $p < 0.01$, $r^2 = 0.88$), reached a maximum at medium levels, and decreased steeply until it was overflowed (Table 1, Fig. 6).

Temporal and Spatial Dynamic of Fish Abundance

In general, the highest abundance of 0+ fish, the number of eurytopic species, and the highest diversity (Shannon-Weaver Index) was found in the "Bay" (Table 2). Total number and density of fish caught varied considerable during the investigation period (Tables 3 and 4). *C. nasus* achieved highest abundance and density of all species (Table 4). Within the water velocity class 0-10 cm·s⁻¹, it ranged from zero to 56±40 (mean of 63 points ± S.E.) individuals per m² (Table 4). Only the most obvious differences in fish abundance were statistically significant, due to high standard errors. Schooling and aggregation of larvae, caused these high standard errors. For example on the 21st June, the fish density

Table 4. Temporal and spatial change in estimated fish density of the most abundant fish species, within the water velocity class < 10 cm.s⁻¹. Given in individuals per m² (mean ± standard error). Cn = *Chondrostoma nasus*, Bb = *Barbus barbus*, Aa = *Alburnus alburnus*, Ll + Rr = *Leuciscus leuciscus* and *Rutilus rutilus*.

	Cn		Bb		Aa		Ll + Rr		Lc	
	mean	S.E.	mean	S.E.	mean	S.E.	mean	S.E.	mean	S.E.
Bay										
10. May	4.12	2.46	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
13. May	14.85	6.89	0.00	0.00	0.00	0.00	0.47	0.28	0.00	0.00
17. May										
24. May	36.85	13.40	0.00	0.00	0.16	0.10	1.44	0.59	0.04	0.04
26. May	7.24	5.07	0.00	0.00	0.00	0.00	0.72	0.66	0.00	0.00
31. May	7.03	2.42	0.47	0.19	1.23	1.23	2.93	1.10	0.00	0.00
09. June	7.03	2.17	0.47	0.20	2.31	1.10	11.32	5.54	7.12	7.08
15. June	6.16	2.53	1.26	0.64	1.08	0.59	17.97	8.65	0.00	0.00
21. June	37.18	30.12	3.16	0.88	4.74	3.02	21.45	12.23	0.13	0.07
29. June	16.83	11.10	8.23	3.50	2.68	1.14	16.27	7.89	2.23	1.51
12. July										
16. Aug										
GB1										
10. May										
13. May										
17. May	2.52	1.98	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
24. May	26.53	22.55	0.00	0.00	0.00	0.00	0.65	0.65	0.00	0.00
26. May										
31. May	5.03	3.97	0.25	0.25	0.00	0.00	0.25	0.25	0.00	0.00
09. June										
15. June	7.93	4.78	0.57	0.41	0.00	0.00	0.00	0.00	0.00	0.00
21. June	56.33	40.33	1.98	1.09	0.00	0.00	3.96	2.37	0.00	0.00
29. June	7.47	5.75	2.49	1.19	0.00	0.00	0.45	0.30	0.00	0.00
12. July	2.26	1.32	10.05	8.15	0.14	0.14	0.57	0.44	0.00	0.00
16. Aug	2.51	1.72	33.57	20.59	0.89	0.64	0.00	0.00	0.00	0.00
GB2										
10. May										
13. May										
17. May	0.53	0.43	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
24. May	2.96	1.39	0.05	0.05	0.00	0.00	0.00	0.00	0.00	0.00
26. May										
31. May	29.94	20.62	0.08	0.08	0.00	0.00	0.34	0.26	0.00	0.00
09. June	4.34	2.79	0.13	0.13	0.00	0.00	0.31	0.16	0.00	0.00
15. June	28.31	22.51	0.57	0.25	0.00	0.00	3.40	2.04	0.00	0.00
21. June	19.90	10.55	0.97	0.25	0.08	0.08	2.59	1.80	0.00	0.00
29. June	1.37	0.64	2.59	0.91	0.89	0.39	0.08	0.08	0.08	0.08
12. July	0.00	0.00	2.89	1.49	3.65	1.43	1.76	0.57	0.00	0.00
16. Aug.	0.00	0.00	4.53	1.60	14.49	9.33	0.00	0.00	0.00	0.00

ranged from zero to 1597 individuals per m² at the 63 sampling points and 35 zero catches occurred. Mean fish density at each stretch and date, was multiplied with suitable habitat area and the total number of *Chondrostoma nasus* at the 100 m long stretches was estimated (Table 5, Fig. 7).

Temporal Dynamics

Highest numbers and most prominent peaks of 0+ *C. nasus* were observed at the “Bay” (Table 5, Fig. 7). The nase population built up significantly from

Table 5. Temporal and spatial change of estimated *Chondrostoma nasus* number at the three sites. The given fish numbers indicate the number of individuals estimated at the 100 m long stretches (calculated from the mean fish density within the suitable habitat, multiplied with the area of suitable habitat).

	Bay		GB1		GB2	
	n	S. E.	n	S. E.	n	S. E.
10. May	2441	1458				
13. May	9213	4227				
17. May			561	441	207	169
24. May	22194	8060	861	734	1645	786
26. May	1952	1368				
31. May	2963	1020	376	297	11902	8224
09. June	3285	1052			2464	1583
15. June	3764	1558	1262	761	7733	6248
21. June	12773	9793	4394	3200	8213	4343
29. June	9995	6568	3136	2413	423	198
12. July			596	349	0	0
16. Aug			1346	922	0	0

2441 ± 1458 (mean ±S.E.) on the 10th May to a maximum of 22194 ± 8060 on the 24th May (Mann-Whitney-U-Test, p<0.05). Then it declined significantly to 1952 ± 1368 individuals on the 26th May (p<0.05). In late June there was a second peak from 3764 ± 1558 to 12773 ± 9793 fish, until the “Bay“ dried out on the 11th of June. Similar patterns could be noticed at “GB2“, but on 24th of May when *Chondrostoma nasus* peaked at the “Bay“, numbers were low at “GB2“ 1645 ± 786. Fish number increased significantly from beginning May up to 11902 ± 8224 on the 31st May (p<0.05). On the 9th of June numbers were rather low and a second peak was observed in the middle of June. Numbers decreased in late June (Fig. 7). In July and August no more fish were caught at “GB2“. The sampling stretch “GB1“ showed low numbers in May and a significant increase from beginning to late June (p<0.05, Table 5). After the 29th June, juvenile *Chondrostoma nasus* were exclusively found at “GB1“ (Table 5).

Spatial Dynamics

C. nasus number differed significantly between the investigated stretches at corresponding sampling dates (Kruskal-Wallis, p>0.05). In the “Bay“, the fish number was significant higher on the 13th May compared with “GB1“ and “GB2“ on the 17th May (Mann-Whitney-U-Test, p<0.05). Also on the 24th May it was significantly higher in the “Bay“ than in “GB1“ and “GB2“ (p<0.05). The inverse situation was observed on the 31st May, where the highest numbers were found at “GB2“. In July and August, *C. nasus* juveniles were caught almost exclusively at “GB1“ (Tables 3, 4 and 5).

Discussion and Conclusions

Space and time function together to shape populations, communities and ecosystems (Lewin et al. 1996). Since mortality is known to be highest during egg and larval stages, the events occurring during this critical phase are believed

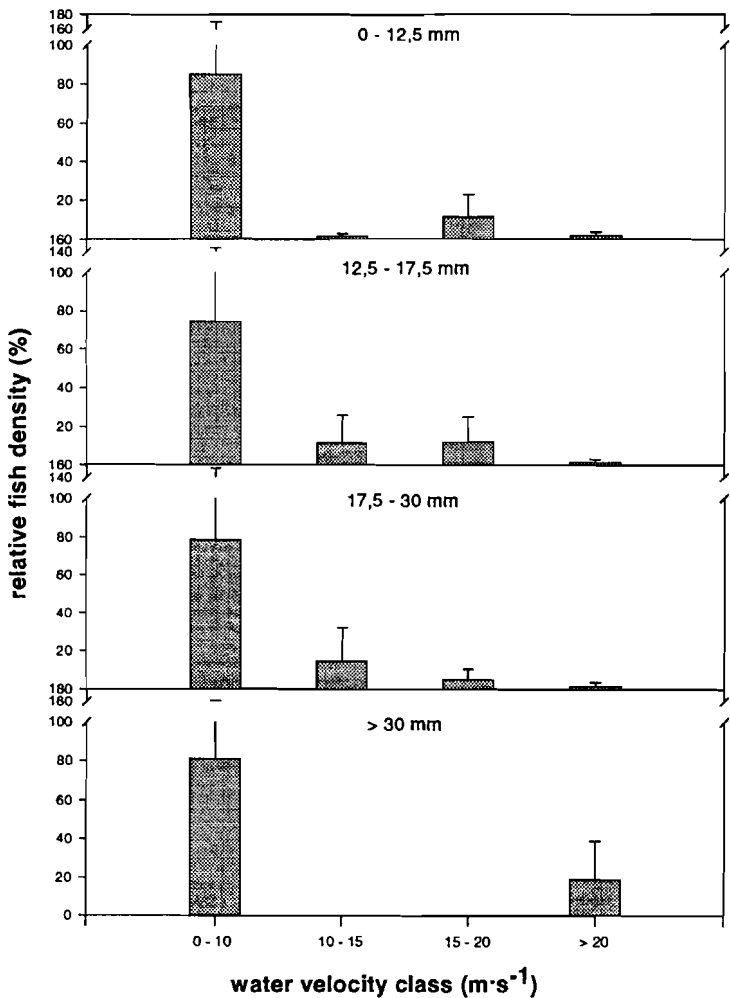


Fig. 5. Habitat preferences of *Chondrostoma nasus* during ontogenetic development concerning water velocity (relative fish density in mean \pm S. E.).

to be the major factors regulating recruitment and population dynamics (H o u d e 1988, C u s h i n g 1988). Knowledge of the central factors regulating variation in fish abundance and recruitment is therefore, a central question not only in fisheries but also in ecology.

Freshly hatched *C. nasus* embryos and larvae were caught over a period of 42 days. This temporal dimension results in a wide range of birth dates and variations in the length and quality of the growing season. Extended breeding periods are very common in freshwater fish and are assumed to affect year class strength and recruitment. C a g n e l l i & G r o s s (1996) reported that 74% of Canadian freshwater fish species have a breeding season longer than one month. This strategy, to enhance the probability bringing the offspring at the right time

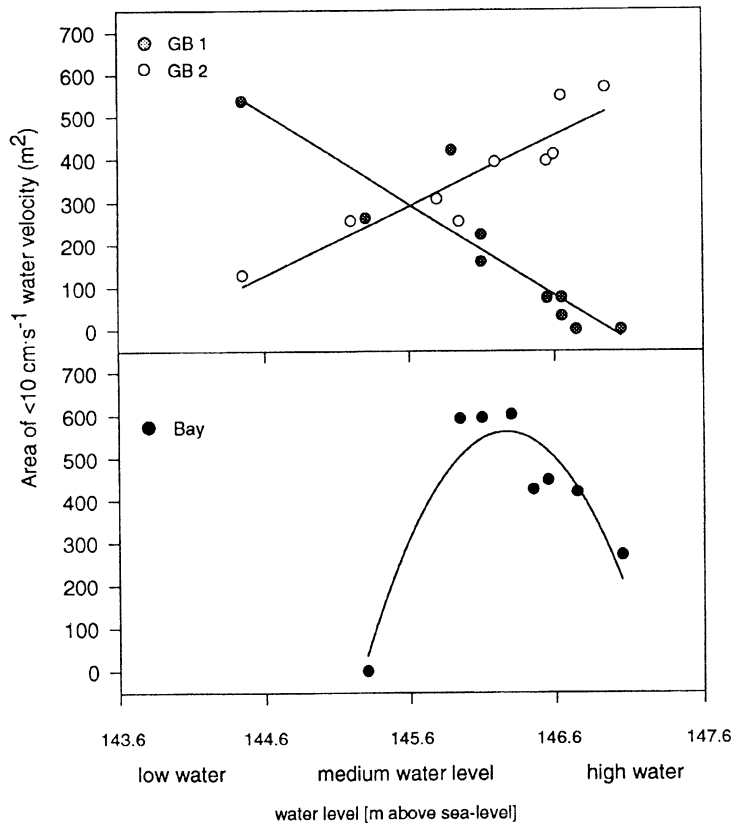


Fig. 6. The influence of hydrology on suitable habitat area. Suitable habitat was defined as the area where water velocity did not exceed $10 \text{ cm}\cdot\text{s}^{-1}$. Regression equations: BAY: $y = -10850789.42 + (156512.13 \cdot x) + (-564.36 \cdot x^2)$, GB1: $y = 28567.85 + (-204.91 \cdot x)$, GB2: $y = -22196.85 + (162.95 \cdot x)$.

to the right place, might be of particular importance in highly stochastic environments like large rivers (Pavlov 1994, Schiemer et al. in press a).

The emerging larvae are known to drift longitudinally and laterally and accumulate at fluvial boundaries or even move into side arms of the river (Heggnes & Traaen 1988, Bodensteiner & Lewis 1994, Pavlov 1994, Persat et al. 1995). The drift of larval fish has been identified as a migratory behaviour related to dispersion and to reach suitable nursery areas (Manteifel et al. 1978, Prokeš & Peňáz 1979).

We investigated the habitat preferences of 0+ *C. nasus* along the “key-factors” water depth and water velocity (Wintersberger 1996, Keckeis et al. 1997) to determine the characteristics of suitable nursery habitats. During ontogenetic development, there were no significant differences in their habitat preferences with regard to water depth and water velocity. Relative densities of all *C. nasus* size classes were higher than 75% in water velocities of $<10 \text{ cm}\cdot\text{s}^{-1}$ and higher than 72% in water depths of $<40 \text{ cm}$. Larger juveniles ($>30 \text{ mm}$), which are feeding on benthic algae, were caught at shallow gravel banks with

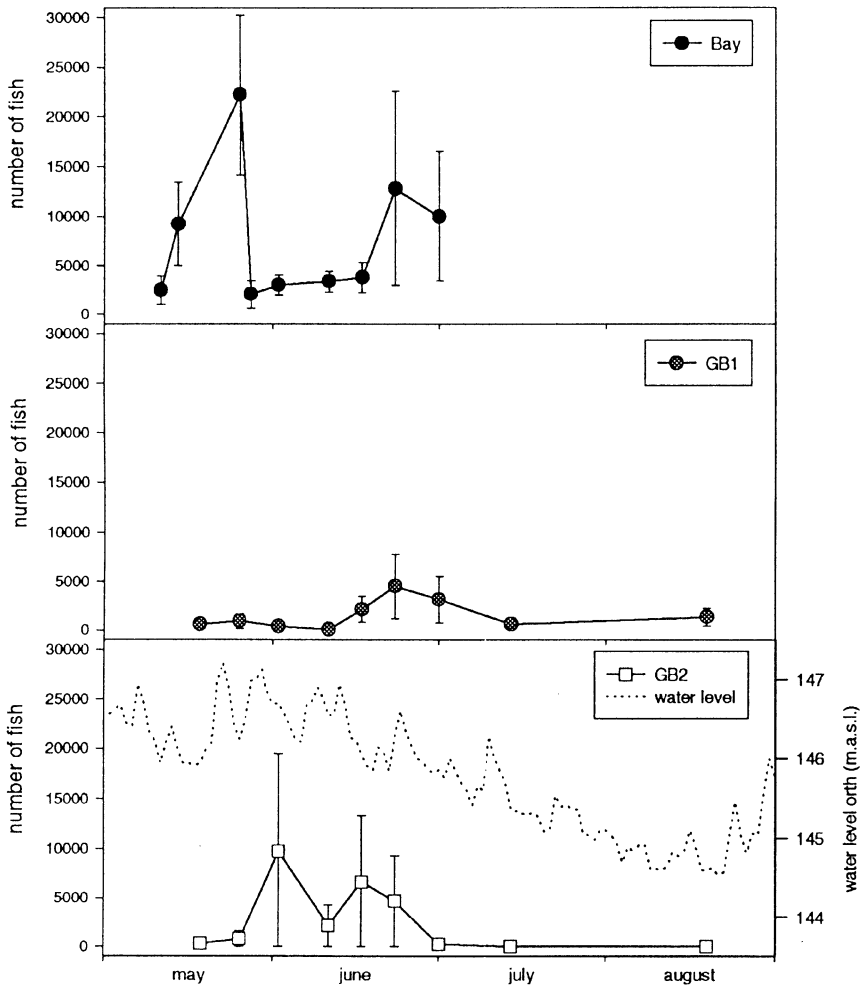


Fig. 7. Temporal and spatial dynamics of 0+ *Chondrostoma nasus* at the three investigation sites. The initial increase in May is due to the emerging larvae. The “Bay” and “GB1” are situated at the head and “GB2” at the end of a nursery zone within an area of uninhabitable straight rip-rap (“GB2” is located 1.5 km downstream of the “Bay” and “GB1”). The next source area (see Schloesser 1995) are similar nursery zones (gravel banks of 2 km length) several kilometres upstream.

coarse substrata and higher water velocities, in general. But they strongly preferred the shallowest zones with water currents $<10 \text{ cm.s}^{-1}$ (more than 80%). Larval and small juveniles ($<30 \text{ mm}$) were bound to sheltered zones, with low water velocities and fine-grained substrata. The restriction of larvae and small juveniles to sheltered, shallow inshore areas may be explained by hydraulic limitation (Jowett & Richardson 1994). Laboratory studies of Flore & Kেকেis (1996) revealed, that the maximal sustainable water velocity of 0+ *C. nasus* was 5 to 7 body lengths per second (8 cm.s^{-1} for 15 mm, to 27 cm.s^{-1} for 56 mm TL). Maximal velocity, where net energy gain was positive, increased

during development from 7 cm.s⁻¹ for 15 mm up to 15 cm.s⁻¹ for 25 mm fish. From these results it was apparent that the critical velocities were in good correspondence with our field results. Higher predation pressure may also restrict 0+ fish to shallow habitats, this may be a reason that we captured more than 72% of all size classes at water depths <40 cm. Power et al. (1985) and SchLOSSER (1987) clearly documented that large piscivores force smaller fishes into shallow-water refuges in streams.

The presented species association and habitat preferences of *Chondrostoma nasus*, were in accordance with the results in the literature. Copp et al. (1994) and KURMAYER et al. (1996), analysed the habitat use of 0+ fish in the floodplains of the Danube. They showed that the abundance of juvenile *C. nasus* was very low and the occurrence was restricted to lotic refuges, in late summer. For the main channel of Danube the dominance of *C. nasus* was demonstrated by Schiemer et al. (1991) and Wintersberger (1996). Larval habitats were characterised as sheltered lentic bays. Both authors observed an ontogenetic habitat shift towards shallow gravel banks.

When interpreting our results, a question was quite obvious: Is there an active ontogenetic habitat shift or is it simply caused by changing physical habitat characteristics, due to seasonal water level fluctuations? We showed that the "Bay" habitat dried at the beginning of July, at a water level of 0.5 m below mean level and this forced the juvenile fish to colonise the adjacent gravel bar. Schiemer et al. (in press) presented some evidence for the "seasonal change of habitat availability" hypothesis. They established a dome-shaped relationship between the diversity of inshore-structure and water level and demonstrated a loss of sheltered bays with decreasing water level, for the free-flowing main channel. On the other hand, the results of the floodplain studies (restriction of older *C. nasus* to lotic refuge habitats) are favouring the "ontogenetic habitat shift" hypothesis. However, a phylogenetic adaptation to the seasonal change in habitat availability, seems to be advantageous and reasonable.

From the determined habitat preferences and laboratory derived maximum sustainable water velocities (FlöRE & KECKEIS 1996) we defined suitable habitat as the area where water velocity does not exceed 10 cm.s⁻¹. Hydrology and shoreline configuration were the "key factors" of environmental characteristics and suitable habitat area for 0+ *C. nasus*, at the inshore nursery zones (Table 1, Fig. 6, see also in KECKEIS et al. 1997). These inshore zones also provide high food availability, by autochthonous production of zooplankton (Schiemer et al., in press) benthic invertebrates (RECKENDORFER et al. 1996), allochthonous material (e.g. Anflug) from adjacent terrestrial zones (WETZEL 1990) and higher temperature (KECKEIS et al. 1997). Thus, allowing fast growth through the critical stages of early development.

Significant variations in temporal and spatial distribution patterns of 0+ *C. nasus* were detected during the investigation period. Short-term fluctuations in abundance, as a result of immigrating individuals from the spawning areas upstream (active emergence, wash-in effects) and emigrating individuals (active migrations, wash-out effects) were observed (Fig. 7). During the emerging period, the *C. nasus* population built up, owing to drift migrations from a close spawning/breeding site upstream. At the end of the emerging period a rise of the water level on the 26th May, resulted in a sudden drop in fish number, apparently

due to wash-out effects which blew off the "Bay". The increase in fish number at the "GB2" (located 1,5 km downstream of the "Bay") a few days later, illustrates the refuge capacity (high suitable habitat area at higher water level, Fig. 6) of this site at higher water levels. This example indicates that the early stages of riverine fry can be passively transported over distances of several kilometres within a short time period and outlines the importance of longitudinal connection/proximity of nursery habitats. The second peak in the middle to the end of June coincided with a longer period of mean water discharge. Such conditions seem to fill up potential appropriate habitats with larvae and juveniles from upstream. The highest abundance of larval *C. nasus* at the beginning of May is primarily explained by spawning time and location of the adults and the decrease during summer may be caused by mortality and massive downstream migrations. The population dynamics suggest that nursery islands and the accompanying 0+ fish assemblage cannot be envisaged as being isolated, but are in a continuous longitudinal exchange. Mass migrations of 0+ fish within water currents are a very common phenomenon in rivers, lakes, and marine ecosystems and it is proposed that the question of "the settled way of life" and "the migratory way of life" ratio, may depend on the particular environment (P a v l o v 1994).

We conclude that, inshore structure determines the microhabitat availability, the extent of refuge capacity at water level fluctuations and the habitat profitability for 0+ fish. For larval fish, this small-scale ecotonal zones form islands in a highly fluctuating environment. Individual and population success seem to rely on the retention-time within these high quality habitats. Massive transport phenomena are influencing fish distribution by moving animals into regions of differing habitat quality. Consequently, a continuous longitudinal sequence of suitable habitats under stochastically changing water level is essential for recruitment.

A c k n o w l e d g e m e n t s

We thank the fishery club of Fischamend for access to the site and the friendly collaboration. We gratefully acknowledge all colleagues who supported and helped our work. Comments on this paper by the reviewers are much appreciated. This study was financed by the Austrian Research Council (Fond zur Förderung der Wissenschaftlichen Forschung) within the FWF Project P-9600 BIO.

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