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Review

The early life history stages of riverine fish: ecophysiological and environmental bottlenecks[☆]

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Abstract

Fish are good indicators of the environmental health of rivers and their catchments as well as important conservation targets. Bioindication has to be based on an understanding of the requirement of characteristic species with regard to: (a) The match/mismatch between reproductive strategies and environmental conditions. (b) The niche dimensions of critical stages vis-a-vis the key conditions. (c) The availability of microhabitats along the ontogenetic niche profiles, i.e. the connectivity from spawning substrates to early life history microhabitats. The main conditions for the embryonic period are temperature and oxygen supply which are responsible for embryonic mortality, the duration of the period, and size and condition of newly-hatched larvae. For the exogenously feeding larvae the functional of food acquisition, growth and bioenergetics to temperature, food availability and current velocity is decisive. Studies concentrated on *Chondrostoma nasus*, a target species for monitoring and conservation in large European river systems. Results obtained in experimental studies are compared with those from field studies in order to evaluate the match/mismatch between performances and microhabitat choice and population dynamics in the field. Discrepancies between requirements and field conditions in regulated rivers underline the significance of inshore zones as microhabitats (expressed in the 'Inshore Retention Concept') and the requirement for ecophysiological studies on target species for river restoration and conservation.

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1. Introduction

1.1. Fish as indicators for the ecological integrity of river systems

It is well established that engineering and intensified land-use have led to deficiencies in the 'ecological integrity' (Karr, 1991) of river systems. Ecological integrity combines structural properties (inshore configuration, connectivity along the river course with the floodplain and the groundwater

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aquifer) and functional processes (hydrology, carbon and nutrient fluxes) of different scale. It evaluates conditions in relation to the original state of the river-floodplain system (Ward and Stanford, 1995; Ward, 1998). Modern—ecologically orientated—river engineering attempts to develop management and restoration schemes that maintain and restore the major properties and functional processes and the characteristic biodiversity. An appropriate indication and monitoring system has to be developed to achieve this goal.

Riverine fish are the most important indicator group for assessing the ecological integrity of rivers (Karr, 1991; Schiemer, 2000). This indication value results from the broad range of habitat requirements of different ecological guilds which integrate during their life cycle, a wide range of riverine conditions from the properties of bottom sediments relevant for egg development to the large scale longitudinal integrity required, for example, for spawning migrations (Schiemer et al., 1991; Persat et al., 1994, 1995).

In this respect the 0+ stages are particularly significant (Schiemer et al., 1991, 2001a) because most of the decline in fish numbers results from starvation of larvae, predation on larvae and from several other factors as non-optimal temperatures, oxygen deficit and dispersal of eggs from viable conditions. These factors vary with time, place and fish species, but always concentrate on early development (Lasker, 1985; Urho, 1999). Therefore, success or failure of a population in terms of year class strength is largely determined during the early life history (Kamler, 1992), where fish suffer highest mortality. The match or mismatch between environmental conditions and requirements during the embryonic and early larval phases is decisive for recruitment (Chambers and Trippel, 1997; Fuiman and Werner, 2002). The bioindication by 0+ fish is fast since the reactions become visible in population dynamics and year class strength. The indication is also precise because of the narrow requirements with regard to structural properties of habitats and the key environmental conditions therein. During the embryonic period, there is a high sensitivity to temperature and the oxygen conditions in the spawning substrates (Kamler, 1992). During the period of exogenous feeding the major environmental variables besides temperature are current velocity pattern and food availability. During early ontogeny, dramatic changes in niche position and dimensions with regard to

environmental conditions which affect microhabitat quality have been found (Schiemer and Spindler, 1989; Copp, 1992; Semperki and Gaudin, 1995; Gaudin, 2001).

The main emphasis of the paper is an analysis of the response of embryos and larvae to the main environmental factors, and a comparison between experimentally defined niche dimensions with the environmental conditions in the field. Suboptimal conditions will lead to reduced growth and retarded development; the key life history events, e.g. hatching and onset of exogenous feeding will be delayed resulting in a higher mortality and hence a reduction of fitness (Fuiman, 1994). A main focus of the paper is to clarify environmental stress on compound life history patterns which are expressed in (a) body size, (b) the morphological development at which a life history event takes place, and (c) the timing and duration of life history events.

The paper presents an overview of field and experimental work on the early life history period of *Chondrostoma nasus*, which has become a major indicator species for the ecological integrity of large rivers and a main research and conservation target (Lusk and Peñáz, 1995; Freyhof et al., 1997).

2. *Chondrostoma nasus*: a target species for highlighting the environmental conditions of large European rivers

2.1. The biology and habitat requirements of early life history stages

A main part of our work has concentrated on *Chondrostoma nasus*, which has become a flagship species for the ecology and conservation of large European rivers. *Chondrostoma nasus* is a characteristic species of the hyporhithral and epipotamal zone. Throughout its life cycle, the species integrates conditions of different spatial and temporal scales associated with a complex array of habitat-use patterns and migratory processes. A high sensitivity especially during the early ontogenetic phase makes the fish a good indicator for structural properties of rivers (Peñáz, 1996; Schiemer et al., 2001b). The spawning areas in the large rivers like Danube or Rhine or in their tributaries are characterized by coarse gravel substrates and high current velocities (1–2 m/s). In the Danube spawning occurs from March to April at ambient

temperatures between 8–12 °C (Keckeis et al., 1996b; Keckeis, 2001). Embryogenesis takes place in the surface strata of the bed sediments and requires high levels of oxygen (Keckeis et al., 1996a). Emerging larvae are transported via drift (Reichard et al., 2001) to the littoral zones of the river which function as nurseries. Larvae are bound to richly structured inshore zones. Our results indicate that their ecological quality as nurseries depends on the extent to which two dynamic processes match:

- a. the ontogenetic shifts in microhabitat requirements during the first months of life (Schiemer and Spindler, 1989; Schiemer and Waidbacher, 1992; Schiemer et al., 2001b), and
- b. short-term water-level fluctuations leading to a continuous change in microhabitat position and quality (Schiemer and Zalewski, 1992).

Inshore structure combines and integrates several elements required for successful recruitment at a micro- and mesoscale, namely (a) the proximity and connectivity of spawning sites and nurseries, (b) the availability of supplementary microhabitats during early ontogeny, (c) the quality of microhabitats with regard to current velocity, temperature, and food availability, and (d) the availability of refugia in the case of spates.

Under regulated conditions such richly structured inshore zones usually form small islands interrupted by embankments with linear shorelines, which are uninhabitable for 0+ fish (Schiemer et al., 1991). In the 50 km regulated but free-flowing stretch of the Austrian Danube downstream of Vienna, we found only 18 inshore 'islands', representing approximately 15% of the total shoreline, which can function as nurseries. The ecological quality of these islands depends on the shoreline configuration. As an index we proposed the length of the shore line in proportion to the length of the river channel which determines the inshore retention capacity (Schiemer et al., 2001c). We found that high index values correlate positively with the number of species present and the number of endangered species in the 0+ fish community of the respective nursery islands (Schiemer et al., 1991; Wintersberger, 1996).

In summary, the early development not only leads to dynamic changes in requirements, but the individual fish has to cope with a highly fluctuating and stochastic micro-environment. The match/mismatch between ecophysiological performances

and environmental conditions is apparently critical. A detailed experimental analysis of requirements set in comparison to the conditions encountered in the field provides insight into the causes of success or failure of the species under a particular environmental setting.

2.2. Temperature dependence of development during embryogenesis and yolk feeding

In *Chondrostoma nasus* the mortality pattern indicates the viable temperature range during embryogenesis and in the yolk feeding larvae. Low experimental mortalities occur between 10 and 19 °C. Below and above these values mortalities increase rapidly.

Table 1 provides a summary of the relationship between temperature and aspects of development, duration of stages, and sizes attained at the different stages. For the experiments egg material derived from a single female was used. Temperature significantly affects the size and the morphological state at which key life history events (for example hatching or onset of exogenous feeding) take place. Fig. 1 compares the size (tissue weight) and the remaining yolk weight of larvae hatching at different temperatures. Inserted in the relationship is the time required to reach this stage. At higher temperature, hatching and the onset of feeding not only occurs earlier but also at smaller size, at an less advanced stage of development and with larger unresorbed yolk reserves (Fig. 1, Table 1). Body growth and tissue differentiation are independent processes (Lindsey and Arnason, 1981). All the three: growth rate, differentiation rate and metabolic rate are positively related to temperature, but their accelerations are not always the same (Kamler, 1992). There are disadvantages and advantages of the combination of delayed hatching and large body size at low temperature. Prolongation of development increases the risk of mortality, but larger body size enhances feeding (Miller et al., 1988; Wanzenböck and Schiemer, 1989), delays the time after which the effects of starvation are irreversible (Miller et al., 1988) and decreases the risk of predation on larvae (Fuiman, 1994). The opposite is true at a high temperature.

2.3. Response of ecophysiological performances of exogenous feeding larvae towards temperature, food and current velocity

For the analysis of the response towards temperature and food availability during the exoge-

nous feeding period, a series of experiments at constant temperatures from 10 to 28 °C and ad libitum food conditions was conducted (Keckeis et al., 2001). In the early larval stages food consisted of *Artemia* sp. and was complemented by larger zooplankton and cut tubificids later on. As mortality above 19 °C during the embryonic phase was 100%, the experiments with larvae at temperatures > 19 °C were carried out with individuals pre-reared at 16 °C and then were adapted for approximately 24 h at the final phase of the mixed feeding stage and full yolk absorption. Larval mortalities were low between 10–28 °C. However, below 13 °C growth rates were very low and development was retarded. We assume that these findings at low temperatures indicate high mortalities in the field situation.

Table 2 provides basic information on the temperature dependence of larval development, finite larval size, specific growth rates and production efficiencies. After yolk resorption the temperature window widens (Fig. 2, Table 2). In externally feeding larvae the optimum temperature now ranges between 16 and 25 °C, based on a combination of data on mortality, growth rates and bioenergetic efficiencies. Fig. 2 compares the temperature

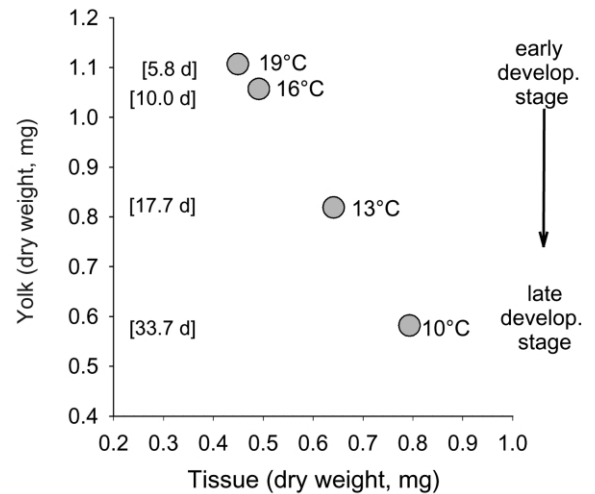


Fig. 1. Relationship between the tissue weight (dry weight) of hatching larvae of *C. nasus* and the weight of remaining yolk at different temperatures. Numbers in brackets refer to hatching times (d). The arrow indicates the increasing morphological state of the newly-hatched larvae with decreasing temperature.

dependences of size specific growth rates of larvae during the yolk-feeding period and after the onset of exogenous feeding. The comparison of weight

Table 1

Temperature dependence of duration (days) and energetics of the yolk feeding stages of *C. nasus* (data from Kamler et al., 1998)

Temperature (°C)	Developmental event	Age	Weight of tissue	Weight of yolk	SGR	Assimilation efficiency	Production efficiency
10	E_6	9.0	0.105	1.559			
	Hatching	33.7	0.793	0.582	8.2	85.4	78.0
	Onset of feeding	40.8	0.932	0.264			
	Full yolk resorption	46.1	1.051	0.000			
13	E_6	5.0	0.113	1.578			
	Hatching	17.7	0.641	0.819	13.7	92.4	74.6
	Onset of feeding	23.0	0.845	0.432			
	Full yolk resorption	28.4	1.091	0.000			
16	E_6	3.0	0.112	1.511			
	Hatching	10.0	0.491	1.057	21.2	82.5	88.7
	Onset of feeding	15.2	0.767	0.549			
	Full yolk resorption	20.8	1.095	0.000			
19	E_6	1.9	0.106	1.610			
	Hatching	5.8	0.449	1.107	37	81.6	89.1
	Onset of feeding	9.7	0.752	0.543			
	Full yolk resorption	13.3	1.082	0.000			

Separated weights (mg dry weight) of tissue and yolk at different developmental stages, and specific growth rates (SGR, mg mg⁻¹ day⁻¹) from the embryonic stage 6 (E_6) to hatching are shown. Definition of stages according to Peñáz (1974). Energetic efficiencies, defined as utilization of yolk, based on tissue production (P), respiration (R) and consumption (C) are computed for the same period as SGR. Assimilation efficiency = $(P + R)C^{-1}100(\%)$; production efficiency = $P(P + R)^{-1}100(\%)$.

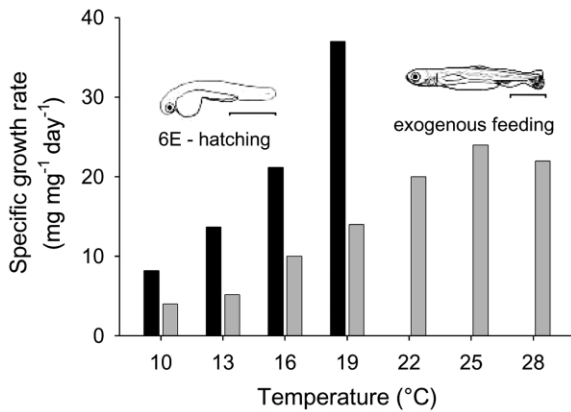


Fig. 2. Temperature dependence of growth rate in the yolk feeding embryos (black bars) and exogenously feeding larvae (grey bars) of *C. nasus*. In yolk feeding embryos tissue was separated from yolk. Values for exogenously feeding larvae refer to the 3 initial days after full yolk resorption.

specific growth rates leads to three main conclusion:

1. Growth rates are distinctly higher in the yolk absorbing period. That can be explained by the smaller body size of the larvae and by higher assimilation efficiencies achieved (Compare Tables 1 and 2).
2. In the older fish the temperature window widens and the optimal range shifts to higher values.
3. In *C. nasus* specific growth rates are high as compared with many fish species (Keckeis et al., 2001).

This high growth potential can be considered adaptive for riverine fish larvae, allowing them to exploit periods of good resource availability in a stochastic environment. The extent to which the high scope for growth can be exploited depends on food availability, temperature conditions and water currents in the micro-environment (see below).

Table 2
Temperature dependence of duration (in days) and energetics of exogenous feeding larvae of *C. nasus*

	10 °C	13 °C	16 °C	19 °C	22 °C	25 °C	28 °C
Larval duration (days from fertilization to juvenile period)	> 80	> 80	78	51	40	34	31
Finite larval size (dry body mass, mg)	–	–	68.4	78.5	56.0	56.9	36.2
Specific growth rate (mg mg ⁻¹ d ⁻¹)	4.0	5.2	10.0	14.0	20.0	24.0	22.0
Assimilation efficiency (P+R) C ⁻¹ 100 (%)	–	79.0	80.0	81.0	67.1	65.3	–
Production efficiency P (P+R) ⁻¹ 100 (%)	–	72.1	74.7	77.8	81.4	82.3	80.7

Data from Keckeis et al., 2001. Specific growth rates for the first days of exogenous feeding period. Assimilation and production efficiencies are calculated for the larval stage 2 (L2) according to Peñáz (1974).

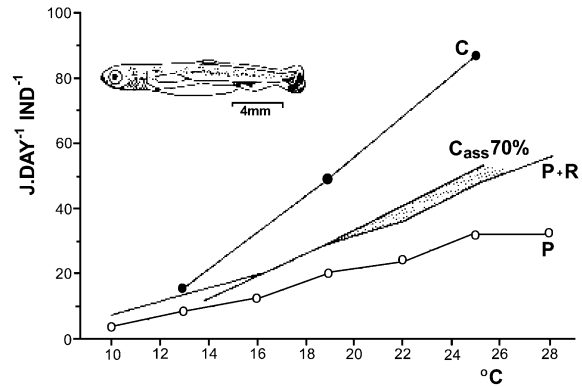


Fig. 3. Elements of an energy budget of larval *C. nasus* of 5 mg dry weight. Consumption (C) over 24 h at 3 temperatures was measured at ad libitum food availability. Production (P) rates are calculated from growth rates obtained at unlimited food supply. Respiration (R) values are based on routine metabolic rates measured with a closed system respirometer using a polarographic oxygen sensor. Active metabolic rates were calculated by multiplying the routine rates by a factor of 2.5 to correct for food searching activity and food-induced thermogenesis. Assimilation was calculated in two ways. Total assimilation (C_{ass70%}) was taken from C assuming assimilation efficiency 70%. It is compared with assimilation from A = P + R. From Schiemer et al., 2001b.

Food consumption rates have been measured in *C. nasus* for the zooplanktivorous larval stage under different temperature (Keckeis et al., 2001). External feeding starts at a larval weight between 0.75 (19 °C) and 0.90 mg dry weight (10 °C), so the onset of feeding at low temperatures occurs later and with a smaller yolk reserve (Kamler et al., 1996). The diet in the field changes with age and size. Earliest larvae feed on planktonic rotifers, which grow in the inshore retention zones (Reckendorfer et al., 1999). With increasing fish size, the mouth gap becomes larger and the mouth position changes from a forward direction to a downward direction. In parallel to these morphological changes, the feeding mode and food selec-

tion shifts from open water drift-feeding and zooplanktivory towards a benthic orientated and later detritivorous diet (Reckendorfer et al., 2001).

A synoptic approach to identify the ecological niche of a species, its constraints and limitations, is to analyze the parameters of an energy budget. Fig. 3 shows the parameters of an energy budget for exogenous feeding larvae over the entire ecological temperature range. Values for consumption, production and respiration were experimentally assessed (for experimental details see figure captions). Total assimilation assumes an assimilation efficiency of 70%. This is a high value recorded for larval cyprinids (Keckeis and Schiemer, 1992; Kamler, 1992). Comparing the calculated total assimilation value with the summed value of production and respiration reveals the tight balance between input and costs. Surplus energy allowing for additional expenditures is only available at a temperature range between 20 and 25 °C (dotted area).

Considering speed of development, bioenergetic efficiencies and mortalities it becomes apparent that from the embryonic to the larval period the optimal temperature continuously shifts to higher values (see below).

A key factor for growth and survival of the larvae of riverine fish is current velocity in the inshore microhabitats. It relates to higher food availability for drift feeding larvae vs. increased swimming costs and an increased risk of wash-out effects. Our experimental work analyzes thresholds of swimming performances as well as optimal velocities with regard to feeding and food particle selection during early ontogenetic development.

Experiments were carried out using a stream channel with a closed water system, in which current velocity, water depth, temperature and particle drift can be controlled. The swimming performances and prey capture reactions of well-acclimatized fish were filmed in a 3-D field using two synchronized video cameras. Main parameters for a foraging model—reactive distance, approach speed of fish towards the prey, capture success and a time budget of prey capture (pursuit, snapping, handling and resting time between food uptake)—were assessed. A model of position choice of riverine fish was applied. The model assumes that, with increasing current velocity, organic drift (i.e. food availability) increases; at the same time, the respiratory cost also will increase and the capture success will be limited.

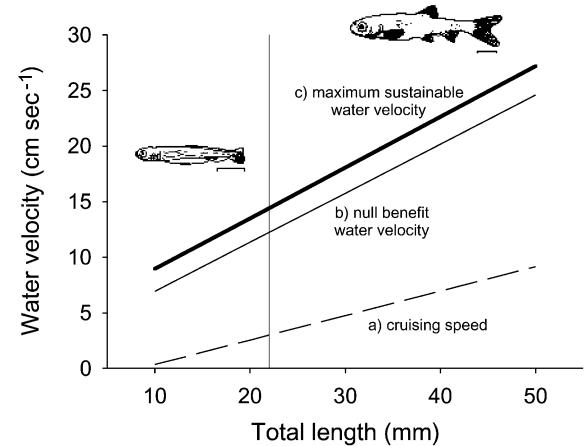


Fig. 4. Relationship of body size of early life history stages of *C. nasus* and three types of critical velocities: (a) average cruising speed of feeding fish; (b) null energy benefit, defined as the current velocity at which the assimilation of consumed food equals the respiratory costs of drift feeding larvae (for explanation see text) and (c) maximum sustainable swimming speed for 30 s. From Flore et al., 2001.

The optimal feeding position is assumed to be that in which energy acquisition is highest (Flore and Keckeis, 1998; Flore et al., 2000, 2001). Such models have so far been tested for adult salmonids (Fausch, 1983; Hill and Grossman, 1993; Hughes and Dill, 1990).

Fig. 4 distinguishes 3 ecologically relevant types of critical current velocities and their relationship to the body size of fish, (a) cruising speed at food search, (b) null energy benefit, at which the assimilated energy equals the respiratory costs and (c) maximum sustainable water velocity (tested for a period of 30 s). Swimming speed was low and increased linearly with body length.

The results on feeding in the flow chamber permit an evaluation of the time budgets and energy budgets in dependence on current velocity and organic food during early ontogenetic development. Using data from the literature on respiratory costs of swimming in the larvae of cyprinids (Kaufmann, 1990), an energetic model was constructed on bioenergetic performances of larval fish in flowing water (Flore et al., 2001).

The ecological niches during the early phases in relation to critical and optimal flow velocities lie within a very narrow range, demonstrating that the scope for development of larval fish in their natural environment is very restricted. With increasing fish size the scope widens.

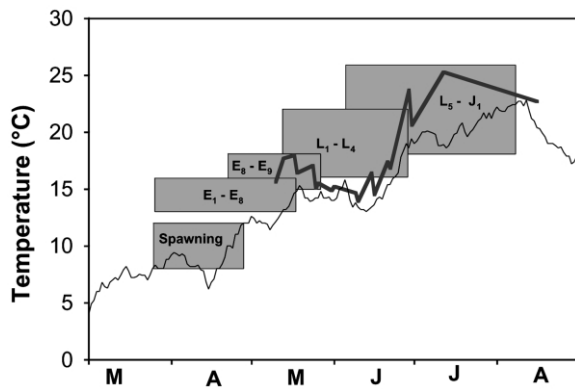


Fig. 5. Temperature in the main channel of the Danube at Vienna (thin line) and in the inshore storage zones (average value of the 3 micro-habitats) during the spawning and early life history development of *C. nasus* in 1994. The inserted boxes are defined by duration of spawning and of consecutive developmental stages in the field (length of boxes), and by the respective ranges of optimum temperatures (height of boxes). Embryonic (*E*), larval (*L*) and juvenile (*J*) developmental stages determined according to Peñáz (1974). Modified from Keckeis et al. (2001).

2.4. Match/mismatch: ecophysiological performances vs. field conditions

How do these ecophysiological performances match with the environmental situation in regulated rivers? To identify critical conditions and thresholds the experimentally obtained performances in relation to temperature, current velocity and food availability has to be compared to the environmental conditions in the field.

Fig. 5 shows the temperature regime in the free flowing Danube downstream of Vienna from March to August 1994. The thin line is based on the daily hydrographic readings at 07.00 h in the main channel. The thick line represents the temperature recording in the inshore zones, i.e. in the actual *C. nasus* microhabitats (Fig. 6b,c). The temperature regime of the inshore storage areas becomes decoupled from main channel conditions to a degree that depends on water retention and exchange. We have formulated this as part of an ‘Inshore Retention Concept’ (Schiemer et al., 2001c). Local temperature conditions will be highly significant for temperature-dependent processes of species bound to the littoral.

Fig. 5 shows the time of occurrence of different stages of *Chondrostoma nasus* in the field together with their temperature optima. Based on experimental data on bioenergetic performances and

mortalities, the optimal temperature shift ranges from 8–12 °C (spawning), to 13–16 °C (embryonic development), 15–18 °C (yolk feeding larvae), 19–25 °C (exogenous feeding larvae), >22 °C (early juveniles). This shift in temperature optima correlates with the temperature increase in rivers after the spawning period of *Chondrostoma nasus*, which usually occurs in March and April. However, there is a mismatch between the optima and the average conditions in a regulated river (hydrographic readings) which illustrates the high significance of the inshore retention zones (Fig. 6).

A detailed study has been carried out at three types of inshore habitat situated within one of the 18, long structured inshore zones that function as fish nurseries in the free-flowing Danube downstream of Vienna. Fig. 6 shows the location of the three inshore zones of 100 m length, representing a bay situation (BAY), an immediately adjacent flat gravel bar (GB1) and a steeper gravel bar (GB2) 0.9 km further downstream. The small-scale inshore bathymetry was assessed and a relief map was constructed in 10-cm-step contour lines using the GIS method. Detailed analyses have been carried out for the period of early fish development from May to September 1994. Temperature and current velocity profiles, the density and composition of plankton, benthos and of drift organisms were assessed in comparison to the distribution pattern of fish larvae, their growth and diet and population dynamics (Keckeis et al., 1997; Winkler et al., 1997; Reckendorfer et al., 1996, 1999, 2001; Schiemer et al., 2001b). The inshore shallow water with a water depth of 40 cm or less is the preferred larval microhabitat. Fig. 6c illustrates the stochastic nature of the larval microhabitat, which, continuously shifts its position with the changing water level of the river.

The importance of current velocity in larval microhabitats is high both for individual growth performances as well as larval displacements and transport processes along the river course and concomitant population losses. Fig. 7 illustrates the average current velocities (v_a) measured in two larval microhabitats in comparison to the critical swimming speed (v_{crit}) of the growing population of *Chondrostoma nasus*. The bay-habitat offers adequate conditions except for periods for short spates, while in the gravel bar habitat the critical swimming speeds are frequently exceeded—which means that microhabitat availability in

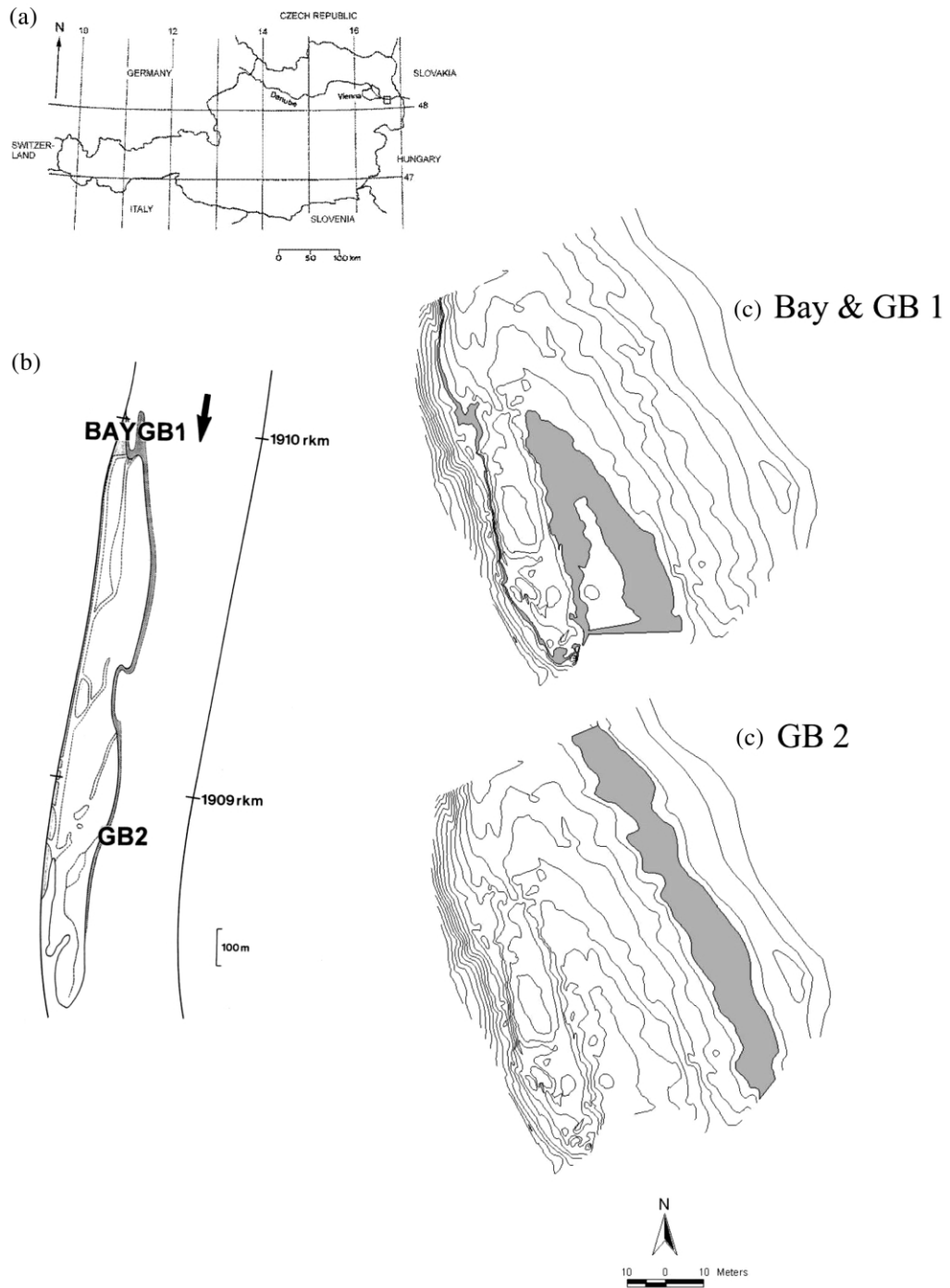


Fig. 6. Austrian Danube (a) with the location of the study site. (b) The position of 3 microhabitat stretches, bay, gravel bar 1 (GB1) and gravel bar 2 (GB2), of 100 m river length each is indicated. (c,d) The contour map at Bay and GB1 and the shift in microhabitat position as delineated the area between flowline and a maximum depth of 40 cm (shaded area). Within this field over 80% of 0+ fish were found.

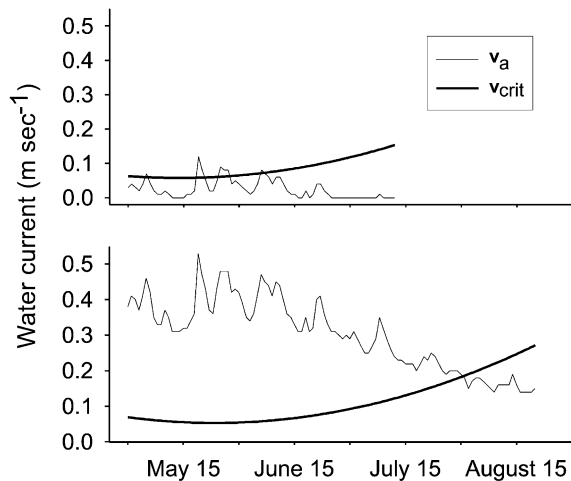


Fig. 7. Average current velocity (v_a) in the 'Bay' (top) and 'GB1' (bottom) microhabitat, set in comparison to the experimentally defined maximal sustainable swimming performances (v_{crit}) of the growing 0+ *C. nasus* population. From Keckeis and Schiemer, 2002.

such areas will be strongly constrained. Under conditions of spates the local populations are decreased by wash-out effects leading to a continuous downstream displacement and loss of larvae. Fig. 8 evaluates the significance of the ratio between the average current velocity, v_a , within a microhabitat area (each data point is the average of 60 measurements) and v_{crit} on the population

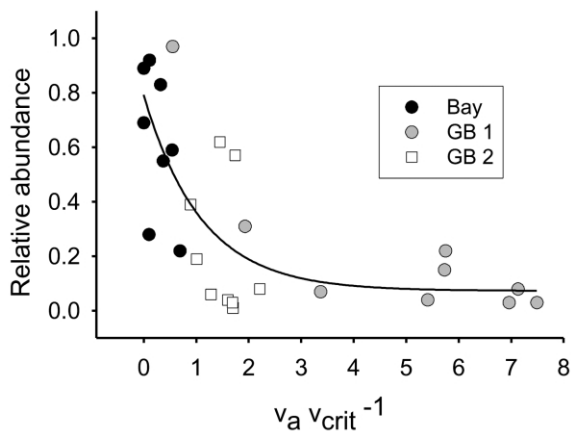


Fig. 8. The relationship between the distribution of the 0+ *C. nasus* population between 3 microhabitats (different signatures) and the ratio between the average current velocity in the field (v_a) and the critical current velocity (v_{crit}) of the growing 0+ populations. The summed catch in the 3 microhabitats at any census is taken as 100%. From Keckeis and Schiemer, 2002.

distribution of *Chondrostoma nasus*. Microhabitat distribution is strongly affected by current conditions in relationship to the swimming performances of 0+ fish. The capacity of a location to retain a high population of 0+ fish against the adverse effects of water level fluctuations and spates depends on inshore sinuosity and inshore retention (Schiemer et al., 2001c).

3. Conclusions

River engineering has led to a reduction in the availability of structured inshore zones and has reduced the synchronization between the physiological program of the species and the environmental temperature regime. For example, the growth of larvae in the field is lower than predicted by the experimentally determined response towards temperature (Reckendorfer et al., 2001) indicating, that not only temperature but also food availability poses constraints. Individual growth profiles obtained from otolith microstructure clearly demonstrate that microhabitat conditions are linked to the retention capacity of the inshore zones. Strong changes in the individual growth profiles indicate a high rate of downstream displacement with a continuous saltatory transport between microhabitats of different quality and a concomitant population loss.

The high scope for growth of *Chondrostoma nasus* apparently can not be fully realized under conditions of regulated rivers. Reduced growth leads to a prolonged development within the critical stages with accumulated risks of high mortality.

The 'Inshore Retention Concept' (Schiemer et al., 2001c) highlights the significance of inshore storage zones, with regard to the physiographic properties in the inshore areas, their productivity with regard to plankton and zoobenthos, and their refuge capacity, e.g. for larval fish, at water level fluctuations. The present study demonstrates the significance of combining experimental studies and field studies and the need for an ecophysiological program with respect to environmental management and conservation.

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