This change in perspective is shaping Great Lakes management decisions from lamprey control to habitat and harvest management. At the same time, studies in the Great Lakes have contributed substantially to our understanding of the important processes affecting survival of fish early life stages in general.

Understanding Conservation Issues of the Danube River

Hubert Keckeis and Fritz Schiemer

11.15 The river and its fish fauna

11.15.1 Geomorphology and longitudinal zonation of the Danube River

The Danube River is the second largest river in Europe, with a drainage area of 805 000 km^2, a length of approximately 2850 km, and a discharge of 6450 m^3 s^{-1} at its mouth. From its source in Germany to its mouth in the Black Sea in Romania, it crosses nine countries (Germany, Austria, Slovakia, Hungary, Croatia, Serbia, Bulgaria, Romania, and Ukraine), representing a large variety of landscapes and climates.

Geomorphological conditions define three distinct sections of the river. The upper section (river km 2850–1750) ranges from Germany to the border of Austria and Slovakia and has an average slope of 40 cm km^{-1}, with a high bedload transport capacity. Before regulation, the morphology of the river in this section alternated between canyons with narrow riparian zones – where the river breaks through massive rocky layers – and braided alluvial sections with many side arms and backwaters in large floodplain areas. This was especially true in the plains in the eastern part of Austria. The middle section is characterized by a drastic reduction in the slope (6 cm km^{-1}) and lower bedload transport capacity. This section is separated from the lower section (river 940–0 km) by a 100-km-long cataract (the "Iron Gate"), where the river cuts through the Carpathian Mountains. In the lower Danube River, the average slope is 3.9 cm km^{-1} and the deposition of suspended solids increases significantly.

11.15.2 Biogeographical aspects

The fish fauna of the Danube River is the richest of any European river, with more than 100 species from 23 families (Busnita 1967, Bacalbaşa-Dobrovici 1989). The fish fauna is dominated by Cyprinidae (39 species), followed by Percidae (11), Gobiidae (11), Cobitidae (eight), Salmonidae (seven) and Acipenseridae (six). There is a clear succession of species associations along the longitudinal course of the river (Bacalbaşa-Dobrovici 1989). The species richness is due to the unique direction of flow of the Danube River. It flows from west to east, which leads to a significant role for it as a biocorridor, connecting the Ponto-Caspic and Central Asian areas in the east with the high mountain alpine regions in the west. The aquatic fauna is sharply delimited against that of Siberia and tropical Africa, but much less different from northeastern Europe and western Asia. Many of the aquatic organisms reveal a Ponto-Caspic distribution, indicating the role of the river as an important migration and recolonization route between and after the ice ages.

11.15.3 Hydrological characteristics and major human impacts in the Austrian section

The hydrological conditions along the Danube River's Austrian stretch are characterized by high and variable flow from the Alps. The long term monthly mean water levels are highest in June and lowest in November, with an amplitude of 2.5 m. Water-level fluctuations, however, are strong and unpredictable, and spates can occur throughout the year. High current velocities in the main channel and coarse-grained substrates characterize the Austrian Danube as a hyporithral* river. Historically, the dynamic hydrology and the high sediment transport from the Alps produced large alluvial fans, especially in the tectonic basins below geomorphological constrictions. This was accompanied by a braided river course with extended floodplains prior to regulation (Figure 11.22).

Severe river regulation in the Austrian Danube was initiated in 1850 and continues to the present. The ecological effects, of course, were not taken into consideration. The main engineering approach was to create a single, straightened channel, stabilized by riverside embankments and ripraps. The former arms of the original braided system were cut off (Figure 11.22). The ecology of the Danube has been strongly affected by land use and changes in its catchment, by pollution, and most importantly by hydro-engineering. Over the past 50 years more than 90% of the upper Danube and its major tributaries have been dammed for hydropower production. The remaining few stretches have been severely affected by regulation. This also holds true for the remaining 50 km, free-flowing section downstream from Vienna. This reach, although considerably impacted by regulation, represents one of the last remnants of a river–floodplain system. Here, the hydrological dynamics, flood pulses, and bedload transport are partially operative and a high potential for re-establishing the hydrological regime remains. As the largest remnant of alluvial landscape in Europe, this stretch was declared a National Park in 1996.

The main features of the regulation scheme and its immediate and long term effects in this area were:

(1) a general reduction of up to 80% of the former alluvial floodplain areas, backwaters, and side arms;
(2) a loss of riverine inshore habitats, which had strong impacts on inshore retention characteristics and on the habitat value for rheophilic organisms; and
(3) reduced hydrological connectivity, both of open surface-water connections and groundwater exchange between river and floodplains.

11.15.4 Status and ecological guilds of the fish fauna

Intensive surveys carried out during the last two decades revealed a large number of fish species. Compared to the historical records, most of the original fauna is still present.

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* Mountain zone.

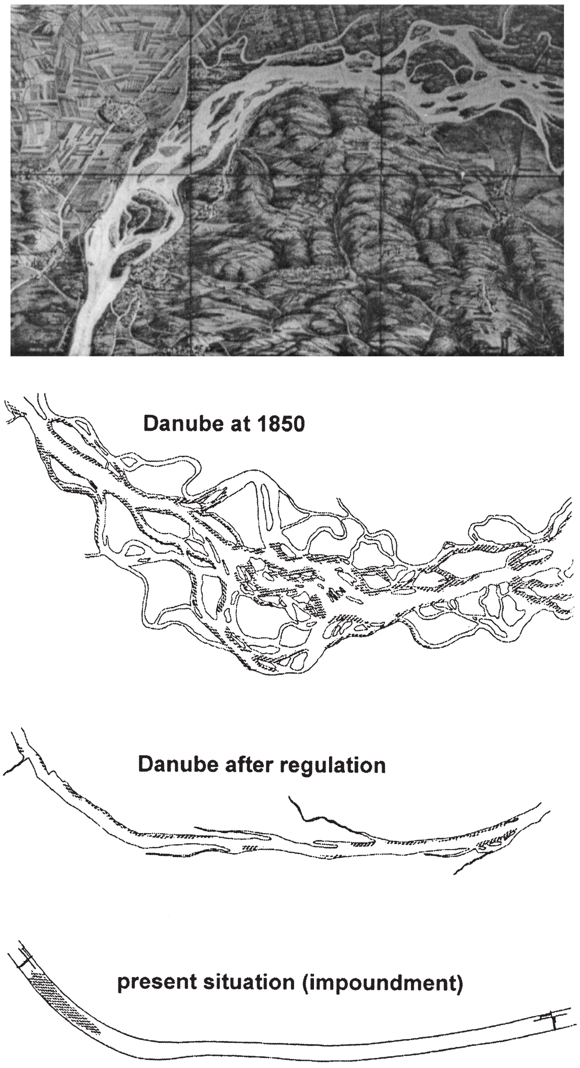

Figure 11.22 (a) Historical map of the Danube River near Vienna showing the character of a braided section before river regulation. (b) Impact of regulation schemes on river morphology and area of the Danube River near Vienna during the era of 1875 to present. (Reproduced with modifications from Zauner 1996 with permission of Hans Winkler.)

Only the large diadromous sturgeons (Acipenseridae: *Huso huso*, *Acipenser gueldenstädti*, *Acipenser stellatus*, and *Acipenser nudiventris*), which historically migrated from the Black Sea more than 2500 km upstream, have completely disappeared in the upper sections. Their migration route was blocked by the construction of large dams at the "Iron Gate" (Serbia, Romania). There are practically no records on the population structure prior to river regulation. The few quantitative data on the impact of river regulation and dam construction on fish abundance show that the populations of the two most characteristic fish species (Cyprinidae: *Chondrostoma nasus, Barbus barbus*) disappeared completely within a period of 2 years (1922–1924) after the construction of a dam in the Inn River, the largest tributary

Table 11.2 Categories for the ecological guilds of the Danube River fish fauna (Schiemer *et al.* 1994).

Category	Description
Rhitrale	Species that migrate at least during their reproductive period into oxygen-rich, cold water streams (upper or lower trout region)
Rheophilic A	Typical riverine species that spend their entire life cycle in the main stream. Larvae and juveniles require species-specific, ontogenetically changing inshore structures
Rheophilic B	Lithophilous species that must migrate into backwaters and side arms during certain seasons (summer-feeding and overwintering habitats)
Eurytopic	Generalist species without any significant preference, occurring either in the main channel, in side arms, or in backwaters. They reproduce mainly in backwaters (primarily phytolithophilous, lithophilous). Species-specific differences exist in diet and feeding habits, microhabitat selection, and preferred temperature
Stagnophilic/Limnophilic	Species that occur throughout their life cycle in abandoned backwaters with dense macrophytic vegetation. Some of these species are specifically adapted to extreme environmental conditions (for example, high water temperature, low oxygen context)
Exotic	Species that were introduced to provide a recreational fishery, escaped from aquaculture ponds, or were released from aquaria.

of the Danube (Waidbacher & Haidvogel 1998). Most of the riverine species found in the Danube and in many other European rivers are on the “Red Lists” of endangered taxa (Lelek 1987; see Chapter 10, Box 10.1). Populations of several fish species have declined during the last decades, indicating that the conditions for sustaining a characteristic fish fauna in the Danube are disappearing. Evaluation of the present situation using qualitative data from numerous surveys and on the basis of species-specific ecological needs revealed six ecological guilds (Table 11.2). It is evident from habitat changes that rheophilic species must have declined in favor of the eurytopic and limnophilic groups (Figure 11.23).

The most significant ecological features for an endangered riverine fish fauna are the specific requirements for the larval and juvenile stages (see Chapter 7). Detailed studies on densities, distribution, and habitat requirements revealed that large numbers of larvae and juveniles of many fish species occur in the main channel of the river (Spindler 1988). A high diversity and a large number of endangered species are found among the populations of 0+ (young-of-the-year) fishes in small bays and in shallow sloped gravel banks of the main river. At artificial shores only a few individuals of eurytopic species are observed (Figure 11.24). Eurytopic forms dominate open backwaters in place of rheophilic and limnophilic species (Kurmayer *et al.* 1996). In disconnected backwaters with dense aquatic vegetation the larval fish associations are composed of eurytopic and limnophilic species.

Examples of clear habitat selection, even in the young larval stages, were also observed. During the first few months of their life, larvae of many riverine fish species undertake

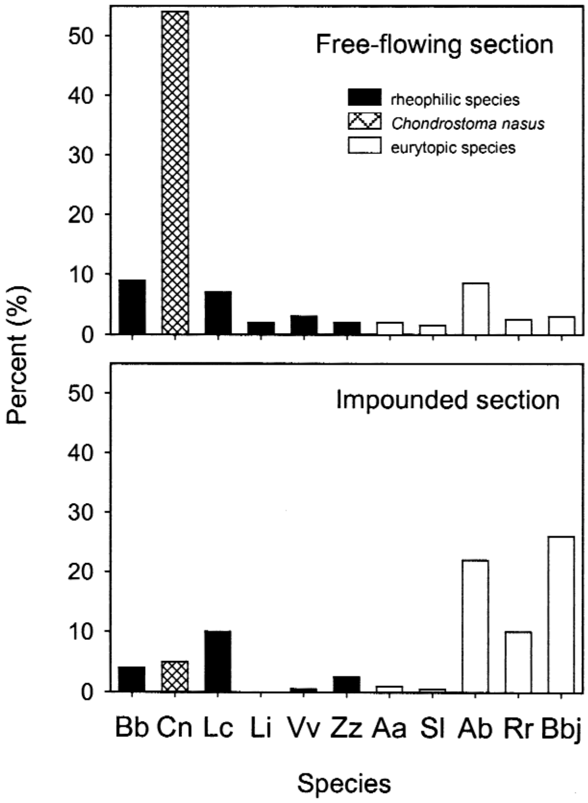

Figure 11.23 Comparison of the adult species composition in a free-flowing and in an impounded section of the Danube in Austria. Bb, *Barbus barbus*; Cn, *Chondrostoma nasus*; Lc, *Leuciscus cephalus*; Li, *Leuciscus idus*; Vv, *Vimba vimba*; Zz, *Zingel zingel*; Aa, *Aspius aspius*; Sl, *Stizostedion lucioperca*; Ab, *Abramis brama*; Rr, *Rutilus rutilus*; Bbj, *Blicca björkna.* (Reproduced from Schiemer & Waidbacher 1992 with permission of John Wiley & Sons Limited.)

ontogenetic niche shifts with significant changes in habitat preferences (Figure 11.25; Schiemer & Spindler 1989). Characteristic 0+ species associations are significantly ordinated along different macrohabitats (lotic, lentic, artificial, parapotamic,* paleopotamic†), the explanatory abiotic variables are current velocity, substrate, depth, and slope of the individual sites (Wintersberger 1996a). A differential utilization of distinct areas by different size classes of the same species also exists. That is, rheophilic species occur in lotic habitats, and are also found in lentic areas, indicating a species-specific ontogenetic habitat shift and size-dependent spatial separation and resource utilization (Wintersberger 1996b).

A general relationship between number of species and shoreline sinuosity of the main river (Figure 11.26) demonstrates the importance of highly diverse inshore structures (gravel banks, bays) as nursery zones for rheophilic fishes. The ecological quality of inshore zones of large rivers can therefore be evaluated on the basis of the ecological requirements

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* Abandoned side arm.

† Oxbow lake.

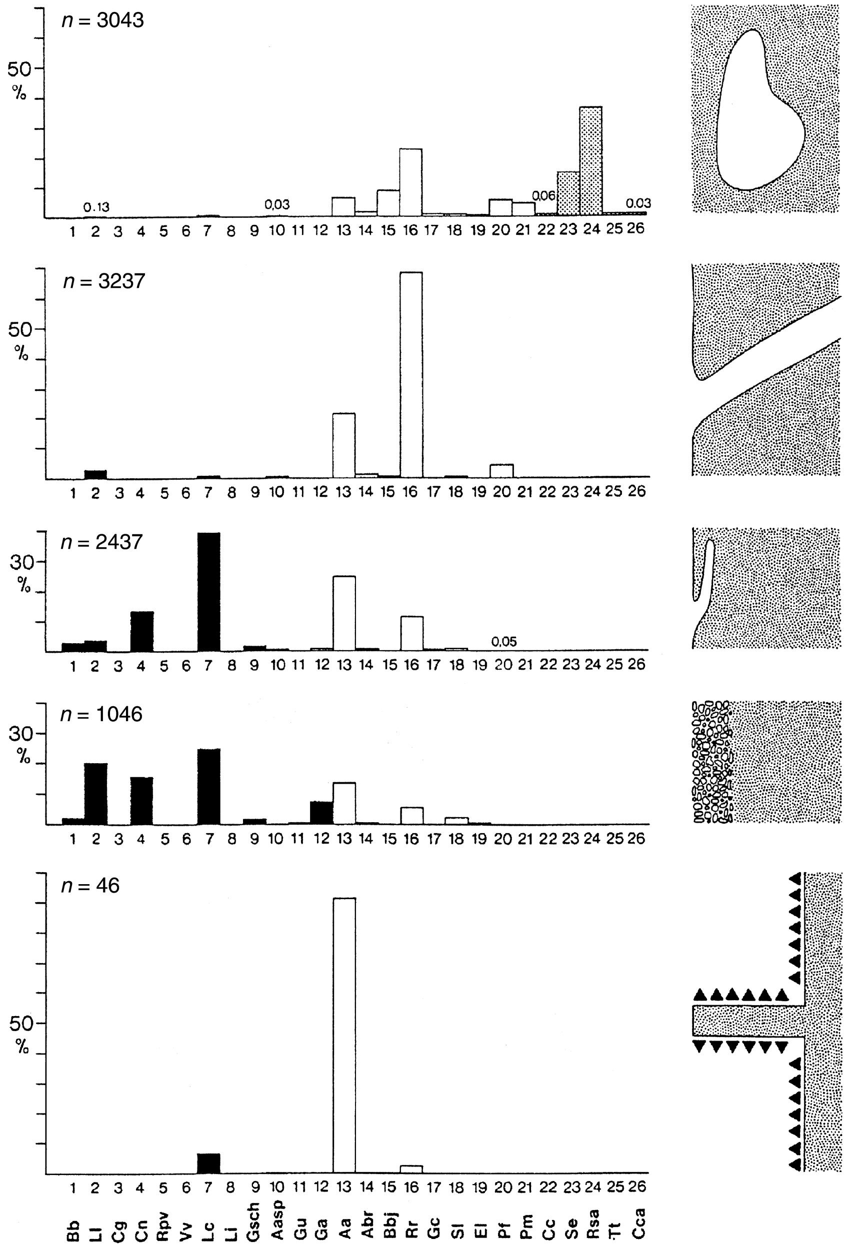

Figure 11.24 Occurrence and densities of species and ecological guilds of early life stages at different types of inshore habitats of the Danube River. Black bars, rheophilic species; white bars, eurytopic species; grey bars, limnophilic species. 1, *Barbus barbus*; 2, *Leuciscus leuciscus*; 3, *Cottus gobio*; 4, *Chondrostoma nasus*; 5, *Rutilus pigus virgo*; 6, *Vimba vimba*; 7, *Leuciscus cephalus*; 8, *Leuciscus idus*; 9, *Gymnocephalus schraetser*; 10, *Aspius aspius*; 11, *Gobio uranoscopus*; 12, *Gobio gobio*; 13, *Alburnus alburnus*; 14, *Abramis brama*; 15, *Blicca björkna*; 16, *Rutilus rutilus*; 17, *Gymnocephalus cernua*; 18, *Stizostedion lucioperca*; 19, *Esox lucius*; 20, *Perca fluviatilis*; 21, *Proterorhinus marmoratus*; 22, *Cyprinus carpio*; 23, *Scardinius erythorphthalmus*; 24, *Rhodeus sericeus amarus*; 25, *Tinca tinca*; 26, *Carassius carassius.* (Reproduced from Schiemer & Spindler 1989 with permission of John Wiley & Sons Limited.)

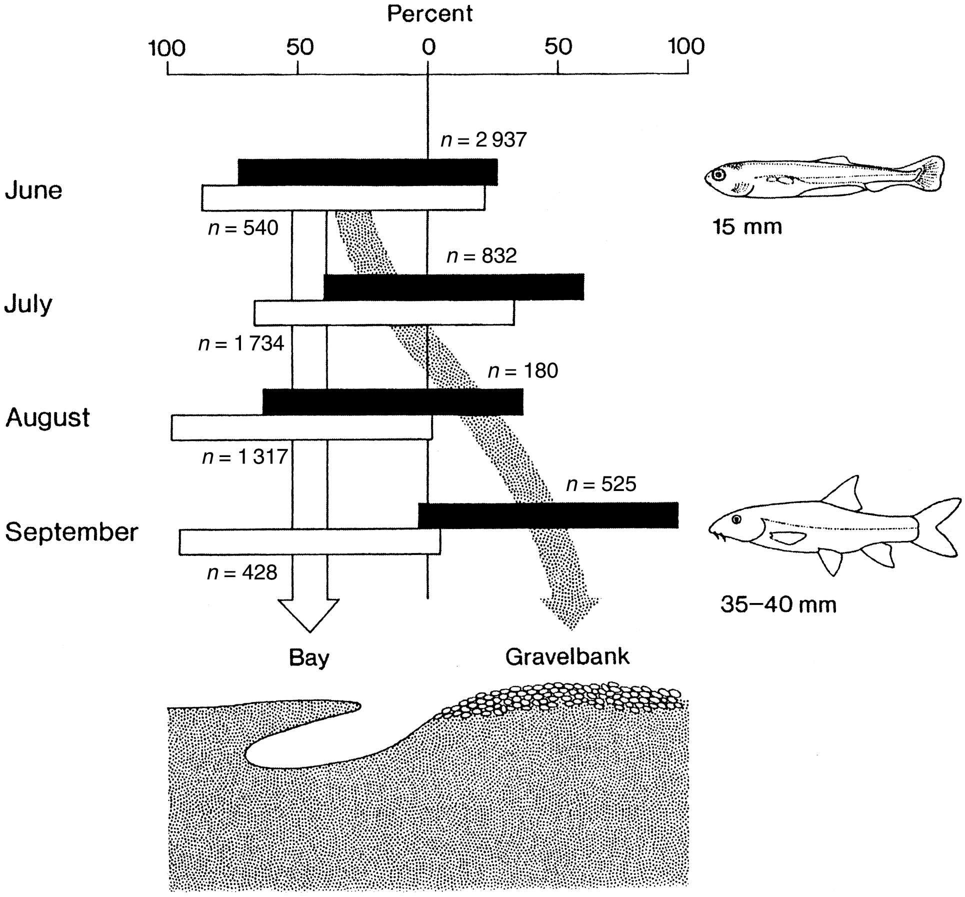

Figure 11.25 Occurrence of larvae and juveniles of the two most abundant fish species of the Austrian Danube River, *Chondrostoma nasus* (☐) and *Barbus barbus* (■). Barbels change their habitat preference during their development from the bay habitat to the gravel banks in the main river, whereas nase stay nearby sheltered bays throughout their early development.

of fish embryos and larvae. It is likely that the present shore structure (see Figure 11.26) is inadequate for long term maintenance of the characteristic fish associations. This idea is supported by the decline of formerly common species that has been observed in recent years.

11.16 The nase: target species for river conservation

Nase (*Chondrostoma nasus*) were abundant in many European rivers, but their stocks have declined dramatically (Lusk & Halačka 1995, Kirchhofer 1996, Kappus *et al.* 1997). Factors that limit populations may change during life history, for example:

(1) Negative effects during the adult period may lead to reduced growth and reduced physiological condition, which can result in poor gamete quality (Trippel *et al.* 1997).

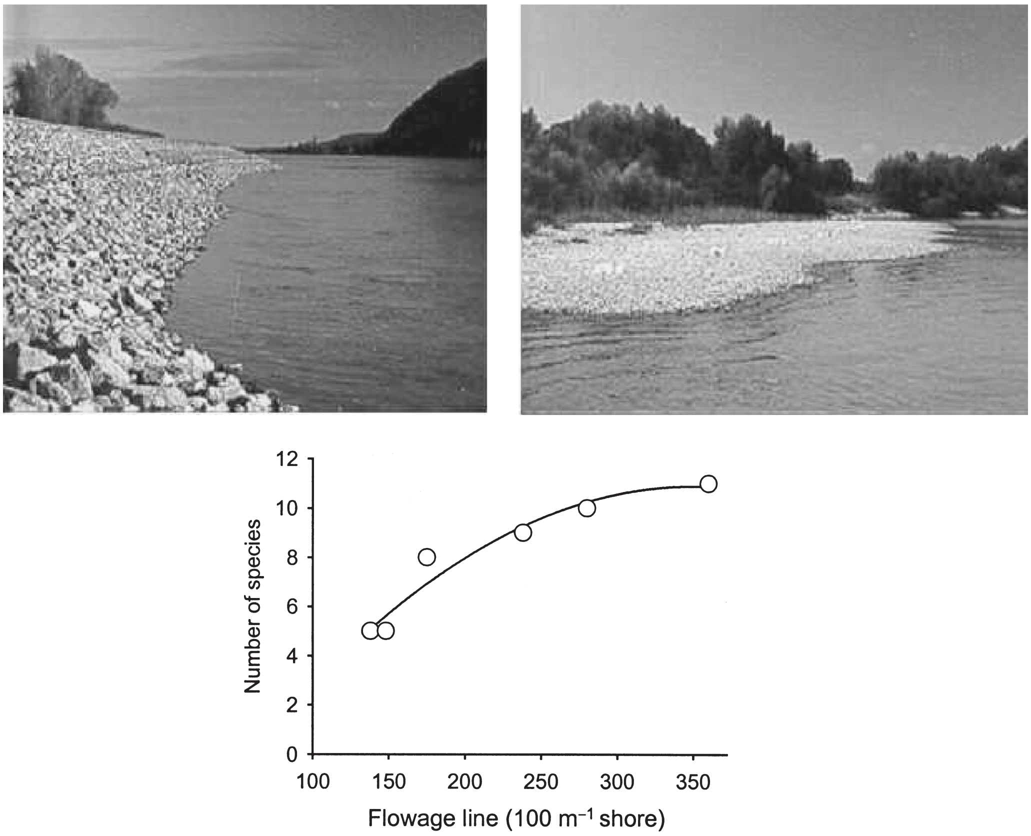

Figure 11.26 Relationship between number of species (age 0+, larvae and juveniles) and inshore sinuosity of the Danube River in Austria. The flowage line (that is, length of the shoreline) is almost straight at artificially constructed shores (left picture) whereas it is longer at natural gravel bars (right picture). (Reproduced from Schiemer *et al.* 1991 with permission of E. Schweizerbart Verlagsbuchhandlungen, www.schweizerbart.de.)

(2) Reduced availability of adequate spawning areas (due to habitat fragmentation, or changes of the natural flow regime) may lead to decreased spawning success.

(3) Alterations of the flow regime as a result of damming and river regulation changes the size-distribution of transported particles, which may lead to silting of eggs with a concomitant reduction in the oxygen supply, which increases the mortality of the embryos (Marty *et al.* 1986; Keckeis *et al.* 1996; Bardonnet 2001).

(4) River channelization reduces the size, number, and quality of habitats available to 0+ fishes. It also alters the position and connectivity of habitats, prohibiting fish larvae and early juveniles from reaching the right place at the right time (that is, disrupted spatial and seasonal habitat relationship), thereby affecting survival of 0+ populations (Schiemer *et al.* 1991, Keckeis *et al.* 1997, Winkler *et al.* 1997). This principle is discussed further in Chapter 7.

The cumulative effect of these disturbances has important implications for the recruitment process.

Table 11.3 Summary of key habitat variables measured at about 80 spawning sites of *Chondrostoma nasus* over their entire distribution (Kamler & Keckeis 2000).

Characteristic	Average	Coefficient of variation (%)
Temperature (°C)	9.5	20
Current velocity (m s^{-1})	0.9	22
Oxygen (mg l^{-1})	10.9	25
Depth (cm)	39.9	37
Area (m^2)	89.5	61
Grain size (mm)	32.5	74

We therefore tried to identify the factors that are responsible for the present decline of *Chondrostoma nasus* populations in rivers. Examining extrinsic and intrinsic factors that influence the performance of the offspring enables a clear identification of the survival potential and helps in the development of successful management criteria based on the ecological demands of the organisms involved. A series of field and laboratory investigations was carried out, which proved to be very helpful for understanding development under natural conditions as well as population fluctuations.

11.16.1 Spawning habitat

Spawning of *Chondrostoma nasus* is tied to the inshore structure of the river itself or its tributaries. The spawning areas are characterized by a narrow range of specific characteristics, such as water depth, average current velocity, and spawning temperature, irrespective of the size and geographical position of the river (Table 11.3). These data may serve as a basis from which to predict or construct usable spawning sites in river restoration projects and to enhance spawning success in this endangered rheophilic cyprinid.

11.16.2 Spawning population, egg quality, and offspring viability

The size and age structure of the spawning population may influence recruitment, and in this respect the pathway from female attributes to egg properties and ultimately to offspring is very relevant. Younger and smaller females, as well as the oldest ones, produce small eggs, which leads to a reduction of offspring viability (Keckeis *et al.* 2000). The age and size structure of *Chondrostoma nasus* populations is affected by habitat modifications and pollution, with the effects being manifested in a heterogeneous size and age structure (Peňáz 1996). A 6-year observation of the structure of the spawning population in a tributary of the Danube revealed that larger individuals of both sexes dominated the population; new recruits of females rarely augmented the population (in only one out of 6 years). New males entered the population in intervals of 1–4 years (Kamler & Keckeis 2000). This record clearly demonstrates that many year classes are missing due to high mortality in early life.

11.16.3 Early development – the endogenous feeding period

Nase eggs and embryos possess many traits that indicate high survival and growth potential (Kamler *et al.* 1996, 1998). Embryos develop successfully over a large range of temperatures, from 9°C to 19°C. Within this range, survival rates are high and the duration of the incubation period ranges from 5.8 days at 19°C to 33.7 days at 10°C. The eggs are large, with a thick egg capsule that protects the embryos against mechanical damage, and yolk-sac larvae appear to be largely independent of minerals supplied from the water. Several traits that are crucial for survival help maximize the size that larvae attain at the end of the yolk-sac phase. Specifically, yolk size, the caloric value of egg dry matter, the efficiency of yolk utilization for growth, and embryonic growth rate are high compared to other species (Kamler & Keckeis 2000). As we have seen in other chapters of this book, the size attained by larvae at the transition from yolk to exogenous feeding is positively associated with survival. The total dry weight of *Chondrostoma nasus* at hatching (tissue + remaining yolk) is 1.485 mg (Kamler *et al.* 1998), which is high compared to the mean of 0.038 mg for marine fish and even other freshwater species (Table 1.1). Body size of *Chondrostoma nasus* at complete yolk absorption is also large, 1.08 mg dry weight, and is independent of temperature between 10°C and 19°C (Figure 11.27). Nase larvae can resist starvation for long periods (Keckeis *et al.* 2000), which gives them an extended window to initiate exogenous feeding. This is beneficial when environmental conditions are unpredictable or highly variable, which is typical of *Chondrostoma nasus* nursery grounds in rivers.

The relatively low metabolic expenditures and fast growth are due to high efficiencies of yolk energy utilization. Yolk-feeding nase have higher conversion efficiencies (K_1) than Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*), and several other freshwater and marine species (averaging 57% in nase compared to 34–52% for others; Kamler *et al.* 1998). Conversion efficiencies continue to be high during exogenous feeding (Figure 11.28). During early ontogeny optimum temperatures increase from 8°C to 12°C for spawning through 13–16°C for embryonic development, 15–18°C for yolk-feeding larvae prior to exogenous feeding, 19°C for exogenous feeding larvae, and 22°C for late larvae and early juveniles. These optimum temperatures for the physiological–biochemical processes in the individual fish closely parallel the spring rise in temperature in their nursery areas (Figure 11.29).

From these findings it can be concluded that nase embryos, larvae, and early juveniles have many intrinsic attributes that indicate high survival potential and help explain the previous success of this species in the Danube River. Low spawning success and low survival rates of young-of-the-year might therefore be attributed to unsuitable extrinsic factors.

11.16.4 Habitat requirements and refugia

As we have seen throughout this book, the success of a year class is primarily determined by reproductive success and mortality in the embryonic and larval periods. In rivers, the conditions along the inshore ecotones are decisive elements in the population dynamics of individual species. Habitat characteristics in rivers are dynamically controlled by hydrology, and, in particular, the patterns of current velocity, depth, temperature, and food availability that depend on the inshore relief and water level of the river (Figure 11.30). For larval

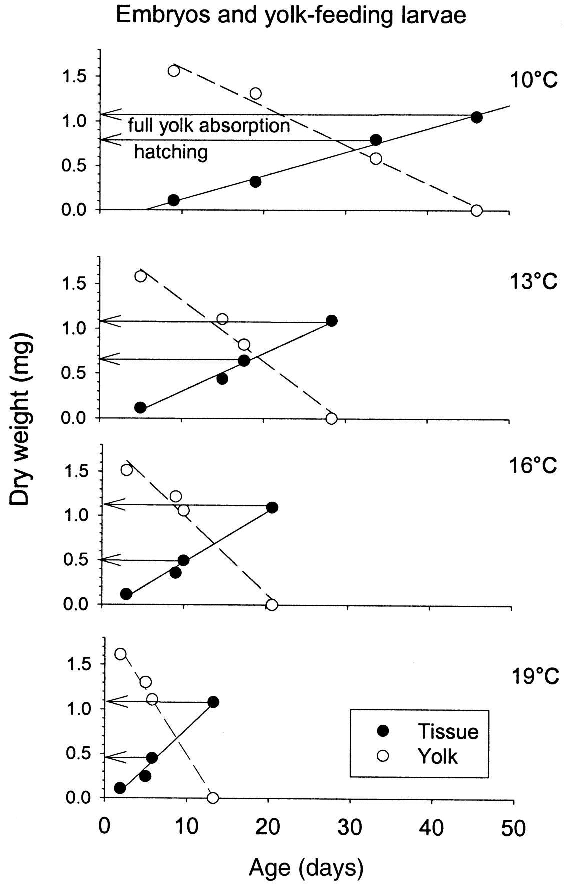

Figure 11.27 Dry weight of tissue and yolk from fertilization to full yolk absorption of *Chondrostoma nasus* embryos at different temperatures. The arrows indicate greater yolk in larvae hatching at higher temperatures. (Data from Kamler *et al.* 1998.)

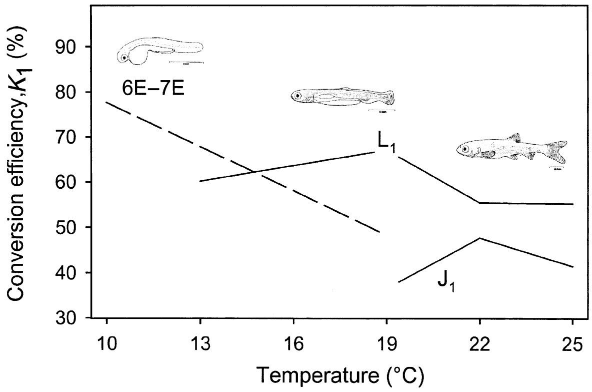

Figure 11.28 Shift of temperature-dependent conversion efficiencies (K_1; calculated as $P \times C^{-1} \times 100$) from embryonic stages 6–7; at larval stage 1, and at the first juvenile stage. (Data from Kamler *et al.* 1998, Keckeis *et al.* 2001.)

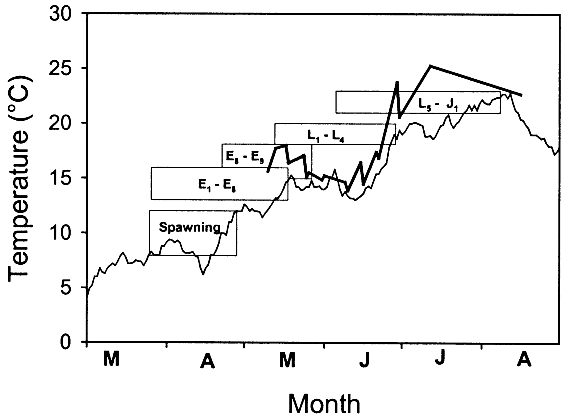

Figure 11.29 Shift in temperature requirements during *Chondrostoma nasus* spawning and early ontogeny in relation to water temperature in the field in 1994. Thin line shows temperatures in Danube River main channel, measured daily at 07:00 a.m. by the River Authority. Thick line shows mean daily temperatures taken in hourly intervals from three actual *Chondrostoma nasus* mesohabitats. Rectangles indicate the occurrence of optimum temperatures in the field. It is evident, that the development at optimal temperatures can only occur in inshore zones with higher temperatures. (Reproduced from Keckeis *et al.* 2001 with permission of Academic Press.)

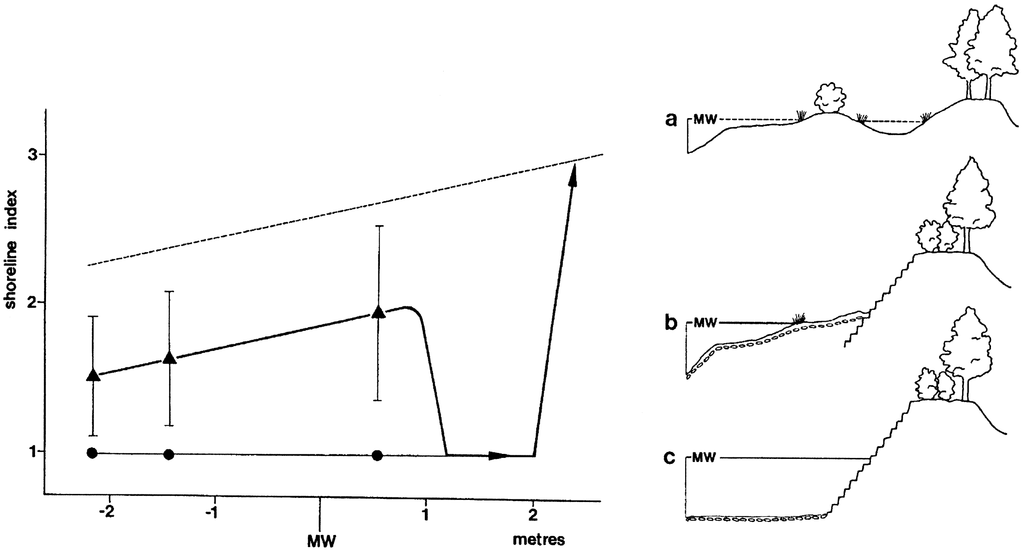

Figure 11.30 Degree of structural diversity of inshore zones in relation to the water level of the Danube River (left graph). The dashed line indicates a hypothetical situation in an undisturbed natural habitat. Inshore structure increases with increasing water level of the river. At the remaining richly structured gravel banks downstream of Vienna, the structural heterogeneity increases with increasing water level, but it is interrupted as the water level reaches the dyke (thick lines, triangles). When the water overflows the dyke, the heterogeneity increases again, as the floodplain is connected with the river. Habitat structure remains low at artificial shores (circles, thin line), so long as the water is higher than the dyke during high water. The inserts on the right side represent cross-sections of the (a) natural shore, (b) present situation at gravel bars of the free-flowing section, and (c) present situation at artificial shores. (Reproduced from Schiemer *et al.* 2001b with permission of E. Schweizerbart'sche Verlagsbuchhandlung.)

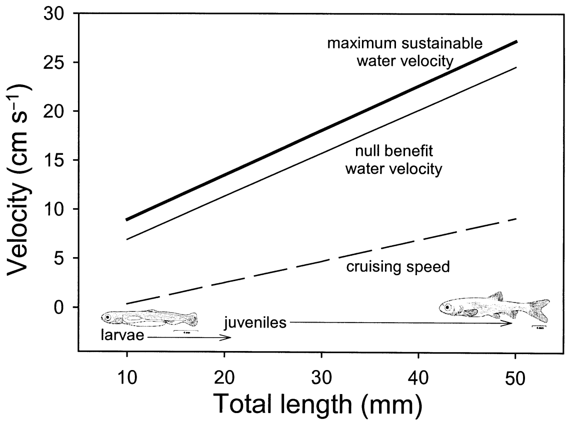

Figure 11.31 Cruising speed, null benefit water velocity, and maximum sustainable water velocity of *Chondrostoma nasus* larvae and juveniles. See text for explanation.

fishes, richly structured, small-scale zones with low water currents, shallow depths, higher temperatures, finer substrate, and dense vegetation form islands in a highly fluctuating stochastic environment.

The structure of the inshore zone also determines the number of refuges and the ecological buffering capacity during rapid water-level changes. Artificial shores are characterized by rapid changes in microhabitat (for example, water current) with changing water level, leading to a wash-out of larval fish populations, whereas along natural shores negative effects are buffered over a broad range of flow conditions (Schiemer *et al.* 2001a). River regulation and reduction of shoreline consequently lead to negative effects on the early stages of riverine fishes.

Habitat quality in rivers is, in addition to the obvious importance of physical conditions, also defined by biotic interactions. The balance between energetic gains and costs, to a large extent, determines an individual's success. Therefore, an individual should select microhabitats where it can maximize its net energy intake. In the context of foraging, water velocity plays a very important role. The tolerance of a fish to water velocity will determine not only its ability to maintain station against a current, but also its escape response and foraging efficiency. Critical swimming speeds for larvae are very low but increase linearly with increasing fish size (Figure 11.31). From a behavioral or energetic perspective, different measures of critical speed must be considered. The null benefit water velocity is defined as the velocity at which the net energy benefit (assimilated energy minus swimming costs; Flore & Keckeis 1998) is zero, whereas the maximum sustainable swimming speed is the lowest water velocity at which a fish fails to maintain its position in the water column (Figure 11.31; Flore *et al.* 2001).

Below these critical values, water velocity influences fish feeding, growth, and metabolism. We found that the energy budget of nase larvae is very tight. That is, the ranges of current velocities and temperatures at which surplus energy was available for an individual fish are very narrow, especially in the early larval stages (Figure 11.32). For example, the water velocity at which a young larva obtains a positive energy balance at optimal food densities

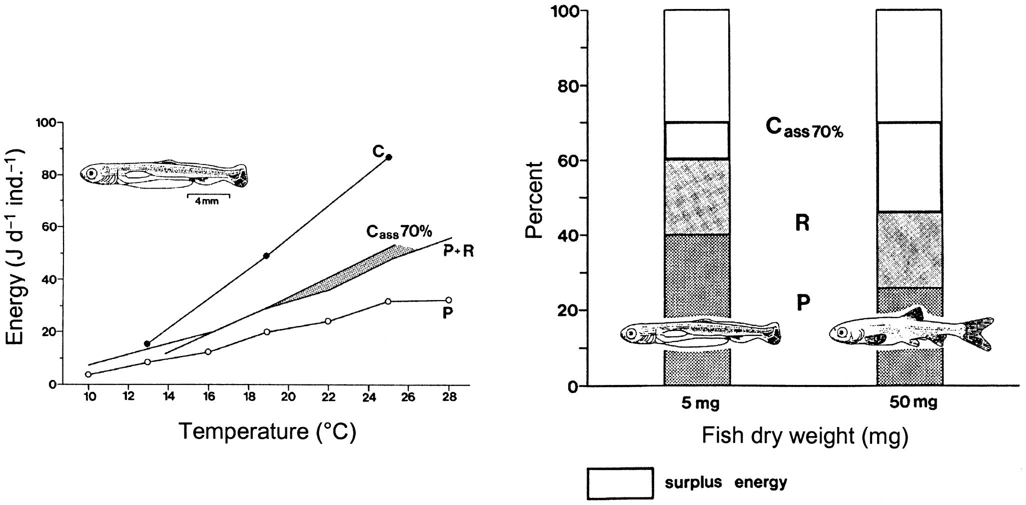

Figure 11.32 Upper: Elements of an energy budget for larval *Chondrostoma nasus* of 5 mg dry weight. Consumption over 24 h at three temperatures was measured at *ad libitum* food availability. Production rates were calculated from growth rates obtained at *ad libitum* food supply. Respiration values were based on routine metabolic rates (RMR) over a period of 24 h (Keckeis *et al.* 2001). Active metabolic rates were calculated by multiplying RMR by a factor of 2.5 to correct for food searching activity and food-induced thermogenesis. (From Schiemer *et al.* 2001a). Lower: Elements of an energy budget at 20°C compared for larvae (5 mg dry weight) and juveniles (50 mg dry weight) of *C. nasus.* The rates are given in percentage of the energy consumed. Production (*P*, dark stippled columns) and respiration (*R*, light stippled columns) as above. The strongly delineated part of the column indicates surplus energy, assuming an assimilation efficiency of 70%. (Reproduced from Schiemer *et al.* 2001b with permission of E. Schweizerbart'sche Verlagsbuchhandlung.)

ranges from 0 to 7 cm s^{-1}. This window widens almost two-fold for a young juvenile (approximately 15 cm s^{-1}; Figure 11.33). Another very important component of fitness is the ability to sustain swimming, since it affects habitat utilization, migration ability, and vulnerability to predation. The water-velocity tolerance of a fish will determine not only its maintenance of station against a current, but also its escape response and feeding efficiency. Measurements of critical water velocities are important for ecological management because they help to determine the limits of 0+ fishes for searching for food, consuming prey, and holding their position.

The transformation of natural shorelines to uniform, fast-flowing channels has a potentially deleterious effect on the survival and distribution of the early life stages of fishes. Inshore areas with very low water velocities, which can be used as refuges, are thus decisive for the recruitment of 0+ rheophilic cyprinids. Combining the results of laboratory studies on critical swimming speeds with the ambient water current at nursery areas (Figure 11.34) and the densities of 0+ nase reveals a significant relationship. The population density drops drastically when the water current exceeds the critical swimming speeds of the fish. This is shown clearly in Figure 11.35, which compares the relative densities of *Chondrostoma nasus* larvae and juveniles at three different nursery areas at the Danube: a sheltered bay habitat (Bay) and two different gravel bank-habitats (GB 1, GB 2). It is clear that young-of-the-year

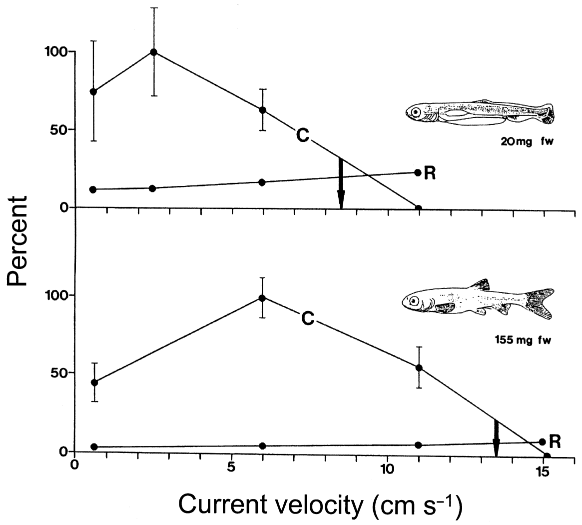

Figure 11.33 Energy acquisition (*C*) of two size classes of *Chondrostoma nasus* in different water currents and associated respiratory costs (*R*). The arrows indicate the water current at which the energy balance of assimilated energy minus the swimming costs equals zero. Feeding at higher currents results in a negative energy budget. (From Flore & Keckeis 1998.)

populations of nase are strongly controlled by the hydrological regime (water-level fluctuations) and the related structural and abiotic properties of the inshore zone of the river.

11.17 Consequences for conservation and future perspectives

The ecology of early life stages proves to be of the greatest significance for planning restoration programs for large rivers. The critical 0+ life stages are dependent on a broad array of conditions connected to the ecological integrity of river systems. They are dependent on the structural properties of the ecotonal inshore zone with high retention characteristics and potential to function as a refuge under fluctuating water levels. They are also dependent on the hydrological and habitat connectivity in a longitudinal sense, as well as the lateral integration between the river and its floodplains. In this respect the requirements of the early life stages are critical for formulating ecological goals for restoration as well as a monitoring tool to test the results of restoration programs.

Fish diversity, population dynamics, and production depend, to a large extent, on the complex and often contradictory effects of water-level fluctuations. The integration of autecological requirements of characteristic fish species helps to define natural conditions to improve structure, functioning, connectivity, and dynamics of the ecosystem. The results of habitat selection and early life history of nase, as one of the most common riverine fish species in central Europe, have been used, together with data for other groups, to design large restoration programs along the free-flowing section of the Danube (Schiemer 1999, Schiemer *et al.* 1999, Tockner *et al.* 1999, Ward *et al.* 1999) and along the main channel in the urban area of Vienna (Chovanec *et al.* 2000). The results of ongoing monitoring programs will hopefully show the extent to which this strategy achieved the planned ecological goals.

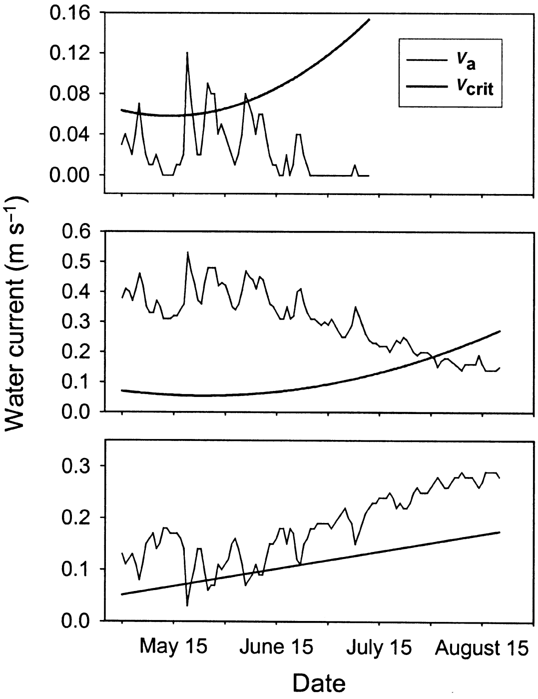

Figure 11.34 Thin line (v_a) represents the seasonal course of the water current at three different nursery areas of the Danube River. The thick line (v_{crit}) represents the critical swimming speed (Flore & Keckeis 1998) related to the size of *Chondrostoma nasus* larvae and juveniles in the habitat. Water current values above this line are unsuitable for holding position, water current values below the line represent suitable situations. The bay habitat (upper graph) is characterized by generally low water currents, the gravel bank (middle graph) had the highest water currents, with suitable conditions only during August, another gravel bank habitat (lower graph) provided suitable conditions at times when the two other nursery zones had high water current situations, thus acting as a refuge with a high inshore retention capacity during periods of floods.

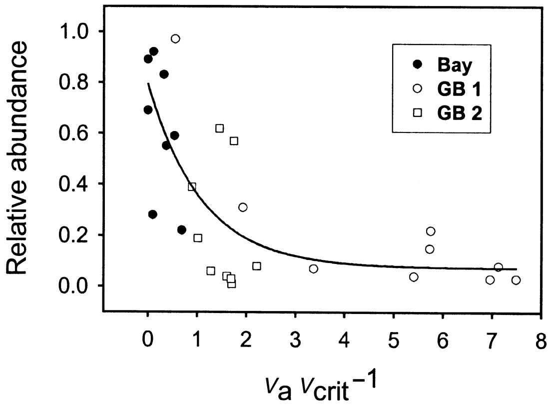

Figure 11.35 Relative density of *Chondrostoma nasus* larvae and juveniles at three inshore areas (one sheltered bay and two gravel banks) of the Danube River in relation to the ratio of the measured average current velocity at the respective habitat (v_a) and the critical swimming speed of the fish (v_{crit}; related to the average fish size at the corresponding site and sampling date). For details see Keckeis *et al.* (1997) and Winkler *et al.* (1997).

11.18 Summary

(1) Since 1875 the Danube River has been considerably affected by land use, pollution and most importantly by hydro-engineering.

(2) The immediate and long term effects were a strong reduction of the former alluvial floodplain areas, a loss of riverine inshore habitats, and reduced connectivity of open-water connections and groundwater exchange between the river and its floodplains.

(3) Most of the historical fish fauna is still present, but populations of most of the riverine species are endangered.

(4) Autecological field and laboratory studies of a target species, nase (*Chondrostoma nasus*), at different life-history periods were initiated to find the factors that limit the populations.

(5) Spawning occurs over a narrow range of distinct habitat conditions throughout the range of the species. A 6-year observation of the age and size structure of a spawning population showed that many year classes are missing due to high mortality in early life.

(6) On the other hand, nase eggs and embryos possess many traits that indicate a high survival and growth potential. Low spawning success and low survival rates of young-of-the-year might therefore be attributed to unsuitable extrinsic factors.

(7) In rivers, the conditions along the inshore ecotones are decisive elements in the population dynamics of individual species. The structure of inshore zones determines the ecological buffering capacity during water-level changes and the quality of refugees. By combining laboratory-derived data of critical swimming speeds with the ambient water current at nursery areas, a significant effect on the abundance of larvae and juveniles was observed. This finding shows that riverine young-of-the-year populations are strongly controlled by water-level changes and related structural properties of the inshore zone of the river.

(8) The results of early life research on nase have been used to design large restoration programs for implementation along the free-flowing section of the Danube River.