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The "inshore retention concept" and its significance for large rivers

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With 4 figures and 1 table in the text

Introduction

The ecology of large rivers is a long neglected but now rapidly expanding field. Several theories have been proposed during the last decade on hierarchically structured determinants of ecosystem processes, community organization and biodiversity (Frissell et al. 1986; Ward 1989; Ward & Stanford 1995b). The applicability of Vannote et al.'s (1980) river continuum concept of carbon flux to high order river reaches with extensive floodplain areas was questioned (Sedell et al. 1989). The floodpulse concept (Junk et al. 1989) refers specifically to these lateral exchange processes between the river and the semi-terrestrial adjoining area, that are inundated by regular or irregular spates. The river productivity model emphasizes, in contrast, that autochthonous production in the channel and connected backwaters may be significant in the carbon dynamics of large artificially constrained rivers (Thorp 1994). In a recent article, Reynolds & Descy (1996) discussed the significance of hydraulic storage as a function of channel morphology for river phytoplankton recruitment and production. They argue that reach retentivity, in relation to growth performances of algal species, can explain the nature of river phytoplankton associations and their productivity.

For streams retentiveness means the physical ability of channels to retain particulate organic matter as food. It also defines the refuge capacity allowing higher community persistence (Hildrew 1991; Hildrew et al. 1996; Lancaster et al. 1996).

We propose that a mechanistic model relating hydraulic retention to biological functions can be applied for different scales of hydrological storage to form a general framework for the understanding of the ecology of large rivers. Inshore retention may be specifically critical in channelized and regulated rivers.

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We present evidence that the structural properties and retention of the inshore zone are significant for the physiographic microhabitat conditions of its biota, and for the productivity of riverine zooplankton, larval fish-growth, and the downstream export and population loss of 0+ fish due to drift and wash-out effects. Inshore retention is, therefore, a major determinant of biological processes and biodiversity in large rivers.

The concept is based on current studies on the ecology of the Austrian Danube, which has been strongly changed by river regulation over the last century (SCHIEMER & WAIDBACHER 1992).

The interaction of inshore topography and hydrology creates the physiographic habitat conditions for the biota

The shape of the inshore ecotones in large rivers is dynamically controlled by hydrology and change considerably with river stage. In the Austrian Danube, for example, the average diel change in the water level is 30 cm; this, combined with high stochasticity and a wide amplitude, causes considerable dynamics in the exchange of water between inshore storage zones and the river. Fig. 1 shows the relationship between inshore sinuosity and river stage for the free-flowing but regulated Danube downstream of Vienna: Highest sinuosity index values occur around mean water level, due to fluvial depositions along the shoreline which form bars, islands and bays within the artificial channel.

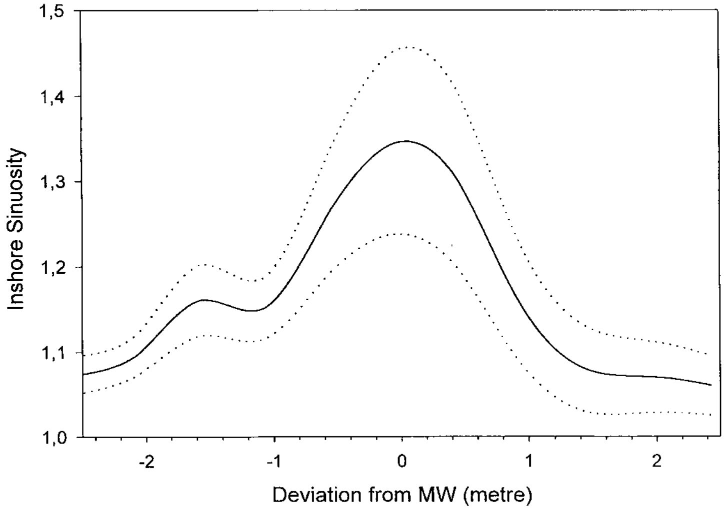

Fig. 1. Relative shoreline length (flowage line) of the Austrian Danube downstream of Vienna referring to 300 m stretches from river-km 1909 to 1920 at different water levels (mean and standard error, n = 39).

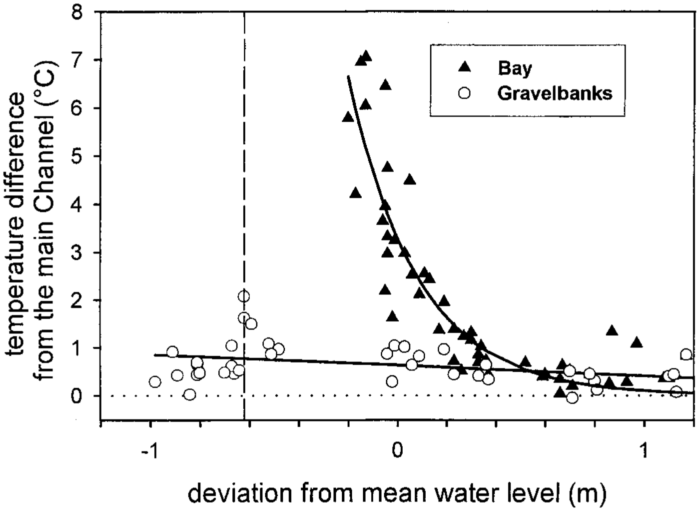

Fig. 2. Relationship between the water level of the Danube and the temperature in two inshore types. The temperature is characterized as deviation from daily (07.00 h) recordings of the river.

Table 1. Temperature dependence of larval duration (range in days) in *Chondrostoma nasus*, a characteristic fish species of hyporithral to epipotamal river stretches in Central Europe. * = high mortality under experimental conditions.

10 °C	13 °C	16 °C	19 °C	21 °C	25 °C	28 °C
47–68*	31–46	22–29	19–23	15–18	13–16*	13–16*

The physiographic conditions within the inshore zone, especially the local patterns of current velocity and temperature, depend on the inshore relief and the water level (see WARD 1985; WARD & STANFORD 1995a). Fig. 2 examines temperature conditions in two types of inshore areas in comparison to the official daily temperature recordings from the main river channel. The temperature regime of the inshore areas becomes decoupled from main channel conditions to a degree that depends on water retention and exchange. Local temperature conditions will be highly significant for temperature-dependent processes of species bound to the littoral zone. A good example would be the temperature-dependent growth of larval riverine fish during a critical period of high risks. Table 1 exemplifies the prolongation of larval duration in *Chondrostoma nasus*, a characteristic riverine species at lower temperatures.

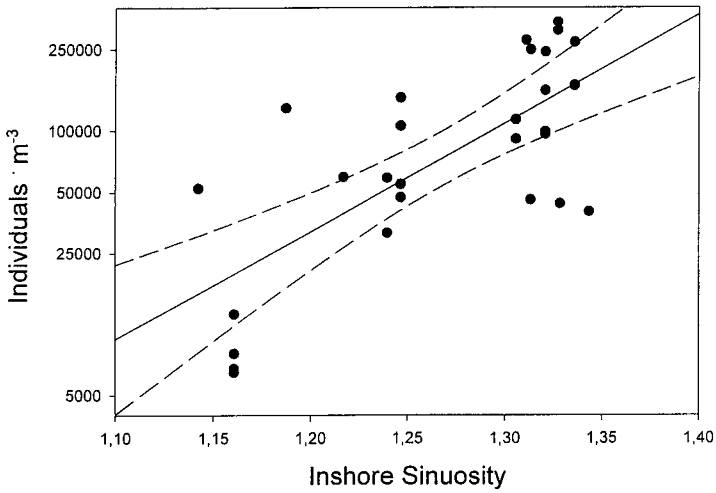

Fig. 3. Relationship between inshore sinuosity (see Fig. 1) and the density of the rotifer *Synchaeta oblonga* in the drift.

Production is linked to inshore sinuosity

Shoreline configuration and water retention not only determine essential physiographic parameters but also the instream production of organic material. REYNOLDS & DESCY (1996) put forward the idea that instream phytoplankton production is linked to storage zones.

Similarly, zooplankton recruitment and production in rivers is limited to current velocities below 10 cm · s^{-1} (VRANOVSKY 1995). Despite this fact the drift of rivers like the Danube or Rhine always contains zooplankton. We have good evidence that this riverine zooplankton is produced in inshore areas with high retention, i.e. in bays forming and being isolated along the shoreline at certain water levels. Large populations of rotifers (esp. *Synchaeta*) develop under such conditions and are released into the channel at increasing water levels and when water exchange is enhanced. We found that zooplankton densities in the river correlate with the index values of shoreline configuration prior to sampling (Fig. 3).

At low-water conditions, coinciding with shrinking boundary areas, the concentration of zooplankton is low. Zooplankton densities in the drift increase with increasing inshore structure at higher water levels. This is taken to mean that the extent of inshore configuration is an immediate correlate to dead zone conditions, which enhance zooplankton production. The time lag between inshore sinuosity and zooplankton abundance depends on the population development rate of specific groups. For instance the highest correlation's for rotifers were found by relating the sinuosity index values 6–10 days prior to sampling, the time required to build up sufficient population sizes.

Retention and refuge capacity of the inshore zone at varying water levels are decisive for the recruitment of riverine fish

Inshore retention has a further important significance, specifically with regard to microhabitat conditions for 0+ fish. High retention fosters recruitment and year class strength.

The larvae of riverine fish drift from neighboring spawning sites in the channel to inshore nursery areas. Larvae and early juveniles are bound to the immediate inshore zone of the river with low current velocities. Critical velocities are in the order of a few cm • s^{-1} at the onset of exogenous feeding and progressively increase with fish size (SCHIEMER et al. 2001).

A high sinuosity of the inshore zone provides the variety of microhabitats required during the course of early ontogenetic development, as well as refugia during spates (SEDELL et al. 1990; SCHIEMER et al. 1991; HILDREW 1996). Suitable nursery zones are scarce under regulated conditions. In rivers such as the Danube or Rhine, such nursery stretches occur like beads on a string along the regulated embankments, which are in general uncolonizable not a suitable habitat for young fish.

In a particular river section microhabitat availability will be compressed or extended with water level fluctuations, depending on the local inshore relief. Changing water levels will lead to wash-out effects, causing high mortality and a unidirectional, downstream shift of the fish fry population. The population of 0+ fish present in a nursery zone is not stable but an assemblage structured by imports from upstream and exports to downstream. Retention in this case is defined both by hydraulic retention and the capability of early juvenile fish actively to escape wash-out effects.

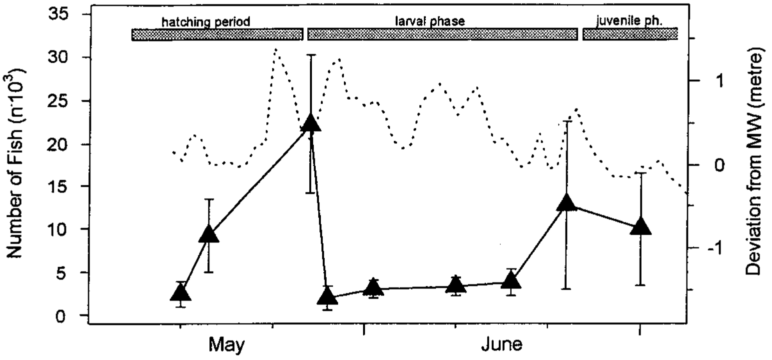

Fig. 4. Temporal dynamics of 0+ *Chondrostoma nasus* in a nursery zone of the Danube. The initial increase in May is due to the emerging larvae. During a period of higher water level the population is diminished. The area is recolonized again by larger larvae and juveniles from upstream.

Fig. 4 shows the population dynamics of 0+ *Chondrostoma nasus* in the first two months of life in a small inshore bay at the head of a nursery island. This nursery island is situated in a sea of inhospitable straight ripraps. The nearest source areas (see SCHLOSSER 1995) are similar nursery stretches several km upstream. We interpret the population dynamics in relation to water level changes (Fig. 4) to mean that nursery islands in regulated rivers cannot be envisaged as being isolated, but are rather in a continuous exchange. There is further evidence for a continuous exchange, based on the apparently high variability of individual growth within one locality, as analysed by otolith microstructure. The individual growth performances deviate from those predicted for temperature-dependent growth at a particular island.

Retention will be advantageous for recruitment both by reducing the unidirectional shift of the larval population as well as – through increased plankton production and higher temperature – allowing faster growth through the critical period and reducing mortality.

Conclusions

River regulation has considerably degraded the structural properties of large rivers, especially with regard to inshore ecotones and the connectivity between the river and its floodplains (DYNESIUS & NILSSON 1994; WARD & STANFORD 1995b). Mitigation and restoration concepts – which are currently being developed – require a detailed understanding of the functioning of the various subunits and their integration in river-floodplain systems (SPARKS 1995; STANFORD et al. 1996).

We propose that retention is a main element for understanding ecosystem processes and biodiversity in large rivers. Its significance becomes apparent in regulated rivers where both retention and the connections between the river and its sidearms have markedly decreased.

We suggest that inshore storage capacity is hydraulically scaled as related to specific biological functions: spatially small storage zones with short retention times allow the production of riverine phytoplankton, while structural properties leading to longer retention will be necessary to allow the development of zooplankton; structural properties on several scales will be required as microhabitats and refugia for larval fish.

For the development of restoration concepts for regulated large rivers the requirements of characteristic target species with regard to hydraulic retentivity will provide a main framework and should become a main research focus in river ecology.

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