

Floods and Fish



Recruitment and distribution of fish
in the Volga River floodplain

Konrad Górski

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Thesis committee:

Thesis supervisor

Prof. Dr. Johan A. J. Verreth
Professor of Aquaculture and Fisheries
Wageningen University

Thesis co-supervisors

Dr. Ir. Leopold A.J. Nagelkerke
Assistant Professor at Aquaculture and Fisheries Group
Wageningen University

Dr. Ir. Hendrik V. Winter
Researcher at Wageningen IMARES, IJmuiden

Other members

Prof. Dr. Ellen van Donk,
Netherlands Institute of Ecology, Nieuwersluis

Dr. Ivan Nagelkerken
Radboud University, Nijmegen

Prof. Dr. Herbert H.T. Prins
Wageningen University

Prof. Dr. Klement Töckner
Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany

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Thesis

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Abstract

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Natural river floodplains are among the most diverse and productive ecosystems on Earth and provide key habitats for foraging, spawning and as a nursery for many riverine fish species. Periodic flooding plays a principal role in the ecological processes in floodplain systems resulting in high productivity and diversity, as formulated in the Flood Pulse concept (FPC, a major conceptual framework for understanding the hydro-ecological processes operating in river-floodplain systems). However, little progress has been made in exploring the FPC over larger spatial scales due to lack of empirical data. The Volga-Akhtuba floodplain (Russian Federation) is still relatively undisturbed, while in Europe and North-America about 90% of floodplains have effectively been lost. This thesis provides a quantitative assessment of the FPC by (1) analyzing flood pulse dynamics in response to changes in river flow regime on various spatial and temporal scales and (2) relating these to recruitment success of riverine fish species that use the floodplain; and (3) identifying the hydro-geomorphic variables that are most involved shaping fish abundance and distribution in the floodplain. The results obtained demonstrate that the flood pulse magnitude in the lower Volga has noticeably decreased due to damming of the Volga upstream from the Volga-Akhtuba floodplain. Still, in spite of this hydrological control, considerable year-to-year variation in flood magnitude and timing has remained. Therefore fish populations in the floodplain still depend on variations in the year-to-year flow regime. Moreover, spring temperature and its match with flooding control the recruitment of young fish at the end of the growing season. However, the main sources of spawning stocks in the large-scale Volga-Akhtuba floodplain originate from local floodplain populations and not from the main river channels. Spatial heterogeneity of hydro-geomorphic attributes of the floodplain water bodies is highly significant for structuring fish abundance and distribution in the floodplain. Therefore, even under changing environmental and social circumstances, it is essential to preserve flood dynamics, which is fundamental not only for fish recruitment success but also governs fish distribution and diversity in the floodplain.

*Moim rodzicom:
Elżbiecie i Jerzemu*

*Издалеку долго
Течёт река Волга,
Течёт река Волга -
Конца и края нет...
Среди хлебов спелых,
Среди снегов белых
Течёт моя Волга,
А мне семнадцать лет.*

*Сказала мать: «Бывает всё, сынок,
Быть может, ты устанешь от дорог, -
Когда придёшь домой в конце пути,
Свои ладони в Волгу опусти».*

*Издалеку долго
Течёт река Волга,
Течёт река Волга -
Конца и края нет...
Среди хлебов спелых,
Среди снегов белых
Течёт моя Волга,
А мне уж тридцать лет.*

*Тот первый взгляд и первый плеск весла...
Всё было, только речка унесла...
Я не грущу о той весне былой,
Взамен её твоя любовь со мной.*

*Издалеку долго
Течёт река Волга,
Течёт река Волга -
Конца и края нет...
Среди хлебов спелых,
Среди снегов белых
Гляжу в тебя, Волга,
Седьмой десяток лет.*

*Здесь мой причал, и здесь мои друзья,
Всё, без чего на свете жить нельзя.
С далёких плёсов в звёздной тишине
Другой мальчишка подпевает мне:*

*«Издалеку долго
Течёт река Волга,
Течёт река Волга -
Конца и края нет...
Среди хлебов спелых,
Среди снегов белых
Течёт моя Волга,
А мне семнадцать лет.»*

1962, Лев Ошанин

From far away for days on end
The Volga River flows,
The Volga River flows, -
The river has no end...
Betwixt ripe crops,
Betwixt white snows,
My Volga River flows,
And I am seventeen.

My mother said: «The world is big, my son,
And roads you take may tire you one day, -
But when you're home after a long journey,
Just dip your palms into the Volga waters».

From far away for days on end
The Volga River flows,
The Volga River flows, -
The river has no end...
Betwixt ripe crops,
Betwixt white snows,
My Volga River flows,
And I am thirty now.

That first look, that first splash of an oar...
I had it all, but it is all flowed away with the river...
I am not sad: though my spring is gone,
Your love is still with me.

From far away for days on end
The Volga River flows,
The Volga River flows, -
The river has no end...
Betwixt ripe crops,
Betwixt white snows,
My Volga River flows,
And I am seventy now.

My berth is here, my friends are here,
All you cannot live behind....
From faraway shores in starry silent night
Some other boy is singing now with me:

From far away for days on end
The Volga River flows,
The Volga River flows, -
The river has no end...
Betwixt ripe crops,
Betwixt white snows,
My Volga River flows,
And I am 17 now.»

1962, Lev Oshanin

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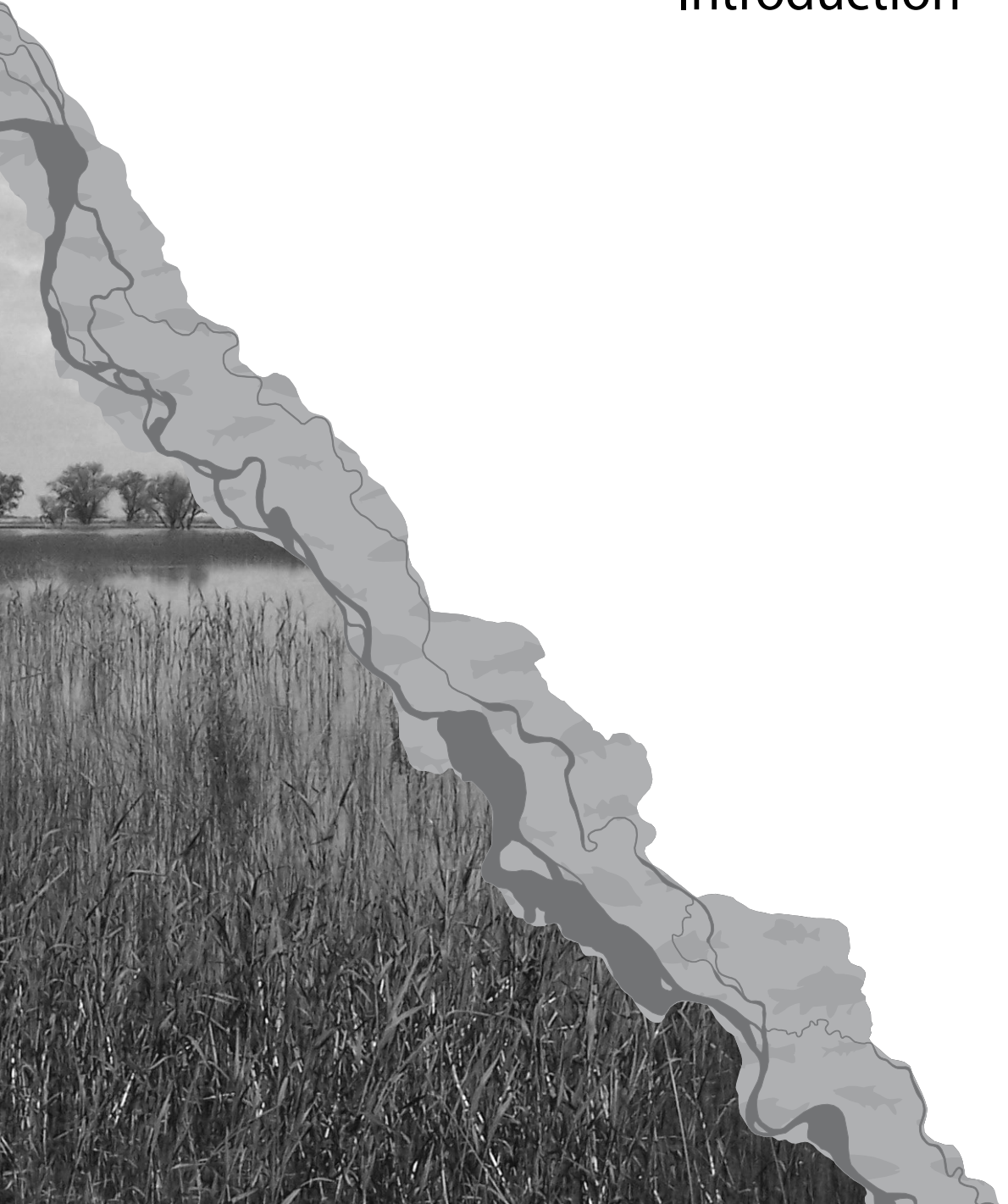
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Chapter 1

Introduction



1.1 Background

1.1.1 Floodplain ecosystems

Natural river floodplains are among the most diverse and productive ecosystems on Earth (Tockner & Stanford, 2002; Ward, Tockner & Schiemer, 1999). Fisheries in large rivers and their associated floodplains provide a major source of food, employment and income which is crucial to sustain the livelihoods of multitudes of people (Arthington *et al.*, 2004). In addition, floodplains play a role in retaining water, mitigating floods, and breaking down pollutants (Costanza *et al.*, 1997).

In floodplain ecosystems, the high spatio-temporal heterogeneity drives a diversity of complex habitats in various stages of succession (Jungwirth, Muhar & Schmutz, 2000). Periodic flooding (flood pulse) plays a principal role in the ecological processes in floodplain systems (Junk, Bayley & Sparks, 1989). Natural variations in the magnitude, duration and timing of the flood pulse continuously change the geomorphology of floodplains, thereby creating high habitat complexity, which in turn results in high biodiversity (Bayley, 1995). In addition, floodplains play a major role in the life cycle of many fish species. A wide range of temporary floodplain habitats are crucial for many species for foraging, spawning and as nurseries. Therefore fish faunas of large rivers are highly adapted to the natural hydrological regime, i.e. the timing and duration of floodplain inundation.

In many rivers the natural flood pulse has been severely altered by river regulation, e.g. construction of dams and dykes, or changes in land use (Dynesius & Nilsson, 1994; Nilsson *et al.*, 2005; Richter *et al.*, 1997). Man-induced alterations of the hydrological regimes and the reduction of floodplain wetlands are considered to be a major threat for biodiversity and natural resource production. In the developing world, natural floodplains are disappearing at an accelerating rate, primarily due to changed hydrology (Poff *et al.*, 1997). In Europe and North-America about 90% of the floodplains are considered functionally extinct (Tockner & Stanford, 2002).

1.1.2 Problem definition

To make rational decisions about the quality and extent of river rehabilitation in relation to fish biodiversity, it is essential to understand the ecolo-

gical functioning of floodplains and its relationship with the characteristics of the flood pulse (Buijse *et al.*, 2002; Galat *et al.*, 1998). Although many theoretical concepts about ecological functioning of rivers in relation to the physical and hydrological environment have been developed, there have been too few rigorous tests of these concepts in real-world floodplains.

1.1.3 Ecological functioning of large rivers – concepts

Over the past decades, a sound conceptual basis has been developed for understanding the functional processes and biodiversity of river systems (Table 1.1; Johnson, Richardson & Naimo, 1995). The longitudinal River Zonation concept focuses on changes in the taxonomic composition of

Table 1.1 Summary of main concepts developed to understand ecological functioning of river systems, with original references.

| Concept | Dimension | Governing abiotic variable | Functional/Structural ecosystem characteristics |
|--|--------------|--|--|
| River Zonation (Nowicki, 1889; Thienemann, 1925) | Longitudinal | Flow velocity, Temperature | Adaptation of fishes and benthic fauna to physical and chemical changes along the river resulting in zonation |
| Nutrient spiralling (Newbold <i>et al.</i> , 1982; Webster & Patten, 1979) | Longitudinal | Flow velocity, Nutrient limitation | Nutrient cycling and downstream transport |
| River Continuum (Vannote <i>et al.</i> , 1980) | Longitudinal | Stream size, Energy source | Progressive shift of physical gradients and energy inputs, Organic matter processing, Primary production/Respiration ratios/shift in trophic organization and biological communities |
| Serial Discontinuity (Ward & Stanford, 1983) | Longitudinal | Position of dams | Organic matter processing, Primary production/Respiration ratios; Abruption from continuum in relation to Dams/Tributary junctions |
| Flood Pulse (Junk, Bayley & Sparks, 1989) | Lateral | Flood pulse: inundation of aquatic terrestrial transition zones bordering the main channel | Exchange of nutrients and organic matter / Habitat complexity / Species diversity |
| Riverine Productivity Model (Thorp & Delong, 1994) | Lateral | Flow velocity / Riparian zone | Importance of the local autochthonous production (phytoplankton, benthic algae, aquatic vascular plants) and direct inputs from the riparian zone during periods not limited to flood pulses |

fauna with respect to physical and chemical changes along the river (Nowicki, 1889; Thienemann, 1925). The *Nutrient Spiralling concept* (Newbold *et al.*, 1982; Webster & Patten, 1979) describes unidirectional spiralling of nutrients along the river continuum, mediated by biotic agents. The *River Continuum Concept* (Vannote *et al.*, 1980) also stresses the longitudinal dimension of the river ecosystem and proposes a progressive shift of physical gradients and energy inputs and an associated shift in trophic organization and biological communities. The related *Serial Discontinuity Concept* (Ward & Stanford, 1983) recognizes that streams do not change uniformly in longitudinal direction, but that changes in the geomorphology (i.e. related to damming) and tributary junctions can interrupt the continuum in an abrupt manner. The transversal *Flood Pulse Concept* (FPC, Junk *et al.*, 1989; Junk & Wantzen, 2004) distinguishes lateral processes from the aforementioned longitudinal concepts. It states that temporary flooding of the aquatic-terrestrial transition zones bordering the rivers is the main determinant of water temperature, turbidity and nutrient content. Hence flooding greatly influences habitat heterogeneity, plant and animal recruitment, as well as ecosystem productivity (Amoros & Bornette, 2002). The FPC provides an integrated idea for complex hydro-ecological processes in river-floodplain systems. Because the FPC is the main transversal concept in large river ecology, proposing mechanisms governing the functioning of floodplains and their role for river ecosystem, it is the main focus of this study and will be discussed in more detail in a later section.

New insights into river functioning have emerged in addition to the abovementioned main concepts. Thorp & Delong (1994) proposed the *Riverine Productivity Model* emphasizing the role of autochthonous production and riparian zones. This model concludes that a substantial portion of the organic carbon assimilated in large rivers can be derived from local autochthonous production (i.e. phytoplankton, aquatic vascular plants) and inputs from the riparian zone adjacent to the river during periods that are not only limited to flood pulses. Furthermore it was recognized that spatial and temporal variability of the 'the natural flow regime' can play a crucial role in the ecological integrity of rivers and can shape the long-term evolution of stream biota (Poff *et al.*, 1997). Therefore 'the natural flow regime' paradigm will have broad implications for river conservation, management and rehabilitation (Poff *et al.*, 1997). Thorp, Thoms & Delong (2006, 2008) put forward '*the Riverine Ecosystem Synthesis*'. This synthesis combines the ecological aspects of fluvial geomorphology with a terrestrial landscape model descri-

bing hierarchical patch dynamics (Wu, 1999; Wu & Loucks, 1995; Fig. 1.1). Thereby it describes rivers as downstream arrays of large hydrogeomorphic patches (e.g. constricted, braided and floodplain channel areas) formed by catchment geomorphology and climate. Different types of these hydrogeomorphic patches are characterised by unique ecological 'functional process zones' because of physiochemical habitat differences which affect ecosystem structure and function (Thorp, Thoms & Delong, 2008).

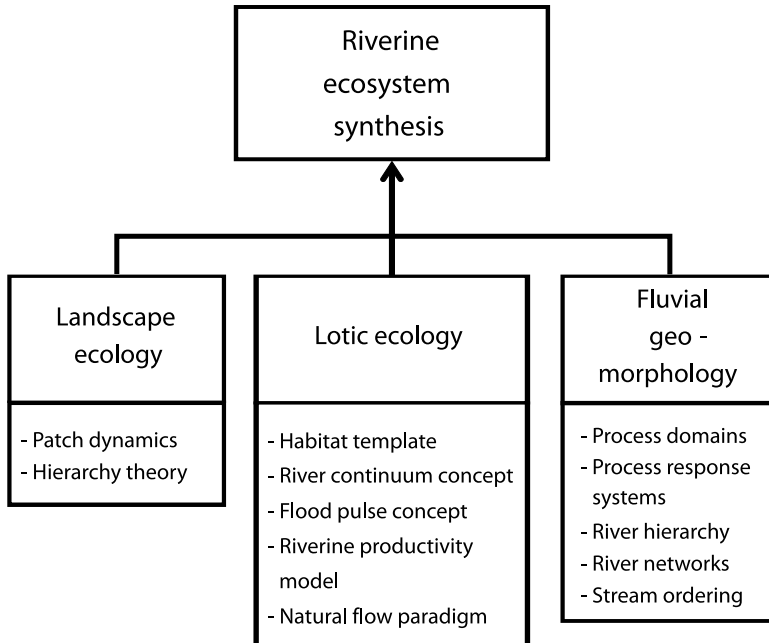


Figure 1.1 Summary of concepts and paradigms which were brought together in the Riverine Ecosystem Synthesis (Modified from Thorp *et al.*, 2008).

1.1.4 The Flood Pulse Concept (FPC)

The FPC states that the principal driving force for habitat heterogeneity in large lowland rivers is the flood pulse, i.e. the temporary flooding of the aquatic-terrestrial transition zones bordering the rivers (Junk *et al.*, 1989). The flood pulse is determined by geomorphologic and hydrological conditions that control its magnitude, timing, duration and predictability. Seasonal inundation maintains the ecological succession at intermediate levels, and hence it is important for sustaining the high biodiversity and productivity of floodplain systems (Petts, 1996). Flooding also mobilizes nutrients, boosts aquatic primary production, provides allochthonous inputs,

and therefore also increases secondary production in floodplain habitats (Thomaz, Bini & Bozelli, 2007). The FPC identifies the predictable advance and retreat of water on the floodplain of a pristine system as the principal agent controlling the adaptations of many terrestrial and aquatic biota, i.e. synchronization of life cycles with water level fluctuation, migration, dispersal abilities, and resistance against inundation or drought (Bayley, 1991). Therefore, the life cycles of diverse fish faunas inhabiting large rivers are highly adapted to the natural hydrological regime, i.e. the timing and duration of inundation (Bailly, Agostinho & Suzuki, 2008; Bayley, 1991; Junk *et al.*, 1989). At the same time, this concept implies that any significant change in the natural hydrological regime has immediate effects on the life cycles of these same ichthyofaunas.

Thus the FPC gives an integrated assessment of the complex hydro–ecological processes operating in river–floodplain systems. However, until now, little progress has been made in exploring the FPC over larger spatial scales and in analyzing temporal changes in spatial heterogeneity in response to fluctuating discharge, due to the notorious lack of empirical data. The FPC suggests that predictable inundation of river floodplains is the major driving force for the maintenance of biotic diversity and the production of plant and animal biomass, including fish. In addition, in temperate systems the FPC stresses the importance of the coincidence of rising temperatures and high flows for successful fish recruitment (Junk *et al.*, 1989). Although research in the tropics demonstrates a high dependence of fish recruitment and fisheries on seasonal flooding (Agostinho *et al.*, 2004; Bailly *et al.*, 2008; Suzuki *et al.*, 2009; Welcomme, 1985), comparable research in large temperate rivers is lacking. This is often due to severe alterations of temperate floodplains, and consequently a lack of empirical data on the required spatial and temporal scales. Studies examining fish recruitment in temperate floodplain systems are limited to relatively small rivers, the middle and upper reaches of larger rivers or to floodplains in the lower reaches of large rivers that are severely altered (Copp, 1989; Grift *et al.*, 2003; Halyk & Balon, 1983; Holland & Huston, 1985). Consequently, fish recruitment mechanisms in large-scale temperate floodplains still remain unclear.

1.1.5 Floodplains and fish recruitment

Recruitment is a crucial component of population dynamics. It plays an essential role in the life history of fish, because the survival of juveniles largely

determines the size of adult populations. Floodplains play a key-role in the life cycle of many fish species, especially in relation to recruitment. The wide array of temporary floodplain habitats can provide essential spawning substrates and nursery grounds; which are crucial for recruitment of many species.

Attempts to explain survival of fish in their early life history stages have resulted in various recruitment models and hypotheses. Cushing (1990) proposed the 'match/mismatch hypothesis', which recognizes that fish spawn at approximately the same time each year, but that food abundance is less predictable and more variable in response to environmental conditions. Thus, in years when larvae and prey coincide or 'match', a strong recruitment will follow, whereas in years when larvae and prey do not coincide ('mismatch'), there will be poor recruitment. Lake (1967) proposed the 'flood-recruitment model', stressing the stimulation of spawning by inundation of terrestrial ground for some species of fish in the Murray-Darling Basin, Australia. However, the generality of this model was questioned and the 'low flow recruitment hypothesis' was proposed, describing the spawning of some species in the main channel and backwaters during periods of low flow and rising water temperatures, yet not dismissing the potential importance of the floodplain (Humphries, King & Koehn, 1999). This suggests a species-specific response to flooding dynamics, depending on life-history characteristics. Therefore more recently the combination of life-history adaptations in the fish fauna and aspects of the hydrological regime such as duration and timing of inundation were proposed to control the response of the recruitment of riverine fish fauna to flooding (King, Humphries & Lake, 2003).

1.1.6 The Volga River and its floodplain

The Volga River in the Russian Federation still accommodates one of the few remaining naturally functioning temperate floodplain systems in its lower reaches.

The Volga, the longest river in Europe (3690 km) and 16th longest in the world, is a water body of outstanding scientific and economic importance (Litvinov *et al.*, 2009; Mordukhai-Boltovskoi, 1979). The major tributaries of the Volga River are the Kama, the Oka, the Vetluga, and the Sura rivers. The Volga and its tributaries form the Volga River system (Fig. 1.2), which drains

an area of about 1.4 million km², covering various biomes from taiga to semi-desert. The Volga is a typical plain-type river, predominantly fed by snow-melt (60% of its water source) and also by groundwater outflow (30%) and rainfall (10%). The climate of the upper Volga basin is moderate continental, the warmest month is July (average temperatures: 16.7 to 19.2 °C), the coldest January (-10.1 to -13.4 °C), whereas in the lower reaches average temperatures are 20.6 to 25.1 °C in July and -9.6 to -6.9 °C in January (Litvinov *et al.*, 2009). The Volga Delta has a length of about 160 kilometres and includes as many as 500 channels and smaller rivers. Each year, a significant part of the Volga is covered by ice for approximately three months.



Figure 1.2 The Volga River system (Source: CABRI-Volga project: <http://cabri-volga.org/VolgaMap.html>).

A cascade of large, shallow reservoirs affects most of the hydrological regime of the Volga, from Tver (near Moscow) to Volgograd. The last in the row of dams is the Volgograd power plant, constructed in 1960. These hydro-constructions changed the appearance of the river and its fish fauna. A small part of the upper Volga and the 580 km long reach downstream of the city of Volgograd have remained unregulated, freely meandering (Fig. 1.3).



Figure 1.3 The banks (rim) of the lower Volga River



Figure 1.4 Bulgakov channel in the lower Volga floodplain during spring flood and in summer after water retreat

Although affected by anthropogenic changes, typical large river fish habitats remained in these stretches. The lower Volga below Volgograd depends strongly on the exploitation regime of the Kuibyshev and Volgograd reservoirs (Mordukhai-Boltovskoi, 1979). However, the discharge regime still follows a cycle of snow-melt floods in late spring (Fig. 1.4). As a result of

this, the lower Volga accommodates some of the few remaining ecologically functional and large-scale floodplain ecosystems in the temperate zone (Fig. 1.5). Directly downstream of the Volgograd dam, the Volga divides into the lower Volga River, the main channel, and the Akhtuba River, a smaller distributary. The rivers run almost parallel down to the Caspian Sea, and bound the Volga-Akhtuba floodplain. The Volga-Akhtuba floodplain extends over a length of 300 km, and is 10-30 km wide. The floodplain is a flat gently sloping area that is dissected by numerous floodplain channels and covered by thousands of lakes and residual floodplain channels. Therefore the lower Volga is an excellent model for studying the processes by which hydrology drives habitat characteristics and recruitment of riverine fishes.

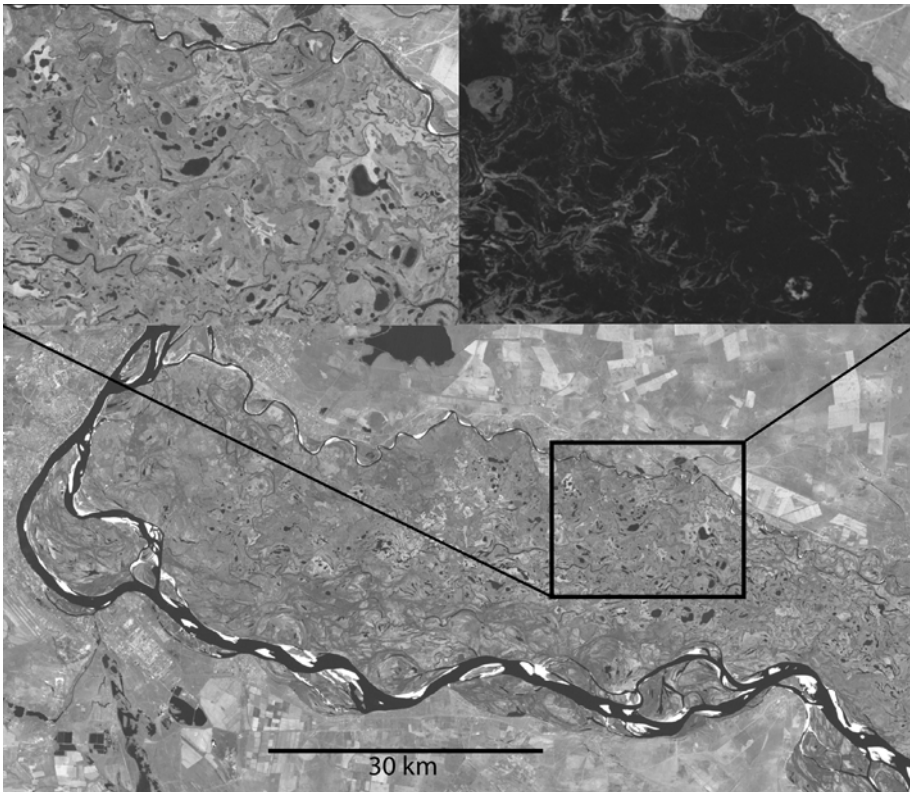


Figure 1.5 Satellite images of the Volga-Akhtuba floodplain; Overview of the upper floodplain in summer; Comparison of inundated surface in summer (low water levels) and during spring inundation; Landsat: P 171/R 26 TM7 ETM+.

1.1.7 Fish fauna and fisheries of the lower Volga

The lower Volga has a highly diverse fish fauna (Litvinov *et al.*, 2009). At present it accommodates 62 fish species (Table 1.2) and is well known for its sturgeon populations migrating upstream from the Caspian Sea. Historically, sturgeon fisheries played a very important commercial role (Fig. 1.6) with catches in the beginning of the twentieth century reaching up to 27 thousand tons (Mordukhai-Boltovskoi, 1979). The aforementioned regulation of the Volga led to barriers for sturgeon migration and consequently caused severe declines in sturgeon abundances. Species such as the Russian sturgeon *Acipenser gueldenstaedtii*, beluga *Huso huso*, and starry sturgeon *A. stellatus* are on the verge of extinction. However, poaching and illegal caviar trade still continue (Górski, pers. obs.). Presently the lower Volga fish community is dominated by eurytopic cyprinids such as roach *Rutilus rutilus*, common bream *Abramis brama*, white bream *Blicca bjoerkna*, blue bream *Abramis ballerus*, common carp *Cyprinus carpio*, bleak *Alburnus alburnus* and ide *Leuciscus idus*. The most common piscivorous fish are perch *Perca fluviatilis*, pike-perch *Sander lucioperca* and wels *Silurus glanis*. In contrast to the upper Volga, which is altered by the cascade of reservoirs, the lower Volga still provides suitable riverine habitats for fish species that are more rheophilic, such as asp *Aspius aspius*, sabrefish *Pelecus cultratus*, dace *Leuciscus leuciscus*, chub *Leuciscus cephalus* and Volga nase *Chondrostoma variable*.

Table 1.2 Fish species of the lower Volga River. Scientific and common names as well as some of the life history characteristics derived from literature (Krizhanovski, 1953; Reshetnikov, 2002) Spawning substrate: Ph - phytophilic, Li - lithophilic, Pe - pelagophilic, In - Indifferent, Ps - Psammophilic, CrEg - Carrying eggs; Migration: P - Potamodromous, A - Anadromous, R - Resident.

| Scientific name | English name | Maximal length | Maximal age | Age at maturity (years) | Spawning season (months) | Spawning substrate | Migration |
|---|-----------------------|----------------|-------------|-------------------------|--------------------------|--------------------|-----------|
| <i>Abramis ballerus</i> (Linnaeus, 1758) | Blue bream | 45 | 10 | 3-4 | 4-6 | Ph | P |
| <i>Abramis brama</i> (Linnaeus, 1758) | Common bream | 80 | 14 | 3-4 | 4-6 | Ph | P |
| <i>Abramis sapa</i> (Pallas, 1814) | White-eye bream | 41 | 8 | 3-4 | 4-5 | Ph | P |
| <i>Acipenser gueldenstaedtii</i> (Brandt & Ratzeburg, 1833) | Russian sturgeon | 152 | 50 | 11-16 | 5-6 | Li | A |
| <i>Acipenser nudiventris</i> (Lovetsky, 1828) | Fringebarbel sturgeon | 220 | 32 | 9-16 | 3-5 | Li | A |

Table 1.2 (continued)

| Scientific name | English name | Maximal length | Maximal age | Age at maturity (years) | Spawning season (months) | Spawning substrate | Migration |
|---|-------------------------|----------------|-------------|-------------------------|--------------------------|--------------------|-----------|
| <i>Acipenser persicus</i> (Borodin, 1897) | Persian sturgeon | 170 | 38 | 15-18 | 6-8 | Li | A |
| <i>Acipenser ruthenus</i> (Linnaeus, 1758) | Sterlet | 125 | 27 | 4-7 | 4-6 | Li | P |
| <i>Acipenser stellatus</i> (Pallas, 1771) | Starry sturgeon | 152 | 35 | 9-15 | 5-8 | Li | A |
| <i>Alburnus alburnus</i> (Linnaeus, 1758) | Bleak | 20 | 12 | 3 | 5-7 | In | P |
| <i>Alosa caspia caspia</i> (Eichwald, 1838) | Caspian shad | 32 | 10 | 2 | 5-6 | Pe | A |
| <i>Alosa kessleri</i> (Grimm, 1887) | Caspian anadromous shad | 44 | 8 | 3-6 | 5-8 | Pe | A |
| <i>Aristichthys nobilis</i> (Richardson, 1845) | Bighead carp | 146 | | 4-6 | | Pe | P |
| <i>Aspius aspius</i> (Linnaeus, 1758) | Asp | 80 | 10 | 3-4 | 4-5 | Li | P |
| <i>Barbatula barbatula</i> (Linnaeus, 1758) | Stone loach | 18 | 7 | 3 | 4-6 | Li | P |
| <i>Barbus brachycephalus</i> (Kessler, 1872) | Aral barbel | 103 | 10 | 5-6 | 4-8 | Li | P |
| <i>Benthophilus granulosus</i> (Kessler, 1877) | Granular pugolovka | 6.6 | 2 | 1-2 | 4-6 | | R |
| <i>Benthophilus mahmudbejovi</i> (Ragimov, 1976) | | 6.6 | 1 | | 5-8 | | |
| <i>Benthophilus stellatus</i> (Sauvage, 1874) | Stellate tadpole-goby | 23 | | 2 | 5-6 | | R |
| <i>Blicca bjoerkna</i> (Linnaeus, 1758) | White bream | 35 | 15 | 3-4 | 5-6 | Ph | P |
| <i>Carassius auratus gibelio</i> (Bloch, 1782) | Gibel carp | 45 | 15 | 2-4 | 5-7 | Ph | P |
| <i>Carassius carassius</i> (Linnaeus, 1758) | Crucian carp | 50 | 12 | 4-5 | 5-6 | Ph | R |
| <i>Caspiosoma caspium</i> (Kessler, 1877) | | 5 | | 1 | 5-7 | | |
| <i>Chalcalburnus chalcoides</i> (Güldenstädt, 1772) | Danube bleak | 40 | 12 | 2-3 | 5-9 | Li | P |
| <i>Clupeonella cultriventris</i> (Nordmann, 1840) | Black Sea sprat | 15 | 6 | 1-2 | 4-6 | Pe | PA |
| <i>Chondrostoma variabile</i> (Yakovlev, 1870) | Volga undermouth | 35 | 8 | | 4-5 | Li | |
| <i>Cobitis taenia</i> (Linnaeus, 1758) | Spined loach | 13.5 | | | 5-7 | Ph | P |
| <i>Cottus gobio</i> (Linnaeus, 1758) | Bullhead | 20 | 9 | 4 | 4-5 | Li | |
| <i>Cyprinus carpio</i> (Linnaeus, 1758) | common carp | 100 | 30 | 3-5 | 4-8 | Ph | P |
| <i>Esox lucius</i> (Linnaeus, 1758) | Northern pike | 150 | 15 | 2-4 | 4-5 | Ph | P |
| <i>Gobio albipinnatus</i> (Lukasch, 1933) | White-finned gudgeon | 22 | 5 | 2-3 | 4-6 | Ps | |

Table 1.2 (continued)

| Scientific name | English name | Maximal length | Maximal age | Age at maturity (years) | Spawning season (months) | Spawning substrate | Migration |
|---|--------------------------------|----------------|-------------|-------------------------|--------------------------|--------------------|-----------|
| <i>Gobio gobio</i> (Linnaeus, 1758) | Gudgeon | 20 | 10 | | 4-6 | Ps | P |
| <i>Gymnocephalus cernuus</i> (Linnaeus, 1758) | Ruffe | 18.5 | 15 | 2-4 | | In | R |
| <i>Huso huso</i> (Linnaeus, 1758) | Beluga | 500 | 100 | 12-18 | 4-5 | Li | A |
| <i>Leucaspius delineatus</i> (Heckel, 1843) | Sunbleak | 9 | 5 | 2 | 5-7 | Ph | R |
| <i>Leuciscus cephalus</i> (Linnaeus, 1758) | European chub | 80 | 18 | 3-4 | 4-5 | Li | P |
| <i>Leuciscus idus</i> (Linnaeus, 1758) | Ide | 100 | 20 | 4 | 4 | Li | P |
| <i>Leuciscus leuciscus</i> (Linnaeus, 1758) | Common dace | 25 | 10 | 2-3 | 4 | Li | P |
| <i>Lota lota</i> (Linnaeus, 1758) | Burbot | 120 | 24 | 2-4 | 12-2 | Ps/Li | P |
| <i>Misgurnus fossilis</i> (Linnaeus, 1758) | Wheatearfish | 30 | 7 | 2 | 4-5 | Ps/Ph | R |
| <i>Neogobius fluviatilis</i> (Pallas, 1814) | Monkey goby | 20 | 5 | 2 | 5-7 | In | R |
| <i>Neogobius gorlap</i> (Iljin, 1949) | | 22 | 3 | 2 | 4-5 | In | R |
| <i>Neogobius gymnotrachelus</i> (Kessler, 1857) | Racer goby | 25 | | 2 | 4-5 | In | R |
| <i>Neogobius melanostomus</i> (Pallas, 1814) | Round goby | 25 | 5 | 2 | 4-8 | Li | R |
| <i>Pelecus cultratus</i> (Linnaeus, 1758) | Sabrefish | 60 | 13 | 2-3 | 4-6 | Pe | P |
| <i>Perca fluviatilis</i> (Linnaeus, 1758) | European perch | 51 | 17 | 2-3 | 2-3 | In | R |
| <i>Proterorhinus marmoratus</i> (Pallas, 1814) | Tubenose goby | 15 | 3 | 1 | 4-7 | Ps | R |
| <i>Pungitius platygaster</i> (Kessler, 1859) | Southern ninespine stickleback | 7 | 3 | 2 | 4-6 | In | R |
| <i>Rutilus frisii</i> (Nordmann, 1840) | Kutum | 70 | 12 | 4-5 | 2-5 | Li | A |
| <i>Rutilus rutilus</i> (Linnaeus, 1758) | Roach | 50 | 20 | 3-5 | 3-5 | Ph | P |
| <i>Salmo trutta</i> (Linnaeus, 1758) | Sea trout | 100 | 20 | 3-4 | 9-12 | Li | A |
| <i>Sander lucioperca</i> (Linnaeus, 1758) | Pikeperch | 130 | 14 | 3-4 | 5-6 | Ps | P |
| <i>Sander volgensis</i> (Gmelin, 1789) | Volga pikeperch | 45 | 8 | 3-4 | 4-5 | Ps | |
| <i>Scardinius erythrophthalmus</i> (Linnaeus, 1758) | Rudd | 36 | 10 | 3-5 | 5-7 | Ph | R |
| <i>Silurus glanis</i> (Linnaeus, 1758) | Wels | 250 | 30 | 3-5 | 3-7 | Ph | R |
| <i>Stenodus leucichthys</i> (Güldenstädt, 1772) | Inconnu | 130 | 22 | 4-6 | 10-11 | Li | A |
| <i>Syngnathus abaster</i> (Risso, 1827) | Black-striped pipefish | 23 | 6 | | 5-6 | CrEg | |
| <i>Tinca tinca</i> (Linnaeus, 1758) | Tench | 63 | 10 | 3-4 | 5-7 | Ph | R |
| <i>Vimba vimba</i> (Linnaeus, 1758) | Vimba | 50 | 17 | 3 | 5-6 | Li | A |



Figure 1.6 *Beluga caught in the lower Volga some decades ago (Source: Mordukhai-Boltovskoi (1979)).*

The lower Volga and upper Volga reservoirs accommodate significant commercial fisheries. More than half of all fish from inland fisheries of the Russian Federation are caught in the Volga catchment (Avakyan, 1998 in: Litvinov *et al.*, 2009). Historically the most valuable commercial fisheries were accommodated in the lower Volga and the Volga Delta (Mordukhai-Boltovskoi, 1979) with yearly catches of about 200 000 tons at the beginning of the 20th century. In the mid 20th century the catches decreased and never exceeded 100 000 tons and dropped further ever since. Presently, the yearly reported catches in the lower Volga are not higher than 1000 tons and consist mainly of common bream, roach, white bream, perch and non-native gibel carp *Carassius gibelio*. This decrease in reported catches is probably the combined result of a rapid drop in diadromous fish stocks (possibly also in riverine and floodplain fish species), a flawed recording system and a decrease in fishing effort. The decrease in fishing effort is a generally perceived, though not officially documented development.

1.2 Thesis rationale and outline

The objective of this study is to reveal mechanisms governing fish recruitment in a large-scale temperate floodplain in relation to flood and temperature dynamics, and thus provide a generic understanding of the relation between the flood pulse and fish recruitment dynamics in floodplains. The study aims at testing the FPC in a large-scale semi-natural floodplain by (1) analyzing flood pulse dynamics in response to changes in river flow regime at various spatial and temporal scales; (2) relating these dynamics to recruitment success of riverine fish species that use the floodplain and (3) identifying the hydro-geomorphic variables that are most involved shaping abundance and distribution of fish populations in the floodplain.

The central hypothesis of the study is that: **'The characteristics of the flow regime ("the flood pulse") determine the recruitment of fish populations that use the floodplains. Thus, there is a quantitative and causal relationship between flood pulse characteristics and fish recruitment.'**

1.2.1 Outline

To address the central hypothesis, the following research questions were put forward, which have been covered in the subsequent chapters.

- How did the construction of the Volgograd dam in 1960 affect the Volga flow regime? How did the flow regime and particularly the characteristics of the annual spring flooding vary in the lower Volga? How did the flood dynamics affect commercial fish catches in the lower Volga and adjoining floodplains? (Chapter 2)
- What is the relationship between the extent and timing of flooding and the timing and duration of spawning of various fish species? What is the proportion of fish entering the floodplain from the main river channel to spawn by comparison with the total number of spawning fishes in the floodplain? (Chapter 3)
- What is the role of flooding in larvae recruitment? (Chapter 4)
- Which habitat characteristics govern recruitment success of young fish (YOY) fish in a large temperate floodplain? (Chapter 5)
- How is the abundance and distribution of fish within the floodplain influenced by hydro-geomorphic variables? (Chapter 6)

To answer these questions the following steps were taken:

First, the characteristics of the annual flood pulse of the lower Volga and its effect on the commercial fish catches in the area were analyzed (Chapter 2). For this, the Volga River discharges before and after dam construction were compared, using long-term historical records. Then the variability of the flow regime and particularly the characteristics of the annual spring flooding were studied in detail for the period after damming (1960 – 2006). Finally, the relationship between the flood dynamics and commercial fish catches in the lower Volga channel and adjoining floodplains were examined.

Chapters 3-5 focus on the effects of flood pulse variability on the recruitment of the consecutive life stages of different fish species using the floodplain. Analyses of fish reproduction and fish recruitment success in relation to flooding and temperature dynamics were performed based on field surveys in three consecutive years (2006-2008). To evaluate the role of the flood pulse on spawning of fishes the relationships between the extent and timing of the spring flood, lateral spawning movements of fish, and timing and duration of spawning in the floodplain were examined (Chapter 3). Subsequently, to evaluate the mechanisms underlying larvae recruitment in floodplain systems the use of flooded terrestrial habitats by fish larvae was studied (Chapter 4). In the following chapter (5) the effects of the ex-

tent, timing and duration of flooding and temperature variability on the recruitment success of young fish (YOY) at the end of the growing season were tested. Finally, Chapter 6 focuses on the effects of flood variability and geomorphology of floodplain water bodies on fish abundance and distribution.

In the general discussion (Chapter 7) the main findings of the study are synthesized. In addition, I reflect upon the biological and methodological issues encountered during the study as well as discuss implications for management and possible future research perspectives.

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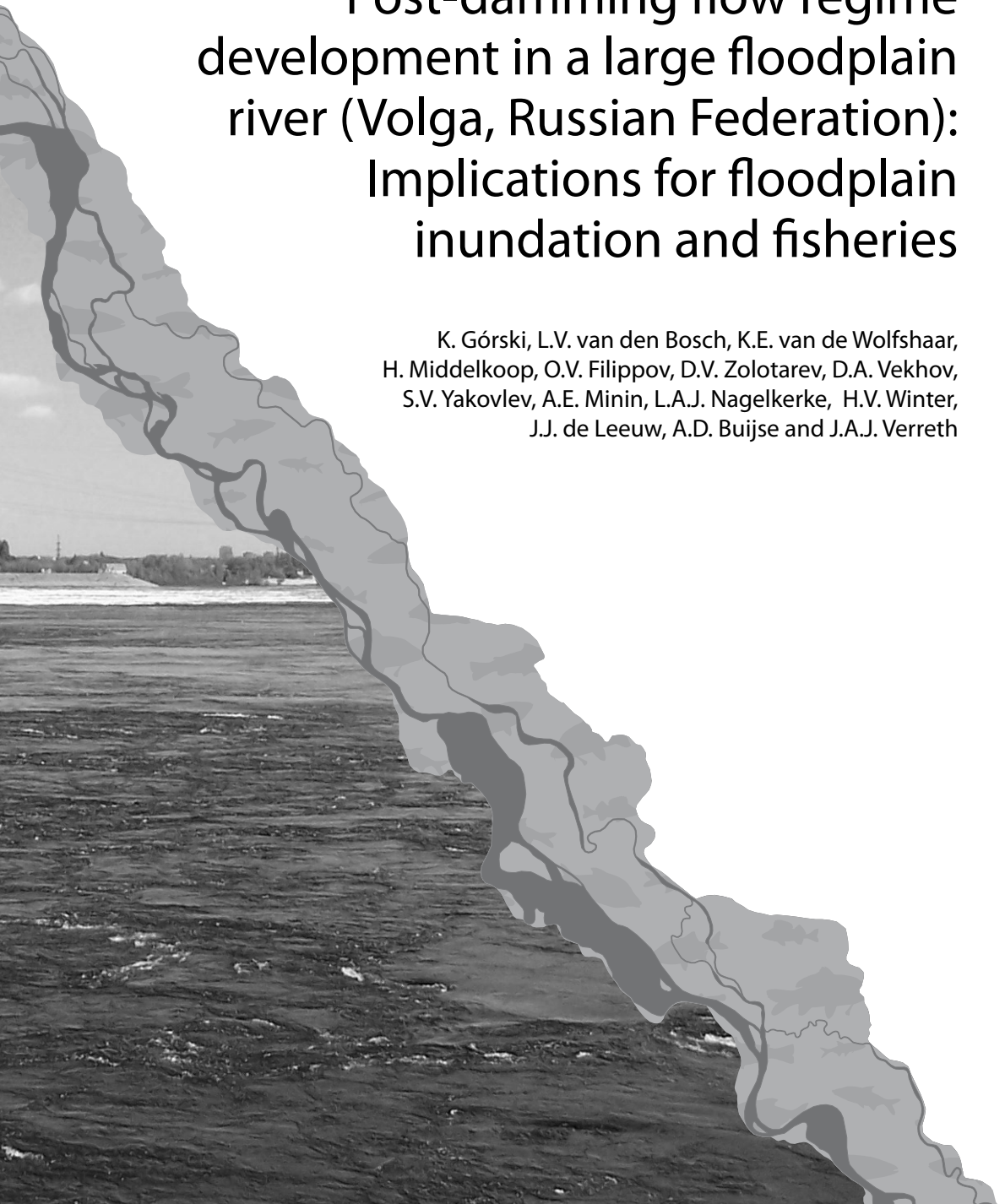
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Chapter 2

Post-damming flow regime development in a large floodplain river (Volga, Russian Federation): Implications for floodplain inundation and fisheries

K. Górski, L.V. van den Bosch, K.E. van de Wolfshaar, H. Middelkoop, O.V. Filippov, D.V. Zolotarev, D.A. Vekhov, S.V. Yakovlev, A.E. Minin, L.A.J. Nagelkerke, H.V. Winter, J.J. de Leeuw, A.D. Buijse and J.A.J. Verreth



Post-damming flow regime development in a large floodplain river (Volga, Russian Federation): Implications for floodplain inundation and fisheries

2.1 Abstract

Periodic flooding plays a key role in the ecology of floodplain rivers. Damming of rivers affects the flow regime and consequently flooding of the floodplain. The Volga River, the largest river in Europe, has a regulated flow regime after completion of a cascade of dams. Here, we study effects of damming on long term discharge variability and flood pulse characteristics. In addition, we evaluate the effects of altered flood pulse on floodplain ecosystem functioning and commercial fish yield dynamics. Our results indicate that both flood pulse and fish populations of the Volga-Akhtuba floodplain have varied considerably over the past decades. After damming, annual maximum peak discharges have decreased, minimum discharges increased, but average discharges remained similar pre- and post-damming. Moreover, due to bed level incision of over one and a half meter, a higher discharge is needed to reach bankfull level and inundate the floodplains. However, despite the significantly altered hydrological regime of the Volga River and following morphological changes, current discharge management provides significant spring flooding, preserving eco-hydrological floodplain functioning mechanisms. We found a strong correlation of commercial fish yield with flood magnitude, suggesting increased fish recruitment and better feeding conditions during high floods. A further understanding of the empirical relations between the Volga discharge and fish catch data requires analysis of the spatio-temporal development of the spawning and nursery habitats within the floodplain, and how these depend on the annual flood pulse.

Развитие водного режима на больших равнинных реках после зарегулирования (Волга, Россия): значение для половодий и рыбного хозяйства

2.2 Резюме

Периодические половодья играют ключевую роль в экологии равнинных рек. Возведение плотин влияет на режим течений и, соответственно, на затопление поймы. На Волге, крупнейшей реке Европы, сток регулируется в результате постройки каскада водохранилищ. В настоящей работе нами исследуется влияние плотины Волжской ГЭС на изменение расходов в долгосрочном периоде и на характеристики половодий. Кроме того, мы оцениваем влияние измененного режима половодий на функционирование экосистемы поймы и на динамику вылова рыбы в коммерческом рыболовстве. Наши результаты показывают, что как режим затопления, так и видовой состав рыбы, существенно изменились за последние десятилетия. После сооружения плотины Волжской ГЭС ежегодные максимальные расходы уменьшились, минимальные расходы увеличились, но средние годовые расходы по сравнению со временем до строительства плотины не изменились. Более того, из-за срезки уровня дна на более чем полтора метра, необходимы большие расходы для достижения водой прежних урезов и заполнения поймы. Однако, несмотря на существенно измененный гидрологический режим Волги и последующие геоморфологические изменения, сегодняшняя система управления сбросом воды через плотину обеспечивает значительное заполнение поймы водой в весенний период, позволяя пойме выполнять свои экологические и гидрологические функции. Мы определили тесную взаимосвязь между объемами коммерческих выловов рыбы и масштабами половодья, означающую увеличение пополнения рыб и улучшение состояния кормовой базы во время высоких половодий. Для дальнейшего объяснения физической связи между расходами Волги и выловами рыбы необходим анализ пространственно-временного развития нереста и условий обитания молоди внутри поймы, и как эти процессы зависят от ежегодного заполнения поймы водой.

2.3 Introduction

River integrity is tightly linked to natural flow regimes (Lowe-McConnell, 1964; Junk, Bayley & Sparks, 1989; Bayley, 1995; Poff *et al.*, 1997) and periodic flooding plays an important role in ecological processes in floodplain systems (Junk *et al.*, 1989). Natural variations in magnitude, duration and timing of the flood pulse drive geomorphologic changes and thereby habitat complexity, resulting in high biodiversity in river floodplain systems (Bayley, 1995). Floodplains offer a wide array of temporarily suitable habitats that can be crucial for many species as feeding, spawning, nursery and refuge areas (Starrett, 1951; Holland and Huston, 1985; Baber *et al.*, 2002). Timing, duration and extent of inundation have been proposed to be the main factors determining the value of floodplains for spawning and growth of fish (Welcomme, 1979; Trifonova, 1982; Bailly, Agostinho & Suzuki, 2008; Balcombe & Arthington, 2009). Therefore, commercial fish stocks are expected to be linked to natural flood pulse dynamics and respond to flood alterations.

Regulation of the flow regime often leads to habitat degradation and species loss in floodplains (Poff *et al.*, 1997; Bowen, Bovee & Waddle, 2003). The effects of damming on downstream areas are variable, and depend on the type of river and dam design (Ligon, Dietrich & Trush, 1995; Magilligan, Haynie & Nislow, 2008). River damming, generally leads to: 1. equalization of floods between years; 2. reduction of high floods (by both levelling off the peak within a year and reducing the probability of a large flood between years); 3. reduction of connectivity between main river channel and floodplain water bodies (Amoros & Bornette, 2002; Miranda, 2005; Thomaz, Bini & Bozelli, 2007). The response of floodplain biota to changes in connectivity of water bodies is dependent on the type of organisms. Macrophytes and macro-zoobenthos show a hump-shaped relationship with increasing connectivity, while for fish the relationship is more gradually increasing. The diversity of amphibians on the other hand, decreases with connectivity (Amoros & Bornette, 2002). Overall, diversity is highest at intermediate connectivity of the floodplain water bodies, as a result of habitat complexity caused by high flood pulse variability.

The largest floodplain ecosystem in Europe, the Volga-Akhtuba floodplain has highly diverse flora and fauna (Litvinov *et al.*, 2009). The geomorphology and vegetation of this floodplain have been preserved in a relatively undis-

turbed state when compared to other large rivers in Europe. The floodplain is situated in the semi-arid continental climatic zone with very dry and hot summers and severe winters (Averina *et al.*, 2000). In 1960, the Volgograd hydropower dam, the last dam in Volga-Kama cascade, was completed. It is the most downstream dam, located just upstream of the Volga-Akhtuba floodplain. Dam construction altered the Volga flow regime, although total annual discharge remained similar (Rakovich, Vyruchalkina & Solomonova, 2003; Litvinov *et al.*, 2009). Moreover, the flow regime in the Lower Volga still follows a semi-natural cycle of large snow-melt floods in late spring that inundate extensive areas (300x20 km) for 5-7 weeks (Gorelits & Zemlyanov, 2005; Middelkoop *et al.*, 2005), since the regulation scheme aims at maintaining a sufficiently large peak flow to provide extensive spawning grounds for fish in spring (Rakovich *et al.*, 2003). Over the past decades numerous studies have reported on the hydrological changes and water balance of the Volga, its effects on the Caspian Sea water level, and the relations with large-scale atmospheric circulation patterns as well as the establishment of the reservoirs and water consumption from the river for various purposes (Rodionov, 1994; Demin & Ismaiyllov, 2003; Rakovich *et al.*, 2003; Sidorenkov & Shveikina, 2006; Arpe & Leroy, 2007; Renssen *et al.*, 2007). However, little attention has been paid to the hydrological changes of the Lower Volga discharge in terms of the inherent characteristics of the annual flood pulse in the Volga-Akhtuba floodplain ecosystem and its effects on floodplain ecological functioning.

The objective of this study is to quantitatively analyze variations in the characteristics of the annual flood pulse of the Lower Volga and to assess whether these are related to fluctuations in commercial fish catches in the area. For this purpose we first compare the Volga River discharge before and after dam construction using long-term data (1879-2006). Then, we study how the flow regime and particularly the characteristics of the annual spring flooding have varied in the period after damming from 1960 until 2006. Finally, we examine the influence of flood dynamics on commercial fish catches in the Lower Volga channel and adjoining floodplains.

2.4 Methods

2.4.1 Study Area

The Volga River (Russian Federation), with a length of 3,690 km and an average annual discharge of $8,103 \text{ m}^3\text{s}^{-1}$, is the largest river in Europe and 16th in the world (Litvinov *et al.*, 2009). It has a combined rainfall / snow-melt flow regime, with a discharge peak in May-June. A cascade of reservoir dams in the Middle Volga, completed in the 1960s, has altered the natural flow regime of the Lower Volga downstream of Volgograd (Mordukhai-Boltovskoi, 1979; Rakovich *et al.*, 2003; Middelkoop *et al.*, 2005). Directly downstream of the Volgograd dam, the Volga divides into the Lower Volga River, the main channel, and the Akhtuba River, a smaller distributary. The rivers run almost parallel down to the Caspian Sea, and bound the Volga-Akhtuba floodplain (Fig. 2.1). The Volga-Akhtuba floodplain extends over a length of 300 km, and is 10-30 km wide (Fig. 2.1). The rivers and floodplain together form a valley within the Caspian plains, bordered by steep cliffs that, for a large part, are still being actively eroded by the Volga River (Korotaev, Babich & Chalov R. S., 2009). The floodplain is a flat gently sloping area that is dissected by numerous floodplain channels and covered by thousands of lakes and residual floodplain channels. The floodplain comprises large nature areas, as well as extensive agriculture (Losev *et al.*, 2008). In the up-

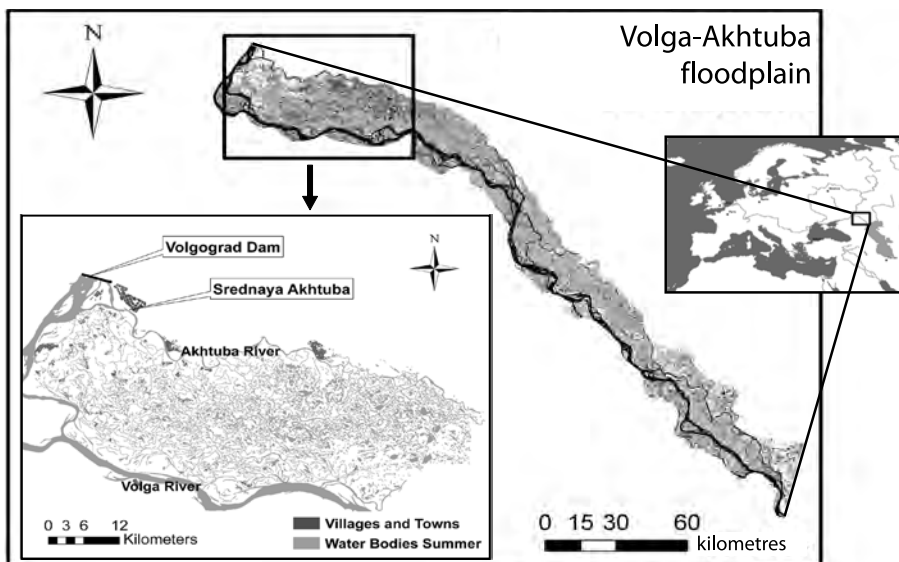


Figure 2.1 Map of the Volga–Akhtuba floodplain and its location in Russian Federation.

stream part, there are small dikes and remains of irrigation systems that provided water for abundant vegetable cultivation before the 1990s. In the upper part of the floodplain the Akhtuba River is the main contributory of floodwater, rather than the Volga itself (Sheppel, 1986). During a flood, river water flows from the upper Akhtuba into the floodplain channels that distribute the water into the floodplain. Floodplain lakes then become connected to the rising water levels in the floodplain channels, and the floodplain surface inundates when the banks of these floodplain channels are overtopped.

2.4.2 Analyses

To assess changes in the flow regime of the Volga River resulting from the construction of the chain of Volga reservoirs in the 1950s-1960s we obtained monthly average discharges for the period 1879-1935 and 1953-1985 at Volgograd from the Oak Ridge National Laboratory Distributed Active Archive Center (ORNL DAAC) (Vörösmarty, Fekete & Tucker, 1998). In addition we obtained scattered daily discharges for 1936-1939 and 1942 from Moscow State University. For the hydrological analyses of the 1960-2006 period after the completion of the Volgograd Reservoir Dam we obtained daily Volga River discharges at the Volga Hydropower Station, water levels, water and air temperatures at the city of Volgograd, as well as water levels and temperatures of the Upper Akhtuba at Srednaya Akhtuba, from the Volgograd Centre of Hydrometeorology and Environmental Monitoring, Volgograd, Russian Federation.

We compared discharges before and after damming using the records of monthly average discharges. For each year we determined the annual total discharge, the lowest monthly discharge and the maximum monthly discharge. This allowed comparing the annual amounts of available water, as well as the effect of the reservoir management regime on the lower and higher extreme discharges.

For the detailed analyses of flood pulse characteristics in different years we identified 18 potentially relevant hydrological variables from the daily data records from 1960-2006. These variables describe a flood in terms of its magnitude, timing, duration and associated water temperature (Table 2.1). Since we were specifically interested in characteristics that affect the floodplain, we determined the minimum water level for which the Akhtuba

Table 2.1 Hydrological and temperature variables selected for analysis.

| Group (corresponding with) | Variable | Description |
|---------------------------------|----------------|--|
| 1. (Flood size) | Hmax | Maximum water level measured at Srednaya Akhtuba |
| | Qmax | Maximum discharge from Volgograd reservoir |
| | Hmeanflood | Mean water level at Srednaya Akhtuba during flooding |
| | Qmeanflood | Mean discharge from Volgograd reservoir during flooding |
| 2. (Flood duration and size) | Qmean | Mean discharge from Volgograd reservoir |
| | Vflood | Sum volume during flood |
| | Wetdays | Number of days with water level (H) above the flooding threshold |
| | DateEndflood | Date of the end of flooding |
| | Tendflood | Water temperature at Srednaya Akhtuba on the last day of flooding |
| 3 and 4. (Low flow period) | Hmin | Minimum water level measured at Srednaya Akhtuba |
| | Hmeandrydays | Mean water level measured at Srednaya Akhtuba excluding flooding |
| | Qmin | Minimum discharge from Volgograd reservoir |
| | Tmeanflood | Mean water temperature at Srednaya Akhtuba during flooding |
| 5. (Flood timing) | DateHmax | Date of maximum water level at Srednaya Akhtuba |
| | DateQmax | Date of maximum discharge from Volgograd reservoir |
| | Tearly | Sum of degree-days during the first 14 days of flooding |
| | DateStartflood | Date of the start of flooding |
| | Tstartflood | Water temperature at Srednaya Akhtuba on the first day of flooding |

River water starts to flow into the floodplain channels. Based on a field survey we determined this level at -6.5 m Mean Sea Level (MSL) measured at Kronstadt, Russian Federation. Periods during which the water level at the Srednaya Akhtuba station (located on Akhtuba River 10 km downstream of its splitting from the Volga River, Fig. 2.1) exceeds this threshold are defined as flood events. Using the 18 selected flood variables we clustered floods according to their similarity using Ward's algorithm (Ward, 1963). In addition, we analyzed the overall similarity of floods with principal components analysis (PCA) using the correlation matrix (Ter Braak & Šmilauer, 2002).

We obtained commercial fishery catch data (aggregated to total catches per species per year) in floodplain lakes (1959 – 2002) and the Volga river channel (1958 – 2003) from the Volgograd Fisheries Inspection. Unfortunately, information on fishing effort was unavailable, rendering it impossible to decide whether long-term changes in catch weight can be contributed to changes in abundance of fishes, or to changes in fishing effort. Moreover, it is unknown how much 'unofficial', and therefore unregistered fishing took

place. Because no major change in applied types of fishing gear occurred, the data can be used e.g. to explore temporal developments of species composition. To summarize overall developments in the commercial catches of both the floodplain and Volga River we performed a principal components analysis (PCA) of the percentage of species composition over the years. Percentages were arcsine-transformed ($\arcsin \sqrt{[\%/100]}$) before the analysis. Only species occurring in both areas, contributing >1% of the total commercial catches were included (Table 2.2).

Table 2.2 Ecological guilds of species making up 95% of the total catches in the River Volga channel and the Volga-Akhtuba floodplain.

| Species | Code | Common name | Family | Ecological guild |
|---|------|--------------|------------|------------------|
| <i>Abramis ballerus</i> (Linnaeus, 1758) | Abba | Blue bream | Cyprinidae | Eurytopic |
| <i>Abramis brama</i> (Linnaeus, 1758) | Abbr | Common bream | Cyprinidae | Eurytopic |
| <i>Aspius aspius</i> (Linnaeus, 1758) | Asas | Asp | Cyprinidae | Rheophilic |
| <i>Blicca bjoerkna</i> (Linnaeus, 1758) | Blbj | White bream | Cyprinidae | Eurytopic |
| <i>Carassius gibelio</i> (Bloch, 1783) | Cagi | Gibel carp | Cyprinidae | Eurytopic |
| <i>Esox lucius</i> (Linnaeus, 1758) | Eslu | Pike | Esocidae | Eurytopic |
| <i>Leuciscus idus</i> (Linnaeus, 1758) | Leid | Ide | Cyprinidae | Rheophilic |
| <i>Pelecus cultratus</i> (Linnaeus, 1758) | Pecu | Sabrefish | Cyprinidae | Rheophilic |
| <i>Perca fluviatilis</i> (Linnaeus, 1758) | Pefl | Perch | Percidae | Eurytopic |
| <i>Rutilus rutilus</i> (Linnaeus, 1758) | Ruru | Roach | Cyprinidae | Eurytopic |
| <i>Sander lucioperca</i> (Linnaeus, 1758) | Salu | Pikeperch | Percidae | Eurytopic |
| <i>Scardinius erythrophthalmus</i> (Linnaeus, 1758) | Scer | Rudd | Cyprinidae | Limnophilic |
| <i>Silurus glanis</i> (Linnaeus, 1758) | Sigl | Wels | Siluridae | Eurytopic |

To investigate the effects of flood variables (explanatory variables) on the variation of fish catches (response variables) redundancy analyses (RDAs) (Ter Braak & Šmilauer, 2002) were performed separately for the floodplain and Volga catch data. In order to remove the effects of long-term changes, and to concentrate on the short-term effects of present and preceding floods on the catch, we calculated the response variables as follows:

- Catches per species (in tonnes) were ¹⁰log-transformed to convert the overall exponential decrease with time into linear trends. In case of zero-catches, these were considered not as true zeroes, but as catch levels below detection level, and were set to half the level of the minimum non-zero catch per species. For gibel carp, a non-indigenous species, zero catches were not filled in for the Volga-area, until it first appeared in the catch in the late 1980s;

- Differences of the log-transformed catches per species between subsequent years were calculated, to emphasize year-to-year variation;
- The overall means of the ¹⁰log-transformed catches per species were calculated, as an indication of the overall level of the catches per species. These values were added to the year-to-year differences so that the final response variables to be entered into the RDA were expressed as the differences between two subsequent years, weighted for the overall mean per species.
- Finally, standardized redundancy analyses (RDAs) were performed with flood variables as explanatory variables, using lag periods of 0 – 4 years (to explore the possible delayed response of the fish community to flooding, related to recruitment to commercial sizes), as well as with the arithmetic means of flood variable values of the current and the two preceding years.

Flood variables that were identified as significantly contributing to the explanation of variation in the year-to-year differences in fish catches in the RDAs, were further examined by linear regression.

2.5 Results

2.5.1 Flood characteristics

The natural flow regime of the Volga River from the pre-damming period 1889 – 1953 shows some clearly different characteristics when compared to the post-damming period (Fig. 2.2). First, the peak flow magnitudes have decreased. Before damming, the maximum monthly reached values between 20,000 and 39,000 m³/s; the high floods of 1926 and 1929 reached maximum discharges of 59,000 and 45,500 m³/s, corresponding to a flood volume of 245 and 207 km³ respectively. The 1930s appear to be years with exceptionally low annual and peak flows (Fig. 2.2C). In the 1950s the peak discharge decreased, while the winter discharge increased as a result of dam building upstream of Volgograd. Reservoir regulation resulted in a considerable reduction of the flood magnitudes: since the 1960s, the highest monthly average discharges decreased by more than 10,000 m³/s compared to the pre-damming period. The largest flood after the dam construction occurred in 1979, with a peak flow of 30,800 m³/s (Fig. 2.2B). The flood of 2006 was exceptionally small, reaching a discharge peak of only 18,300 m³/s. The reduced flood volume is a consequence of artificially

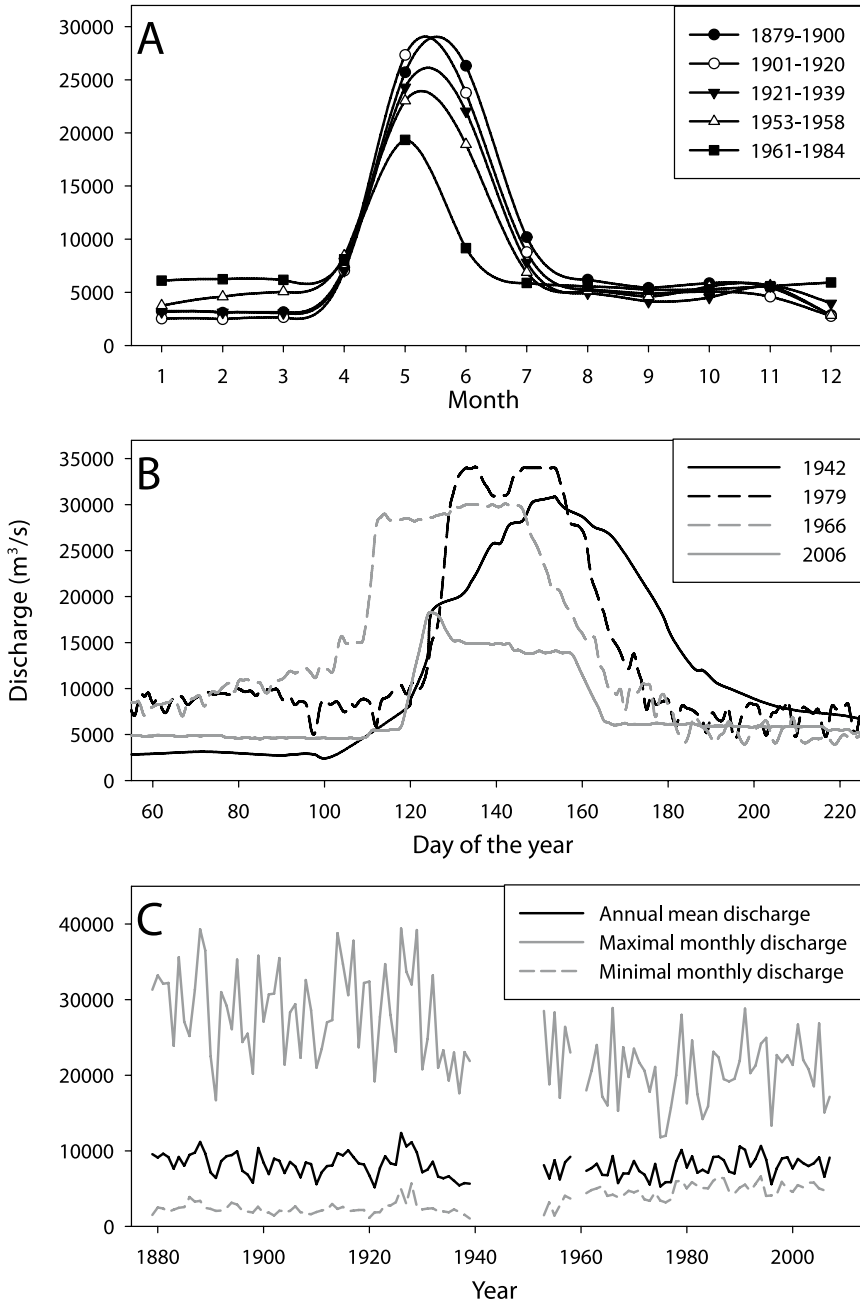


Figure 2.2 (A) Changes in the monthly average discharge of the Volga River measured at Volgograd. (B) Daily discharge of the Volga River for 1942, 1979, 1966 and 2006 representing a pre-dam flooding event, and postdam flooding of a high, average and low flooding event. (C) Mean annual discharge, monthly maximum and monthly minimum discharge for the period 1879-2006. Note that monthly averages mask peak discharges when flooding events occur at the transition from one month to the next.

maintaining a higher discharge than the natural flow during the rest of the year. The natural Volga flow decreased in summer to less than 2000 m³/s, with occasional low flow in early winter of less than 1000 m³/s. To date the reservoir management artificially maintains a minimum flow of about 6,000 - 6,500 m³/s (Fig. 2.2A). In contrast to what was suggested in some literature (Asarin, 1985) the total annual discharge of the Volga has only decreased slightly after damming: the average annual discharge in the period 1897 - 1930 was about 268 km³ (s.d. = 46.2 km³), while it was on average about 250 km³ (s.d. = 42.7 km³) per year over the period 1961-2006, therefore a decrease of less than 7%.

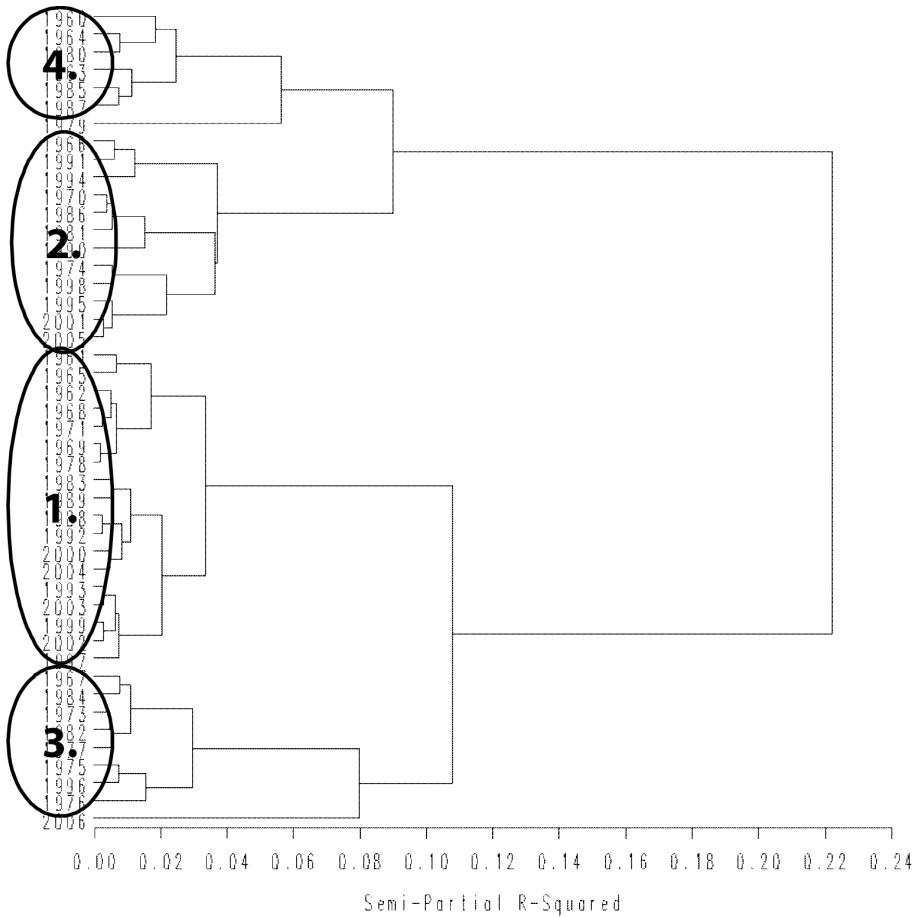


Figure 2.3 Clustering result of floods (Ward method).

Reservoir regulation also changed the timing and the rise and recession of the floods. The natural rise of a flood could take up to a few weeks (Fig. 2.2B), peak values lasted only for a few days, and recession of the flood continued until low flow conditions were reached by mid-July. The regulated floods show a steep rise in discharge at the onset of the flood: within two weeks the peak flow is reached. Furthermore, high discharge levels are maintained at a constant level for 1-2 weeks, before they fall back to lower, but still elevated values. At the end of the flood by mid-June, discharge decreases more rapidly than the natural flood recession to low flow values.

Cluster analysis of the floods in the period of 1961-2006 resulted in 4 distinguishable clusters plus the floods of 1979 and 2006 which were so anomalous that they are separate from floods from other years (Fig. 2.3).

The PCA resulted in 42.5% of the total variance among the flood characteristics explained by PC1 and 18.5% by PC2. PC1 strongly correlated with variables describing flood magnitude: Q_{max} , Q_{mean} , V_{flood} and $Wetdays$. PC2 strongly correlated with variables describing the timing of a flood event: $Tearly$, $DateStartflood$, $DateQ_{max}$ and $DateH_{max}$ (Fig. 2.4A). Plotting the floods in the $V_{flood} - DateQ_{max}$ plane, representing the dominating variables correlating with PC1 and PC2, illustrates the clustering of floods from different years (Fig. 2.4B).

Floods from the years before damming (with the exception of very low flood in 1937, falling in cluster 3) do not fall in any cluster, and are characterized by a higher and later flood than after damming. It should be noted that the pre-damming floods presented in this graph are still considerably smaller than flooding events occurring before the 1930s (Fig. 2.2).

The following types of floods are identified:

- Cluster 1: Floods of average volume with early timing
- Cluster 2: Larger than average floods with early timing
- Cluster 3: Smaller than average floods with late timing
- Cluster 4: Floods of average volume with late timing
- 1979: Very large flood with late timing
- 2006: Very small flood with early timing

Floods of type 1 and 2 have become relatively more frequent since the mid-1990s, while floods of type 3 and 4 have become rarer (Fig. 2.5). In other words, average, or larger than average floods with early timing have become more frequent than average, or smaller than average floods with late timing.

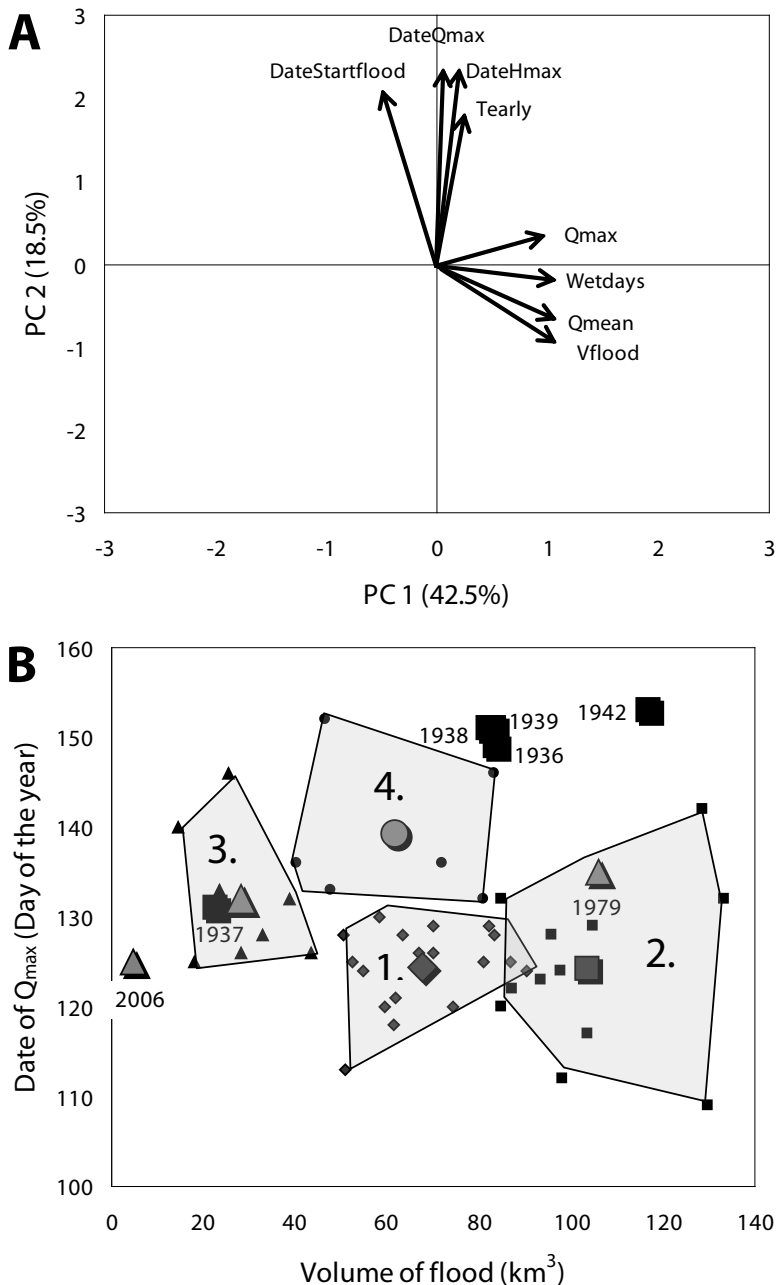


Figure 2.4 (A) Flood variables correlating most with PC1 and PC2 of the flood years 1960-2007. (B) Cluster averages and the envelopes around clusters of individual flood years plotted in flood volume and date of Q_{max} plain (corresponding with PC1 and PC2). The flood clusters correspond to those in Fig. 3 and were assigned post hoc. 1936-1939 and 1942 were added post hoc for comparison with pre-damming flooding events.

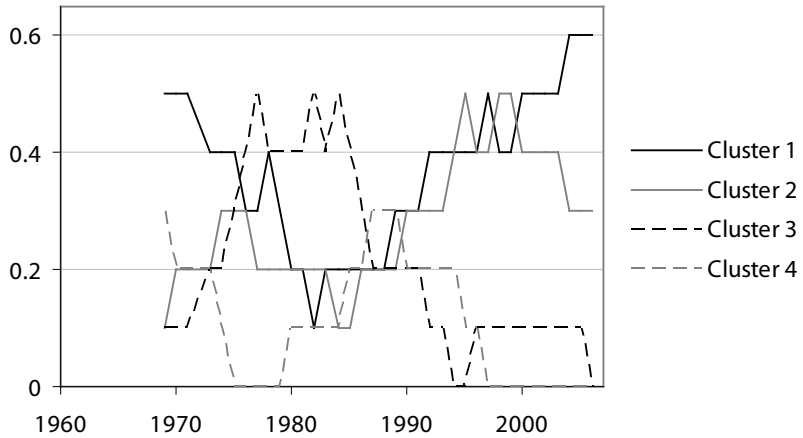


Figure 2.5 10-year moving average of frequency of occurrence of the 4 clusters of flood types. The clusters are as in Figure 4.

2.5.2 Fish catches

Commercial catches in the Volga channel and floodplain lakes in the Volgograd Region already dropped by 50% immediately after the Volgograd dam closure (Delycyn, 1967). Catches continued to decrease in both the Volga channel and floodplain with time (Fig. 2.6). Catch composition consistently differed between the Volga channel and the floodplain lakes according to the flow preference of fish species, with a larger abundance of rheophilic species in the Volga channel (especially asp, ide and sabrefish), and limnophilic (especially phytophilic) species more abundant in the floodplain (pike, gibel carp, and rudd). Eurytopic species such as white bream, roach and perch were relatively more important in the floodplain catches, while common bream and pike-perch were more abundant in the Volga channel catches.

In addition to the clear differences between floodplain lakes and Volga channel catches, there is a remarkable difference in the fish catches in the periods before and after 1990 (Fig. 2.7A). This distinction can be attributed to a large extent to the importance of asp in the Volga, and perch in the floodplain (distinction between areas) and the importance of gibel carp after 1990 (Fig. 2.7B).

The ordinations by redundancy analysis (RDAs) indicated that for the floodplain lakes the flood variables significantly explain the differences in fish

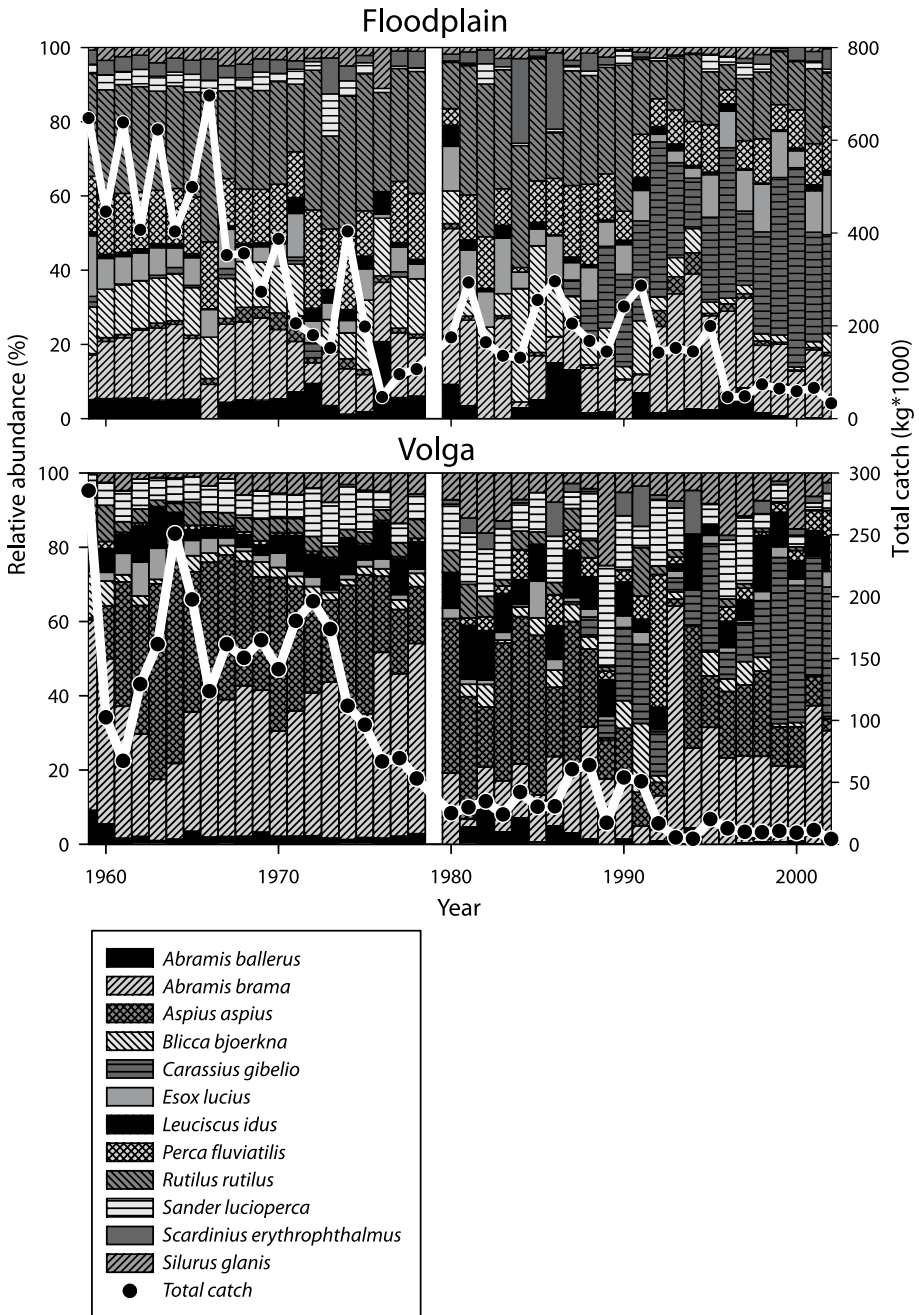


Figure 2.6 Official statistics of commercial fish catches in the floodplain lakes (top) and in the margin of the main channel of the Volga (bottom).

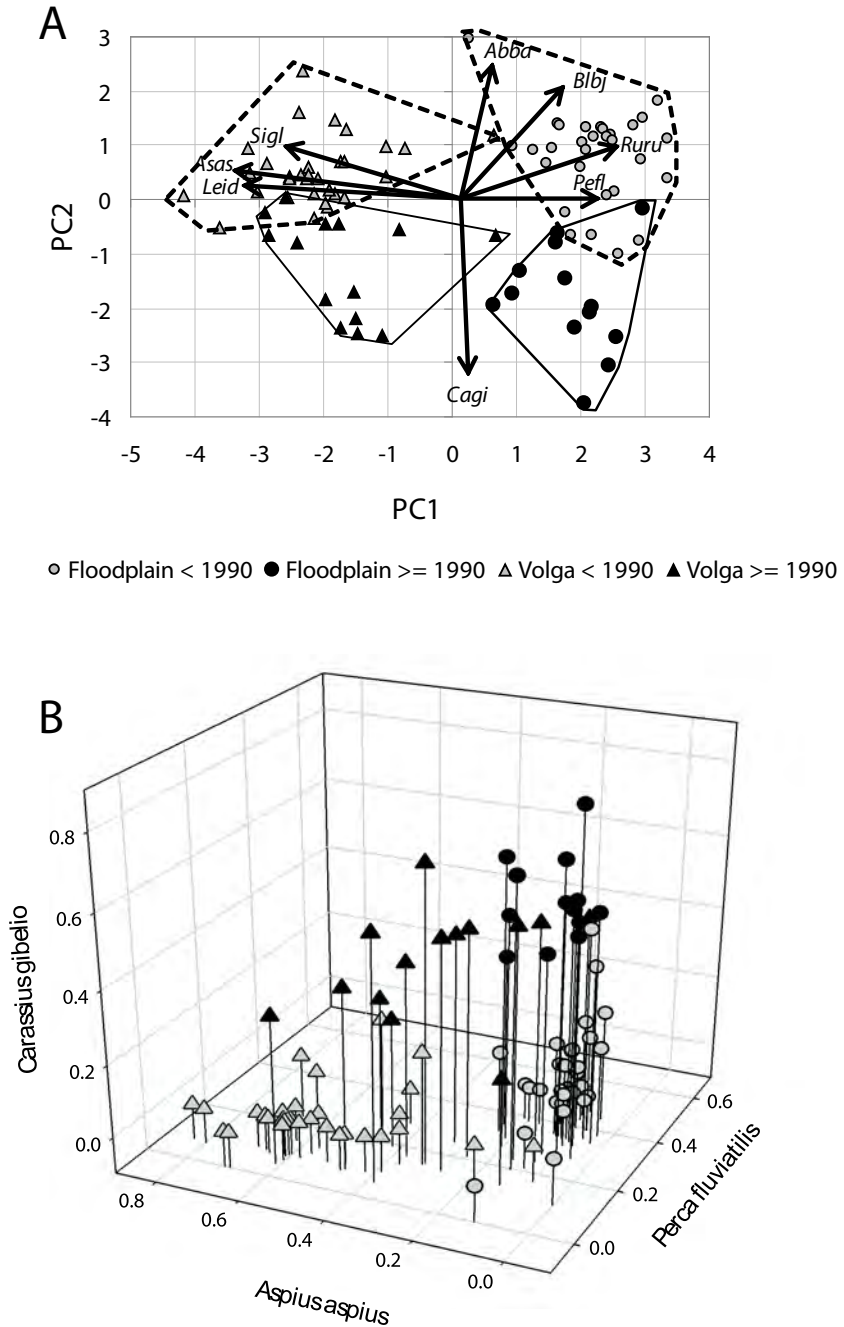


Figure 2.7 (A) Biplots of the principal components analysis of commercial catches in the Floodplain and Volga channel. (B) 3D-plot of the three fish species that distinguish the Floodplain and Volga commercial catches in the periods until 1990 and thereafter.

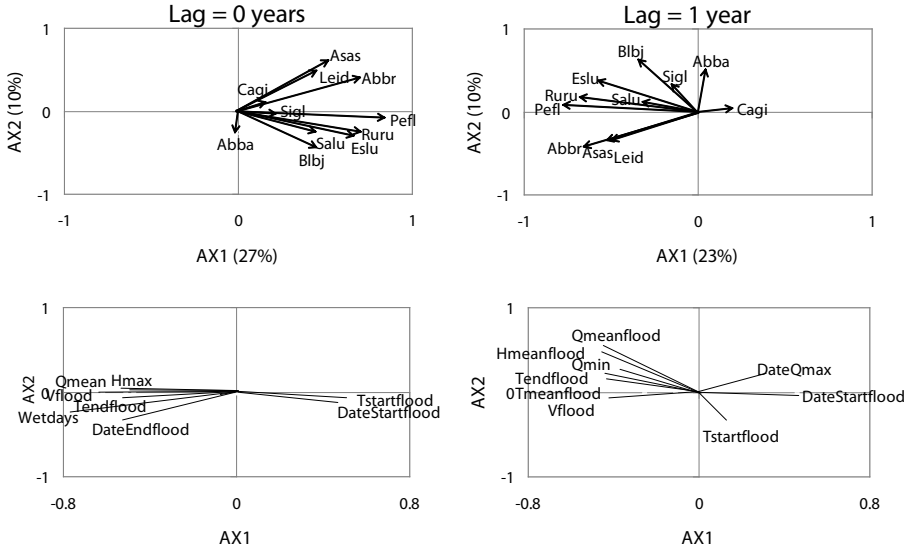


Figure 2.8 Redundancy analysis (RDA) of year-to-year differences between log10-transformed fish catches in the commercial catches in the Floodplain water bodies from 1960 – 2002 explained by flood variables. Shown significant RDAs were performed with lags of 0 and 1 for the flood variables.

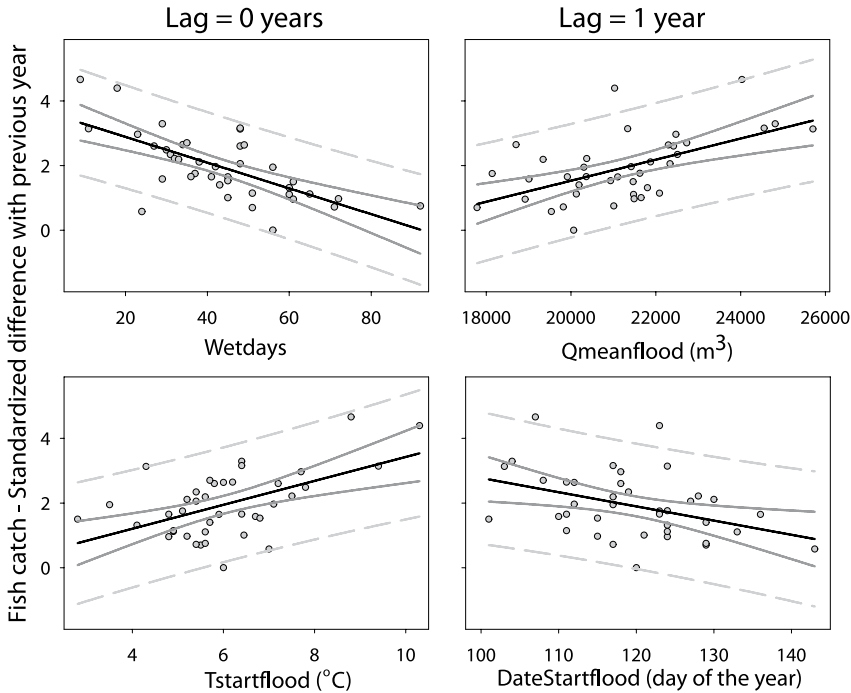


Figure 2.9 Linear regression (with 95% Confidence and prediction bands) of standardized difference in total fish catch with previous year and significantly correlated flood variables.

catches between the current (lag=0) and preceding year (lag=1). The flood variables of the preceding year (lag=1) also significantly explain these differences. However, flood variables do not significantly explain the year-to-year differences in fish catches from the Volga channel. For the significant ordinations 55 – 60 % of the variance in channel fish catches is explained by flood variables, with 40 – 44% explained in the first three PC axes (Fig. 2.8). For the floodplain, a large and long flood (large *Vflood*, *Wetdays* and *DateEndflood*) in the current year correlates with lower catches of most fish species compared to the preceding year. This effect is particularly strong for perch, bream, roach, asp and pike. A late start of the flood and high temperatures at the start of the flood resulted in higher catches in that year. As expected, the effects of flood variables in the preceding year (lag=1) are more or less opposite to those in the current year (lag=0). For the floodplain, a high flood discharge, early start of the flood, and high flood water levels in the previous year resulted in relatively higher fish catches in the current year, while a late start of the flood in the previous year resulted in lower catches. Here too, the effect on perch, bream, roach, asp and pike was strongest. Total fish catch differences with preceding years show significant negative correlations with flood duration (*Wetdays*) and positive with the temperature at the start of flooding in particular year (*Tearly*) (Fig. 2.9). Moreover, fish catches in a particular year were positively correlated with flood magnitude (*Qmeanflood*) and negatively with the date of start of the flooding (*DateStartflood*) in the preceding year (Fig. 2.9).

2.6 Discussion

2.6.1 Flood pulse changes

The flood pulse magnitude of the Lower Volga River has shown considerable variation over the past century, with a major reduction in magnitude after the completion of the Volga-Kama cascade of reservoirs. The variation in the amounts of water that have entered the floodplain each year – both before and after completion of the reservoirs - are due to different processes. Some of these underlying processes show a cyclic variation, other are progressive; they operate at different time scales, and are climatic, geomorphologic or anthropogenic in nature.

Before the construction of the reservoirs, the Volga discharge regime was mostly determined by climatic variables, i.e. the net precipitation surplus and a seasonal snow melt peak in spring. These climate variables have shown a considerable year-to-year variability, resulting in a large variation in total annual Volga discharge, as well as in the spring flow. Since variations in the annual Volga discharge contribute for 80% to changes in the Caspian Sea water balance and inherent sea level changes, several researchers have attempted to detect cyclicity in the annual discharge magnitude, and to find statistically significant correlations with large-scale atmospheric circulation patterns, ENSO and NAO (Rodionov, 1994; Sidorenkov & Shveikina, 2006). Arpe *et al.*, 2000 found – after attempting various lags and shifts in the start month for the hydrological year – that annual Volga discharge significantly correlating with Niño-4 sea surface temperatures (SSTs) when the latter are averaged from spring to next winter, and the averaging of annual Volga River Discharge starts in the winter of the SST averaging period. The amounts of snow accumulation in the Volga River basin might be larger during years of positive NAO index, causing larger amounts of moisture into NW Europe (Trigo, Osborn & Corte-Real, 2002; Zveryaev, 2004). We compared the magnitude of the Volga annual (Nov-Sep) and spring flow (April-Jun) during the pre-damming period (1879-1939) to Jones' Gibraltar-Iceland winter (Oct-Mar) NAO-index (Jones, Jonsson & Wheeler, 1997). However, neither annual discharge nor the spring flow showed a significant correlation with the NAO index. The runoff regulation after the construction of the reservoirs since the 1960s has strongly affected potential correlations between discharge and NAO: both fluctuations in peak flow and annual flow are considerably damped by the reservoirs; while varying amounts of water extraction for agriculture and evaporation losses from the reservoirs have further affected the natural discharge of the lower Volga. Nevertheless, the amounts of precipitation surplus and snow melt water from the Volga basin, both annually and in spring time, remain controlled by semi-periodic variations in atmospheric circulation patterns over N-Europe, associated with NAO and ENSO (Rodionov, 1994).

After the reservoirs of the Volga-Kama cascade became operational, increasing amounts of Volga water were withdrawn for industrial use and agriculture until the 1990s (Demin & Ismaiyllov, 2003). In the 1970s, about 20% of the annual discharge was extracted from the natural Volga flow. To fulfil the demands for navigation in the lower Volga and for energy production, the reservoir management programs provided a higher minimum water flow

during periods of low natural discharge (Vasilevskii *et al.*, 2001). Although this resulted in a reduction of the amount of water released during the spring discharge peak, the regulation scheme aims at maintaining a sufficiently large peak flow to provide extensive spawning grounds for fish in spring (Rakovich *et al.*, 2003). Still, water extraction and retention of water in the reservoirs have considerably reduced the flood pulse magnitude for the Volga-Akhtuba floodplain.

In addition to the reduced flood pulse magnitude, a second factor causing less water entering the floodplain lies in the morphological changes in the river channels that occurred after the reservoir was built. Firstly, the natural entry of the Akhtuba was artificially replaced by a canal downstream of the dam. However, the unfavourable lay-out of the new bifurcation and sand bars developing in the upstream parts of the Akhtuba decreased the discharge capacity of this river, and caused within channel deposition of sand in the Akhtuba channel (Chalov, 2005). Secondly, in the same period, sediment trapping in the reservoir has led to channel bed degradation in the Volga downstream of the reservoir dam (Ivanov *et al.*, 2006). Consequently, the river water level at Volgograd resulting from a given discharge has dropped in the course of years, which occurs especially at lower discharges. At a discharge of $10,000 \text{ m}^3\text{s}^{-1}$ the water level has dropped over 1.5 meter in nearly 50 years after completion of the Volgograd Dam (Fig. 2.10). This has resulted in a decrease in inundation duration of adjacent floodplain as higher discharges are needed to reach bankfull water levels (Page *et al.*, 2005; Frazier & Page, 2006). To date the Volga discharge needs to be about $3,100 \text{ m}^3\text{s}^{-1}$ larger than before dam building to reach the water level that causes the water starting to penetrate into the Volga-Akhtuba floodplain via the floodplain channels.

Our analysis of the characteristics of the spring peak flows during the period of Volga regulation (1960-2006) shows that the frequency of occurrence of the identified clusters changes towards larger flood discharges (Fig. 2.5). This might be due to the economic set-back in the Russian Federation in the early 1990s, reducing water demand by industry and for irrigation of agricultural lands and the increase of water recirculation (Demin, 2005). Demin & Ismaiyllov (2003) report a drop in water withdrawal from 37 to 29 km^3 during the early 1990s, despite an increase in water demand for households. This economical effect on water demand contrasts damming effects elsewhere, as damming generally results in decreased flood mag-

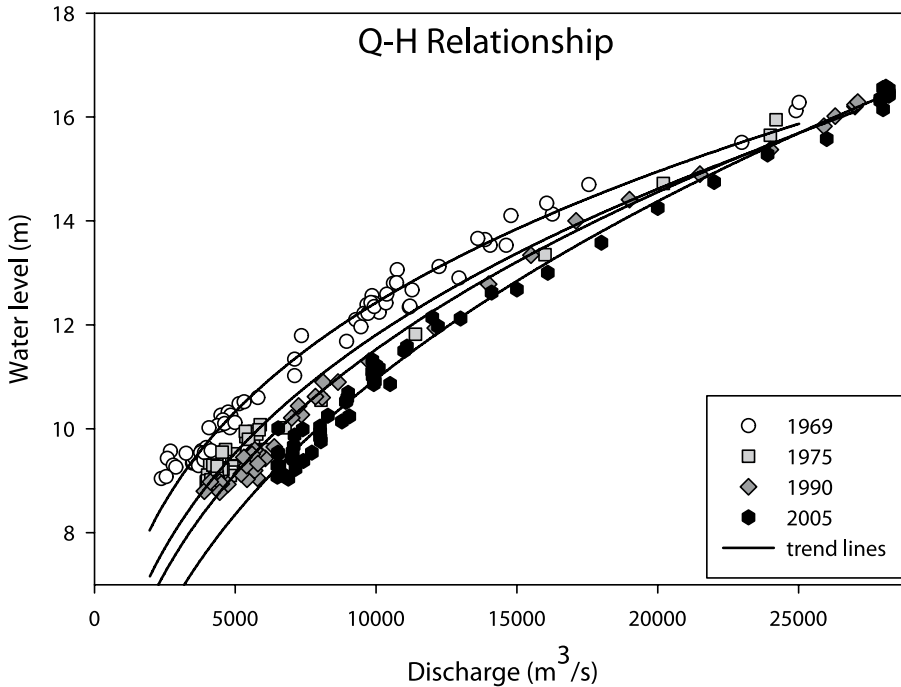


Figure 2.10 Relationship between daily water level and daily discharge (upcoming water only) for 4 years representing the time span of the data set (data points and polynomial trend line). Trend line equations: 1960: $y = 1.1172x^{0.2613}$ ($R^2 = 0.9755$), 1975: $y = 0.7384x^{0.3006}$ ($R^2 = 0.9784$), 1990: $y = 0.5396x^{0.3323}$ ($R^2 = 0.99$), 2005: $y = 0.2929x^{0.3932}$ ($R^2 = 0.9905$). Water levels are raised by 20 to create positive values in order to calculate the trend line.

nitude and peak discharge (Poff *et al.*, 2007). Due to the opposite effects of channel bed incision below the Volgograd reservoir dam and increased Volga discharge, there has not been significant change in flood duration over the past decades. However, as bed incision continues, a reduction in flood duration is anticipated when water demand resumes in response to economic recovery.

In conclusion, the flood pulse magnitude of the Volga-Akhtuba floodplain has considerably decreased due to the reservoir construction. In spite of regulation, considerable year-to-year variation in flood magnitude and timing has remained. However, the combination of hydrological changes, channel bed degradation downstream of the Volgograd dam, and silting-up of the Akhtuba has led to decreasing amounts of flood waters entering the Volga-Akhtuba floodplain over the past decades.

2.6.2 Implications for fish populations and reproduction

The damming of the Volga River and its resulting flow alterations and environmental changes was followed by a dramatic decrease in fish catches observed in both the floodplain lakes and the Volga channel (Fig. 2.6). Even though the catch data are potentially flawed it is highly unlikely that the observed 10 to 20-fold decrease in total fish catches is entirely due to registration errors, or misreporting. Moreover, similar drastic drops in commercial catches as a result of damming were reported for many other temperate and tropical large rivers such as the Danube, Missouri, Columbia, and Niger (Welcomme, 1979; Holčík, 2003). Dam construction resulted in blocking of longitudinal fish migration routes and therefore led to a dramatic decrease in abundance of migratory species such as sturgeons in the Volga River (Khodorevskaya *et al.*, 1997; Billard & Lecointre, 2001; Usova, 2005). In addition to the blockage of longitudinal fish migration routes, equalization of floods after damming, combined with changes in the timing and duration of the floods decreased habitat variability in the floodplain, favouring more eurytopic fish species. Moreover, flow regulation promotes invasion success of non-native species (Moyle & Light, 1996a; Marchetti & Moyle, 2001), which are often better adapted to the new conditions. The most important factor determining fish invasions in streams and estuaries was shown to be the match between the invader and the abiotic environment, while biotic resistance (Case, 1991) seemed to play a minor role (Moyle and Light, 1996b). The sudden increase of gibel carp around 1985 in the Volga-Akhtuba floodplain is an indication of these effects. A similar drop in catches and gibel carp invasion was observed in the Danube delta lakes following the construction of upstream dams (Navodaru, Buijse & Staras, 2002). This confirms that changes in flood pulse characteristics change the ecological functioning of floodplains for aquatic organisms (Junk *et al.*, 1989; Ligon *et al.*, 1995). Especially for species that rely on (temporarily) submerged terrestrial vegetation for food, shelter and spawning, such as insects and fish, decreased floodplain availability may result in growth reduction, mortality and reproduction failure (Sommer *et al.*, 2001; Magalhaes *et al.*, 2007; Wantzen *et al.*, 2008).

Flood timing in the Volga-Akhtuba floodplain shifted towards earlier onset and flood peak (types 1 and 2, Fig. 2.5). This is expected to have major ecological implications, because in temperate regions temperature and light availability are highly critical for many ecological processes such as primary

production, metabolic processes, and as spawning and hatching cue for insects and fish (Blaxter, 1992; Menzel & Fabian, 1999; Mingelbier, Brodeur & Morin, 2008). Earlier flooding can result in a mismatch between flooded habitat availability and temperature-driven processes, such as growth (Schramm & Eggleton, 2006). Likewise, flood-driven processes, such as fish migration to spawning grounds (Abe *et al.*, 2007) may be triggered at low temperatures that are not optimal for spawning. This mismatch may result in prolonged hatching times, limited food and habitat availability, and therefore increased mortality of offspring (Blaxter, 1992; Avakyan, 1998). Moreover, during spring flooding water is released from the bottom of the reservoir, which leads to lower water temperatures during the flood compared to the pre-damming situation. Such dam-induced thermal alteration has significant effects on productivity and the reproduction, growth and assemblage structure of organisms (Haxton & Findlay, 2008). The faster drop in relative abundance of early and one time spawning fish species such as asp and bream compared to more warm-water, batch spawners is corroborated by this mechanism. The fact that we only observed this effect in the catches from the Volga main channel and not in the catches from floodplain lakes could be explained by the buffering effect of the morphological and resulting thermal complexity of the Volga-Akhtuba floodplain during flooding (Górski *et al.*, 2010), as well as by faster warming of shallow waters. Fish populations in the Volga-Akhtuba floodplain still depend on variations in the year-to-year flow regime, besides flow alterations and long-term environmental changes. A large flooding in a particular year generally resulted in a higher fish catch in the subsequent year, suggesting that the abundance of catchable fish will increase, probably through better survival and growth during high flood (Junk *et al.*, 1989; Grift, 2001; Barko, Herzog & O'Connell, 2006). Moreover, larger floods are reported by the fishermen to have the effect of releasing fish imprisoned within floodplain water bodies and increasing the recruitment, therefore leading to better catches in the source as subsequent years (Welcomme, 1985). Similar correlations between fish catch in any year and flood magnitude in the preceding year were reported in the Danube River system (Holčík & Bastl, 1977). No such relationships were found for the floodplains of the Mississippi river system, which are highly disconnected from the main river (Risotto & Turner, 1985). Magnitude and duration of floods was reported to relate directly to fish yields also in other tropical and temperate floodplain river systems (Welcomme, 1985; Moses, 1987; Bayley, 1991). Additionally, improved catches during low waters are known from most fisheries as shallower waters fa-

your the capture of fish (Welcomme, 1985). This could be further explanation to the observed higher catches in years with short floods, although it is unlikely that this completely explains the observed differences.

Despite the significantly altered hydrological regime of the Volga River after damming, discharge management still provides significant spring flooding, preserving eco-hydrological functioning of the floodplain. As such, the Volga River distinguishes itself from many other regulated rivers worldwide, where dam constructions do not allow for any flooding period to be maintained (Postel & Richter, 2003). Future management strategies should carefully take regime requirements of the native fish fauna into consideration. Post-damming changes in floodplain morphology may require additional management actions in order to preserve floodplain diversity and productivity.

2.7 Acknowledgements

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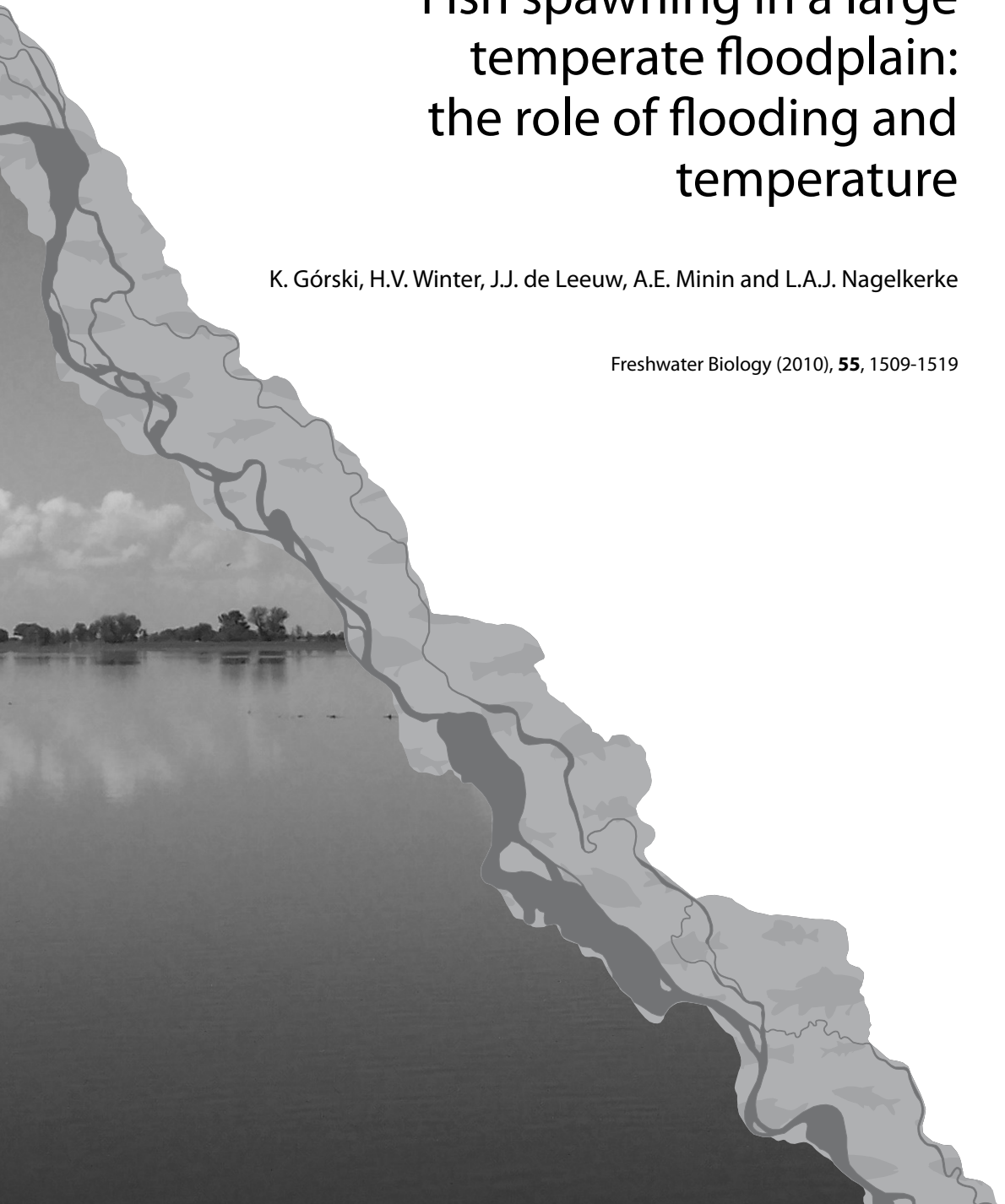


Chapter 3

Fish spawning in a large temperate floodplain: the role of flooding and temperature

K. Górski, H.V. Winter, J.J. de Leeuw, A.E. Minin and L.A.J. Nagelkerke

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Fish spawning in a large temperate floodplain: the role of flooding and temperature

3.1 Abstract

Floodplains are a key habitat for foraging, spawning and as a nursery for many riverine fish species. The lower Volga floodplains (Russian Federation) are still relatively undisturbed, while in Europe and North-America about 90% of floodplains have effectively been lost. We examined relationships between the extent and timing of the spring flood, lateral spawning movements of fish species, and timing and duration of spawning in the floodplain by sampling during spring 2006 and 2007. Only the spawning of rheophilic species, that released their eggs in the floodplain, coincided with the flood. In contrast, the timing of spawning by eurytopic and limnophilic species was unrelated to flooding. For most fish species we found no indication that the majority of spawners in the floodplain originated from the main river channel, with the exception of sabrefish *Pelecus cultratus*. We postulate that in the vast Volga-Akh-tuba floodplain fish spawning stocks mainly originate from permanent floodplain water bodies, whereas hydrological conditions are dominated by the river. Both the river and water bodies on the floodplain may serve as sources for recolonization after local extinction due to extreme environmental conditions, such as freezing or desiccation.

Нерест рыб в пойме большой реки умеренного климата: роль половодий и температурного режима

3.2 Резюме

Поймы рек являются ключевым местом кормления, нереста и роста молоди для многих речных видов рыб. Пойма Нижней Волги (Российская Федерация) относительно нетронута человеком, в то время как в Европе и Северной Америке фактически около 90% всех пойм потеряны. Мы изучали взаимосвязи между масштабами и временем весеннего половодья, латеральным перемещением различных видов рыб во время нереста и временем наступления и продолжительностью нереста в пойме путем выборочного облова в весенние периоды 2006 и 2007 годов. Только нерест реофильных видов рыб, которые мечут икру в пойме, совпадает с половодьем. Напротив, время нереста эвритопных и лимнофильных видов не было связано с временем наступления половодья. Для большинства видов мы не обнаружили признаков того, что большинство нерестящихся особей заходит в пойму из русла реки. Исключение составляет чехонь *Pelecus cultratus*. Мы постулируем, что по всей Волго-Ахтубинской пойме рыба выходит на нерест из временных пойменных водоемов (ериков и озер), несмотря на то, что гидрологические условия доминируются рекой. Как река, так и пойменные водоемы могут служить источником реколонизации после локальных заморозов вследствие экстремальных экологических условий, таких как промерзание или обсыхание.

3.3 Introduction

The Flood Pulse Concept states that the predictable inundation of floodplains is the major driving force for the maintenance of biodiversity and the production of river ecosystems (Junk, Bayley & Sparks, 1989; Tockner, Malard & Ward, 2000). Seasonal flooding increases connectivity between floodplain water bodies, and facilitates the exchange of nutrients, organisms and energy between aquatic and terrestrial compartments of river ecosystems (Thomaz, Bini & Bozelli, 2007). At present, relatively undisturbed large floodplains can still be found in the tropics and the Arctic, but are very rare in temperate regions, where most large rivers are highly modified (Bayley, 1995; Nilsson *et al.*, 2005).

Floodplains offer a wide array of different temporarily suitable habitats that can be crucial as fish feeding, spawning and nursery areas as well as refugia for many species (Baber *et al.*, 2002; Holland & Huston, 1985; Poizat & Crivelli, 1997; Starrett, 1951). The timing, duration and extent of inundation have been proposed to be the main factors determining the value of floodplains for spawning and growth of fish (Bailly, Agostinho & Suzuki, 2008; Balcombe & Arthington, 2009; Trifonova, 1982; Welcomme, 1979; Welcomme & Halls, 2004). Nevertheless, remarkably few studies have examined migrations of fish from the main channel into the floodplains (lateral migrations) in naturally functioning, large scale, river floodplains (Lucas & Baras, 2001). Some studies on the lateral migration of fish in large natural floodplains are available for tropical rivers (Castello, 2008; Wantzen *et al.*, 2002). However, in the temperate zone studies on lateral migration are available only for relatively small rivers, the middle and upper reaches of larger rivers (Barko, Herzog & O'Connell, 2006; Holčík, 1996), or for floodplains in the lower reaches of large rivers that are severely altered (Grift *et al.*, 2001; Molls, 1999; Reynolds, 1983).

The Lower Volga and its adjoining floodplains in the Russian Federation are still relatively undisturbed. The flow regime in the Lower Volga shows a semi-natural cycle of large snow-melt floods in late spring, resulting in an annual high-amplitude flood pulse that inundates extensive areas (300x20 km) for 5-7 weeks (Middelkoop *et al.*, 2005). Therefore, the Lower Volga provides the opportunity to study lateral movements of fish in large natural floodplains in the temperate zone.

This paper focuses on lateral spawning migration of adult fish. Our main objectives were to examine: 1) the relationship between the extent and timing of flooding and the timing and duration of spawning of various fish species and 2) the proportion of fish entering the floodplain from the main river channel to spawn in relation to the total number of spawners in the floodplain, including those from the permanent floodplain water bodies. Given the limited number of inlets from the main channel to the vast inundated floodplains of the Lower Volga during flooding, we hypothesize that if, for a given species, the spawners in the floodplain mainly originate from the main channel, then the number of fish moving into the floodplain through these inlets is expected to be very much higher than the number of fish moving within the vast floodplain, due to dispersal. If spawners mainly originated from floodplain water bodies, then no such difference in numbers would be expected. To test this, and to relate the timing and duration of spawning to the extent and timing of flooding, we monitored fish abundance and maturity stages with gill-nets at inlets and within the floodplain during the course of spring flooding in 2006 and 2007.

3.4 Methods

3.4.1 Study area

The Volga River (Russian Federation), with a length of 3,690 km and average annual discharge of 8,103 m³s⁻¹ is the largest river in Europe and 16th in the world (Litvinov *et al.*, 2009). It has a combined rainfall / snowmelt flow regime, with peak discharge in May-June. A series of upstream dams, completed in the 1960s, only moderately altered the flow regime of the Lower Volga downstream of Volgograd (Middelkoop *et al.*, 2005; Mordukhai-Boltovskoi, 1979). Directly downstream of the Volgograd dam, the Volga splits into the Lower Volga River, the main channel, and the Akhtuba River, a smaller side-arm. The Volga-Akhtuba floodplain is over 300 km long, is bordered by the Lower Volga River and Akhtuba River, and is 10-30 km wide.

The geomorphology and vegetation of the Volga-Akhtuba floodplain have been preserved in a relatively undisturbed state, the floodplain is situated in the semi-arid continental climatic zone with very dry and hot summers and severe winters (Averina *et al.*, 2000). Shallow water bodies in the floodplain may dry up in late summer, and freeze entirely in winter. The vegetation of the floodplain consists mainly of meadows (Averina *et al.*, 2000)

used for extensive grazing of cattle and hay production (Losev *et al.*, 2008). Woodlands are restricted to about 3% (Zolotarev, 2005). As water level rises at the start of the spring flood, the floodplain is inundated via a maze of permanent and temporary side channels, though there are relatively few inlets from either the Akhtuba River or the Lower Volga River itself (Fig. 3.1). These inlets would have to serve as the only possible entrances for fish moving onto the floodplain from either river.

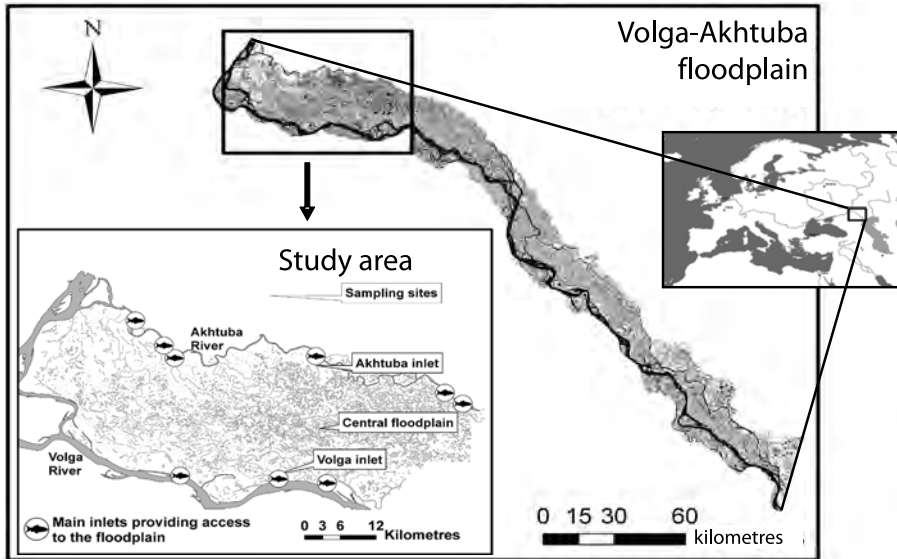


Figure 3.1 A map of the Volga–Akhtuba floodplain and selected sampling sites.

3.4.2 Sampling strategy

To compare lateral movements of spawning fish from the river channels into the floodplain with dispersal of spawners within the floodplain we monitored fish abundance at three sites. One inlet was selected on the Lower Volga River ('Volga inlet', with a width of 100 m prior to flooding and increasing to c. 300 m during flood, 48°29'3.22"N, 45° 6'46.06"E), one inlet on the Akhtuba River ('Akhtuba inlet', width 20 m prior to flooding increasing to c. 80 m during flooding, 48°41'13.30"N, 45°11'40.40"E). To measure the dispersal within the floodplain we selected one channel in the largest channel system of the central part of the upstream section of the Volga-Akhtuba floodplain ('Central floodplain', width 150 m prior to flooding extending to approximately 800 m during flooding, 48°34'11.29"N, 45°13'17.41"E) (Fig. 1). All sites were sampled during spring floods of 2006 and 2007.

3.4.3 Environmental variables

Daily discharge, water level, water temperature and air temperature at Volgograd were available for 1997-2007 and obtained from the Volgograd Centre of Hydrometeorology and Environmental Monitoring. For the Volga inlet and Central floodplain in 2006 and 2007, water levels and temperatures were measured almost daily from neighbouring bridges across the channels sampled. In addition, in 2007 water temperature was recorded at one hour intervals on the Akhtuba River, Akhtuba inlet and Central floodplain using automatic data loggers (UA-002-64 HOBO® Temperature/Light Data Logger).

3.4.4 Fish sampling

Fish movements were examined using gill-nets during the spring flood from 13 April to 8 June in 2006. Inlets were not sampled until the onset of the flood, because before that the river discharge was very low in 2006 (Fig. 3.2). In 2007 sampling was repeated from 14 April until 14 June. All sites were sampled three to four times per week. For each sampling a set of three commercial monofilament, nylon gill-nets was used, each with a different mesh size (70, 100 and 140 mm stretched mesh size). Each net was 90 m long and 2m deep. Nets were set overnight (11 h exposure) across the inlet channels at a depth of 3–4 m. At the Akhtuba inlet nets were crossing approximately the entire channel, whereas at the Volga inlet and the Central floodplain they crossed between 10–30% of the channel. We tried to minimise bias in abundance data by always using the same sampling strategy, including the use of the same set of nets, the same exposure time and a similar placement of nets across the channels at similar depths. Abundance was expressed as catch per unit of effort (CPUE) with number of fish per setting (N/setting) as unit.

Each individual caught was measured, weighed and inspected for the maturity of the gonads. Gonad maturity was classified in six stages (Nikolski, 1963). Stages I and II correspond to immature individuals, stages III and IV to maturing and mature individuals, stage V represent fish spawning ('running'), and stage VI is reserved for post-spawners ('spent'). Juveniles were not considered for the analysis. All English and scientific names, abbreviations used, reproductive guilds and minimum spawning temperatures for each of the fish species observed are given in Table 3.1.

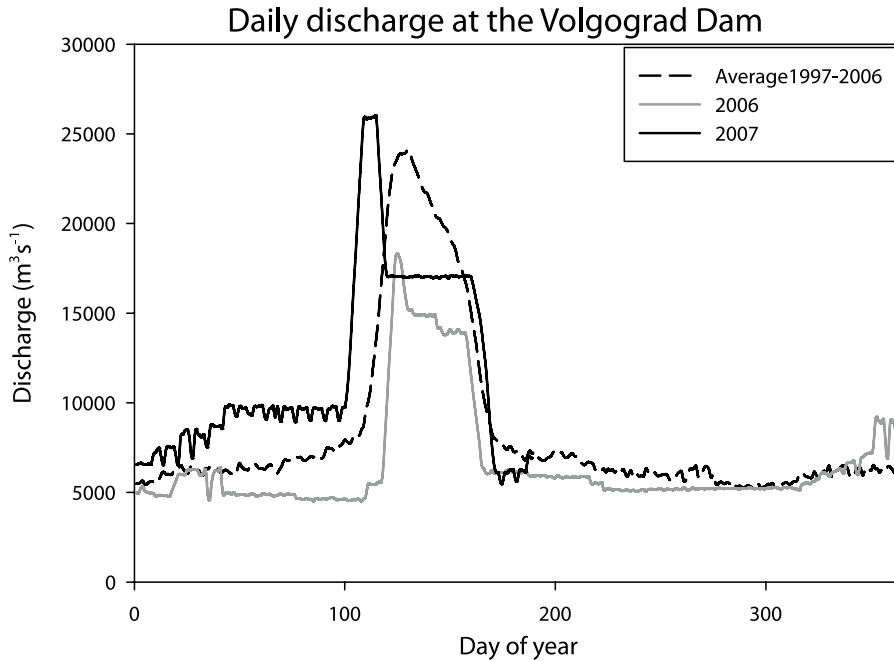


Figure 3.2 Daily discharge at the Volgograd Dam in 2006 and 2007 (the study years; data were available up to June 2007) and the mean for 1997-2006.

Table 3.1 Spawning temperatures and reproductive guilds for selected species from the Volga-Akhtuba floodplain; Reproductive guilds: I = indifferent, Li = lithophilic, Pe = pelagophilic, Ph = phytophilic (Bănărescu & Paepke, 2002; Kottelat & Freyhof, 2002; Reshetnikov, 2002).

| Species abbrev. | Scientific name | Common name | Minimum spawning temperature (°C) | Reproductive guild |
|-----------------|---|-----------------|-----------------------------------|--------------------|
| Abba | <i>Abramis ballerus</i> (Linnaeus, 1758) | Blue bream | 8 | Ph |
| Abbr | <i>Abramis brama</i> (Linnaeus, 1758) | Common bream | 12 | Ph |
| Absa | <i>Abramis sapa</i> (Pallas, 1814) | White-eye bream | 8 | Ph |
| Asas | <i>Aspius aspius</i> (Linnaeus, 1758) | Asp | 4 | Li |
| Blbj | <i>Blicca bjoerkna</i> (Linnaeus, 1758) | White bream | 15 | Ph |
| Caca | <i>Carassius carassius</i> (Linnaeus, 1758) | Crucian carp | 17 | Ph |
| Cagi | <i>Carassius gibelio</i> (Bloch, 1783) | Gibel carp | 18 | Ph |
| Chva | <i>Chondrostoma variable</i> (Yakovlev, 1870) | Volga nase | 15 | Li |

Table 3.1 (continued)

| Species abbrev. | Scientific name | Common name | Minimum spawning temperature (°C) | Reproductive guild |
|-----------------|--|-------------|-----------------------------------|--------------------|
| Cyca | <i>Cyprinus carpio carpio</i> (Linnaeus, 1758) | Carp | 16 | Ph |
| Eslu | <i>Esox lucius</i> (Linnaeus, 1758) | Pike | 3 | Ph |
| Gyce | <i>Gymnocephalus cernuus</i> (Linnaeus, 1758) | Ruffe | 4 | I |
| Leid | <i>Leuciscus idus</i> (Linnaeus, 1758) | Ide | 5 | Li |
| Pecu | <i>Pelecus cultratus</i> (Linnaeus, 1758) | Sabrefish | 12 | Pe |
| Pefl | <i>Perca fluviatilis</i> (Linnaeus, 1758) | Perch | 7 | I |
| Ruru | <i>Rutilus rutilus</i> (Linnaeus, 1758) | Roach | 8 | Ph |
| Salu | <i>Sander lucioperca</i> (Linnaeus, 1758) | Pikeperch | 15 | I |
| Scer | <i>Scardinius erythrophthalmus</i> (Linnaeus, 1758) | Rudd | 18 | Ph |
| Titi | <i>Tinca tinca</i> (Linnaeus, 1758) | Tench | 19 | Ph |
| Vivi | <i>Vimba vimba</i> (Linnaeus, 1758) | Vimba | 18 | Li |

3.4.5 Statistical analyses

Differences in fish abundance between sites were tested using the non-parametric Kruskal-Wallis test given the non-normal distribution of the abundance data. This non-parametric test was suitable because of data heteroscedasticity and numerous zero catches for some species.

Logistic regression models (Jongman, ter Braak & van Tongeren, 1995) were used to derive the spawning dynamics of different species in time. Individuals recorded in maturity stages V and VI (running and spent) were categorized as '1', stages II, III and IV as '0'. Maturity stage I was classified as juveniles and excluded from the analysis. The response variable (p_{ij}) was defined as:

$$p_{ij} = \frac{n_{ij}(\text{stages V and VI})}{n_{ij}(\text{stages V and VI}) + n_{ij}(\text{stages II, III and IV})}$$

where: p = response variable (fraction of running and spent); n = number of individuals caught; i = sex, j = the day of a calendar year ('yearday')

The analysis was performed for species, sites and years separately. A logit function $g(M)$ was used to link the expected value of the response variable (p) to the linear predictor:

$$g(M) = \ln \frac{p}{(1-p)}$$

where: $g(M)$ = expected value of fraction of running and spent; M = overall mean.

The linear predictor for the expected fraction of running and spent was defined using the following model:

$$g(M) = M + \text{sex}_i + \text{yearday}_j + \varepsilon_{ij}$$

where: sex_i = effect of i th sex; yearday_j = effect of j th yearday; ε_{ij} = error.

In the process of analysis the differences between sexes were compared and if they were not significantly different ($P < 0.05$) so the sexes were pooled.

3.5 Results

3.5.1 Flooding dynamics

Compared to the average flood pulse during 1997-2006, the peak flow in 2006 was smaller and shorter, whereas in 2007 it was earlier and longer (Fig. 3.2), and a larger fraction of the floodplain was inundated.

During the flooding period, water temperature in the Akhtuba River gradually increased, with very small daily fluctuations (Fig. 3.3), whereas water temperature in the Central floodplain was about 6°C higher with marked daily fluctuations. Water temperature in the floodplain dropped rapidly when the area was first flooded, but within 10 days temperature was 6-9°C higher than in the Akhtuba River once again. Differences of 6-15°C between the Akhtuba and the Central floodplain were observed through the entire flood event.

Initial water level prior to flooding was about 3 m lower in 2006 than in 2007 and, even during peak flow, water level was about 2 m lower in 2006 than in 2007 (Figs 3.4 & 3.5). Flooding started at around 5th of May (125th day of the year) in 2006 and 26th of April (116th day of the year) in 2007.

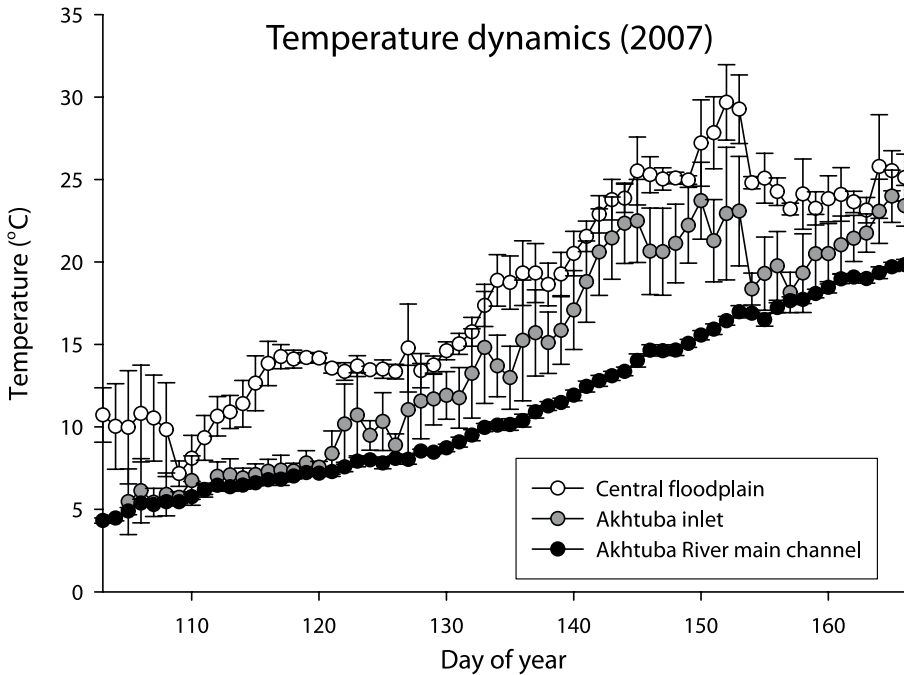


Figure 3.3 Daily water temperature (mean \pm range) in selected sampling sites and in the River Akhtuba.

3.5.2 Timing of spawning

Spawning fish were observed in both years at all three sites (Fig. 3.4). In 2006, seven species began to spawn in the Central floodplain before flooding. In 2007, for most species spawning started earlier in the Central floodplain than in either inlet. Moreover (unlike 2006), in 2007 the sequence in which spawning of the different species occurred was as expected based on minimal spawning temperature. Spawning rheophilic species were found only (*i.e.* white-eye bream and Volga nase) or mainly (*i.e.* ide, asp and sabrefish) in both inlets. Moreover, the timing of spawning of rheophilic species appeared to be related to the peak of the flood in both years. Spawning limnophilic species (*i.e.* crucian carp, tench, rudd) were found only in the Central floodplain and late in the season, as would be expected from their high minimal spawning temperatures.

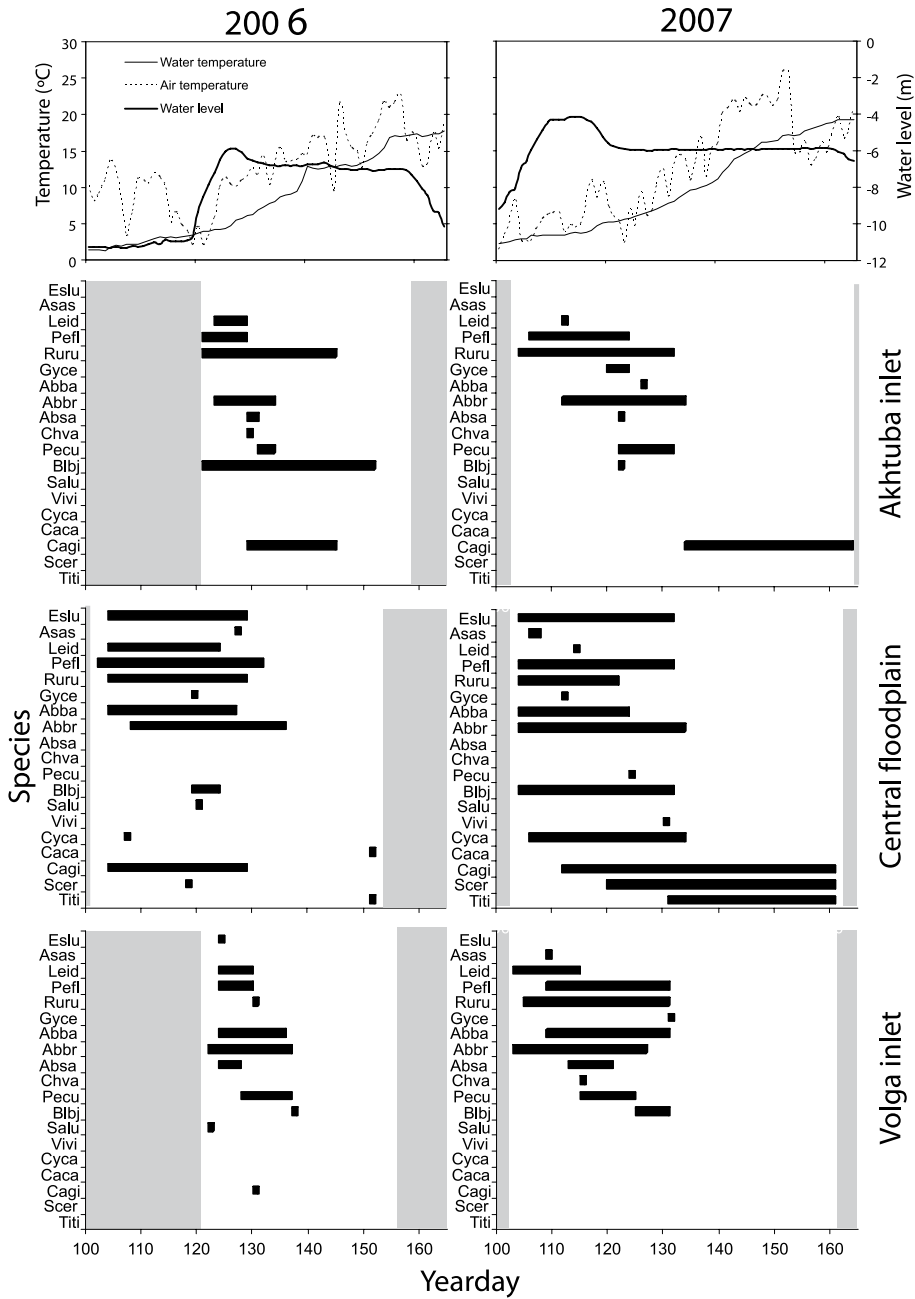


Figure 3.4 Water level and temperature of the Volga channel and air temperature in Volgograd in 2006 and 2007 (top panels). Duration of running individuals occurrence in sampled sites of the floodplain. Full species name for species abbreviations given in Table 3.1.

3.5.3 Abundance and maturity

The largest number of fish in both years were caught in the Central floodplain (1913 adult fish in total), followed by the Volga inlet (948) and the Ahktuba inlet (531). For the five most abundant species, comparisons of relative abundance (CPUE) and maturity over time between the Volga inlet and the Central floodplain were made (Fig. 3.5, Table 3.2). Similar depth, transparency and sampling strategy allowed direct abundance comparisons between these sites. In 2006, blue bream, common bream and sabrefish were more abundant at the Volga inlet than in the Central floodplain, whereas perch and roach were more numerous in the Central floodplain (Table 3.2). In 2007, blue bream, perch and roach were more numerous in the Central floodplain. Sabrefish was slightly more numerous at the Volga inlet and common bream in the Central floodplain, but the differences for these two species were not statistically significant (Table 3.2).

Abundance of blue bream appeared to increase with water level at the Volga inlet in 2006, with the highest abundance occurring well after the peak of the flood (Fig. 3.5). In 2007, however, the abundance peak was less clear, and occurred simultaneously with the highest water levels. Spawning periods of blue bream appeared to be of extended duration (shallow slopes of the logistic regression curves) in both 2006 and 2007 (Fig. 3.5). Common bream showed no peak of abundance at the Volga inlet or the Central floodplain in either 2006 or 2007 (Fig. 3.5). In 2006 it did show a short spawning period (steep regression slopes), while it had an extended spawning period in 2007 (shallow slope). Sabrefish catches reached a maximum a few days after the peak of the flood at the Volga inlet in both years. In 2006, only one spent female sabrefish was recorded in the Central floodplain, whereas in 2007, sabrefish were also abundant in the Central floodplain, though most were spent females, 43 of the 59 individuals examined having full stomachs. Steep logistic regression curves for sabrefish in both years (Fig. 3.5) indicate a short spawning period, timed directly after the peak of flooding. Perch and roach were the most abundant species in the Central floodplain and were present in low numbers at the Volga inlet in both years. No clear abundance peaks were found for either of these species with the possible exception of roach in the Central floodplain in 2006, where the highest catches were made when also the water level peaked. The inflection points of the logistic curves for perch were placed before sampling started or just at the beginning, suggesting an early onset of spawning in this species. The

inflection points of the logistic curves for roach usually followed the flood peak (Fig. 3.5), suggesting later spawning than in perch.

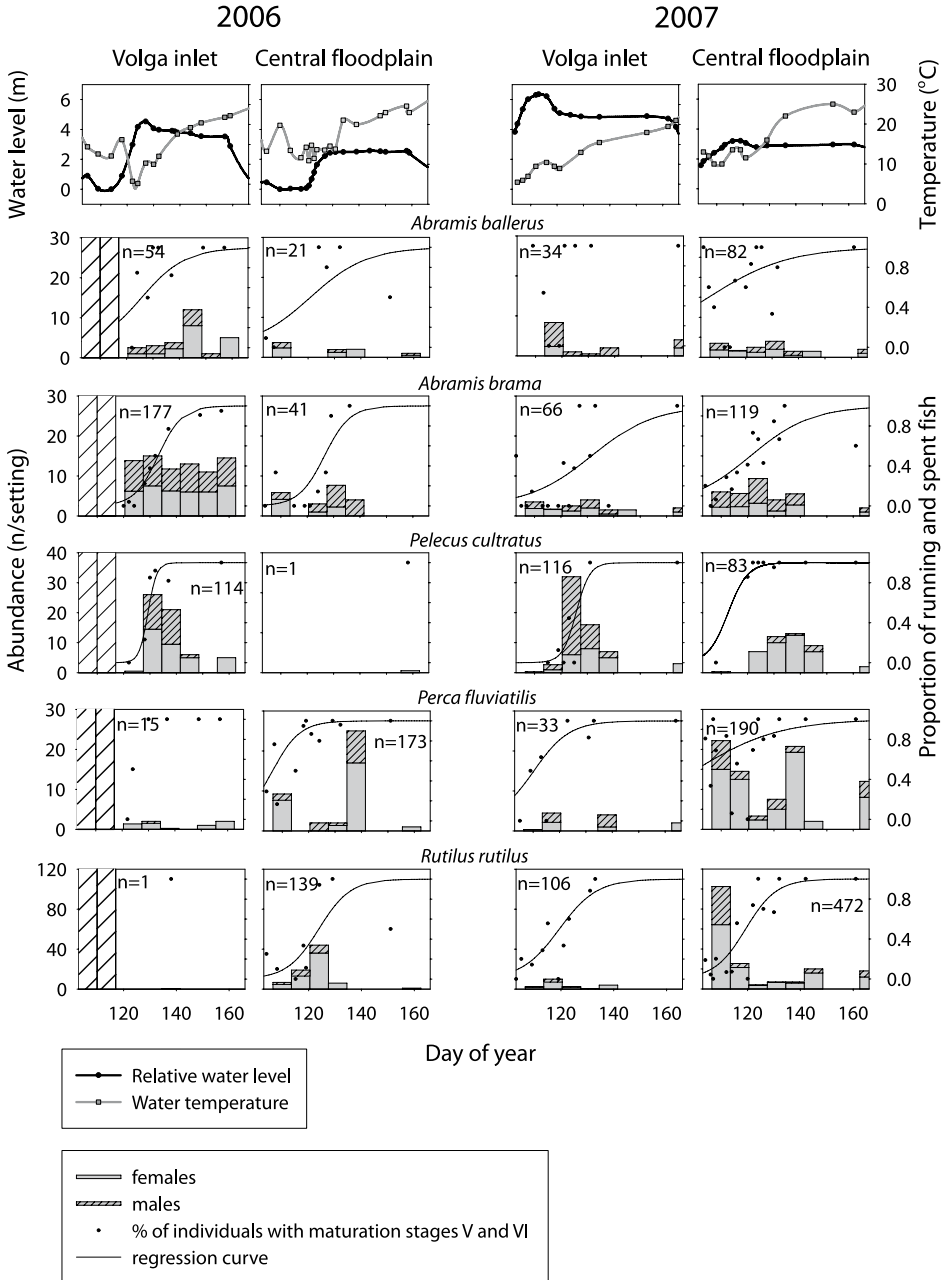


Figure 3.5 Water levels and temperatures as well as abundance and spawning dynamics (proportion of spawners, logistic regression curves shown where significant) of fish at the River Volga inlet and in the Central floodplain in 2006 and 2007.

Table 3.2 Differences in mean CPUE (N/setting) of the five most abundant fish species between the Volga inlet and the Central floodplain sites (Fig. 1). Significance of differences is indicated by *P* (based on Kruskal-Wallis test), *H*: test statistic; *n.s.*: non-significant.

| Year | Species | Volga Inlet | | | Central Floodplain | | | H | P |
|------|-----------------------|-----------------------|--------------------|----|-----------------------|--------------------|----|------|-------------|
| | | Mean CPUE (N/setting) | Standard deviation | n | Mean CPUE (N/setting) | Standard deviation | n | | |
| 2006 | <i>A. ballerus</i> | 6 | 8.8 | 9 | 2 | 3.3 | 15 | 4.7 | <.05 |
| | <i>A. brama</i> | 20 | 11.4 | | 3 | 4.1 | | 10.8 | <.01 |
| | <i>P. cultratus</i> | 13 | 17.4 | | 0 | 0.3 | | 8.3 | <.01 |
| | <i>P. fluviatilis</i> | 2 | 1.6 | | 14 | 18.1 | | 4.9 | <.05 |
| | <i>R. rutilus</i> | 0 | 0.3 | | 12 | 15.2 | | 6.9 | <.01 |
| 2007 | <i>A. ballerus</i> | 2 | 4.5 | 12 | 5 | 3.8 | 16 | 5.7 | <.05 |
| | <i>A. brama</i> | 4 | 2.7 | | 7 | 7.3 | | 0.6 | <i>n.s.</i> |
| | <i>P. cultratus</i> | 8 | 11.4 | | 5 | 6.8 | | 0.08 | <i>n.s.</i> |
| | <i>P. fluviatilis</i> | 2 | 3.5 | | 12 | 9 | | 12.8 | <.01 |
| | <i>R. rutilus</i> | 7 | 11.8 | | 30 | 40.6 | | 6.9 | <.01 |

3.6 Discussion

3.6.1 Is spawning triggered by flooding?

As expected, our results show that only the rheophilic species that spawn in the floodplain are timing their spawning activity in relation to the flood pulse, whereas the timing of spawning of eurytopic and limnophilic species seems to be more or less indifferent to the flood pulse. Spawning of the eurytopic common bream showed a stronger link with timing and duration of the flood in 2006, which was a year with a small flood pulse (Fig. 3.5), probably due to spawning habitat limitation. Therefore, it seems that for some eurytopic species flooding could enhance spawning, but it is not strictly required, whereas for rheophilic species (*i.e.* sabrefish) spawning seems to depend more strongly on the flood pulse. Directly linking the timing of spawning to water temperature is made difficult by the large temporal and spatial variance in water temperatures (Fig. 3.3) in the complex and dynamic Volga floodplain (Fig. 3.1). Aquatic habitats within the floodplain have a broader temperature range than the river itself (Tockner, Malard & Ward, 2000). Fish, however, are very well capable of finding patches with suitable spawning temperature, as was shown for pike in the floodplain of the St. Lawrence River (Mingelbier, Brodeur & Morin, 2008). This might also explain why species with different minimum spawning temperatures (Table 3.1) showed simultaneous spawning periods (Fig. 3.4).

3.6.2 Is there mass spawning migration from the river into the floodplain?

High spring discharge increases connectivity between temporary and permanent waters and, therefore, it is important for fish movements and exploration of temporarily flooded habitats (Baber *et al.*, 2002). However, in this study we did not observe mass migrations into seasonally flooded areas for most species. This is in contrast to observations of mass migrations by tropical floodplain fish, although these migrations seem to be related primarily to feeding (Wantzen *et al.*, 2002; Welcomme, 1985). Backwaters and oxbow lakes might be important spawning habitat for riverine-originating species (Hohausova, Copp & Jankovsky, 2003), but our results suggest that, in the vast floodplain system of the lower Volga the spawning stocks mainly originate from the permanent water bodies within the floodplain rather than riverine habitats. Therefore, the Volga-Akhtuba floodplain appears to be dominated by external hydrological factors, but its fish populations appear to stem largely from water bodies within the floodplain, with only a relatively marginal input of adult river fish. From the perspective of river fish the floodplain is probably important as a spawning habitat, but the fringing floodplain may be enough to fulfill these requirements (Grift *et al.*, 2001; Molls 1999).

Sabrefish seemed to be the only species with a spawning stock that mainly originated from the main channel, where spawning took place mostly at the entrance. After spawning, some females probably migrated deep into the central floodplain to feed. The degree of floodplain penetration for this species was determined by hydrological conditions and probably related to water level (Cucherousset, Carpentier & Paillisson, 2007). Full stomachs for the majority of sabrefish caught in the Central floodplain suggest they used the floodplain to feed and to replenish energy reserves after spawning, which has also been observed in tropical floodplain systems (Fernandes, 1997). The fact that, after the construction of a series of reservoirs on the upper Volga River, the abundance of sabrefish decreased around 10 fold in the newly formed reservoirs (Minin, 2005) confirms the importance of seasonal flooding for this species.

Given the limited number of inlets sampled we cannot exclude the possibility of mass migration through other inlets. Nevertheless, based on the similar character of the inlets this seems unlikely. Another alternative to ex-

plain the low number of fish migrating from the river into the floodplain during flooding would be that this migration had already taken place prior to inundation, as shown in the Upper Mississippi (Knights, Johnson & Sandheinrich, 1995), resulting in spawning stocks already being present in the floodplain when the flooding and our sampling started. This seems unlikely, because of the small extent, or absence of inlets during low flow conditions. Therefore, our conclusion that the majority of the adult fish that use the Volga floodplain for spawning originate from floodplain water bodies rather than the main channel seems justified.

Next to spawning in the floodplain, some species may spawn in main channel habitats close to inlets prior to flooding events to enable their larvae to drift into the floodplain with the incoming flood (King, Humphries & Lake, 2003). Even though we did not address lateral movements of larvae and juveniles, in the Lower Volga such a strategy could only successfully be performed by species that can spawn and hatch in the very low water temperatures of the main channel prior to flooding. This holds only for a few species present in the Volga.

We postulate that in large-scale floodplain systems, the floodplain can be important for river fish populations that spawn along the flooded fringes, but deeper within the floodplain itself, river spawners are probably outnumbered by the population of resident fish. The main river channel primarily acts as a source of water and nutrients, and also as a source of recolonists of fish after the local extinction of fish caused by extreme environmental conditions such as prolonged freezing or desiccation. However, more studies in large temperate floodplains are needed to determine whether this is a general principle.

3.7 Acknowledgments

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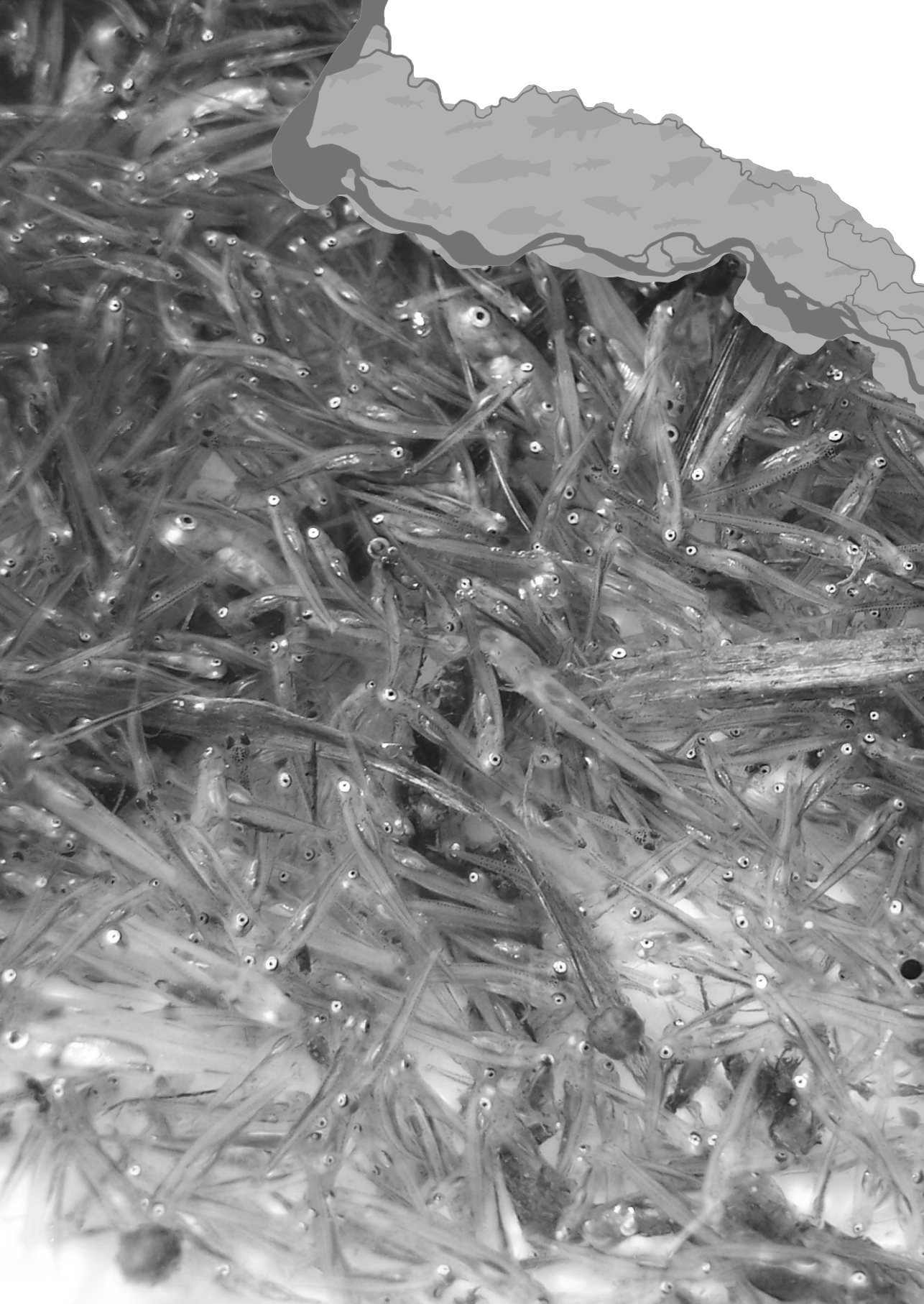
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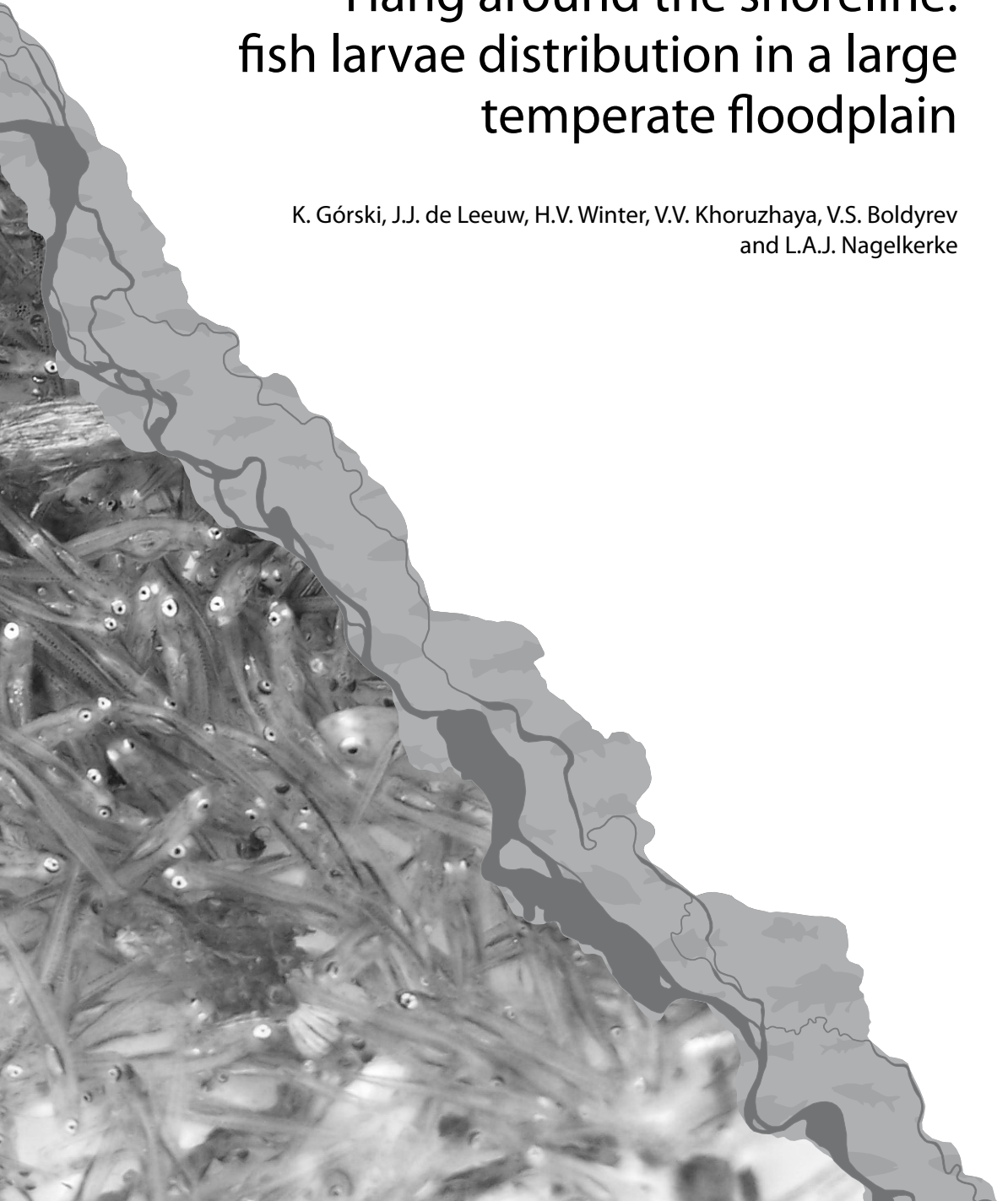
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Chapter 4

Hang around the shoreline: fish larvae distribution in a large temperate floodplain

K. Górski, J.J. de Leeuw, H.V. Winter, V.V. Khoruzhaya, V.S. Boldyrev
and L.A.J. Nagelkerke



Hang around the shoreline: fish larvae distribution in a large temperate floodplain

4.1 Abstract

We examined the use of flooded terrestrial habitats by fish larvae in a semi-natural large floodplain (Volga, Russian Federation) by comparing densities at the shoreline of permanent water bodies with flooded terrestrial habitats. Fish larvae were collected using hoop-nets in four permanent floodplain water bodies and adjacent flooded terrestrial habitats during the flooding seasons of 2007 and 2008. We found that overall larval densities at the shoreline of permanent water bodies were 6- to 10-fold higher compared to flooded terrestrial habitats. Shorelines appear to offer significantly better habitat for newly-hatched larvae, most likely because here there is an influx of food and warmer water from flooded terrestrial habitats, combined with refuge from cold, open water of permanent water bodies. At the same time the risk of hypoxia of shallow flooded terrestrial habitats, and the risk of predation by fish from the permanent water bodies is reduced. Therefore, the main importance of terrestrial flooded areas for the floodplain fish community appears to be the production of food organisms that comes available for larvae and juveniles with retreating water after flooding. However, given the large extent of flooded terrestrial areas, even at low densities they may accommodate large numbers of fish larvae.

Вдоль береговой линии: распределение местообитаний личинок рыб в пойме большой реки умеренного климата

4.2 Резюме

Мы исследовали использование наземных затопляемых мест обитания личинками рыб в антропогенно измененной пойме крупной реки (Волга, Российская Федерация) путем сравнения плотности личинок у береговой линии постоянных водных объектов с плотностью во временно затопляемых понижениях рельефа. Личинки рыб вылавливались с помощью вентерей в четырех постоянных водоемах поймы и прилегающих к ним затопляемых участках поймы во время половодий 2007 и 2008 годов. Нами определено, что общая плотность личинок у береговой линии постоянных водоемов от 6 до 10 раз выше по сравнению с временно затопляемыми участками. Прибрежья являются значительно более подходящими местами обитания для только что появившихся личинок, что, наиболее вероятно, связано как с притоком корма и теплой воды с временно затопленных территорий, так и с тем, что прибрежные местообитания являются убежищем от холодной воды постоянных водоемов, которая недавно очистилась ото льда. В то же время, снижается риск гипоксии, существующий в мелких временно затопленных понижениях, и риск нападения хищников, присутствующий в водах постоянных водоемов. Следовательно, главная роль временно затопляемых территорий для пойменных рыб заключается в том, что они поставляют кормовые организмы, доступные для личинок и молоди, с уходящей после половодья водой. Однако, давая огромную протяженность временно затопляемых территорий, даже с низкой плотностью кормовых организмов, они могут обеспечивать большое количество личинок рыб.

4.3 Introduction

Natural river floodplains are among the biologically most productive and diverse ecosystems (Tockner & Stanford, 2002; Ward, Tockner & Schiemer, 1999). Biodiversity and production of plants and animals inhabiting floodplain, are primarily driven by the seasonal water level fluctuations as formulated in the Flood Pulse Concept (Junk, Bayley & Sparks, 1989; Lowe-McConnell, 1964; Tockner, Malard & Ward, 2000).

The wide array of temporal floodplain habitats is crucial for many species, especially in relation to spawning and nursery as well as to feeding and refuge (Baber *et al.*, 2002; Copp, 1989; Poizat & Crivelli, 1997; Starrett, 1951). Floodplain backwaters, oxbows and lakes are important for fish larvae recruitment (King, 2004; Sheaffer & Nickum, 1986; Turner *et al.*, 1994). Moreover temporarily flooded terrestrial habitats were shown to support faster larvae growth (Sommer *et al.*, 2001) by providing high production of autochthonous food (Herwig *et al.*, 2004).

However, in temperate floodplains when spring flooding reaches its maximum, water levels in the floodplain stabilize and temperatures increase. Because of the large concentrations of organic material in the habitat this results in increased bacterial metabolism, often resulting in reduced oxygen levels in the water (Fontenot, Rutherford & Kelso, 2001), which can be disadvantageous for fish larvae. This in turn may result in avoidance of inundated terrestrial flooded areas by fish larvae if water quality is unsuitable (Gehrke, 1991).

River habitat use by fish larvae has been studied, but not with an emphasis on the use of large, temperate, naturally functioning floodplains. Numerous studies elaborated on habitat preferences and use by fish larvae in the main river channels (Copp, 1992; Scheidegger & Bain, 1995) and on anthropogenically modified rivers (Brown & Coon, 1994; Garner, 1996; Jurajda, 1999; Sabo & Kelso, 1991). Some studies have focused on patterns of downstream larval drift (Martin & Paller, 2008; Pavlov *et al.*, 2008; Pavlov, 1994), or on lateral exchange of larvae between main river channels and backwaters (Csoboth & Garvey, 2008). However, the distribution of fish larvae in large river floodplains remains unclear.

The Volga River, a large lowland river, still accommodates semi-naturally functioning floodplains with relatively well-preserved geomorphology compared to other large rivers in Europe. Therefore it can serve as a model for studying the distribution and habitat use of larvae in large temperate floodplains. The present study aims at examining the use of flooded terrestrial habitats by fish larvae. Our main hypothesis is that the densities of fish larvae in flooded terrestrial habitats will be high compared to permanent water bodies, because of their higher temperatures, food availability and relatively low predation risk.

4.4 Methods

4.4.1 Study area

The Volga River (Russian Federation), with a length of 3,690 km and average annual discharge of $8,103 \text{ m}^3\text{s}^{-1}$ is the largest river in Europe (Litvinov *et al.*, 2009). It has a combined rainfall / snowmelt flow regime, with a discharge peak in May-June. A series of upstream dams, completed in the 1960s, moderately altered the flow regime of the Lower Volga downstream of Volgograd (Middelkoop *et al.*, 2005; Mordukhai-Boltovskoi, 1979). Directly downstream of the Volgograd dam, the Volga splits into the larger Lower Volga River, and the smaller Akhtuba River. The Volga-Akhtuba floodplain extends between these two rivers over a length of 300 km, and is 10-30 km wide. The floodplain is situated in the semi-arid continental climatic zone with very dry and hot summers and severe winters. The geomorphology of the floodplain has been preserved to a large extent (Averina *et al.*, 2000). The vegetation of the floodplain mainly consists of meadows (Averina *et al.*, 2000) used for extensive grazing of cattle and hay production (Losev *et al.*, 2008). With rapidly rising water levels in spring (Fig. 4.1) within approximately 2 weeks 50-85% of the floodplain is inundated through permanent and temporary side channels, resulting in expansion of the permanent water bodies (Fig. 4.2).

Four floodplain water bodies with different hydrological and morphological characteristics were chosen to analyse habitat use by fish larvae (Fig. 4.2). Two water bodies are in the southern part of the floodplain and experience relatively small size expansions during the flooding season. These are (1) Kalinov, a permanent channel connected to the Volga River, and (2) Zo-

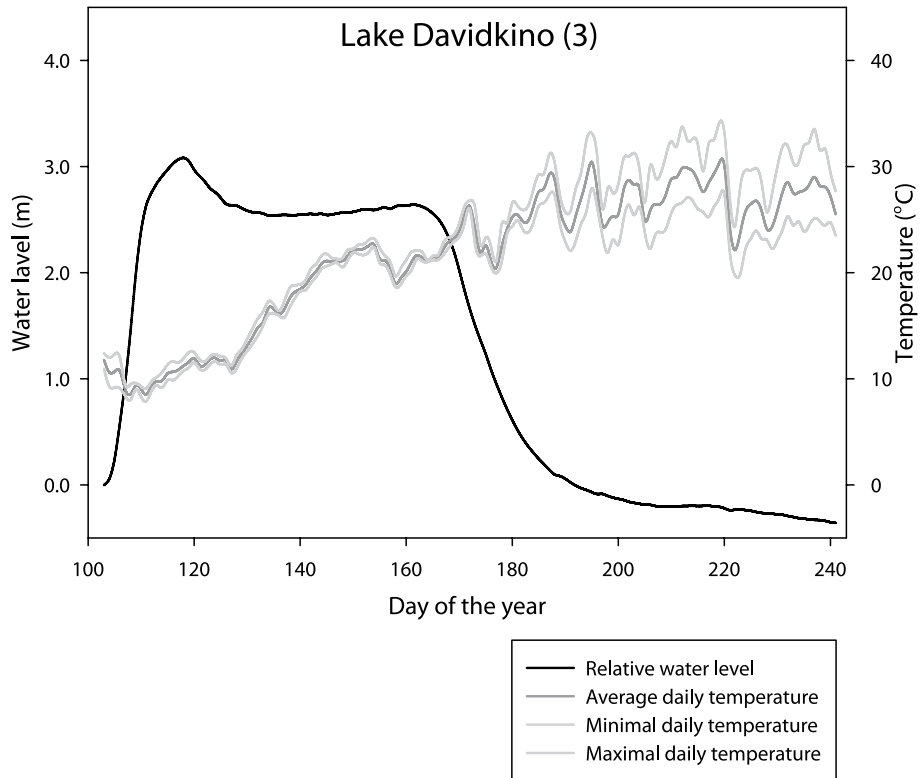


Figure 4.1 Relative water level and temperature dynamics in Lake Davidkino (3) during spring 2007.

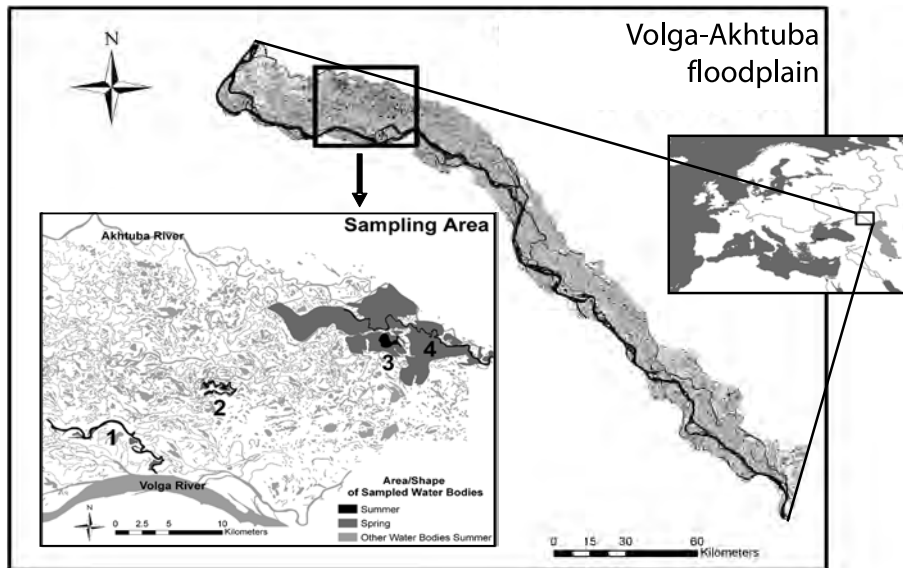


Figure 4.2 A map of Volga–Akhtuba floodplain and selected study sites.

lotoy, a permanent elongated lake in the central floodplain. Two other water bodies are in the northern part of the floodplain, which turns into one big flooded area with some dry patches during the flooding season. These are (3) Davidkino, a large (minimum of 240 ha at the end of summer) shallow floodplain lake connected to the Akhtuba River during flooding, and (4) Staraya Akhtuba, a permanent channel connected to the Akhtuba River.

4.4.2 Sampling and analysis

Fish larvae were sampled in four different water bodies in two habitats (shore of permanent water body and shallow flooded terrestrial habitats adjacent of the flooded shoreline) from 17 May – 23 June in 2007 and 18 – 30 May in 2008. Larvae were sampled in each water body in both habitats once every 2-3 days with hoop-nets (30 cm diameter opening, 1mm mesh size). The net was dragged along a transect of ca. 5 meters, moving at a constant speed of ca. 0.5 m/s. Samples for each water body and habitat type consisted of three transects. For each sample, larvae were counted and catch per unit of effort (CPUE, in number per meter) was calculated.

To verify the gradient in larvae densities from the shore to the open water, shown for shallow temperate lakes (Mooij, 1996), on 25 May 2008 four additional samples were collected at different distances from the shore of Lake Davidkino (water body 3), by dragging the hoop net from a boat for about 90 meters parallel to the shore at a speed of approximately 1 m/s. Collected larvae were preserved in 5% formaldehyde solution and analyzed to species level, based on morphological features and pigmentation (Koblitskaya, 1981). Water temperature was measured at each sampling location. In addition, in 2007 oxygen concentrations were measured using a standard temperature/oxygen probe (Marvet Junior 2000, Elke Sensor LLC). Water level and temperature were recorded at one hour intervals in Lake Davidkino (3) using automatic data loggers (Diver® Water Pressure Logger, Schlumberger Water Services, Sugar Land, TX, USA; UA-002-64 HOBO®, Onset Computer Corporation, Bourne, MA, USA).

The effect of habitat type on fish larvae densities was estimated by pairwise comparison of mean densities, with confidence intervals calculated using a bootstrapping method (Efron & Tibshirani, 1993; Zhou & Gao, 1997), given the low sample number and non-normal distribution of the data. To compare larvae densities between shoreline and terrestrial flooded habitat we

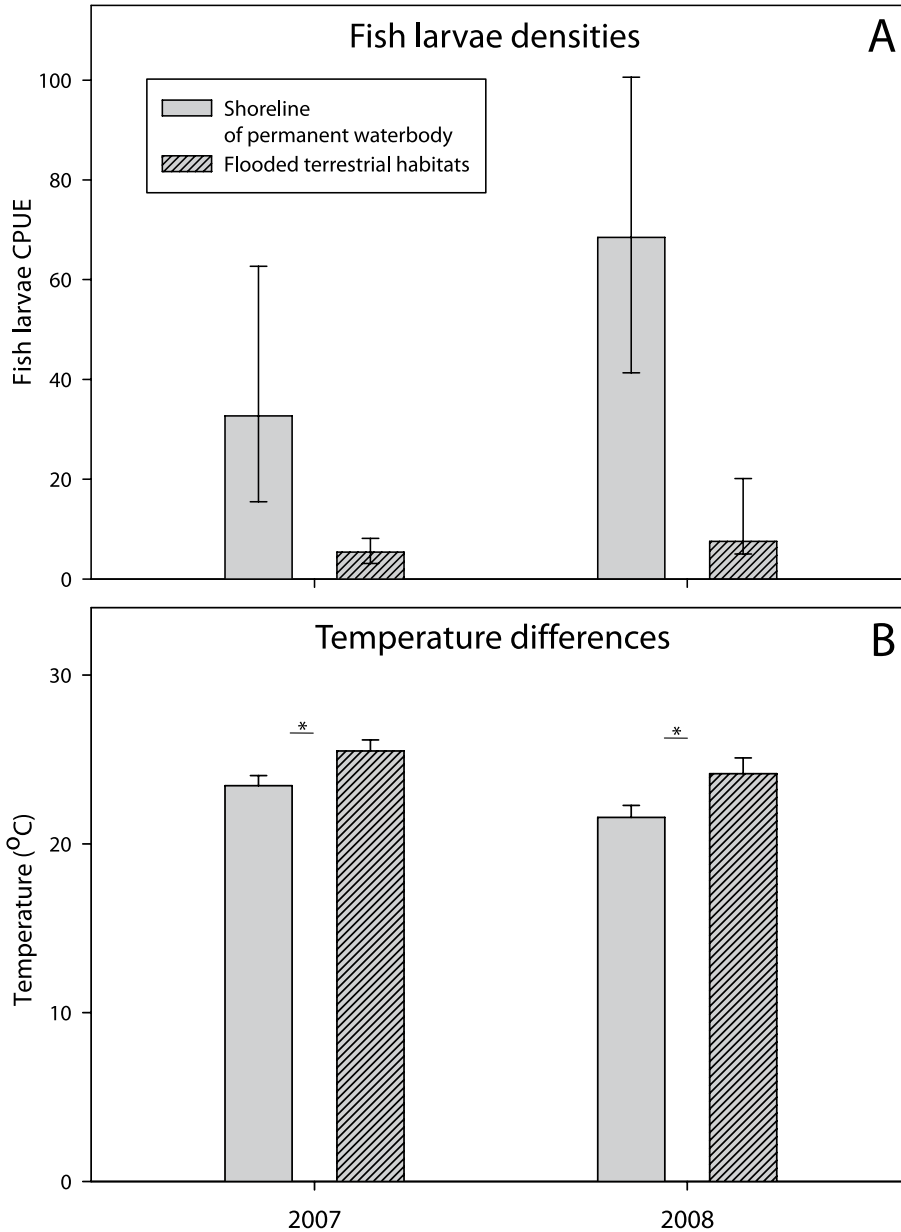


Figure 4.3 (A). Differences in fish larvae CPUE between the shoreline of permanent water bodies and flooded terrestrial habitats with confidence intervals estimated using bootstrapping method. (B). Average temperature and standard error in two sampled habitats. Consistent lower temperature at shoreline in both years ($p < 0.05$), based on ANOVA.

used 10,000 bootstrap replications of samples from each habitat and year separately. We then calculated the differences between means with bias-corrected and accelerated confidence intervals (Efron & Tibshirani, 1993). Only samples collected on the same date and similar time in two different habitats in each location were used as pairs for this analysis (A total of 26 samples in each year). The differences in water temperature and dissolved oxygen between habitats were tested using Analysis of Variance.

4.5 Results

Fish larvae densities were significantly higher at the shore of permanent water bodies compared to the adjacent flooded terrestrial habitats (Fig. 4.3A), with mean densities 6-fold (2007) to 10-fold (2008) higher at the shoreline. Water temperature was lower in shoreline habitats than in the flooded terrestrial areas in both years (Fig. 4.3B). No significant differences in oxygen concentration were found between the two habitats in 2007, when data were available.

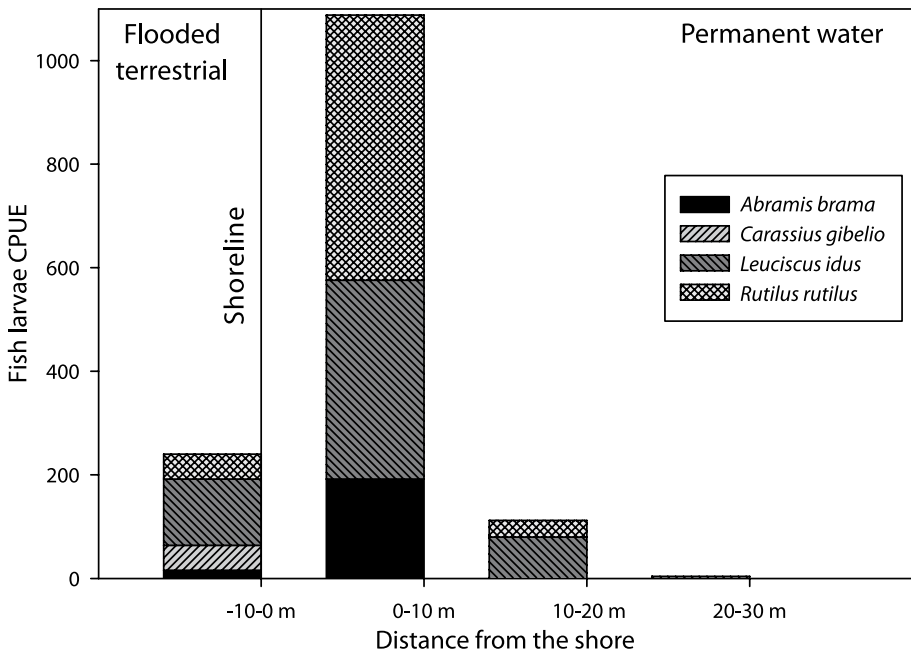


Figure 4.4 CPUE and species composition of fish larvae in relation to distance from the shore in Lake Davidkino (3) in 2008.

In Lake Davidkino (water body 3), roach *Rutilus rutilus*, ide *Leuciscus idus* and common bream *Abramis brama* were the most abundant species (>90%), with consistently higher densities for all species at the shore compared to both flooded terrestrial habitats and into the open water zone of the lake (Fig. 4.4). Gibel carp *Carassius gibelio* was present only in the flooded terrestrial habitats.

Temporal patterns in larvae densities were consistent in different water bodies and years and were characterized by a clear peak at the shoreline during 10-15 days and low densities in the flooded terrestrial habitats (Fig. 4.5).

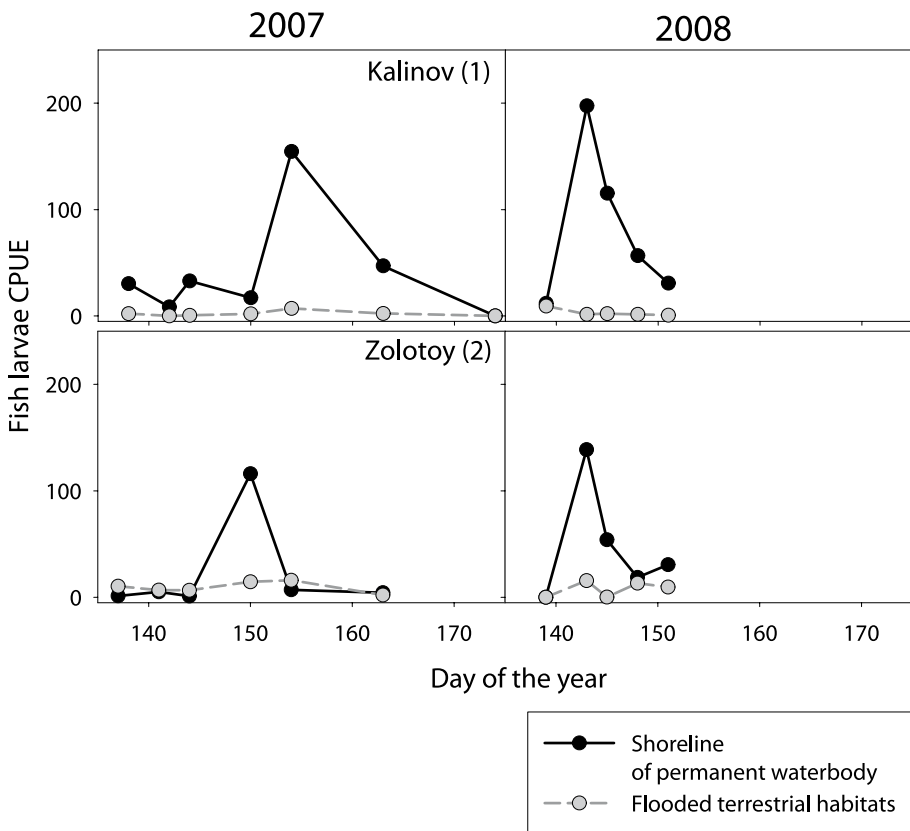


Figure 4.5 Temporal patterns of fish larvae CPUE in two frequently sampled locations.

4.6 Discussion

Habitat choice is a result of trade-offs between relative costs and benefits, in terms of food availability, metabolic cost, predation and other mortality risks. The importance of floodplain habitats as fish larvae nursery had been previously recognized (Copp, 1989; Grift, 2001; Sheaffer & Nickum, 1986). Therefore we did not expect that the observed densities in the flooded terrestrial habitats would be six to ten times lower than at the shoreline of the permanent water bodies.

The spatial distribution of fish larvae could be an effect of: 1) Selection of the spawning site by adults (Bialetzki *et al.*, 2005); 2) Active selection by larvae themselves, as shown for coral reef fish (Doherty *et al.*, 1996; Leis & Carson-Ewart, 1998); 3) Passive transport by water currents or wind (Carassou *et al.*, 2008; Fowler, Leis & Suthers, 2008). The last mechanism seems unlikely in the Volga-Akhtuba floodplain since the current in sampled habitats was low/absent and the floodplain is exposed to little wind in spring (sampling days with high wind speed (> 3 Beaufort) accounted for less than 5%). Our data suggest that hatching predominantly takes place in the shorelines (Fig. 4.5) (spawning sites selection by adults) and is followed by limited subsequent dispersal (with the exception of gibel carp).

So why do fish larvae in the Volga floodplain prefer these shorelines and do not massively penetrate into temporally flooded areas, which provide the favoured structurally complex habitats (Garner, 1996)? We propose that a trade-off between increased food availability and increased risk of mortality due to high temperatures, hypoxia or desiccation is the key to this distribution pattern. For the recruitment success of many fish species maximizing growth is crucial in the first few weeks after hatching (Kirjasniemi & Valtonen, 1997). Staying in the shoreline can maximize growth of fish larvae, because they can take advantage of food produced in the flooded areas which flows back into permanent water bodies with retreating water (Wilzbach *et al.*, 2002). In addition, epiphyton production, providing a source of food, is expected to be highest at the shoreline (Azim, 2005; Welcomme, 1979; Welcomme, 1985), especially compared to the poor feeding conditions of the open water (Garner, 1996). Moreover, the structural complexity of the shorelines of permanent water bodies in the Volga floodplain is similar to that found in flooded terrestrial habitats (Fig. 4.6) and provides similar refuge from predators.



Figure 4.6 Vast naturally functioning Volga floodplains. Flooded surroundings of Lake Davidkino (3).

At the same time, by residing close to the open water fish larvae avoid being stranded when the water levels drop (Brown & Colgan, 1982; Paller, 1987) and the risk of hypoxia, which is higher in flooded terrestrial habitats than in the littoral zones of permanent waterbodies (Gehrke, 1991). All in all the shoreline seems to provide superior conditions for newly hatched larvae of most fish species.

The only notable exception appears to be Gibel carp larvae, which showed higher densities in shallow waters compared to the shoreline. This species is known for its tolerance to high water temperatures and hypoxia (Lushchak *et al.*, 2001; Roesner *et al.*, 2008), possibly allowing it to take more risk.

In conclusion, the importance of flooded terrestrial habitats for fish larvae recruitment appears crucial in the Volga floodplain, but possibly through a slightly other mechanism than through providing direct nursery habitat. Rather, flooded terrestrial habitats produce food organisms that can flow back towards the main water bodies when water levels retreat after the flood pulse. These food organisms can be used by fish larvae that dwell in

the shoreline regions thereby reducing their risk of desiccation, high water temperatures, hypoxia, or predation. However, even though the densities of fish larvae may be low in flooded terrestrial habitats compared to permanent water body shorelines, given their extended surface area, they still accommodate substantial numbers of fish larvae.

4.7 Acknowledgements

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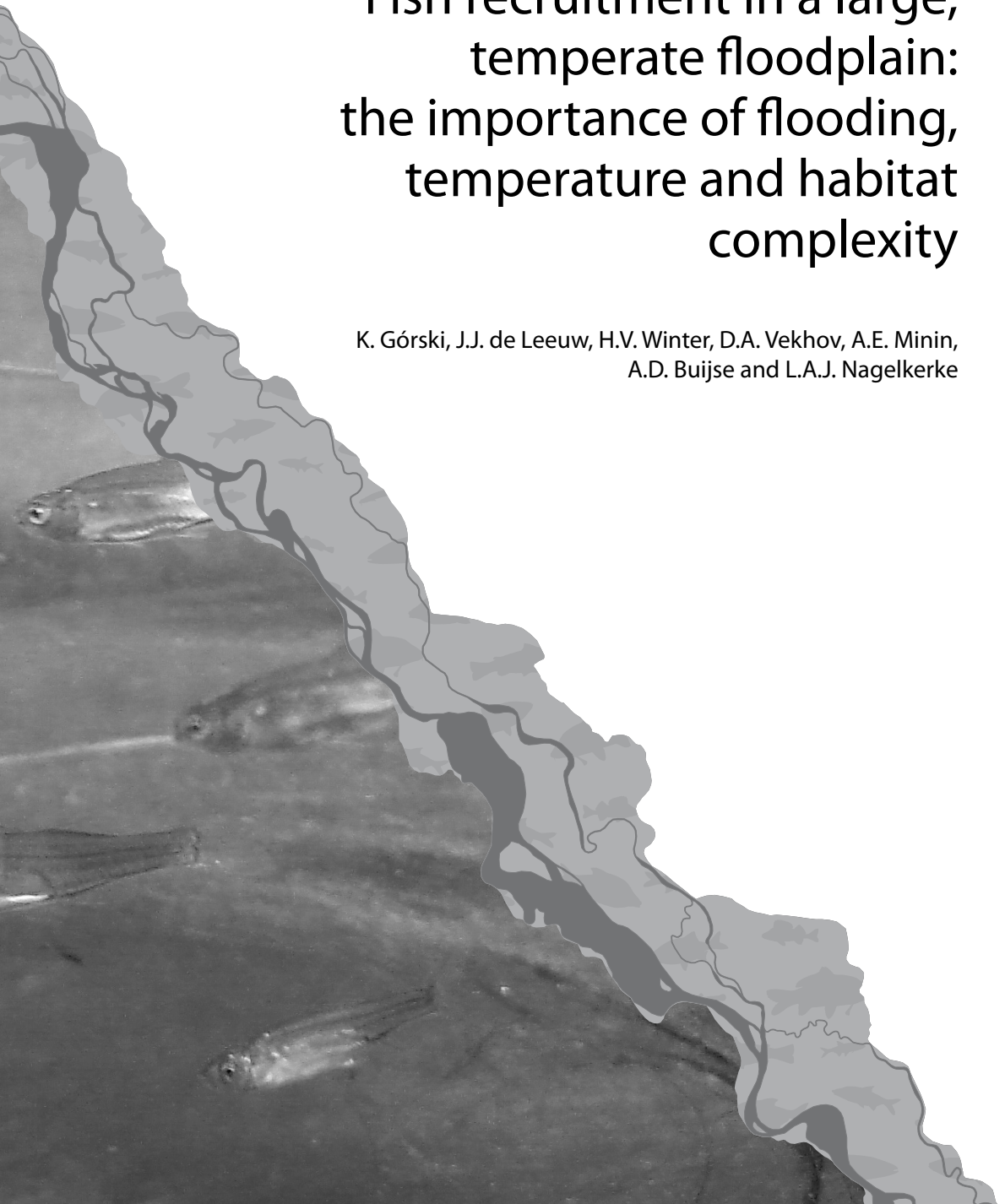
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Chapter 5

Fish recruitment in a large, temperate floodplain: the importance of flooding, temperature and habitat complexity

K. Górski, J.J. de Leeuw, H.V. Winter, D.A. Vekhov, A.E. Minin,
A.D. Buijse and L.A.J. Nagelkerke



Fish recruitment in a large, temperate floodplain: the importance of flooding, temperature and habitat complexity

5.1 Abstract

Large river floodplains are considered key habitats for nurseries of many riverine fish species. The lower Volga River floodplains (Russian Federation) are still relatively undisturbed serving as a suitable model for studying the influence of flooding and temperature on fish recruitment in floodplains. We examined the effect of flooding and its co-occurrence with spring water temperature development on the recruitment success of young of the year (YOY) fish after the first growing season in the lower Volga floodplain by sampling in four areas with different flooding regimes, in three consecutive years (2006-2008). Our results support the governing role of temperature, coupled with flooding for fish recruitment in temperate floodplains. In areas with large flood extents in the warm years 2006 and 2007 the biomass of YOY of most fish species was about three times higher compared to the cold year 2008. Floodplain areas with a large extent and longer duration of flooding accommodated significantly higher densities of young fish, especially species characterized by periodic life history traits (large-body size, delayed maturation, high fecundity and low parental investment) such as pike, roach and ide. This confirmed that extended inundation improves recruitment success of river fish. Gibel carp, a species tolerant to high temperatures and hypoxia, did especially well in small water bodies in the driest parts of the floodplain. Spring temperature and its coupling with flooding appear to be one of the most important factors in YOY fish recruitment in the lower Volga floodplain. Flood timing synchronized with temperature enhances recruitment success of all species. Regulation of the Volga River for hydropower production resulted in shorter floods with an earlier onset, increasing the probability of a flood-temperature mismatch, which will reduce fish recruitment success.

Пополнение рыб в пойме большой реки умеренного климата: значение половодья, температурного режима и многообразия условий обитания

5.2 Резюме

Поймы крупных рек считаются ключевым местообитанием для нагула молоди многих речных видов рыб. Пойма Нижней Волги (Российская Федерация) до сих пор относительно незначительно изменена человеком являясь подходящим модельным участком для изучения влияния половодья и температурного режима на воспроизводство популяций рыб в поймах. Мы исследовали влияние половодья и его взаимного влияния с динамикой температурного режима воды во время весеннего паводка на успешность пополнения рыб (сеголетки) после первого вегетационного сезона в пойме Нижней Волги путем облова четырех пойменных участков с разным режимом затопления в течение трех последовательных лет (2006-2008). Наши результаты подтверждают руководящую роль температурного режима совместно с затоплением в воспроизводстве рыб в поймах умеренного климата. На участках с большой площадью залития в теплые годы 2006 и 2007 биомасса сеголеток большинства видов рыб была почти в три раза выше по сравнению с холодным 2008 годом. Участки поймы с большими площадями затопления и продолжительным половодьем обеспечивали существенно большее количество молоди, особенно видов рыб с характерными чертами жизненного цикла (большой размер тела, позднее созревание, высокая плодовитость и незначительное участие родителей): щука, плотва и язь. Это подтверждает, что большее затопление улучшает успех воспроизводства речных видов рыб. Серебряный карась, вид, толерантный к высоким температурам и гипоксии, чувствовал себя особенно хорошо в мелких водоемах в самых засушливых участках поймы. Динамика температуры воды весной и ее связь с половодьем являются одними из важнейших факторов в пополнении рыбных запасов в пойме Нижней Волги (за счет сеголеток). График подачи воды на пойму, синхронизированный с ходом температуры воды, повышает успех воспроизводства популяций всех видов рыб. Зарегулирование Волги для производства электричества привело к тому, что половодья стали короче по продолжительности по сравнению с предыдущим периодом, повышая вероятность несовпадения хода температур и уровней воды в пойме, что снижает успешность пополнения запасов рыб.

5.3 Introduction

Natural river floodplains are among the most productive and diverse freshwater ecosystems (Ward, Tockner & Schiemer, 1999; Tockner & Stanford, 2002). Seasonal flooding increases habitat extent and complexity by temporary inundation of terrestrial habitats. This inundation leads to mobilization of organic matter (Robertson *et al.*, 1999), and facilitates exchange of nutrients between aquatic and terrestrial compartments of the riverine ecosystem. Increased nutrient availability and frequent disturbance in turn results in high biodiversity and production of plants and animals inhabiting the floodplains, as envisaged in the Flood Pulse Concept (FPC) (Junk, Bayley & Sparks, 1989; Junk & Wantzen, 2004; Lowe-McConnell, 1964; Tockner, Malard & Ward, 2000). For many species of river fish, floodplains provide a wide range of temporarily available habitats that are important as feeding, spawning and nursery areas, as well as providing refuge against predation (Baber *et al.*, 2002; Holland & Huston, 1985; Poizat & Crivelli, 1997). The timing, duration and extent of inundation have been proposed to be the main factors determining the importance of floodplains for successful fish recruitment (Welcomme, 1979; Welcomme, 1985; Bayley, 1991; Bailly, Agostinho & Suzuki, 2008).

Fish recruitment at the end of the growing season in inundated floodplains is likely to be influenced by a number of interrelated factors: 1) predictability of flooding; 2) rate of rise and fall of the water table; 3) extent of inundated area; 4) duration of inundation and 5) degree of coupling of flooding and changes in temperature (King, Humphries & Lake, 2003; Trifonova, 1982). After the water retreats, the carrying capacity of permanent water bodies and resulting food competition, as well as predation and hypoxia risks, appear to play a decisive role in the survival of young of the year (YOY) fish and therefore in recruitment success (Grenouillet, Pont & Olivier, 2001; Nunn, Harvey & Cowx, 2007).

The notion of the flood pulse alone controlling fish recruitment is too simple, because not all species will be equally affected by habitat complexity and temperature in the floodplain (King *et al.*, 2003; Zeug & Winemiller, 2008). Survival chances of YOY, and therefore their recruitment success, will be different for species with different life history strategies. Such life history strategies can be defined as 'periodic', 'opportunistic' and 'equilibrium' (Winemiller, 1989; Winemiller & Rose, 1992). Species with periodic

life history traits (large-bodied, with delayed maturation, high fecundity and low parental investment) such as common bream *Abramis brama* (Linnaeus, 1758), ide or pike are adapted to seasonal variation and large-scale spatial variation in environmental conditions. These species would possibly depend on, but also benefit most from, predictable seasonal dynamics. Opportunistic strategists, such as sunbleak *Leucaspis delineatus* (Heckel, 1843) and gibel carp are more flexible and characterized by early maturation, continuous spawning and a particular ability to frequently colonize new habitats. These would also be expected to recruit successfully in the floodplains. Finally, equilibrium strategists with delayed maturity, low fecundity and well-developed parental care, for which the survival of eggs and larvae depends on the condition of adults and the integrity of the adult habitat, are expected to be more indifferent to seasonal flood dynamics.

Despite the importance of floodplains for river fishes and the fact that the role of the floodplains may, differ according to the life history strategies of these fishes, little attention has been paid to the role of floodplain complexity in influencing fish recruitment (Turner *et al.*, 1994). Few studies have examined fish recruitment in naturally functioning, large-scale river floodplains. Some recent studies are available for the tropics (Agostinho *et al.*, 2004; Bailly *et al.*, 2008; Suzuki *et al.*, 2009). In the temperate zone, available studies of fish recruitment are limited to relatively small rivers, the middle and upper reaches of larger rivers (Copp, 1989; Halyk & Balon, 1983; Holland & Huston, 1985), or to severely modified floodplains in the lower reaches of large rivers (Grift *et al.*, 2003).

The Lower Volga and its adjoining floodplain in the Russian Federation is one of the few remaining naturally functioning temperate floodplains (Górski *et al.*, 2010) and it therefore provides an opportunity to study recruitment of young fish in such systems that were formerly widespread.

Our main objectives were:

- 1) To examine the effects of the extent, timing and duration of flooding on the recruitment success of fish in floodplain systems. We hypothesized that a higher magnitude and duration of flooding would enhance the production of young fish, as predicted by the FPC.
- 2) To examine the effect of temperature and its relationship to flooding on recruitment success. Since temperature is the main driver of many biological processes we expected the coupling of high temperatures with flooding to increase fish recruitment.

- 3) To assess the selective impact of flooding and temperature on different fish species with various life history strategies. We expect species adapted to seasonality or large scale spatial variation (periodic strategists) and flexible, fast colonizers (opportunistic strategists) to be most successful in the floodplain environment.

5.4 Methods

5.4.1 Study Area

The Volga River (Russian Federation), (length 3,690 km, mean annual discharge $8,103 \text{ m}^3\text{s}^{-1}$), is the largest river in Europe (Litvinov *et al.*, 2009). It has a combined rainfall / snowmelt flow regime, with peak discharge in May-June. A series of upstream dams, completed in the 1960s, moderately altered the flow regime of the Lower Volga downstream of Volgograd (Middelkoop *et al.*, 2005; Mordukhai-Boltovskoi, 1979). Directly downstream of the Volgograd dam, the Volga splits into the larger Lower Volga River, and the smaller Akhtuba River. The Volga-Akhtuba floodplain extends between these two rivers over a length of 300 km, and is 10-30 km wide. The floodplain is situated in the semi-arid continental climatic zone with very dry

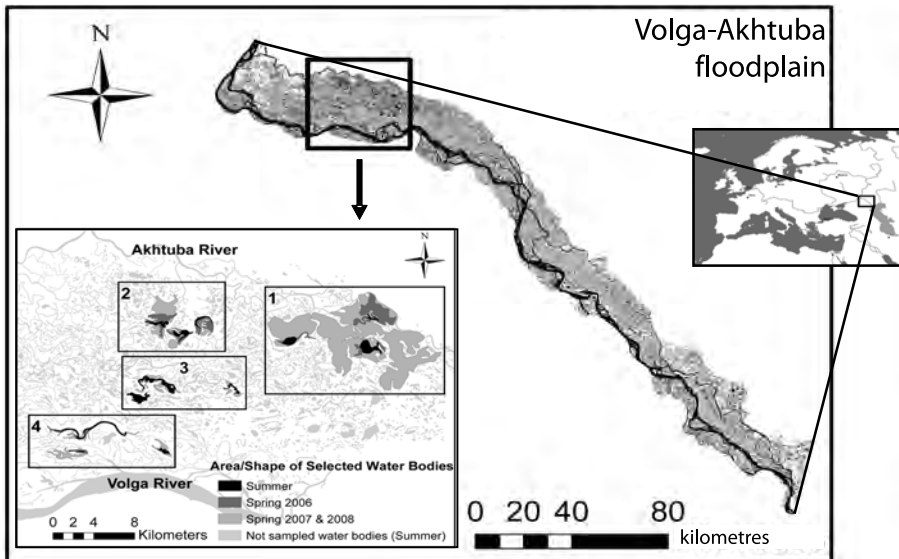


Figure 5.1 A map of Volga–Akhtuba floodplain and selected study area, indicating sampled water bodies in four areas with different hydrological regimes.

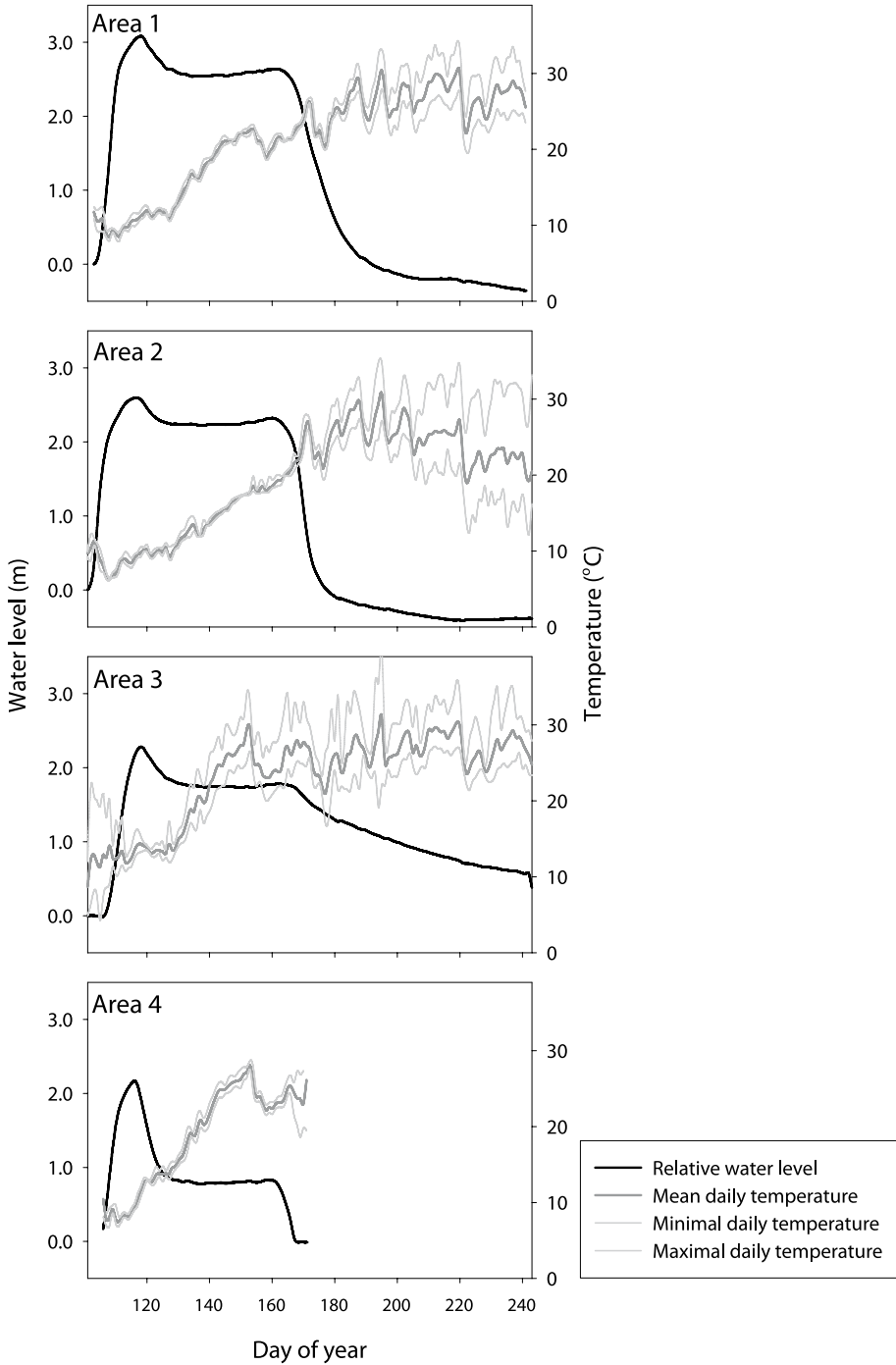


Figure 5.2 Water levels and temperature dynamics in different sampling areas in 2007.

and hot summers and severe winters. Its geomorphology is largely intact (Averina *et al.*, 2000). The vegetation of the floodplain mainly consists of meadows (Averina *et al.*, 2000) used for extensive grazing of cattle and hay production (Losev *et al.*, 2008). With rapidly rising water levels in spring, 50-85% of the floodplain is inundated through permanent and temporary side channels within approximately two weeks.

To analyse fish recruitment patterns, 12 floodplain water bodies in four areas (three in each area) with different hydrological characteristics were chosen (Fig. 5.1). Water level and temperature were recorded at one hour intervals in one water body of each Area using automatic data loggers (Diver® Water Pressure Logger, Schlumberger Water Services, Sugar Land, TX, USA; UA-002-64 HOBO®, Onset Computer Corporation, Bourne, MA, USA) in 2007. Areas 1 and 2 were characterized by a similar rapid rise (ca. 2 weeks from onset of the flood until maximum water level) and large magnitude (approximately 3 m) of the flood, followed by stable inundation of about 7 weeks and then a fall for about two weeks (Fig. 5.2). The total area inundated around water bodies sampled was significantly greater in Area 1 than in Area 2 (Fig. 5.1). In Area 3 the rise of the flood was also rapid (ca. 2 weeks as in Areas 1 and 2, and the magnitude was about 2 m) but the decline was slow and prolonged (ca. 12 weeks) (Fig. 5.2). In Area 4 a rapid rise (ca. 2 weeks) to a maximum water level of about 2 m was followed by two stages of rapid decline, the first (of about 1.5 m) just after two weeks from the initial rise and the second at the same time as in other areas (Fig. 5.2).

5.4.2 Data collection

Daily Volga discharge and air temperature at Volgograd were available for 1997-2008 and obtained from the Volgograd Centre of Hydrometeorology and Environmental Monitoring.

For all floodplain water bodies, surface area, perimeter and distance between the water body and the nearest channel connection to the main river channel (Volga or Akhtuba) were estimated from available maps and Landsat images. Interpretations from maps and images were verified by field observations during fish sampling. The proportion of each vegetation type in the flooding area of each lake was calculated from the Volga Floodplain Ecological Map (Losev *et al.*, 2004). Average depth of water bodies was estimated from measurements in many locations (on average 20) using

standard measuring tape. The relative surface area covered by submerged vegetation was determined by combining visual estimates with the collection of plants with a rake while wading through the water in each sampling year.

In each year (2006, 2007, 2008) fish were sampled in the same twelve water bodies from the end of August to the end of September. On average three (two-five) samples were collected in each water body using a beach seine (30 m long, 1.5m deep, 10 mm stretched mesh size). For each sample, fish were identified to species based on morphological features and pigmentation (Koblitskaya, 1981), fish were counted and length-frequencies of (sub) samples were determined based on standard length to the nearest mm. In each water body, a subsample of fish was weighed and length-mass relationships were calculated. Fishing effort was calculated as total area covered per seine haul.

A literature search was conducted for life history parameters of fish inhabiting the Volga-Akhtuba floodplain. Most fish species exhibit considerable variation in life history traits over their geographical ranges. Therefore, only data indicating the origin of the fish sampled as the South of Russia were used. Data compiled by Krizhanovski (1953) and Reshetnikov (2002) covered most of the parameters needed for analysis. Data were obtained for the following life history traits: (1) maximum length, (2) age at maturation, (3) egg size, (4) length of breeding season (in months), (5) spawning mode categorized as: 1 – single spawning per year, 2 – from two to four spawning events per year, 3 – more than four spawning events per year, (6) fecundity as the average number of oocytes of mature females in a single spawning season, and (7) parental care as classified following Winemiller (1989) which for our species resulted in just two categories: nesting species (with a score of 3), and non-nesting species with spawning habitat selection (scoring 1).

5.4.3 Data analysis

YOY fish were distinguished from older fish by evaluating length-frequency distributions, which showed clear cut-off lengths for all abundant species. We collected YOY of 23 species (Table 5.1). Data for the 11 most abundant fish species (> 99% in numbers) were used for further analysis. The mean catch per unit effort (CPUE) values in numbers and biomass were calculated for each species for each water body in each year. To assess the effect of

flood and temperature on the production of young fish, overall CPUE (gm-2) of YOY including all species was compared between different years and areas with Analysis of Variance (ANOVA). The data used in the analysis were log10-transformed to achieve an approximately normal distribution.

Table 5.1 Abbreviations, English and scientific names, numbers of caught fish species as well as some of the life history characteristics derived from literature Krizhanovski (1953); Reshetnikov (2002). Abbreviations of 11 most abundant species shown in bold.

| Abbrev | Scientific name | Common name | Total n of YOY caught | % of total YOY caught | n of water bodies where present | Maximum length (cm) | Maturation age (years) | Average Fecundity (n of eggs *1000) | Parental care | Spawning mode |
|-------------|--|---------------|-----------------------|-----------------------|---------------------------------|---------------------|------------------------|-------------------------------------|---------------|---------------|
| Abba | <i>Abramis ballerus</i> (Linnaeus, 1758) | Blue bream | 210 | 0.141 | 7 | 45 | 3 | 28 | 1 | 1 |
| Abbr | <i>Abramis brama</i> (Linnaeus, 1758) | Common bream | 15971 | 10.705 | 12 | 80 | 3 | 215 | 1 | 1 |
| Alal | <i>Alburnus alburnus</i> (Linnaeus, 1758) | Bleak | 7104 | 4.762 | 12 | 20 | 3 | 6.5 | 1 | 2 |
| Asas | <i>Aspius aspius</i> (Linnaeus, 1758) | Asp | 3 | 0.002 | 2 | 80 | 3 | 281 | 1 | 1 |
| Blbj | <i>Blicca bjoerkna</i> (Linnaeus, 1758) | White bream | 19040 | 12.762 | 12 | 35 | 3 | 60 | 1 | 2 |
| Caca | <i>Carassius carassius</i> (Linnaeus, 1758) | Crusian carp | 24 | 0.016 | 2 | 50 | 4 | 218 | 1 | 2 |
| Cagi | <i>Carassius gibelio</i> (Bloch, 1783) | Gibel carp | 1513 | 1.014 | 11 | 45 | 2 | 215 | 1 | 2 |
| Cota | <i>Cobitis taeni</i> (Linnaeus, 1758) | Spined loach | 425 | 0.285 | 10 | 20 | 4 | 0.3 | 1 | 1 |
| Cyca | <i>Cyprinus carpio carpio</i> (Linnaeus, 1758) | Carp | 12 | 0.008 | 3 | 100 | 3 | 948 | 1 | 1 |
| Eslu | <i>Esox lucius</i> (Linnaeus, 1758) | Pike | 662 | 0.444 | 12 | 150 | 2 | 118 | 1 | 1 |
| Gyce | <i>Gymnocephalus cernuus</i> (Linnaeus, 1758) | Ruffe | 1693 | 1.135 | 8 | 18.5 | 2 | 53 | 1 | 2 |
| Lede | <i>Leucaspis delineatus</i> (Heckel, 1843) | Sunbleak | 4978 | 3.337 | 5 | 9 | 2 | 1.4 | 3 | 2 |
| Leid | <i>Leuciscus idus</i> (Linnaeus, 1758) | Ide | 1022 | 0.685 | 10 | 100 | 4 | 76 | 1 | 1 |
| Mifo | <i>Misgurnus fossilis</i> (Linnaeus, 1758) | Weather-fish | 1 | 0.001 | 1 | 30 | 2 | 125 | 1 | 1 |
| Nefl | <i>Neogobius fluviatilis</i> (Pallas, 1814) | Monkey goby | 172 | 0.115 | 1 | 20 | 2 | 1.5 | 3 | 2 |
| Pefl | <i>Perca fluviatilis</i> (Linnaeus, 1758) | Perch | 8747 | 5.863 | 12 | 51 | 2 | 156 | 1 | 1 |
| Prma | <i>Proterorhinus marmoratus</i> (Pallas, 1814) | Tubenose goby | 313 | 0.210 | 7 | 15 | 1 | 0.6 | 3 | 2 |

Table 5.1 (continued)

| Abbrev | Scientific name | Common name | Total n of YOY caught | % of total YOY caught | n of water bodies where present | Maximum length (cm) | Maturation age (years) | Average Fecundity (n of eggs * 1000) | Parental care | Spawning mode |
|--------|---|------------------------|-----------------------|-----------------------|---------------------------------|---------------------|------------------------|--------------------------------------|---------------|---------------|
| Ruru | <i>Rutilus rutilus</i> (Linnaeus, 1758) | Roach | 82306 | 55.167 | 12 | 50 | 3 | 51 | 1 | 1 |
| Salu | <i>Sander lucioperca</i> (Linnaeus, 1758) | Pikeperch | 5 | 0.003 | 2 | 130 | 3 | 625 | 3 | 1 |
| Scer | <i>Scardinius erythrophthalmus</i> (Linnaeus, 1758) | Rudd | 4776 | 3.201 | 12 | 36 | 3 | 118 | 1 | 2 |
| Sigl | <i>Silurus glanis</i> (Linnaeus, 1758) | Wels catfish | 3 | 0.002 | 3 | 250 | 3 | 455 | 3 | 1 |
| Syab | <i>Syngnathus abaster</i> (Risso, 1827) | Black-striped pipefish | 131 | 0.088 | 6 | 23 | 1 | 0.1 | 3 | 2 |
| Titi | <i>Tinca tinca</i> (Linnaeus, 1758) | Tench | 82 | 0.055 | 8 | 63 | 3 | 565 | 1 | 2 |

To analyse the effects of year and area on the densities of YOY fish of each of the 11 most abundant species we used a two-way ANOVA, after ranking the data and applying Blom's transformation, which adjusts rank scores to achieve an approximately normal distribution (Blom, 1958). After ANOVA we performed pair-wise comparisons between different years and areas, using 10,000 bootstrap replications of samples from each group and year separately. Subsequently, means with bias-corrected and accelerated confidence intervals were compared (Efron & Tibshirani, 1993) using a Bonferroni-correction of the α -level for multiple comparisons (Sokal & Rohlf, 1995) (α -levels for comparison between years and areas were set to 0.0167 and 0.0125, respectively).

To analyse the effects of year and area on the length data for each species we also used two-way ANOVA. Length data were first log-transformed producing an approximately normal distribution. Differences between years and areas were analysed using multiple pairwise comparisons with Tukey's method (Sokal & Rohlf, 1995).

Different species will have different proportions of various life history traits. To assess which life history traits recruit successfully in the floodplain, we compared the relative abundance of fish in in each category of life history

strategy (periodic, opportunistic or equilibrium; Winemiller & Rose, 1992) weighted by YOY abundance in each area and year. The relative proportion of each life history category was calculated as follows. The main life history traits for each species were weighted based on the relationships of these traits with each life history strategy (Winemiller & Rose, 1992; Table 5.2). Next, for each species a total score per life history strategy was calculated, by summing the scores for each trait. These total scores were expressed as percentage values of each strategy for each species. Finally, the proportion of each strategy was weighted by the abundance of each species in each area and year.

Redundancy Analyses (RDAs) (based on correlation matrices) (Jongman, ter Braak & van Tongeren, 1995; ter Braak & Šmilauer, 2002) were performed to examine the relationship between YOY fish abundance of different species and water body characteristics (Table 5.3). Global Monte Carlo permutation tests (1000 permutations) were performed to determine the significance of the ordination at $\alpha = 0.05$. Species data were square-root transformed prior to analysis to diminish the effect of outliers (Jongman *et al.*, 1995).

Table 5.2 Relationships between life history traits and how they affect different life history strategies (-1, negative; 0, neutral; 1, positive relationship between size of the life history trait and the life history strategy).

| | MaturityAge | Fecundity | Survivorship (egg size*parental care) |
|----------------------|--------------------|------------------|--|
| Opportunistic | -1 | 0 | -1 |
| Equilibrium | 1 | -1 | 1 |
| Periodic | 1 | 1 | -1 |

Table 5.3 Environmental variables of sampled water bodies, related to geomorphology, connectivity, and vegetation.

| Variable | Description |
|-----------------|---|
| SpArea | Surface area in spring (m ²) |
| SuArea | Surface area in summer (m ²) |
| SLI | Shore Length Index (the ratio of shore length to water body area) |
| SLD | Shore Line Development (the ratio of the length of the shore line to the length of the circumference of a circle of area equal to that of the water body) |
| Depth | Average depth |
| Forest | Percentage of forests in the flooded area around water body (arcsine transformed) |
| Grasslands | Percentage of grasslands in the flooded area around water body (arcsine transformed) |
| Helophytes | Percentage of helophytes in the flooded area around water body (arcsine transformed) |
| Submerged | Percentage of submerged macrophytes in the water body (arcsine transformed) |
| MCD | Distance to the main channel (km) |

5.5 Results

5.5.1 Flooding and temperature

Compared to the average flood pulse during 1997-2006, the peak flow in 2006 was smaller and shorter (maximum discharge: $17.5 \times 10^3 \text{ m}^3 \text{ s}^{-1}$), whereas peak flows in 2007 and 2008 were both earlier and reached a higher maximum ($26\text{-}27 \times 10^3 \text{ m}^3 \text{ s}^{-1}$) (Fig. 5.3, Table 5.4). A conspicuously larger fraction of the floodplain was inundated in 2007 and 2008 than in 2006 (Fig. 5.1). Peak flow duration in 2007 was about three weeks longer than in 2008. The growing season was the warmest in 2007 (1560 cumulative degree-days (dd) above 12°C air temperature), followed by 2006 (1387 dd) and 2008 (1236 dd) (Fig. 5.4).

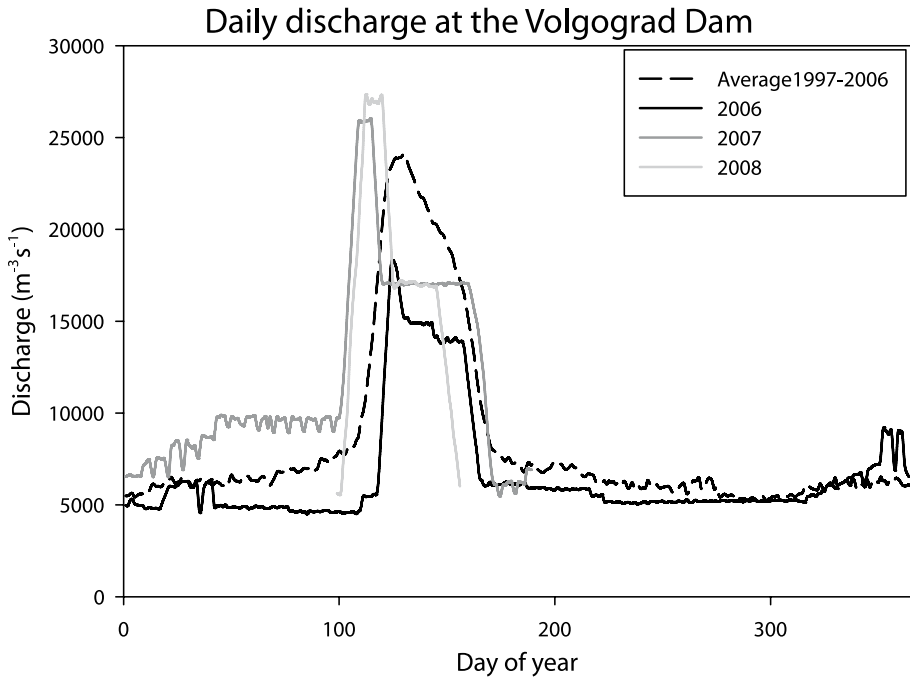


Figure 5.3 Daily discharge of Volga River during sampling years.

Table 5.4 Summary of flood/temperature conditions in years covered by the study.

| Year | flood | | | temperature |
|------|--------|-----------|--------------|--------------|
| | timing | magnitude | duration | |
| 2006 | late | low | short | intermediate |
| 2007 | early | high | long | high |
| 2008 | early | high | intermediate | low |

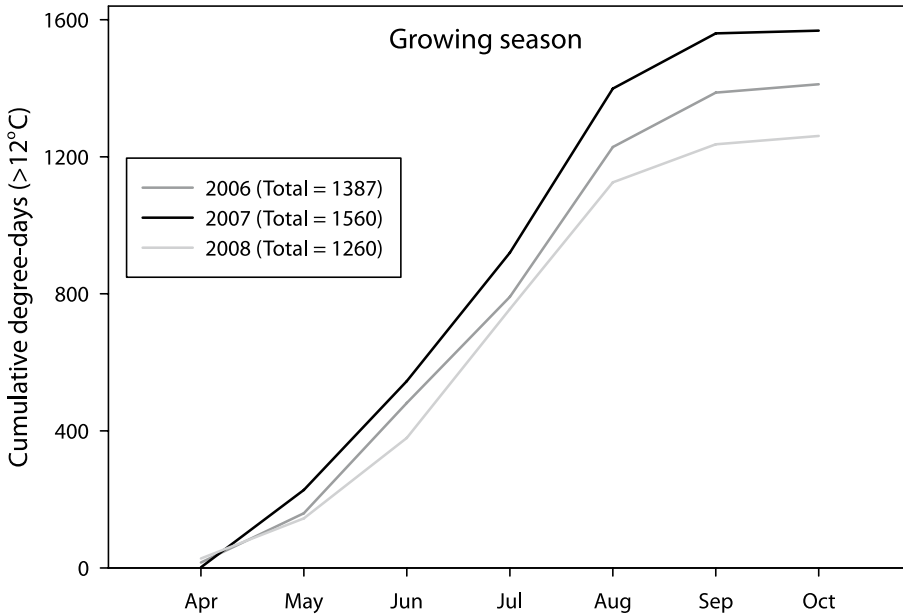


Figure 5.4 Air temperature - Summary of degree-days in sampling years.

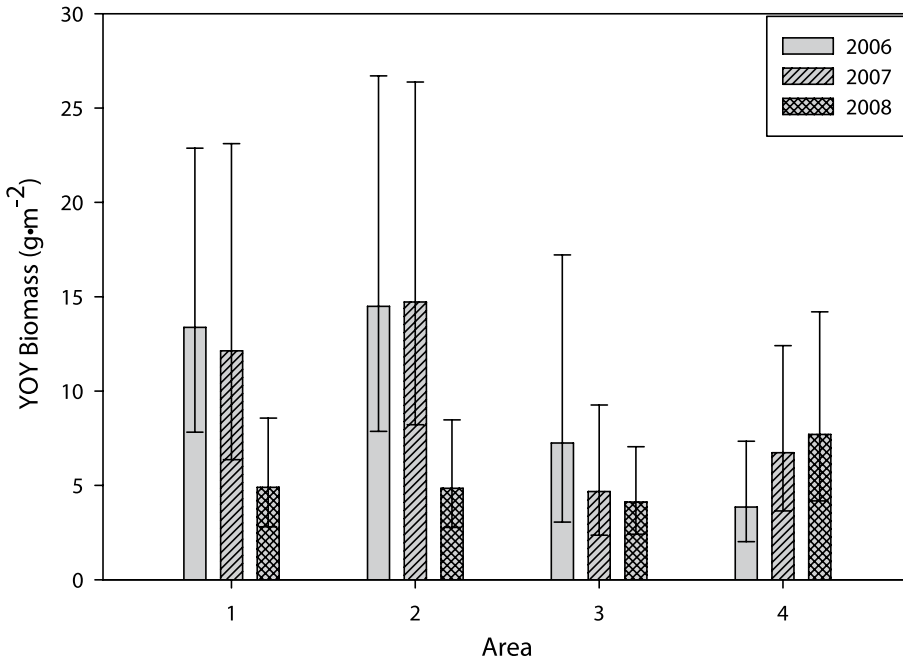


Figure 5.5 Comparison of the biomass of YOY (mean and 95% confidence limits as estimated by the statistical model) in different years and areas.

5.5.2 Overall production of recruits

We recorded the highest overall CPUE biomass of YOY in Areas 1 and 2 in 2006 and 2007 (12-14 gm⁻², Fig. 5.5, Table 5.5). The CPUEs in Areas 3 and 4 were lower in all three years (4-7 gm⁻²). In 2008, CPUE in Areas 1 and 2 was much lower (4-5 gm⁻²) than in previous years. CPUE of YOY was highest in Area 4 (approximately 7 gm⁻²) in 2008, while in Area 3 it ranged between approximately 4 (2007, 2008) and 7 gm⁻² (2006).

Table 5.5 ANOVA table of overall CPUE biomass (g-m⁻²) of YOY fish. DF, degrees of freedom; SS, sums of squares; F, F-statistic; P, probability. 10log-transformed data were used in the analysis.

| | SS | DF | F | P |
|-----------|------|-----|------|------|
| Year | 1.44 | 2 | 4.07 | 0.02 |
| Area | 1.83 | 3 | 3.46 | 0.02 |
| Year*Area | 2.44 | 6 | 2.3 | 0.04 |
| Error | 19.5 | 110 | | |

5.5.3 Recruitment of different species

For the 11 most abundant species, comparisons of abundance (CPUE, (nom-2) and mean length between different years and areas were made (Fig. 5.6A,B). Roach was the most numerous species in all years (mean of 4.90 m⁻²), making up more than half of the catch, followed by common bream (1.01 m⁻²) and white bream (0.95 m⁻²). We did not find any significant effect of area, year or their interaction for common bream, white bream, perch, sunbleak, ruffe or rudd (Table 5.6). For the more opportunistic species bleak and gibel carp, there was a significant effect of year (Table 5.6), with the highest CPUE in 2006 and the lowest in 2008 for both species (Fig. 5.6A,B). For bleak, CPUE in 2007 was less than half compared to 2006, while in 2008 it was negligible (ca. 2% of its abundance in 2006). For gibel carp in 2007, CPUE was less than 4% and <1% in 2008 compared to 2006. Sunbleak showed high abundances in 2007 and Area 2, but in other years only a few individuals were found. In contrast ruffe, another opportunistic species, was more abundant in 2008 than in the two previous years and three times more abundant in Areas 2 and 4 than in Areas 1 and 3. For the more periodic species pike, ide, and roach, there was a significant effect of area (Table 5.6). Pike had the highest CPUE values in Area 2 (CPUE was on average 3.7 times lower in Area 3). For ide, mean CPUE values in Areas 1 and 2 were more than

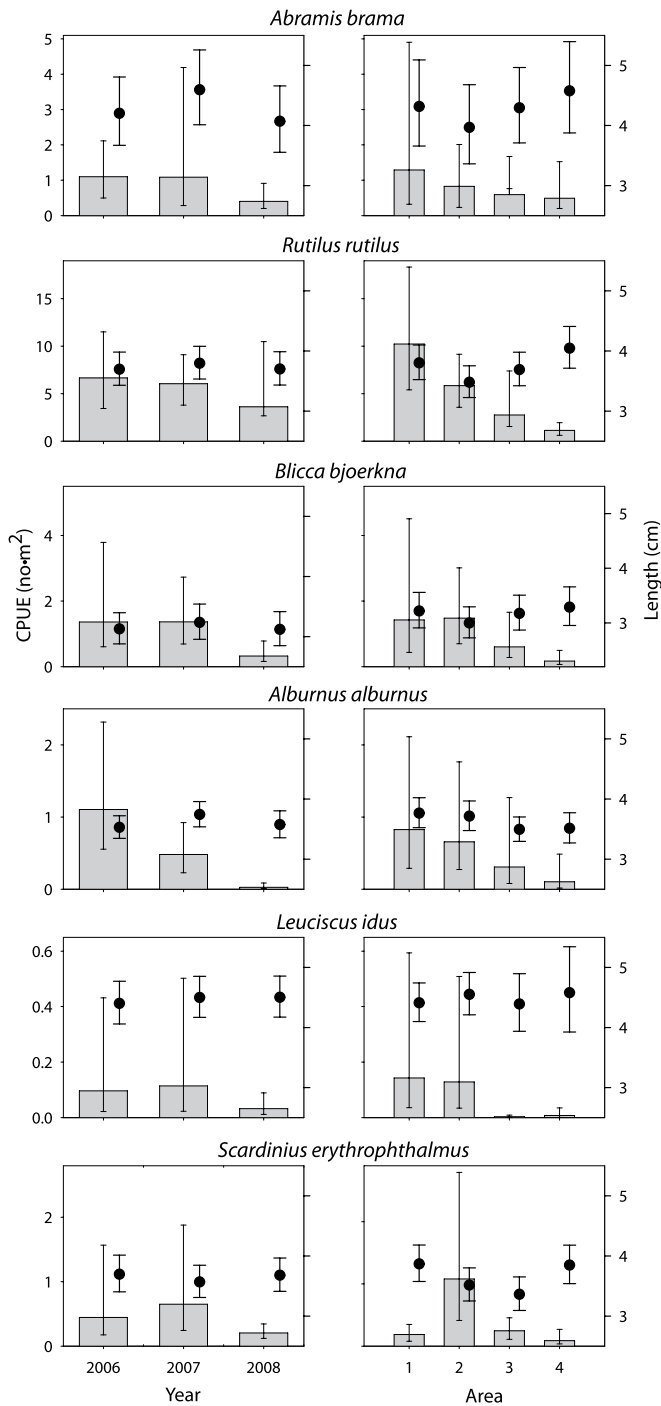


Figure 5.6A Comparison of densities (bars) and length (dots) of YOY in different years and areas. Letters indicate significant differences in CPUE based on Tukey's multiple comparison test.

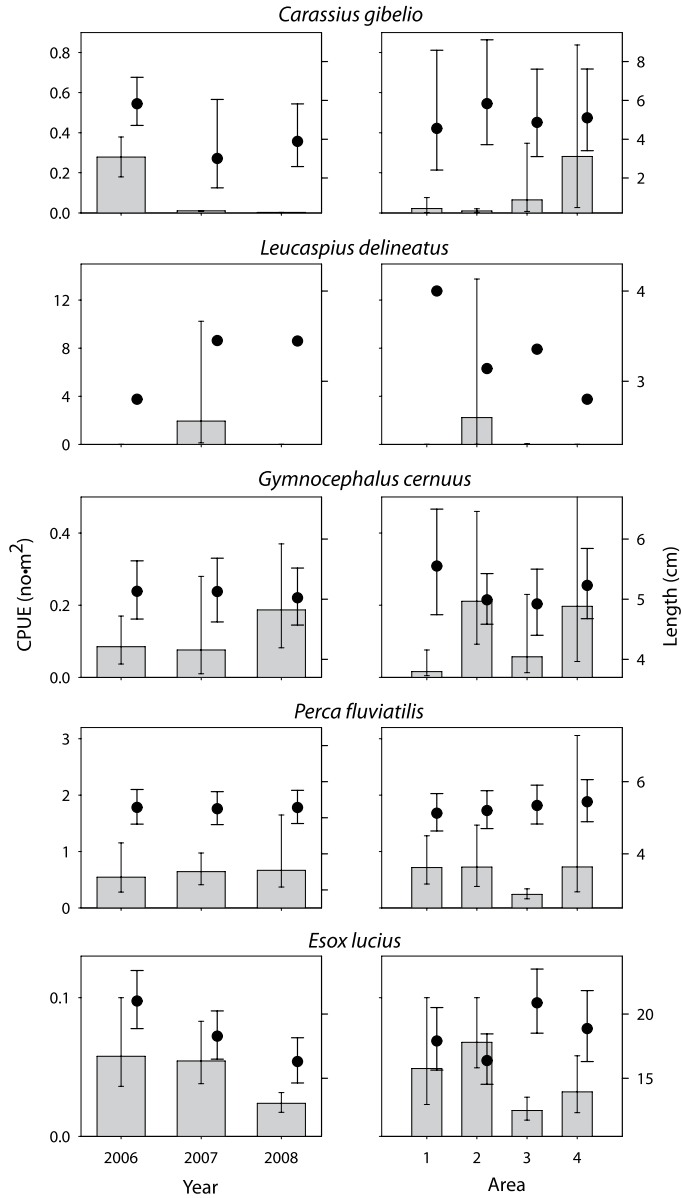


Figure 5.6B Comparison of densities (bars) and length (dots) of YOY in different years and areas. Letters indicate significant differences in CPUE based on Tukey's multiple comparison test.

20 times greater than in Areas 3 and 4 (Fig. 5.6A). Roach showed the lowest CPUE in Area 4 (Fig. 5.6A).

For most species, neither area nor year had a significant effect on YOY length. Exceptions were bleak, pike and rudd. Bleak showed significant effects of area ($F=4.76$, $P=0.014$) and for the area \times year interaction term ($F=3.34$, $P=0.017$). This was mostly caused by the exceptionally small YOY in 2008 in Area 4 (standard length 2.7 cm, while in all other year-area combinations it ranged between 3.3 and 3.9 cm). Pike showed significant effects of area ($F=4.82$, $P=0.009$) and year ($F=7.53$, $P=0.003$). YOY from Area 2 (mean length varying between 15.2 and 18.2 cm among years) were significantly smaller than those from Area 3 (18.4 – 25.4 cm). YOY in 2006 (mean lengths of 18.2 – 25.4 cm among areas) were significantly larger than in 2008 (15.2 – 18.4 cm). Finally, rudd showed a significant effect of area ($F=3.09$, $P=0.042$), with Area 3 (annual means of 3.1 – 3.5 cm) having smaller YOY than area 4 (3.7 – 4.2 cm).

At the overall community level, 'periodic' life history traits made up the highest proportion in all areas and years analyzed (approximately 50 %), whereas both opportunistic and equilibrium traits ranged between 21-

Table 5.6 ANOVA table of the CPUE (n^*m^2) of YOY fish of the most abundant species. DF, degrees of freedom; SS, sums of squares; F, F-statistic; P, probability. Blom-transformed rank scores were used in the analysis.

| Species | Mean CPUE (n/m ²) | Factor | DF | SS | F | P |
|------------------------------------|-------------------------------|--------|----|-------|-------|-------|
| <i>Abramis brama</i> | 1.01 | | | | | NS |
| <i>Alburnus alburnus</i> | 0.47 | Year | 2 | 9.22 | 6.60 | 0.004 |
| | | Error | 33 | 23.06 | | |
| <i>Blicca bjoerkna</i> | 0.95 | | | | | NS |
| <i>Carassius gibelio</i> | 0.12 | Year | 2 | 13.16 | 17.46 | 0.000 |
| | | Error | 33 | 12.44 | | |
| <i>Esox lucius</i> | 0.04 | Area | 3 | 8.01 | 3.42 | 0.029 |
| | | Error | 32 | 24.95 | | |
| <i>Gymnocephalus cernuus</i> | 0.10 | | | | | NS |
| <i>Leuciscus idus</i> | 0.08 | Area | 3 | 11.68 | 6.90 | 0.001 |
| | | Error | 32 | 18.06 | | |
| <i>Leucaspis delineatus</i> | 0.68 | | | | | NS |
| <i>Perca fluviatilis</i> | 0.61 | | | | | NS |
| <i>Rutilus rutilus</i> | 4.90 | Area | 3 | 12.29 | 6.25 | 0.002 |
| | | Error | 32 | 20.98 | | |
| <i>Scardinius erythrophthalmus</i> | 0.43 | | | | | NS |

27%. There were no clear differences between years and areas in the proportion of different strategies, with the exception of Area 4, where the opportunistic traits were more abundant (27% in Area 4, compared to 21-23% in the other areas).

Results of the redundancy analyses showed that environmental variables explained much of the variation in YOY fish abundance in each year sampled (Table 5.7). In each year, water body area in summer, submerged macrophyte cover and shore length index (SLI) were important explanatory variables (Fig. 5.7). In addition to these three, helophyte cover was also an important explanatory variable in 2006. In 2007, water body depth and water body area in spring contributed markedly to explaining the YOY fish abundance. Finally, distance to the main channel and grassland cover were important explanatory variables in 2008. Most of the variation in YOY fish abundance can be assigned to gibel carp, common bream and ruffe in 2006; common bream, bleak, perch and roach in 2007; and common bream, white bream, ruffe and ide in 2008. The ordination revealed large variability in species – environment associations between years, emphasizing the influence of variability between years on recruitment. However, we also observed some consistent patterns over the years. Common bream showed positive correlations with the water body area in spring, the area of flooded grasslands, and depth, and a negative correlation with submerged macrophyte cover. Bleak correlated negatively with shore line index, and positively with water body area in summer. Roach also correlated positively with summer area. Gibel carp and sunbleak correlated negatively with the extent of grassland and with water body area in spring. Rudd correlated positively with submerged macrophyte cover in all years.

Table 5.7 Redundancy analyses of the environmental variables explaining the abundance of YOY fish.

| Year | P* | The proportion of the total variance explained | Eigenvalues | | | |
|------|------|--|--------------------------------|-------|-------|-------|
| | | | Cumulative percentage variance | | | |
| | | | I | II | III | IV |
| 2006 | <.01 | 0.612 | 0.2 | 0.181 | 0.093 | 0.052 |
| | | | 20 | 38.1 | 47.4 | 52.5 |
| 2007 | <.01 | 0.604 | 0.214 | 0.12 | 0.095 | 0.081 |
| | | | 21.4 | 33.4 | 43 | 51.1 |
| 2008 | <.01 | 0.42 | 0.116 | 0.1 | 0.063 | 0.042 |
| | | | 11.6 | 21.6 | 27.9 | 32 |

* Based on 1000 permutations (test of significance of the first canonical axis vs. all canonical axes gave the same results)

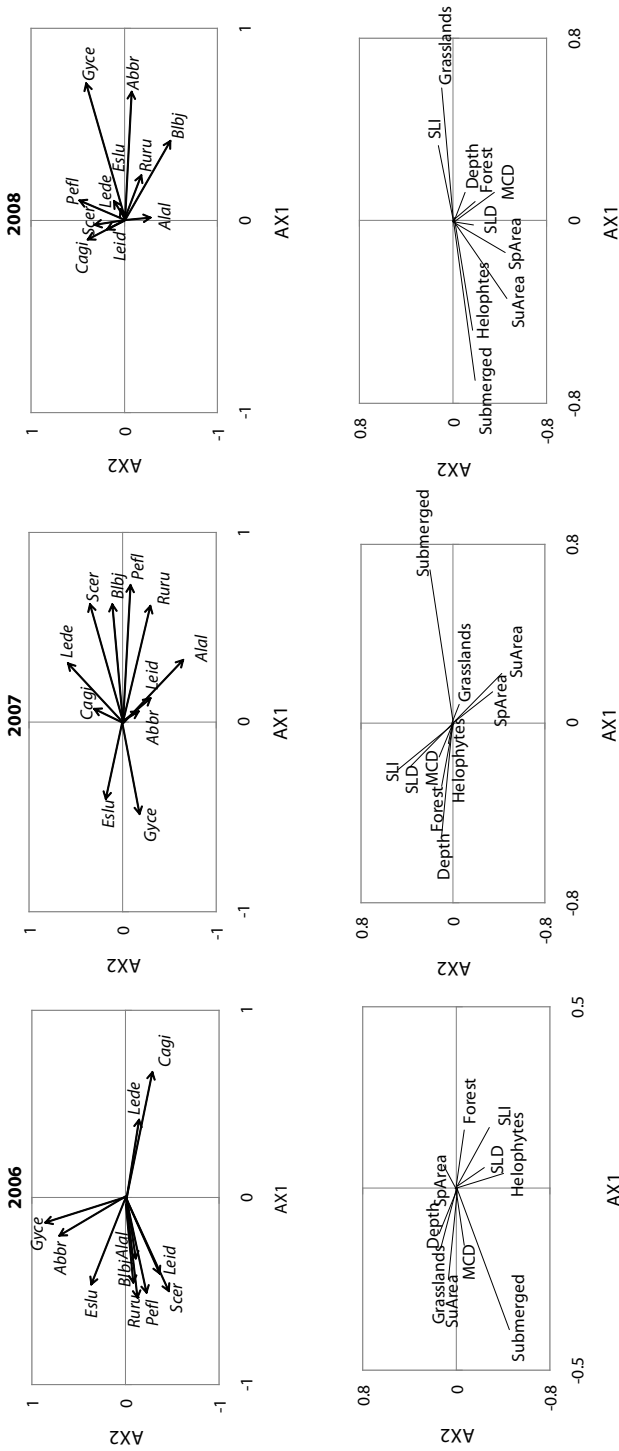


Figure 5.7 Relationship between species relative abundance and specific characteristic of each water body. Redundancy analysis of YOY fish densities of different species explained by Geomorphology / Connectivity / Vegetation variables.

5.6 Discussion

5.6.1 Temperature and flood driven production of YOY

Our results indicate the potential importance of temperature coupled with flood conditions in fish recruitment in a temperate floodplain. In contrast, Nunn *et al.* (2003) suggested that discharge rather than spring temperature may be the key factor in young fish recruitment in some temperate lowland rivers, but their conclusions were based on a study on a smaller, more severely altered river. We observed the overall biomass of YOY fish to be about three times higher in warmer years and areas with a large flood extent, compared to the coldest year 2008. Of course our dataset is only limited to three years of data collection and we cannot be completely sure how generic the pattern is that we see, but it appears to be corroborated by other studies (King *et al.*, 2003; Trifonova, 1982). On the other hand, in areas with a smaller flood extent, biomass was similar despite the differences in temperature. These observed differences in YOY biomass between different areas support the hypothesis that the flood pulse immediately affects productivity in the floodplains (Welcomme, 1985). The smaller extent of flooding in Areas 3 and 4 resulted in a much lower recruitment of all the species compared to areas with a large flood extent. This corroborates the importance of high productive flooded terrestrial habitats for fish production in floodplains (Herwig *et al.*, 2004). It is also consistent with experimental findings stressing the importance of temperature and food availability for exogenous feeding fish fry (Schiemer, Keckeis & Kamler, 2002). Interestingly, we found no marked differences in YOY fish biomass between 2006 and 2007, despite the lower temperatures and lower flood amplitude and duration in 2006. However the flood peak in 2006 was late and therefore co-occurred with suitable temperatures for fish recruitment. This possibly resulted in better recruitment. Moreover, lower peak discharge in 2006 resulted in an average depth of water bodies at the end of summer about 0.2 m lower in all the areas compared to 2007 and 2008. Therefore, CPUE densities could have been biased by the lower volume of some water bodies in 2006. With an average depth of water bodies of 1.5 m the bias would have been on average 15%. The higher abundance of pelagic bleak caught with the beach seine in 2006 compared to 2007 could be a (partial) reflection of this. Additionally, the high abundance of gibel carp in 2006 could have been a direct effect of the very low flood pulse in 2006. This low flood pulse resulted in a reduced water volume of some of the floodplain water bodies,

favouring this species, known for its tolerance to high water temperatures and hypoxia (Lushchak *et al.*, 2001; Roesner *et al.*, 2008). Another factor potentially affecting spawning and recruitment success is the abundance of the spawning stock. We do not have quantitative data on spawner abundance, but we do not expect it to play an important role in the number of recruits, since the relationship between spawning adults and recruitment success is shown not to be strong (Mooij, 1996).

Differences in YOY abundances were more pronounced between 2007 and 2008 despite the fact that peak discharge, filling the water bodies, was similar in these year. This resulted in similar water depths, despite probably higher evaporation in 2007 due to higher air temperatures. However, flood duration in 2008 was about 4 weeks shorter than in 2007, possibly causing a decoupling of flooding and suitable temperatures reducing YOY fish recruitment. Considering that flooding now occurs earlier than before the Upper Volga regulation (Mordukhai-Boltovskoi, 1979), this will significantly decrease the time window in which floodings providing suitable habitat and suitable water temperatures are in synchrony. Potentially this could lead to a long-term decrease of recruitment success.

In addition to the co-occurrence of flooding and favourable temperatures there are other potential mechanisms influencing recruitment success. In the time between the end of the flooding and late summer both abiotic (such as anoxia and desiccation) and biotic (competition and predation) processes may have influenced, or even partially masked the effect of successful spawning. In our case however, selected water bodies did not desiccate, nor were there any signs of extensive anoxia (although locally this may have played a role). It is therefore more likely that the temperature conditions that we report actually enhanced the effect of (un)successful spawning. For instance, the cold summer temperatures of 2008 may possibly have additionally reduced recruitment in that year, because of lower productivity. Moreover, the non-significant differences in fish length for most of the species do not indicate that density-dependent processes such as competition for food would have been important for recruitment success.

5.6.2 Recruitment of different species

The large extent of floods in Areas 1 and 2 compared to 3 and 4, ensured that flooding was coupled with suitable temperatures. Therefore Areas 1 and 2

accommodated significantly higher densities of young fish, especially more periodic species such as common bream and roach. This supports findings that large inundation improves the reproductive success of fish species that frequently reproduce on floodplains (Killgore & Baker, 1996). Consequently, the higher densities of pike in Areas 1 and 2 could have resulted from the available higher cyprinid larvae densities which are suitable prey for young pike. Moreover, extended and prolonged connectivity of Areas 1 and 2 with the main channel could have made these areas a more suitable nursery habitat for periodic fish, also the most rheophilic of the analysed fish species. The small extent and duration as well as lower predictability of flooding, often resulting in low water levels, high temperatures and possibly hypoxic conditions in Area 4, severely reduced YOY fish abundances of most species, especially periodic strategists. The more opportunistic species gibel carp, also known for its high temperature and hypoxia tolerance showed high recruitment success here (Lushchak *et al.*, 2001; Roesner *et al.*, 2008).

5.6.3 Recruitment of different life history traits at the community level

As expected periodic life history traits which are adaptive to large-scale, predictable changes dominate fish species that recruit in floodplains. Equilibrium and opportunistic traits play a minor role. Even with variability of recruitment success between species, the composition of life history traits remains stable between years. However, when the environment becomes less predictable, opportunistic strategists might take an advantage as shown for Area 4. Therefore, further alterations of flood pulse might result in fish community shifts towards more opportunistic strategists.

5.6.4 Role of permanent water body characteristics

Even though flood and temperature variability between years seems to dominate fish recruitment in the Volga-Akhtuba floodplain, we found that more permanent characteristics of the water bodies also played a role in determining recruitment success for some species.

Common bream revealed a strong association with submerged grassland area in spring, probably related to its phytophilic spawning preferences (Reshetnikov, 2002). Moreover, the negative correlation of common bream abundance with submerged macrophyte cover could be an effect of breams

ability to deteriorate growth conditions for macrophytes (Scheffer, 1998). Pelagic bleak was associated with larger water bodies with a low shoreline index, which is in line with its open-water habitat preference. As expected, limnophilic rudd was strongly correlated with submerged macrophyte cover, and thus probably short flood duration as shown in other floodplain river systems (Heiler *et al.*, 1995; Van Geest *et al.*, 2003). Hypoxia-tolerant gibel carp was the only species surviving in desiccating water bodies, which are usually small, therefore showing negative correlations with size and extent of flooded grasslands.

We hypothesize that in the lower Volga floodplain spring temperature and its match with flooding is the most important factors in YOY fish recruitment. A mismatch of flood timing and temperature reduces recruitment success of all species, especially periodic strategists (Cushing, 1990). The shorter flood durations caused by the regulation of the Volga River increase the probability of such a mismatch and therefore might reduce fish recruitment success in the long run. Independent of flooding events, however, long-term characteristics of the water bodies within the floodplain, especially related to their morphology, hydrology, and vegetation, also explain a large part of fish recruitment success.

5.7 Acknowledgments

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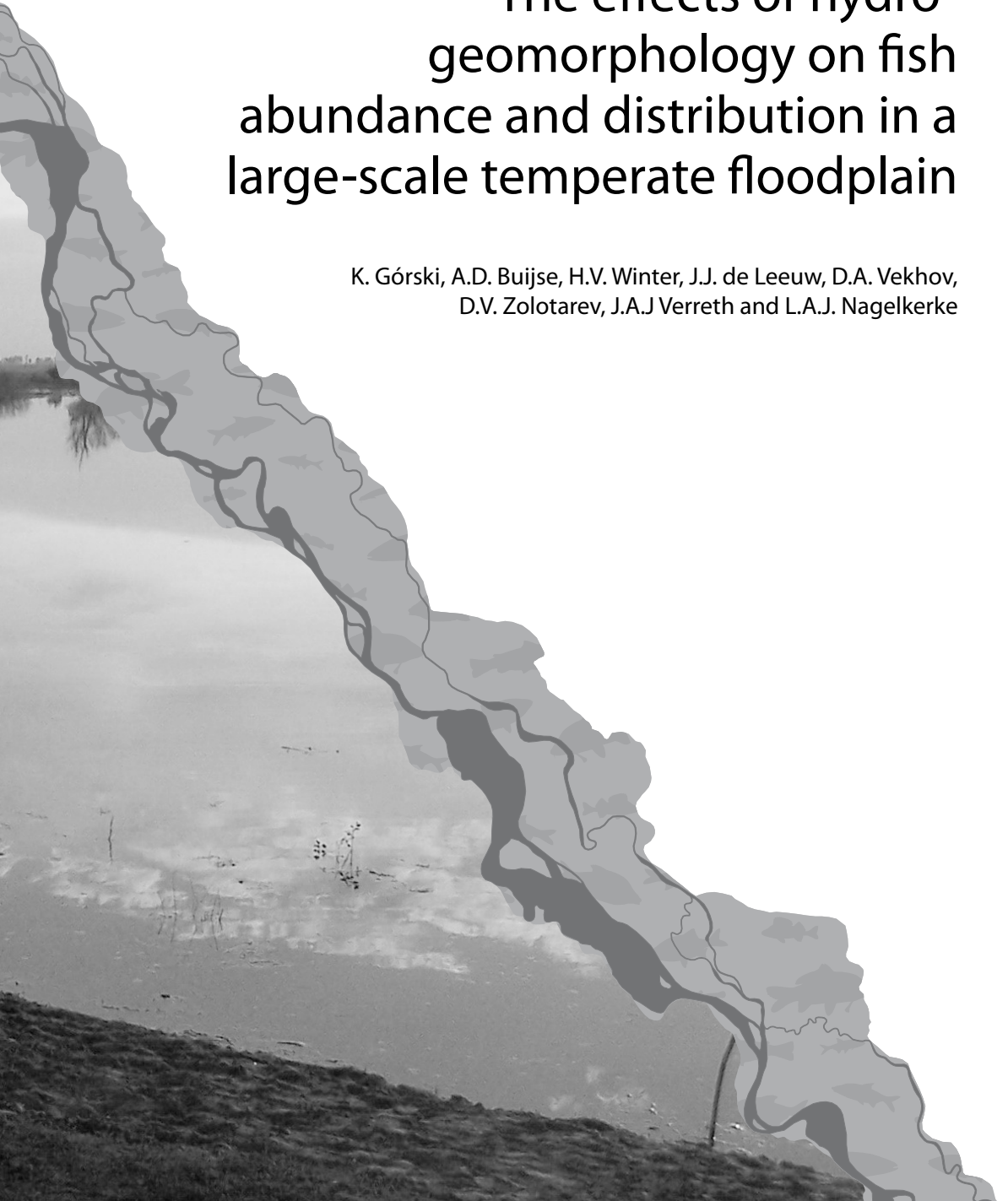
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Chapter 6

The effects of hydro-geomorphology on fish abundance and distribution in a large-scale temperate floodplain

K. Górski, A.D. Buijse, H.V. Winter, J.J. de Leeuw, D.A. Vekhov,
D.V. Zolotarev, J.A.J Verreth and L.A.J. Nagelkerke



The effects of hydro-geomorphology on fish abundance and distribution in a large-scale temperate floodplain

6.1 Abstract

Natural river-floodplain systems are characterized by a dynamic hydro-geomorphology resulting in a wide range of habitats that support high fish diversity and production. Various factors (e.g. hydrological dynamics, water quality, biotic processes) have been proposed to explain fish abundance and distribution in large river floodplains, but it is still widely acknowledged that the mechanisms involved might vary in diverse floodplain systems and that they are not fully understood. To examine whether flooding dynamics and floodplain geomorphology influence fish abundance, and species distributions across the Volga-Akhtuba floodplain, Russian Federation we examined (1) the inter-annual variation in species abundance and (2) the distributions of eight species with respect to variables reflecting floodplain hydro-geomorphology. We used both ANOVA and boosted regression trees analysis to analyse the data. We found that inter-annual flood variability caused variation in overall abundances of most fish species. However, prevalence of the majority of most abundant species remained stable. The distribution of fish species was strongly influenced by geomorphology and flooding. The geomorphic heterogeneity of the floodplain creates suitable habitats across ranges of fish guilds (rheophilic, eurytopic and limnophilic) resulting in high diversity of the floodplain ichthyofauna. We conclude that this diverse habitat availability is a highly significant factor influencing fish abundance and distribution in the Volga-Akhtuba floodplain and that its effects can be more pervasive than the effects of inter-annual variability in flooding, except for temporary deviations in part of the water bodies occurring during extreme years.

Влияние гидро-геоморфологических условий на численность рыб и ее распределение в крупномасштабных поймах умеренного климата

6.2 Резюме

Естественные системы река-пойма характеризуются динамическими гидро-геоморфологическими процессами, формирующими широкий диапазон условий обитания, который поддерживает высокое разнообразие видов рыб и их продуктивность. Для объяснения численности и распределения рыб в больших поймах рек предлагаются различные факторы (например, гидрологическая динамика, качество воды, биотические процессы), однако до сих пор общепризнано, что оказывающие влияние механизмы могут различаться в несходных пойменных системах и что эти механизмы не до конца поняты. Чтобы определить, влияет ли динамика половодья и геоморфология поймы на численность рыб и распределение видов в Волго-Ахтубинской пойме, Российская Федерация, мы исследовали (1) межгодовые вариации в количестве видов и (2) распределение восьми видов в зависимости от переменных, описывающих гидрологические и геоморфологические условия. Для анализа данных мы использовали дисперсионный анализ (ANOVA) и метод расширяемых регрессионных деревьев (boosted regression trees analysis). Мы выявили, что межгодовая изменчивость затоплений поймы служила причиной различий в общей численности большинства видов рыб. Однако, доминирование большинства наиболее многочисленных видов оставалось стабильным. На распределение видов рыб существенно влияли геоморфологические условия и характер затопления. Геоморфологическая неоднородность поймы создает подходящие местообитания для различных экологических групп рыб (реофилы, эвритопы и лимнофилы), выражаясь в высоком разнообразии ихтиофауны поймы. Мы приходим к выводу, что доступность разнообразных мест обитания является одним из наиболее значимых факторов, влияющим на изобилие и распределение рыбы в Волго-Ахтубинской пойме, и что действие этого фактора может быть более существенным по сравнению с межгодовой изменчивостью затопления, за исключением временных отклонений в части водных объектов, проявляющихся в экстремальных по гидрологическим условиям годам.

6.3 Introduction

Natural river floodplains are among the most productive and diverse freshwater ecosystems (Tockner & Stanford, 2002; Ward, Tockner & Schiemer, 1999). Seasonal flooding inundates terrestrial habitats, and this in turn expands habitat availability and increases habitat complexity for aquatic organisms. Flooding also mobilizes organic matter (Robertson *et al.*, 1999), and facilitates the exchange of nutrients between the aquatic and terrestrial compartments of the riverine ecosystem. Increased nutrient availability and frequent disturbances are caused by regular flooding, which result in high production and biodiversity of floodplains (Junk, Bayley & Sparks, 1989; Lowe-McConnell, 1964; Tockner, Malard & Ward, 2000). Water bodies in the floodplain can show strong environmental dynamics (Baker, Killgore & Kasul, 1991; Sabo & Kelso, 1991), largely driven by the seasonal flood pulse (Miranda, 2005; Schramm & Eggleton, 2006). Because of the dynamic nature of river-floodplain systems and the spatial and temporal extent of connectivity, floodplain water bodies are characterized by varying hydrogeomorphic features e.g. water body size, shape, and distance to the main channel. They provide a wide range of habitats that support high fish diversity and production (Amoros & Bornette, 2002; Welcomme, 1985).

Various mechanisms have been proposed to explain fish abundance and distribution patterns in floodplain systems (Lowe-McConnell, 1987; Martelo *et al.*, 2008; Saint-Paul *et al.*, 2000; Welcomme, 1985). Some studies propose that fish abundances and distributions are random in floodplain water bodies (Lowe-McConnell, 1987). Other authors suggest active habitat selection by fish species (Martelo *et al.*, 2008; Saint-Paul *et al.*, 2000; Welcomme, 1985), which in turn may be influenced by water quality parameters of the floodplain water bodies such as turbidity (Tejerina-Garro, Fortin & Rodriguez, 1998). Recently, flood pulse dynamics (e.g. frequency, magnitude, timing and duration of floodplain inundation) were suggested as a major factor structuring abundance and distribution of fish in tropical as well as arid floodplains (Arthington *et al.*, 2005; da Silva, Petry & da Silva, 2010; Sousa & Freitas, 2008). The aforementioned studies indicate that the mechanisms shaping fish abundance and distribution in large river floodplains are highly variable and not fully understood. Some recent studies demonstrate the importance of hydrological dynamics in structuring fish abundance and distribution in tropical floodplains in South America (Arthington & Winemiller, 2006; Espírito-Santo *et al.*, 2009; Martelo *et al.*, 2008)

and Australian arid rivers (Balcombe & Arthington, 2009). Few studies have been carried out in large temperate floodplains (Lasne, Lek & Laffaille, 2007; Winemiller *et al.*, 2000), of which most examined fish abundance and distribution in floodplains that were severely altered by human activity (Feyrer, Sommer & Harrell, 2006; Gehrke & Harris, 2000; Grift, Buijse & Van Geest, 2006; Jurajda, Reichard & Smith, 2006). This is related to the scarcity of undisturbed large temperate floodplains in temperate zones since up to 90 % of the floodplains in Europe and North America are considered functionally extinct due to river regulation (Tockner & Stanford, 2002).

The lower Volga floodplain is still relatively undisturbed (Middelkoop *et al.*, 2005), and thus provides an excellent opportunity to study factors that control fish abundance and distribution. In this study we aim to determine how the abundance and distribution of fish species in such a floodplain is influenced by hydro-geomorphic conditions. Therefore our objectives were to 1) determine the effects of flooding and geomorphology of floodplain water bodies on floodplain fish abundance; 2) determine which hydro-geomorphic features play the most important roles in the distribution of various species within the floodplain and 3) predict fish distribution in the floodplain, based on relationships between the occurrence of selected species and hydro-geomorphic variables.

6.4 Methods

6.4.1 Study Area

The Volga River (Russian Federation), with a length of 3,690 km and an average annual discharge of $8,103 \text{ m}^3\text{s}^{-1}$, is the longest river in Europe and 16th longest in the world (Litvinov *et al.*, 2009). It has a combined rainfall / snowmelt flow regime, with peak discharge in May-June. A series of upstream dams, completed in the 1960s, moderately altered the natural flow regime of the lower Volga downstream of Volgograd (Middelkoop *et al.*, 2005; Mordukhai-Boltovskoi, 1979). Directly downstream of the Volgograd dam, the Volga splits into the larger Volga River, and the smaller Akhtuba River. The Volga-Akhtuba floodplain extends between these two rivers over a length of 300 km, and is 10-30 km wide. The Western part of the floodplain (the study area, Fig. 6.1) accommodates about 3500 water bodies (shallow floodplain lakes and streams) with a wide range of sizes and shapes.

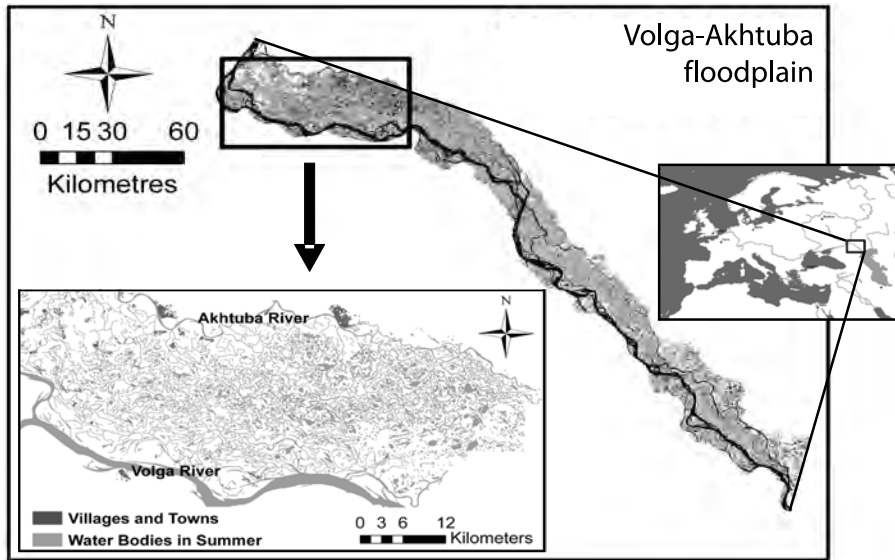


Figure 6.1 Map of the Volga–Akhtuba floodplain and its location in Russian Federation.

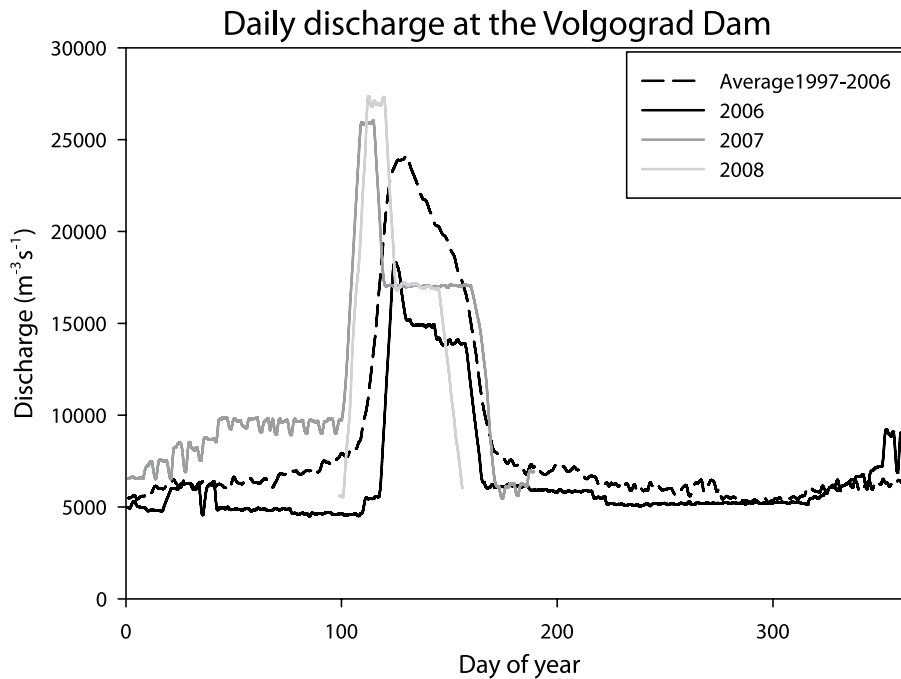


Figure 6.2 Daily discharge of Volga River during sampling years.

The depth of most of the floodplain lakes ranges between 1-2 metres. The Volga-Akhtuba floodplain is situated in the semi-arid continental climatic zone with very dry, hot summers and severe, cold winters (Averina *et al.*, 2000). Its geomorphology has been preserved to a large extent (Averina *et al.*, 2000). The vegetation of the floodplain mainly consists of meadows (Averina *et al.*, 2000), which are used for extensive grazing of cattle and hay production (Losev *et al.*, 2008). When water levels rapidly rise in spring (Fig. 6.2), 50-85% of the floodplain is inundated within approximately two weeks through permanent and temporary side channels as well as through overflowing terrestrial areas.

6.4.2 Data collection

The geomorphology of 3518 water bodies was described by determining the surface area and perimeter from available digitised topographic maps (scale 1:85,000) using ArcGIS and by calculating shoreline development (SLD) and shoreline index (SLI) (measures for shoreline complexity and water body shape) from these (Table 6.1). Flood extent was derived from a sequence of five satellite images and field observations and classified into 4 levels: (1) no overbank expansion of the water body; (2) overbank expansion, but water bodies do not merge (3) large overbank expansion, water bodies merge, but large non-flooded patches remain; and (4) very large overbank expansion, resulting in one large water table.

Table 6.1 Variables used in the classification of water bodies.

| Variable | Description |
|----------|---|
| Area | Surface area in summer (ha) |
| SLI | Shore Length Index (the ratio of shore length to water body area; m^{-1}) |
| SLD | Shore Line Development (the ratio of the length of the shore line to the length of the circumference of a circle of area equal to that of the water body) |
| Extent | Flood extent (categories 1-4) From low to high |

Fish were sampled in water bodies which were selected to cover a broad range of hydro-geomorphic characteristics. Sampling was performed from the end of August until the end of September in 2006 (19 water bodies), 2007 (27 water bodies), and 2008 (40 water bodies). Fifteen water bodies were repeatedly sampled across all three years. On average three samples were collected in each water body using a beach seine (30 m long, 1.5 m high, 10 mm stretched mesh size). The beach seine was hauled over a distance of 20 – 40 m, sweeping an area of 600 – 1200 m^2 . For each sample,

fish were identified to the species level (Koblitskaya, 1981), counted and measured (standard length). In each water body, a subsample of fish was weighed and length-weight relationships were derived. Catch per unit effort (CPUE) was expressed as g·m⁻² area swept by the seine. Scientific and common names, flow guilds and totals of individuals caught for each of the fish species are given in Table 6.2.

Table 6.2 List of all the species caught with their flow preferences (Reshetnikov, 2002; Schiemer & Spindler, 1989).

| SPECIES | | | |
|---|-------------------------|------------------------|----------------------------|
| Scientific name | Common name | Flow preference | Total number caught |
| <i>Abramis ballerus</i> (Linnaeus, 1758) | Blue bream | Eurytopic | 344 |
| <i>Abramis brama</i> (Linnaeus, 1758) | Common bream | Eurytopic | 26,069 |
| <i>Alburnus alburnus</i> (Linnaeus, 1758) | Bleak | Eurytopic | 38,835 |
| <i>Alosa kessleri</i> (Grimm, 1887) | Caspian anadromous shad | Rheophilic | 2 |
| <i>Aspius aspius</i> (Linnaeus, 1758) | Asp | Rheophilic | 20 |
| <i>Blicca bjoerkna</i> (Linnaeus, 1758) | White bream | Eurytopic | 44,706 |
| <i>Carassius carassius</i> (Linnaeus, 1758) | Crucian carp | Limnophilic | 207 |
| <i>Carassius gibelio</i> (Bloch, 1783) | Gibel carp | Eurytopic | 10,547 |
| <i>Clupeonella cultriventris</i> (Nordmann, 1840) | Black Sea sprat | Rheophilic | 7,485 |
| <i>Cobitis taenia</i> (Linnaeus, 1758) | Spined loach | Rheophilic | 1,291 |
| <i>Cyprinus carpio carpio</i> (Linnaeus, 1758) | Carp | Eurytopic | 466 |
| <i>Esox lucius</i> (Linnaeus, 1758) | Pike | Eurytopic | 1,128 |
| <i>Gymnocephalus cernuus</i> (Linnaeus, 1758) | Ruffe | Eurytopic | 2,731 |
| <i>Leucaspis delineatus</i> (Heckel, 1843) | Sunbleak | Limnophilic | 11,331 |
| <i>Leuciscus idus</i> (Linnaeus, 1758) | Ide | Rheophilic | 1,770 |
| <i>Misgurnus fossilis</i> (Linnaeus, 1758) | Weatherfish | Limnophilic | 2 |
| <i>Neogobius fluviatilis</i> (Pallas, 1814) | Monkey goby | Eurytopic | 811 |
| <i>Perca fluviatilis</i> (Linnaeus, 1758) | Perch | Eurytopic | 18,116 |
| <i>Proterorhinus marmoratus</i> (Pallas, 1814) | Tubenose goby | Eurytopic | 342 |
| <i>Rutilus rutilus</i> (Linnaeus, 1758) | Roach | Eurytopic | 124,382 |
| <i>Sander lucioperca</i> (Linnaeus, 1758) | Pikeperch | Eurytopic | 19 |
| <i>Scardinius erythrophthalmus</i> (Linnaeus, 1758) | Rudd | Limnophilic | 10,207 |
| <i>Silurus glanis</i> (Linnaeus, 1758) | Wels | Eurytopic | 5 |
| <i>Syngnathus abaster</i> (Risso, 1827) | Black-striped pipefish | Eurytopic | 931 |
| <i>Tinca tinca</i> (Linnaeus, 1758) | Tench | Limnophilic | 342 |
| | | | 302,089 |

6.4.3 Data Analysis - Abundance

Mean CPUE values were calculated for each species and each water body (WB) in each year (2006-2008). CPUE-values of the 12 most abundant species were tested by analysis of variance (ANOVA) for the effect of year and WB, using the model: $CPUE = year + WB + year \times WB + \epsilon$. Because of the non-normal distribution of CPUE values, data were ranked and ranks were transformed using Blom's method, which adjusts the rank scores to an approximately normal distribution (Blom, 1958). In this way we could use ANOVA on the transformed ranks, allowing for testing for interactions. This would not have been possible when using a non-parametric method on non-transformed ranks. The fifteen water bodies that were sampled across all years were used for this analysis.

6.4.4 Data analysis - Occurrence

The occurrence of eight species were described with respect to flood extent, surface area of water body, shoreline development (SLD) and shoreline index (SLI) for 43 sampled water bodies, using Boosted Regression Trees Analysis (Elith, Leathwick & Hastie, 2008; Friedman, 2001; Friedman, 2002). Boosted regression trees have recently been shown to be a powerful approach for ecological modelling studies (De'ath & Fabricius, 2010; Elith *et al.*, 2008; Leathwick *et al.*, 2008). The approach consists of two components: fitting regression trees and boosting. The algorithm of fitting regression trees involves iteratively partitioning the data in parts in such a way that the sum of the squared deviations from the mean in the separate parts is minimised. This has a number of advantages in comparison to classical regression techniques, e.g. the ability to deal with missing data and to automatically model interactions. However, regression trees are prone to misclassification. To overcome misclassification errors, the boosting algorithm stochastically combines regression trees in different combinations and fits these to the data to produce a robust predictor. The algorithm iteratively improves the fit by focusing on the observations which are the hardest to predict in each cycle until an optimal solution is found (Elith *et al.*, 2008).

To identify the importance of each of the environmental variables in explaining fish occurrence, binomial models were run for each of the 8 selected species separately. We did not analyze statistically rare species (occurring less than 20%). The tree complexity and learning rate of the models was

optimized in all cases so that a maximum of ~1000 trees was fitted. Ten-fold cross-validation was used to assess the performance of each model. Cross-validation compares the fitted values from ten individual models, based on 10 random subsets of the data, to withheld portions of the raw data (Elith *et al.*, 2006; Leathwick *et al.*, 2006). Predictive performance of the models was assessed using the area under the receiver operating curve (AUC) (Bradley, 1997). Values for AUC give a measure of the degree to which fitted values discriminate between observed presences and absences; values can be interpreted as indicating the probability that a presence for a species drawn at random from the data will have a higher fitted probability than an absence drawn at random (Leathwick *et al.*, 2008). To account for the year effect in each of the species models the water bodies that were repeatedly sampled across all years were placed into a single cross-validation fold and were down-weighted so that the contribution of each replicate year represented a fraction of the total. In addition, because of the low sample sizes in this study the cross-validated BRT performance measures were estimated, based on 5 replicate model runs.

The importance of each predictor variable was assessed by calculating the contribution of each predictor to the model, averaged across all trees (n.trees in Table 6.4; Ridgeway 2006). Spatial predictions of fish occurrence for each species were predicted across the sampled area using the final model and estimated information for the other 3518 water bodies across the Volga-Akhtuba floodplain. All BRT models were fitted in version 2.6.0 of R using the 'gbm' library (Ridgeway, 2004).

6.5 Results

6.5.1 Abundance dynamics

During the 2006 – 2008 surveys more than 300,000 fishes representing a total of 25 species were caught (Table 6.2). Eurytopic fish species such as roach, perch, pike, common bream and white bream accounted for the highest CPUE in weight ($\text{g}\cdot\text{m}^{-2}$) (Table 6.3). Small-bodied bleak, sunbleak and Black Sea sprat were also numerous (Table 6.1), but their contribution to CPUE expressed in $\text{g}\cdot\text{m}^{-2}$ was smaller. CPUE values showed a high variation between years and water bodies, but there were some consistent patterns. Roach was the most abundant species in all years followed by perch and

Table 6.3 ANOVA table of the CPUE ($g \cdot m^{-2}$) of the most abundant fish species.; *P*, probability; *WB*, water body.

| Abbrev | Species | Mean CPUE (SE) ($g \cdot m^{-2}$) | | | WB (df=14) | Year (df=2) | WB-year (df=28) |
|--------|------------------------------------|-------------------------------------|-------------|------------|------------|-------------|-----------------|
| | | 2006 | 2007 | 2008 | | | |
| Abbr | <i>Abramis brama</i> | 1.2 (0.4) | 1.7 (0.6) | 1.3 (0.5) | <.0001 | 0.3398 | <.0001 |
| Alal | <i>Alburnus alburnus</i> | 1.0 (0.4) | 0.6 (0.1) | 0.2 (0.06) | 0.0016 | <.0001 | <.0001 |
| Blbj | <i>Blicca bjoerkna</i> | 2.0 (1.0) | 0.9 (0.3) | 0.4 (0.2) | <.0001 | <.0001 | <.0001 |
| Cagi | <i>Carassius gibelio</i> | 2.7 (1.2) | 0.51 (0.4) | 0.4 (0.2) | <.0001 | <.0001 | <.0001 |
| Cyca | <i>Cyprinus carpio</i> | 1.2 (0.5) | 0.06 (0.04) | 0 | <.0001 | <.0001 | <.0001 |
| Eslu | <i>Esox lucius</i> | 4.8 (1.1) | 3.4 (1.0) | 2.0 (0.4) | <.0001 | 0.0487 | <.0001 |
| Gyce | <i>Gymnocephalus cernuus</i> | 0.25 (0.1) | 0.5 (0.2) | 0.7 (0.3) | <.0001 | 0.0019 | <.0001 |
| Leid | <i>Leuciscus idus</i> | 0.14 (0.1) | 0.2 (0.1) | 0.2 (0.1) | <.0001 | 0.5814 | <.0001 |
| Pefl | <i>Perca fluviatilis</i> | 2.0 (0.7) | 2.4 (0.6) | 6.0 (2.6) | 0.0004 | 0.0326 | <.0001 |
| Ruru | <i>Rutilus rutilus</i> | 5.0 (1.5) | 4.8 (1.1) | 6.4 (2.4) | 0.0004 | 0.6572 | 0.0003 |
| Scer | <i>Scardinius erythrophthalmus</i> | 0.95 (0.4) | 1.2 (0.4) | 0.4 (0.16) | <.0001 | 0.0025 | 0.0002 |
| Titi | <i>Tinca tinca</i> | 0.07 (0.05) | 0.09 (0.06) | 0.1 (0.06) | <.0001 | 0.79 | 0.0321 |

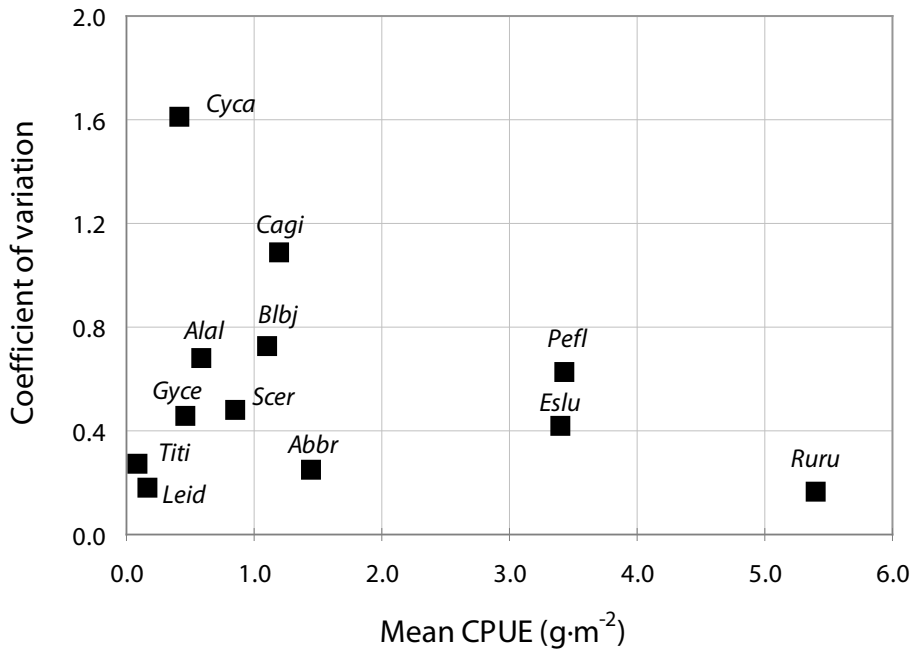


Figure 6.3 Mean CPUE and CV between years for the 12 most abundant species (abbreviations as in Table 6.3).

pike (Table 6.3; Fig. 6.3). Common bream, ide, roach and tench showed the lowest variation between years (no significant effect of year; Table 6.3; Fig. 6.3), whereas common carp and gibel carp showed the largest variation in abundance between years, with CPUE about 6-fold higher in 2006. Bleak and white bream showed the highest CPUE in 2006, with a 2 to 5-fold lower level in respectively 2007 and 2008. Pike also showed the highest CPUE in 2006, but with a 1.5-fold decrease in the following years. By contrast, ruffe and perch demonstrated the lowest CPUE in 2006 and an approximately 2 to 3-fold increase in 2007 and 2008 respectively. All species showed a significant effect of the WB and the interaction term between WB and year, suggesting that hydro-geomorphology plays an important role in shaping abundance patterns within the floodplain.

6.5.2 Hydro-geomorphic variables and fish distribution

BRT model performances were relatively high (cross-validated AUC > 0.7) for most individual species models, with the exception of common bream and tench (Table 6.4). Water body size was the most important predictor explaining the probability of occurrence of eurytopic bream and ruffe and rheophilic ide (Table 6.4), whereas flood extent was the most significant predictor explaining the occurrence of eurytopic white bream and black-striped pipefish (Table 6.4). Common bream and ruffe were most frequently present in large water bodies, whereas the distribution of white bream was also strongly positively associated with large flood extent (Fig. 6.4A,B). Similarly rheophilic ide and spined loach were most frequently found in large water bodies with a large flood extent (Fig. 6.4A,B). For limnophilic tench and eurytopic gibel carp the shore line development and shoreline index were the most important predictors explaining their occurrence. Tench was found across a range of water body sizes and showed a strong association with well-developed shorelines, just like gibel carp, which also showed a negative association with flood extent. Eurytopic black-striped pipefish were strongly associated with intermediate flood extent and well-developed shorelines.

Predictions of species occurrence across the 3518 water bodies identified that distribution patterns varied across the species, as shown for the distribution of common bream, white bream, gibel carp and ide (Fig. 6.5A,B). Common bream was predicted to occur most frequently in large water bodies and they were predicted to occur along the whole study area (Fig.

6.5A). Spatial predictions for white bream and ide identified that across the water bodies which were not sampled, these species could occur more frequently in the North-Eastern part of the study area (Fig 6.5A,B) where there is a large flood extent (Fig. 6.6). Gibel carp, on the other hand, was predicted to occur most frequently in smaller water bodies and in the South-Western part of the floodplain associated with a low flood extent (Fig. 6.5B).

Table 6.4 Average percentage contributions of environmental variables to species distribution (bold indicates the variable explaining the highest proportion of the variation) and summaries of the optimal binomially distributed boosted regression tree models for species with intermediate prevalence. All models were fitted with a tree complexity of 3; lr, learning rate; n.trees, number of trees; AUC, area under the receiver operating tree; lr was optimized for each species model so that an optimal number of trees was fitted. Mean and standard errors (SE) for the predictive deviance and AUC were calculated using tenfold cross-validation.

| | Contributing variables | | | | | prevalence (%) | lr | n.trees | Null deviance | Predictive deviance (SE) | AUC (SE) |
|------------------------------|------------------------|-------------|-------------|-------------|------|----------------|--------|---------|---------------|--------------------------|----------------|
| | extent | loga-rea | SLD | SLI | year | | | | | | |
| <i>Abramis brama</i> | 5.3 | 63.3 | 23.2 | 7.6 | 0.6 | 71 | 0.0003 | 1450 | 0.63 | 0.58 (0.09) | 0.66 (0.04) |
| <i>Blicca bjoerkna</i> | 46.2 | 22.0 | 9.8 | 16.4 | 5.6 | 78 | 0.0013 | 1150 | 0.63 | 0.47 (0.08) | 0.84 (0.04) |
| <i>Carassius gibelio</i> | 21.4 | 28.5 | 13.0 | 35.4 | 1.7 | 63 | 0.0013 | 1200 | 0.65 | 0.57 (0.1) | 0.76 (0.07) |
| <i>Cobitis taenia</i> | 32.1 | 40.0 | 8.9 | 15.2 | 3.8 | 63 | 0.0006 | 1050 | 0.69 | 0.6 (0.08) | 0.72 (0.07) |
| <i>Gymnocephalus cernuus</i> | 3.7 | 70.1 | 16.4 | 9.1 | 0.7 | 44 | 0.0003 | 1000 | 0.66 | 0.64 (0.05) | 0.7 (0.06) |
| <i>Leuciscus idus</i> | 38.0 | 45.0 | 2.9 | 6.9 | 7.2 | 51 | 0.0013 | 1000 | 0.68 | 0.48 (0.09) | 0.87 (0.03) |
| <i>Syngnathus abaster</i> | 34.9 | 19.6 | 23.2 | 19.1 | 3.2 | 29 | 0.005 | 1200 | 0.57 | 0.36 (0.1) | 0.9 (0.03) |
| <i>Tinca tinca</i> | 7.4 | 12.7 | 39.1 | 33.9 | 6.9 | 45 | 0.0003 | 1100 | 0.68 | 0.67 (0.04) | 0.6 (0.04) |

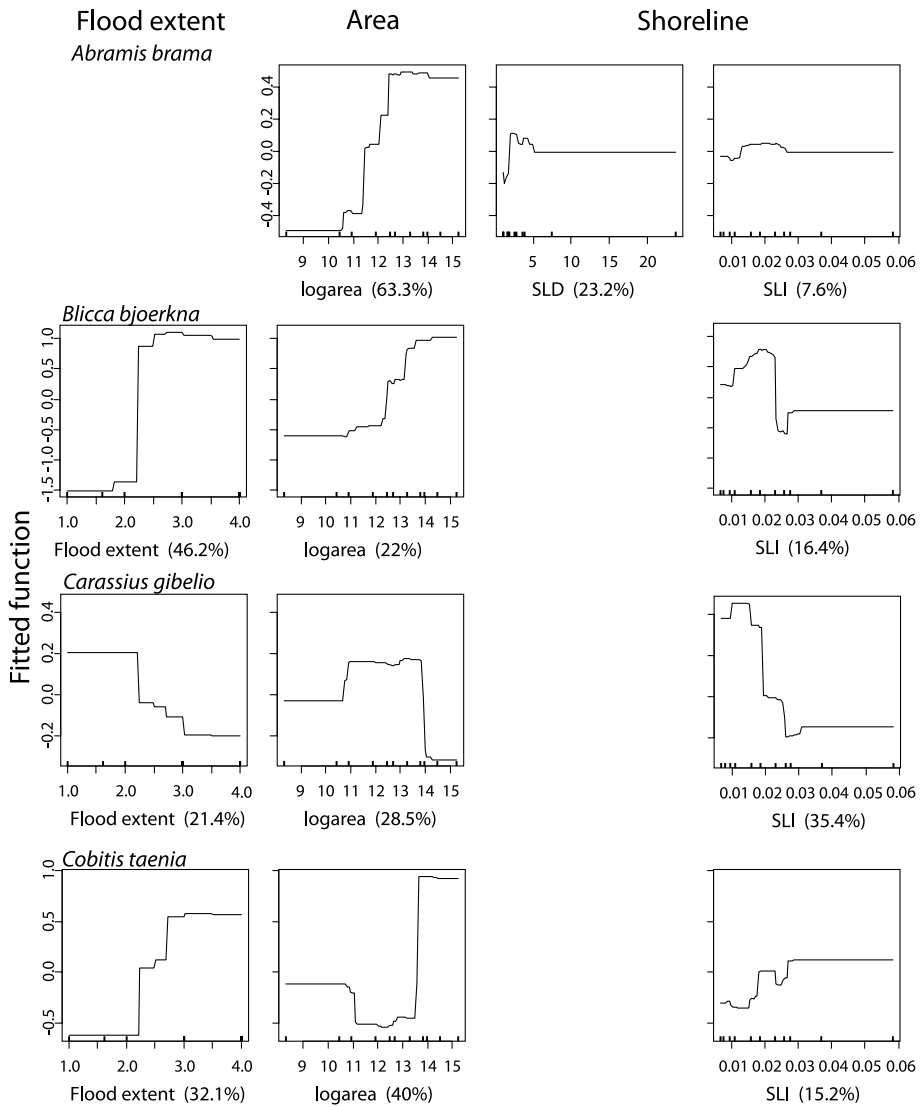


Figure 6.4A Functions fitted for the three most important predictors for four species. The functions fitted by the BRT models relate the probability of occurrence to flood extent and some features of water body geomorphology.

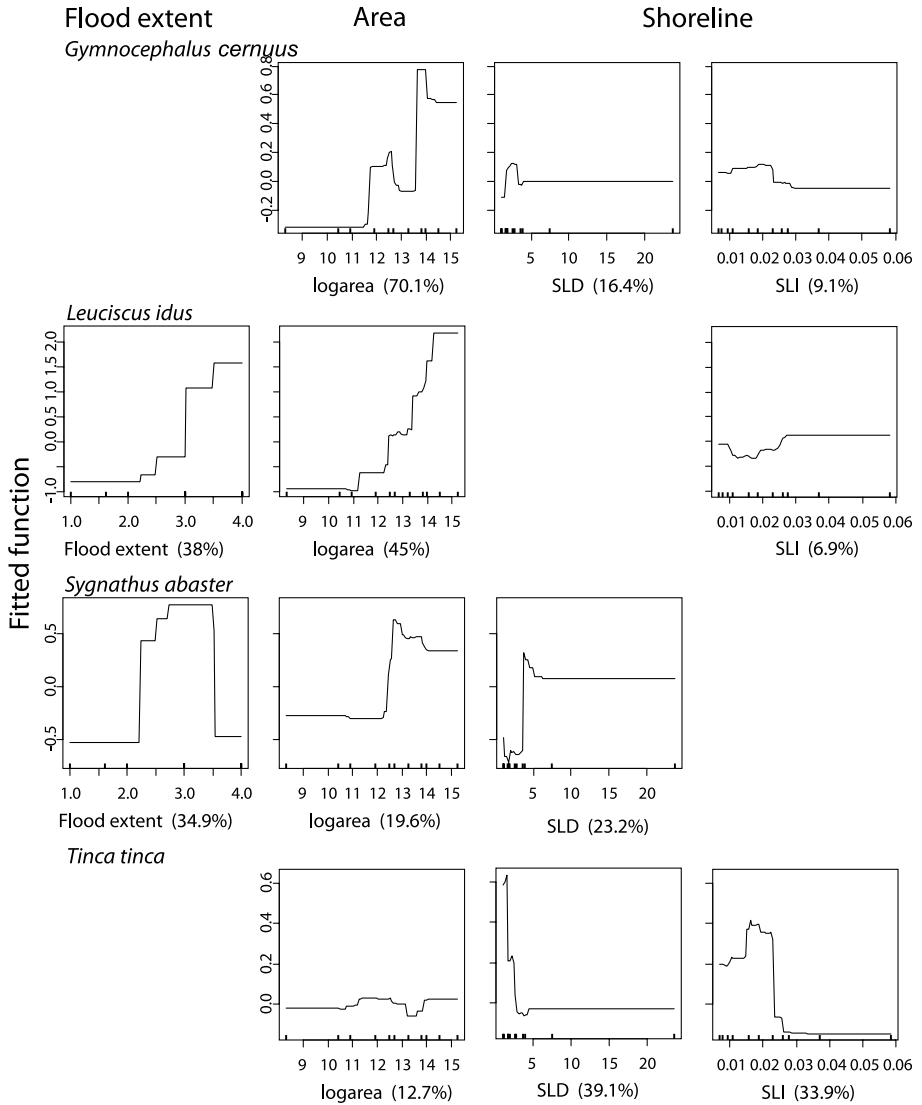


Figure 6.4B Functions fitted for the three most important predictors for four species. The functions fitted by the BRT models relate the probability of occurrence to flood extent and some features of water body geomorphology .

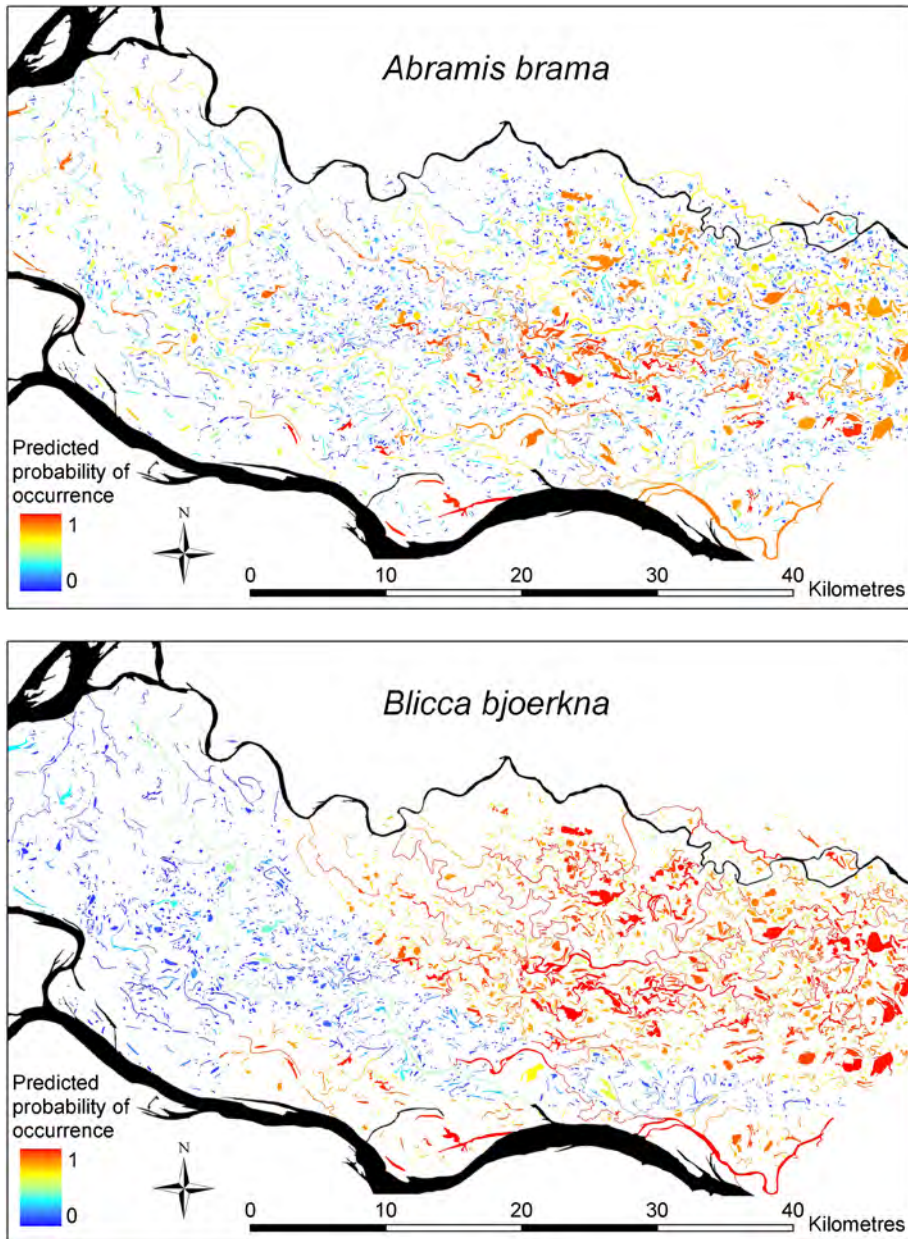


Figure 6.5A Spatial distribution of predicted probabilities of occurrence of common bream and white bream. The distributions were predicted across the sampled area using the final BRT models and estimated information for the other water bodies across the Volga-Akhtuba floodplain.

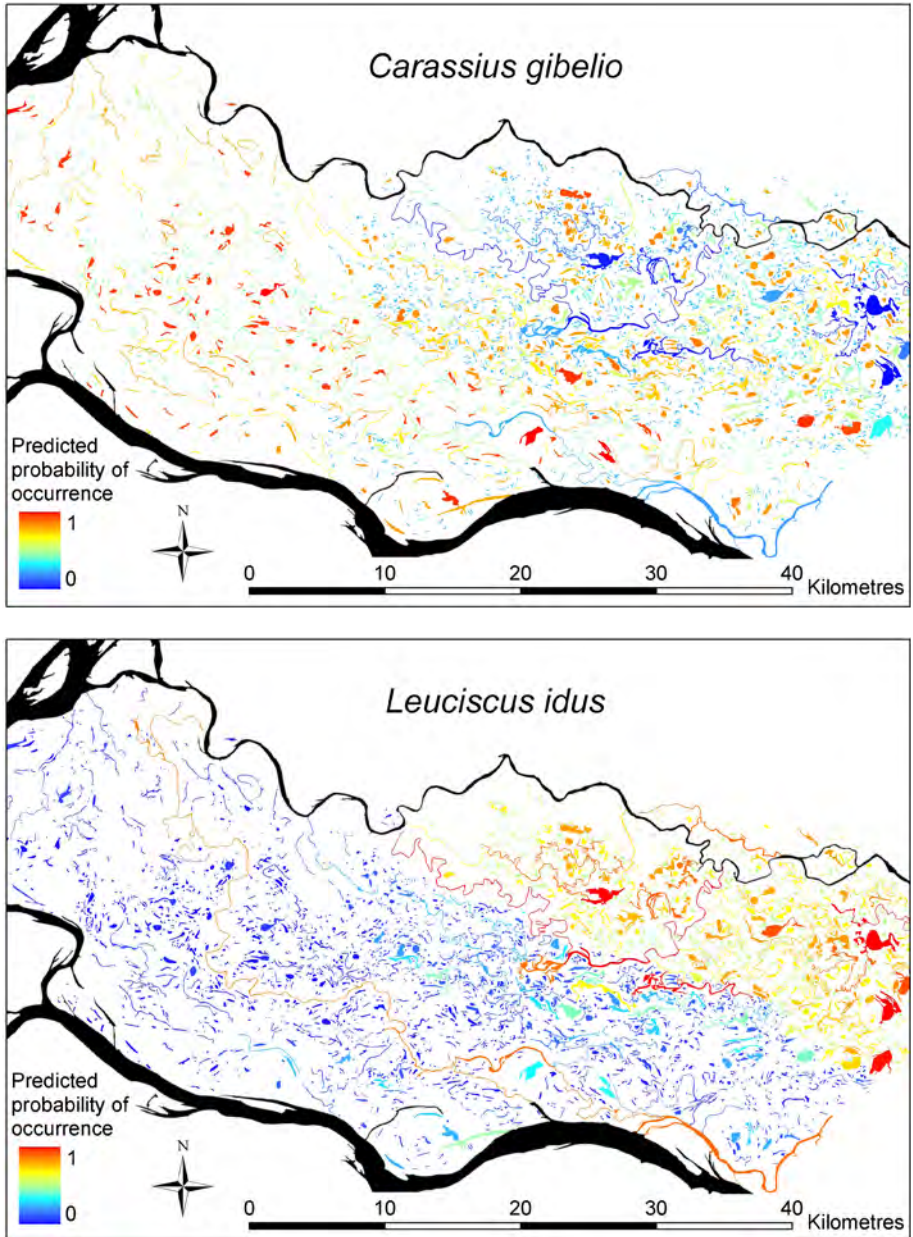


Figure 6.5B Spatial distribution of predicted probabilities of occurrence of gibel carp and ide. The distributions were predicted across the sampled area using the final BRT models and estimated information for the other water bodies across the Volga-Akhtuba floodplain.

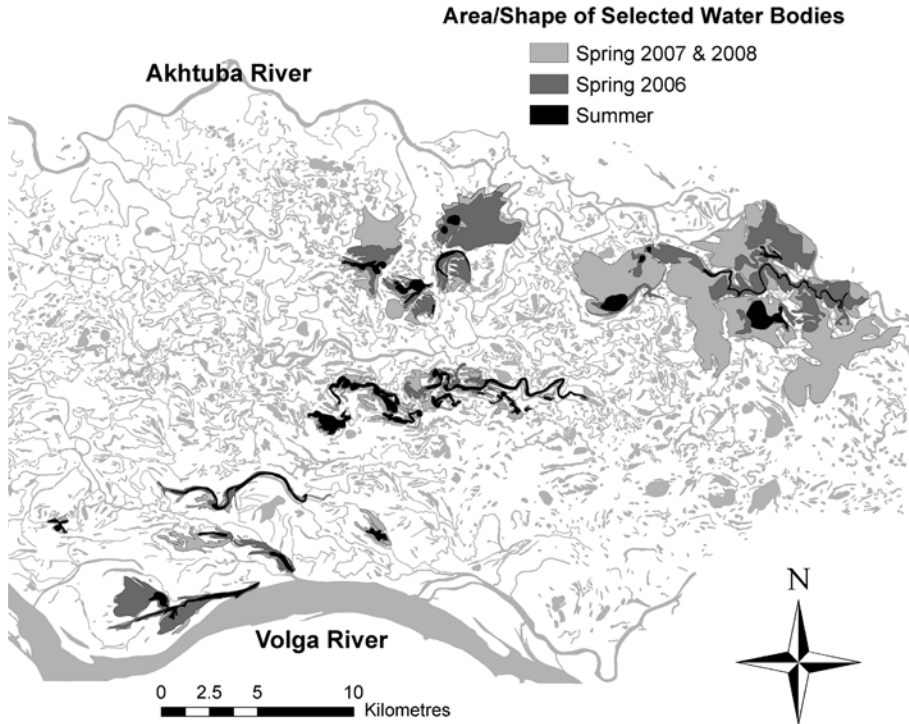


Figure 6.6 Illustration of the flood extent for selected water bodies within the floodplain in different years.

6.6 Discussion

Species occurrence at a particular location and time may be due to a combination of large-scale factors (i.e. climate, catchment geomorphology), whereas the relative abundance or biomass of a species in an assemblage is more likely driven by processes operating at the local scale, such as habitat availability and biotic interactions (Rahel, 1990). In this study we found that species distributions were strongly associated with large scale hydro-geomorphology of the floodplain whereas abundance was strongly influenced by both local geomorphology of water bodies and inter-annual flood variability.

6.6.1 Methodological uncertainties

We are aware of the possible methodological uncertainties and limitations of our data sets, which we will subsequently discuss below. Fish data were collected using a seine net, which may cause bias. However, seining was

reported to be the most effective method for sampling shallow offshore sites, compared to other methods i.e. electrofishing (Lapointe, Corkum & Mandrak, 2006). Moreover as shown by Jurajda *et al.* (2009), who also used a seine net with 10mm mesh size and compared it to point-sample electrofishing and continuous electrofishing, reported that estimates of the size structure of the fish assemblages obtained using the beach seine were similar to those obtained by electrofishing. As mentioned in the Methodology section, the analysis of the effect of year and water body on CPUE was based on 15 water bodies only. These water bodies were selected to cover a range of hydro-geomorphic features, but the conclusions drawn should be taken with caution. We observed high CV values for some species with low CPUE values (Fig. 6.3). This indicates higher variation in abundance between years for these species. However, it may also suggest that for rarer species data become more uncertain. Further difficulty arises from possible temporal auto-correlation between years within water bodies, which may obstruct the interpretation of the results of ANOVA (Nagelkerke & van Densen, 2007). These uncertainties would require larger spatial and temporal resolution of the dataset. However, because we did not find any indication of temporal auto-correlation and extensive long-term datasets are lacking for large temperate floodplains we believe that the patterns found hold important clues for further unravelling the effects of hydro-geomorphology on fish in large temperate floodplains.

6.6.2 Does variability in fish abundance relate to environmental variability?

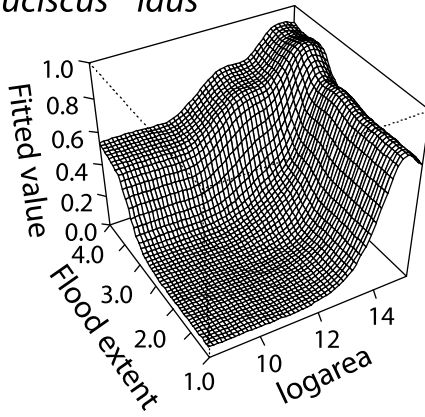
The abundances (CPUE) of many species showed significant inter-annual variation. In 2006 the abundance of common carp and gibel carp was much higher compared to 2007 and 2008, despite the severe winter hypoxia with extensive fish mortality (Sorokin, V.N.; pers. comm.) and the desiccation of some water bodies in the following summer due to low flood magnitude in 2006. In 2007 and 2008 the winters were less severe and desiccation did not occur. Both these species are known for their hypoxia tolerance (Lushchak *et al.*, 2001; Van Raaij *et al.*, 1996) and therefore might have had a selective advantage compared to other species from the specific environmental conditions occurring in 2006. Winter hypoxia may also have provided a selective advantage in recruitment for these species. Similar results were found indeed for common carp in the Midwest shallow lakes in the USA (Bajer & Sorensen, 2010). In eutrophic lakes in Finland, severe winter morta-

lities were found to lead to high zooplankton abundances, which resulted in clear water, thereby favouring visual predators such as perch and pike (Jeppesen *et al.*, 1997). In 2006, we observed slightly higher abundances of pike, but the abundances of perch did not corroborate the results of Jeppesen *et al.* (1997). Possibly, pike depends more on water clarity in capturing prey than perch that is also successful in turbid waters (Chapman & Mackay, 1984; Granqvist & Mattila, 2004; Hoogland, Morris & Tinbergen, 1956). An alternative explanation might be that annual flooding allowed dispersal and re-colonisation (Miranda, 2005), thereby reducing or diluting possible effects of winter hypoxia. The abundances of eurytopic common bream and roach, rheophilic ide and limnophilic tench did not show significant year effects, despite the differences in flood magnitude and duration between sampling years (Fig. 6.2). For all these species we found a significant effect of water body and water body \times year interactions (Table 6.3). This suggests that the role of inter-annual flood variability in structuring fish abundances is especially relevant at the spatial scale of individual water bodies and not so much on the scale of the entire floodplain. This may be a result of the large geomorphic diversity of the Volga-Akhtuba floodplain. Consequently, even with different flood magnitudes required habitats for various fish species (e.g. rheophilic to limnophilic) remain available in all years. Moreover occurrences of the most abundant species remain stable suggesting that the hydro-geomorphic characteristics maintain the distribution of fishes in the floodplain water bodies (Fig. 6.5A,B).

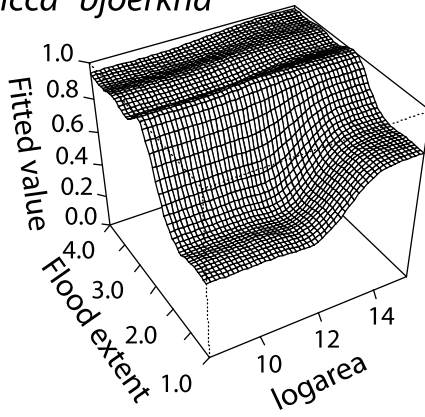
6.6.3 Does hydro-geomorphology govern fish distribution?

Large-scale geomorphology, controlling the flood extent, in combination with smaller scale geomorphology (water body size, shore line complexity) seems to control the prevalence of various flow guilds within the floodplain (Fig. 6.7). Rheophilic ide and spined loach were most prevalent in large water bodies with a high flood extent. A similar but weaker association, was found for the more eurytopic white bream (which is more often associated with running waters; Grift *et al.* (2001) reported that this species avoids isolated floodplain water bodies). By contrast, eurytopic gibel carp (often associated with stagnant waters (Lasne *et al.*, 2008)) was more prevalent in smaller water bodies with a small extent of flooding. Small water bodies with low flood extent have higher probability of exposure to harsh conditions (such as winter hypoxia or desiccation, as shown in 2006). Hypoxia to-

Leuciscus idus



Blicca bjoerkna



Carassius gibelio

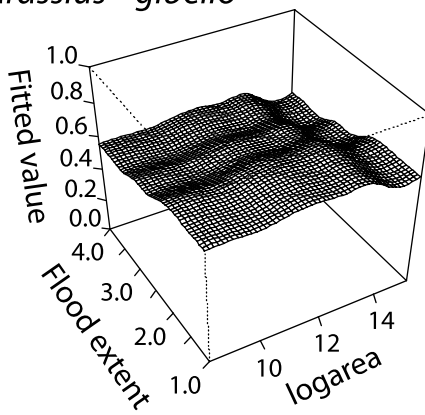


Figure 6.7 Effects of interactions between flood extent and water body area on probabilities of occurrence of selected species. The plots are based on the probability functions fitted by the BRT models.

lerance possibly allows gibel carp to take advantage in these environments over other species (Nilsson & Östlund-Nilsson, 2008; Roesner *et al.*, 2008). The distributions of eurytopic common bream and ruffe were associated with large water body size. Large floodplain water bodies often show a higher turbidity and lower macrophyte cover (Van Geest *et al.*, 2003). Turbid waters are preferred habitats for these species. Ruffe is able to select moving prey items under high turbidity (Hölker & Thiel, 1998) and does not rely on macrophytes as spawning substrate (Reshetnikov, 2002). Also common bream is typically found in turbid open waters (Lammens, Nes & Mooij, 2002) and has superior feeding abilities in these environments (Diehl, 1988). The distribution of limnophilic tench was associated with shore line complexity. Tench avoids open, clear waters (Kotrschal *et al.*, 1991), and therefore complex, usually vegetated, shorelines may be very important for its distribution. In addition, a decline in tench populations was shown to be related to a decline in littoral zone complexity (Mamcarz & Skrzypczak, 2006).

The hydro-geomorphic variables which we used seem to explain a large part of the variation in distribution patterns for many species. However, other variables may play a role too, i.e. distance to the main channel, flow velocity or chemical water quality parameters (Araujo, Pinto & Teixeira, 2009; Rodríguez & Lewis, 1997). In addition macrophyte abundance may also explain a large part of the variability in the distribution of species such as tench (Navodaru, Buijse & Staras, 2002) or black-striped pipefish (Luzhnyak & Korneev, 2006; Malavasi *et al.*, 2007). Nevertheless, some of these variables could possibly correlate with the variables we used (e.g. turbidity with lake geomorphology (Hamilton & Lewis, 1990)) and, therefore, the patterns observed would not change markedly.

6.6.4 The flood pulse, geomorphology and floodplain fish

The annual flooding and the high degree of connectivity among the water bodies of the Volga-Akhtuba floodplain enable fish dispersal during spring flooding. However, the specific characteristics of the floodplain such as flood extent are strongly associated with large-scale geomorphology. This results in significant differences between different areas which appear rigid to most of the variation in flood pulses, except perhaps for extreme flood pulses. Therefore, flooding reduces the spatial variability in environmental conditions and resulting fish communities (Thomaz, Bini & Bozelli, 2007),

but on the other hand the geomorphology influences flood characteristics and increases spatial variability.

Our main conclusion is that spatial heterogeneity of hydro-geomorphic characteristics of floodplain water bodies and the hydrological connectivity results in a spatial gradient in the occurrence of fish, as shown for 8 analysed species across the floodplain. This may suggest that assemblage structure for other species is driven by similar factors. This conclusion corroborates the results from neotropical and tropical floodplain systems (Petry, Bayley & Markle, 2003; Pouilly & Rodríguez, 2004; Rodríguez & Lewis, 1994; Rodríguez & Lewis, 1997; Saint-Paul *et al.*, 2000), proposing that fish assemblages are driven by hydro-geomorphic variables. In the Volga-Akhtuba floodplain the influence on fish distributions of inter-annual flooding may be reduced as a result of its large scale and because of the hydro-geomorphic complexity resulting in the availability of many different and extensive habitats. Consequently, the Volga-Akhtuba floodplain has more or less stable fish communities, associated with different parts of the floodplain, despite of its great dynamics. The diverse hydro-geomorphology of the floodplain, which results in high habitat diversity, was shown to be a highly significant factor influencing fish abundance and distribution and to have the ability to buffer the ecological effects of flood events that differ in magnitude. In addition, this diverse hydro-geomorphology, creates suitable habitats across ranges of fish guilds (rheophilic, eurytopic and limnophilic) resulting in high diversity and biocomplexity of the floodplain (Amoros & Bornette, 2002).

6.7 Acknowledgements

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Chapter 7

General discussion



River floodplains are increasingly appreciated for their possible role in flood protection in combination with river rehabilitation (Buijse *et al.*, 2002; Galat & Zweimüller, 2001). In addition, floodplains provide a necessary habitat for many river fishes, in particular for feeding and recruitment (Baber *et al.*, 2002; Holland & Huston, 1985; Poizat & Crivelli, 1997). Because only few naturally functioning floodplains remain, particularly in temperate regions (Tockner & Stanford, 2002), their importance for fish recruitment and diversity has mostly been explored in conceptual and semi-quantitative terms. Empirical evidence to corroborate the concepts is generally poorly available. The present study aimed at increasing such empirical knowledge on the reproduction, recruitment and distribution of fish in a temperate river floodplain. We assessed the availability, the accessibility and the predictability of floodplain habitats for the recruitment of various fish species, in an attempt to link the interactions between the floodplain's hydrology and geomorphology to fish recruitment. In this chapter the main findings of the study are summarized and discussed. Directions for future research and implications for floodplain fisheries and floodplain restoration in temperate regions are also considered.

7.1 Main findings

The present study provides a quantitative assessment of the flood pulse concept (FPC). Therefore it offers a more generic understanding of the relationship between the flood pulse and fish recruitment dynamics in temperate floodplains, which in turn may allow the assessment of potential changes in fish production and diversity under changing hydrological conditions.

Analysis of time series of discharges of the Volga at Volgograd (1879-2006) demonstrated that the flood pulse magnitude in the Volga-Akhtuba floodplain has noticeably decreased due to construction in 1960 of the Volgograd Reservoir, directly upstream of the floodplain. Still, in spite of this hydrological control, considerable year-to-year variation in flood magnitude and timing has remained (Fig. 7.1). Flood control is geared to maintain and regulate hydropower production and improve navigation, but fisheries benefits are also considered. Therefore, discharge management still provides significant spring flooding. This yearly flooding preserves the eco-hydrological functioning of the floodplain and fish populations in the Volga-Akhtu-

ba floodplain can still depend on year-to-year variations in the annual flow regime. In addition, a strong correlation was found between commercial fish catch in the floodplain and flood magnitude, suggesting increased fish recruitment and better feeding conditions in years following high floods. This corroborates with the FPC. The fact that no significant correlation was found for the commercial catch in the main channel of the Volga, suggests that fish present in the main channel benefit much less from high floods (Chapter 2).

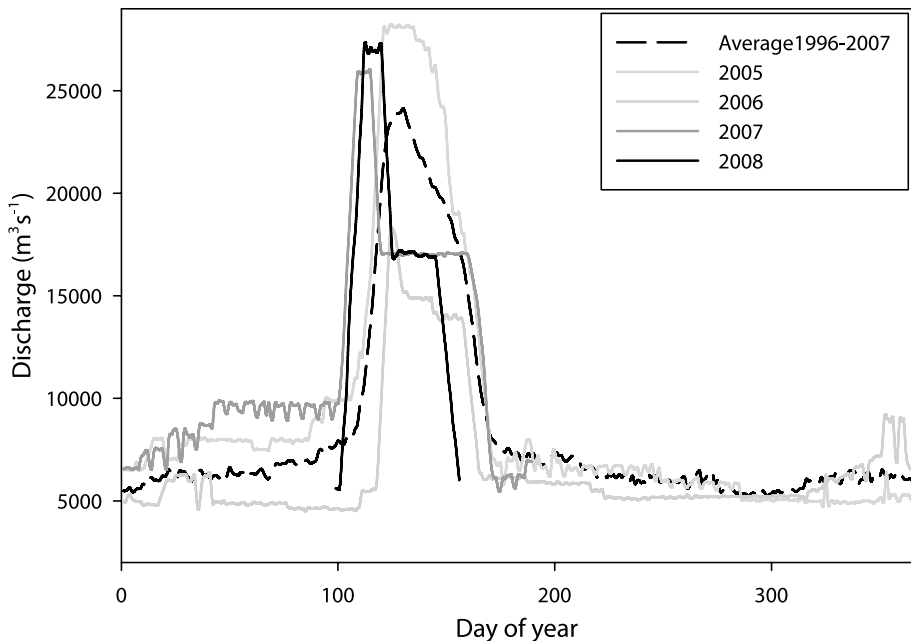


Figure 7.1 Daily discharge at the Volgograd Dam in years 2005-2008 and the mean for 1996-2007.

The field study on fish recruitment during three consecutive growing seasons (2006-2008), from spawning to 0⁺ recruits (YOY) (Chapters 3-5, Fig. 7.2) yielded the following: Spawning of rheophilic species, that release their eggs in the floodplain, was found to coincide with the flood. In contrast, the timing of spawning by eurytopic and limnophilic species was unrelated to flooding (Chapter 3). This confirms a strong species-specific response to flood dynamics, depending on life-history characteristics (King, Humphries & Lake, 2003). In addition, in the Volga-Akhtuba floodplain the main river channels (Volga, Akhtuba) act as a source of *water* for the floodplain, but not of spawning fish.

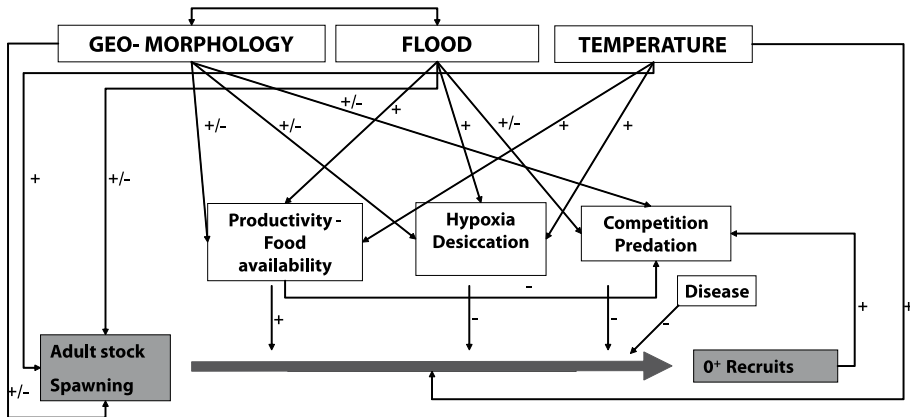


Figure 7.2 Simplified conceptual model of factors driving fish recruitment in large temperate floodplains within a growing season ('+' and '-' indicate possible positive and negative effects).

Larvae recruitment corroborates the FPC in terms of the potential importance of the high productivity of flooded terrestrial habitats. Even though during flooding larvae of most fish species were dwelling in the shoreline regions of *permanent* water bodies (Chapter 4), they may still potentially benefit from the extra food production in shallow areas. A substantial part of the production of food organisms in the flooded terrestrial habitats will be conveyed towards the main water bodies with the retreating water after the flood pulse has peaked and subsequently become available for fish fry.

The survival and growth of fish larvae results in Young of the Year (YOY, 0+) recruitment at the end of the growing season. In agreement with the FPC, YOY recruitment appeared to be primarily controlled by spring temperature and its match with flooding (Chapter 5), as shown by significantly higher YOY fish abundance in areas with extensive flooding, compared to those areas where flooding was less widespread. However, fish recruitment was also related to long-term characteristics of the water bodies within the floodplain e.g. water body size and macrophyte cover.

The diverse hydro-geomorphology of the Volga-Akhtuba floodplain, on a long time scale driven by the flood pulse, creates suitable habitats for a range of fish guilds (rheophilic, eurytopic and limnophilic) resulting in high diversity and biocomplexity of the floodplain, as predicted by the FPC (Chapter 6). On a smaller time scale the diverse hydro-geomorphology of the floodplain also buffers the ecological effects of year-to-year differences in the magnitude of the annual flood events.

7.2 Methodological considerations

This study offers substantial insight into the ecology of early life stages of fish in large river floodplain systems (order 10^1 – 10^2 km width and length). Yet, the available data are insufficient to fully explore mechanisms driving fish diversity and production in temperate floodplain systems.

The indication that the spawning stocks mainly originate from water bodies *within* the floodplain rather than from the main river channel (Chapter 3) imply that the fringes of the large-scale Volga floodplains may be enough to fulfil spawning habitat requirements for fish dwelling in the main channel, similar to backwaters and oxbow lakes which act as spawning habitats for riverine species in smaller river systems (Grift *et al.*, 2003; Hohausova, Copp & Jankovsky, 2003). Consequently, the spatial scale of the floodplain system plays an important role in its functioning. Fish populations in small or altered floodplains will depend to a larger extent on the main channel as spawning stock source (Grift *et al.*, 2001), while sources of fish may exist within large floodplains. In the latter case, the flood pulse connections between channel and habitats occur 'nested' within the large floodplain. Thus, the fish population dynamics within the large Volga-Akhtuba floodplain could be considered as 'separate' from the main channel, controlled by the flood pulse connections between the floodplain channels, lakes and terrestrial habitats. However, additional studies in large temperate floodplains are needed to determine whether this is a general principle. Moreover, the spatial scale of fish movements between different floodplain water bodies needs additional quantification.

We proposed that the significantly higher abundances of fish larvae along permanent water body shorelines compared to extensive flooded terrestrial habitats are the result of a trade-off between food availability and mortality risk due to e.g. hypoxia, desiccation and predation (Chapter 4). Despite the fact that we did not have data on food densities and predation risks, these conclusions are supported by other studies (Brown & Colgan, 1982; Gehrke, 1991; Paller, 1987). Yet, additional field sampling to quantify food availability and mortality risks associated by utilising the flooded areas is needed to confirm or falsify the proposed mechanism.

This study also supports previous hypotheses (King *et al.*, 2003; Trifonova, 1982) that flooding and its coupling with temperature is important for dri-

ving recruitment success of floodplain fish (Chapter 5). These conclusions are based on data from the relatively short time-span of three annual spawning seasons. Three years of data is more than many studies provide (King *et al.*, 2003; Zeug & Winemiller, 2008), but still, given the complexity of fish recruitment, these patterns should ideally be tested across longer time-scales.

Spatial heterogeneity of hydro-geomorphic characteristics of floodplain water bodies and the hydrological connectivity have significant effects on the distribution and abundance of most frequently occurring fish species. However, the number of water bodies we used for the analysis (43) was small, therefore these conclusions have to be considered with caution and should be verified when more data becomes available. In addition, to address distribution patterns of rare species, a more intensive sampling effort is needed. The distribution patterns of these species may indeed be more influenced by year-to-year variations in flooding and by other environmental factors. In this study, we only used a limited number of hydro-geomorphic variables. As a consequence, we did not account for all aspects of connectivity (i.e. water body permanency, distance to main channel, flow velocity). Distance to main channel and flow velocity could give additional explanations to the patterns observed in fish distribution. We also did not take into account water quality parameters. However, environmental variables such as temperature, dissolved oxygen concentration, pH and conductivity proved to be less important factors for structuring the distribution of fish communities in floodplain systems (Araujo, Pinto & Teixeira, 2009).

7.3 Flood dynamics and fish recruitment

This study confirms that flooding coupled with suitable temperatures can be essential for spawning, nursery and resulting recruitment of fish species that use the floodplain (Chapters 3-5), as hypothesized in the FPC (Junk, Bayley & Sparks, 1989).

Inter-annual variability of floods and ambient temperature in the Volga-Akhtuba floodplain is substantial (Fig. 7.3). The match between species-specific environmental requirements for spawning and growing with the environmental conditions occurring during a specific year in terms of timing, duration and height of the flood pulse and water temperature, results in 'opportunity windows' which are suitable for the spawning or growth of

young fish of a particular species. Since different fish species in the floodplain have different life-history strategies this will result in complex and diverse recruitment responses (King *et al.*, 2003; Zeug & Winemiller, 2008). In the following I will use this concept of opportunity windows to further explore and discuss the potential for fish recruitment, depending on floodplain topography, flood pulse magnitude and other environmental factors.

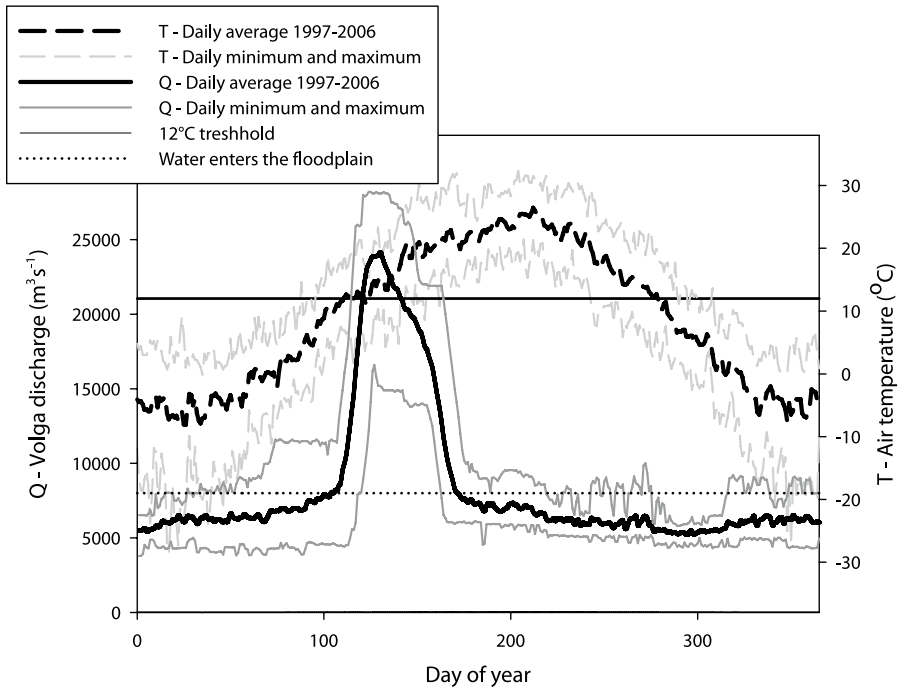


Figure 7.3 Seasonal dynamics of mean, maximum and minimum discharge and air temperature during 1997-2006.

The majority of fish species inhabiting the Volga-Akhtuba floodplain such as roach *Rutilus rutilus*, common bream *Abramis brama*, perch *Perca fluviatilis* and pike *Esox lucius* spawn once per year (Chapter 5, Table 5.1). Spawning is more or less synchronized, because these species are dependent on opportunity windows in which suitable spawning temperatures become available in suitable floodplain habitats (Górski *et al.*, 2010). As emphasized by the FPC (Junk *et al.*, 1989), **flooding coupled with suitable temperatures** can be essential for growth and recruitment of these species because spring and summer are associated with high food production for larval fish in the floodplain. A decoupling of flooding and suitable temperatures (i.e. mismatch) will result in poor recruitment because of the limited availability of spawning and nursery areas, or because of a reduction in food producti-

on. More opportunistic species, with multiple spawning events throughout spring and summer, such as gibel carp *Carassius gibelio*, sunbleak *Leucaspis delineatus*, and ruffe *Gymnocephalus cernuus*, might be less dependent on such spawning opportunity windows. They may also recruit successfully when suitable spawning temperatures and flooding are decoupled, and then might have a selective advantage over one-time spawners. However, also these species will depend on the growing opportunity window for YOY recruits and benefit from high food production when flooding is coupled with warm temperatures.

Next to flooding coupled with suitable temperatures, flood magnitude, flood duration, inter-annual predictability of floods, and the rate of change in the water level, appear to be the main aspects of flooding that can influence the opportunity windows for spawning and growing.

First, **flood magnitude** controls the extent of the inundated area and therefore the availability of temporarily flooded habitats (Fig. 7.4A, B). These habitats are associated with high productivity (Herwig *et al.*, 2004) and hence floodplain productivity will increase when larger parts of terrestrial areas are flooded, resulting in a strong positive impact on recruitment (Wilzbach *et al.*, 2002). In systems such as the Volga-Akhtuba floodplain where groundwater influence is small for most of the water bodies (Sheppel, 1986), flood magnitude also controls the water levels of water bodies during summer. Floods of low magnitude, such as the one in 2006, caused drying of some of the more isolated water bodies (Fig. 7.5) and favoured hypoxia-tolerant species (such as gibel carp). Recruitment of this species may be driven by environmental instability such as hypoxia (Bajer & Sorensen, 2010). Furthermore, drying out also consolidates sediments and favours aquatic macrophyte dominance in the subsequent year (Van Geest *et al.*, 2005) creating a more suitable habitat for macrophyte-associated species such as rudd *Scardinius erythrophthalmus* and tench *Tinca tinca*.

Secondly, **flood duration** controls the strength of biotic responses to flooding (Poff *et al.*, 1997). Longer flood durations will increase the probability of the co-occurrence of flooding and suitable temperatures for spawning and growth and thus extend the duration of the opportunity windows (Chapter 5, Fig. 5.2). However, very long duration may create areas of poor water quality (low oxygen levels) in the floodplain and can again reduce fish recruitment (Gehrke, 1991; Junk *et al.*, 1989).



Figure 7.4A Flooded terrestrial habitats of the Volga-Akhtuba floodplain – grasslands



Figure 7.4B Flooded terrestrial habitats of the Volga-Akhtuba floodplain – forested habitats



Figure 7.5 Dried water bodies after low flood in 2006

Thirdly, the **predictability of annual floods** favours the development of morphological, behavioural, and physiological adaptations of aquatic organisms to flooding (Bayley, 1991; Junk *et al.*, 1989) and therefore it is essential for successful fish recruitment. Floods in the Volga-Akhtuba floodplain are relatively predictable since they result from snowmelt in the upper catchment and are controlled by the Volga cascade management, whereas heavy rains causing smaller flood pulses are absent due to the reservoir regulation and dry local climatic conditions (Averina *et al.*, 2000). Consequently, species that are adapted to flooding, i.e. adjusted to large scale temporal and spatial variability, have the most successful recruitment in this floodplain. Such species are usually large sized, long lived, and spawning once per year (having periodic life history traits *sensu* Winemiller (1989)). Common bream, roach and pike seemed to have better recruitment in areas with larger flood extent (Chapter 5). However, more opportunistic species may have a selective advantage when floods become less predictable as a result of, for example, Volga cascade management changes (Chapter 2). We observed much higher abundances of the more opportunistic, batch-spawning gibel carp in 2006 (extremely low flood, compared to average after Volgograd dam construction).

Fourthly, the **rate of rise and fall of the water level** will influence the range and strength of biotic responses to flooding. A slow or moderate rise and fall in water level is likely to improve recruitment, since young fish benefit from the habitat availability as the slowly retreating water will provide a source of food from highly productive flooded grasslands (Junk *et al.*, 1989). Sudden changes in the water level may result in fish displacement downstream (Nunn *et al.*, 2003), and in fish stranding. These processes appear not to play an important role in large scale floodplain systems such as the Volga-Akhtuba floodplain, because flow velocities over the inundated floodplain are reduced due to its complex geomorphology. Only in the main floodplain channels, flow velocities in the order of 0.2 – 0.8 m/s were observed. In smaller scale floodplains and possibly along the margins of large scale floodplains these processes may play a more important role.

The coupling of a sufficiently high temperature with the availability of inundated habitats creates opportunity windows which are essential for fish recruitment in floodplains. However, this relationship between flood pulse, temperature and fish recruitment may differ between rivers. As classified by Winemiller (2004), rivers display at least three general patterns in relation to

flow and temperature dynamics: 1) temperate with aseasonal flood pulses, 2) temperate with seasonal flood pulses and 3) tropical with seasonal flood pulses. The relationships between flooding and fish spawning and recruitment are probably most tight in seasonal systems. The flood pulses in the lower Volga show a cyclic pattern of high spring flows related to the melting of snow (Chapter 2), providing a relatively predictable flow and temperature regime to which fish may respond adaptively (Resh *et al.*, 1994).

Fish recruitment analyses within this study concentrated on the spring flood period. However, conditions operating outside this period may also play an important role in fish recruitment. We did not have quantitative data on possible factors influencing YOY recruitment after water retreat during summer. We only measured the result of these processes and expressed them as abundance of YOY at the end of growing season (Chapter 5). Nevertheless, initial spawning conditions need to be favourable to enable successful recruitment in the first place and the concept that both flooding and temperature can have a positive effect on both spawning and recruitment is already well documented (Winemiller, 2004). Of course, extreme summer conditions, both abiotic (such as anoxia and desiccation) and biotic (competition and predation) may influence, and in extreme circumstances even obscure, the effect of successful spawning. It is however more likely that successful or unsuccessful spawning is enforced by subsequent higher or lower temperatures. For instance, the relatively cold summer in 2008 may have additionally reduced recruitment in that year, because of decreased productivity of food organisms (Chapter 5).

7.4 Winter mortality

In addition to spring and summer temperatures and flood pulse dynamics, winter mortality also has to be considered to understand fish recruitment and the resulting fish communities in the Volga-Akhtuba floodplain. The floodplain lies in the continental climatic zone (Averina *et al.*, 2000), and is exposed to severe winters with long periods of air temperatures below 0°C (Fig. 7.3). Subsequently freezing of water bodies may result in massive fish mortality. For instance, the severe winter of 2005/2006 caused extensive fish mortality (Fig. 7.6), which in 2006 may have led to a lower predation pressure on YOY, and thus a very abundant year-class, in spite of the relatively small flood magnitude that spring (Chapter 5). A similar mechanism

was also demonstrated for perch *Perca fluviatilis* and roach *Rutilus rutilus* in eutrophic lakes in Finland (Ruuhijärvi *et al.*, 2010). In lakes, winter fish-kills can have cascading effects on the lower trophic levels, which in turn, may lead to conspicuous changes in the fish community (Jeppesen *et al.*, 1997). For instance, if the majority of zooplanktivorous fish die during winter, the abundance, body size and grazing pressure of zooplankton increase, potentially resulting in a clear water phase in the next spring. In turn, clear water favours visual predators such as perch and pike over benthivorous fish, reducing sediment disturbance, maintaining the clear water phase and facilitating macrophyte growth (Scheffer, 1998). In floodplain ecosystems, seasonal flooding allows for the connection and exchange of fish stocks during spring and as a consequence possibly diminishes these effects of winter freezing. Winter hypoxia may also provide a selective advantage for the recruitment of specific species such as common carp *Cyprinus carpio*, a world-spread invasive species originating from the lower Volga region. In shallow lakes in the Midwest of the USA this species could only recruit in significant numbers when shallow spawning habitats suffered from severe winter hypoxia. When common carp used these disturbed habitats, competition with other species and predation on early life stages was reduced, resulting in a more successful recruitment (Bajer & Sorensen, 2010).



Figure 7.6 Freezing mortality of fish in winter 2005/2006 in lake Bezchasnoye

7.5 Flooding and floodplain: fish meta-community dynamics

Meta-community dynamics can create spatial and temporal resilience of floodplain fish communities. A meta-community consists of a network of communities that are linked by the dispersal of potentially interacting species (Holyoak, Leibold & Holt, 2005; Leibold *et al.*, 2004). Meta-communities can exist as spatially structured communities along environmental gradients whose constituent species are linked by dispersal processes. However, the spatial location of the communities and their constituent species can change through time (Holyoak *et al.*, 2005; Leibold *et al.*, 2004). Understanding the processes that sustain the network of constituent communities will add to our understanding of how fish diversity would be impacted by fragmentation of habitats and loss of connectivity between communities.

The fish communities constituting the meta-community of the floodplain ecosystem are spread along environmental gradients and are connected by seasonal flooding. In the Volga-Akhtuba floodplain these environmental gradients underlie patterns in fish communities (Chapter 6). The inter-annual flood pulse variability may influence these gradients and, consequently, the long term availability and quality of aquatic habitats and their associated fish species. For example, year-to-year variability of flood magnitude may result in annual variations in the depth of water bodies and thus change resource availability in the floodplain by controlling terrestrial inputs. It will also alter the susceptibility of these water bodies to winter mortalities or desiccation. This may cause local (and temporary) extinctions and favour certain communities (in this case a hypoxia tolerant community, such as reported in the Volga-Akhtuba floodplain in 2006, Chapters 5 and 6). Communities may not re-establish in the same location after extinction and may be replaced by a different community type. Subsequent flooding may then result in homogenization of the meta-community, by allowing connection and exchange of stocks. The main river channels as well as some floodplain water bodies which are less prone to environmental changes may act as a source for various species and therefore provide a mechanism facilitating recruitment after local extinctions. In conclusion, the flood pulse seems to have a governing role in structuring floodplain fish communities by on one hand creating spatial habitat heterogeneity and, on the other hand,

homogenizing the meta-community through connecting the communities during high water periods. Large-scale floodplain systems such as the Volga-Akhtuba floodplain accommodate many 'refugia' for recolonisation; therefore the resilience of the meta-community is maintained.

7.6 The possible effects of human-induced pressures on fish recruitment in the floodplain

Worldwide, floodplains have been utilized by humans since the dawn of civilisation (Junk & Wantzen, 2004; Tockner *et al.*, 2010). River-floodplain systems provide a wide array of ecosystem goods and services such as supply of fresh water and food (agriculture and fisheries), but also recreation, transport, water quality protection and wildlife habitat (Costanza *et al.*, 1997; Tockner *et al.*, 2010). The extensive availability of resources and services also makes floodplains highly attractive for human exploitation resulting in the majority of floodplains being threatened by human activity (Tockner *et al.*, 2010; Tockner & Stanford, 2002).

Like many floodplains in the world, the Volga-Akhtuba floodplain is exposed to multiple human-induced alterations (Fig. 7.7) either directly, such as damming, water extraction, land-use change and fishing, or indirectly through possible climate change. These alterations affect floodplain geomorphology, change the dynamics of the flood pulse or affect fish stocks by legal and illegal fisheries. These may all impact the ecological functioning of the floodplain and hence fish recruitment.

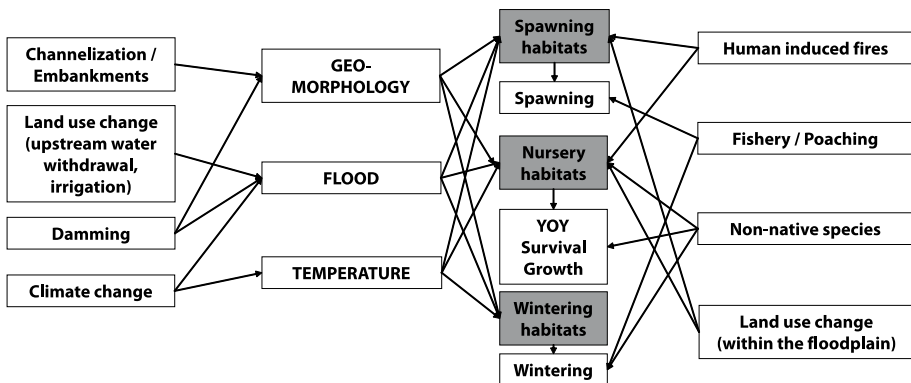


Figure 7.7 Schematic overview of human activities affecting floodplain functioning and fish recruitment

One of the major alterations is the construction of the cascade of reservoirs in the upper Volga. These reservoirs reduced the magnitude and duration of spring flood pulses and altered their timing (Chapter 2). The shorter flood durations could be associated with a de-coupling of flooding and suitable temperatures for spawning and growth of young fish, which might reduce fish recruitment. Moreover, human settlement within the floodplain and use of the floodplain grasslands for cattle grazing and hay production increased (Fig. 7.8). Many kilometres of dikes were constructed in the Western floodplain to protect settlements and agricultural lands from flooding, substantially reducing flooded habitats for fish.



Figure 7.8 Grasslands used for hay production in the Volga-Akhtuba floodplain

Commercial fisheries (with catches in the water bodies of the Western floodplain making up to 97 and 180 tons in respectively 1999 and 2001 (unpublished data from Leninsk Fisheries Inspection; fishing companies also operate in other years, but no further data is available), sport fishing (Fig. 7.9) and poaching (Fig. 7.10) may impact spawning stocks.

Due to an increased human presence in the floodplain in recent years, the Volga-Akhtuba floodplain has been exposed to frequent human-induced



Figure 7.9 Recreational fisherman in the Volga-Akhtuba floodplain



Figure 7.10 Examples of various poaching techniques used in the lower Volga; 'Barrel' used to catch fish at the shorelines of shallow lakes; large hooks used for sturgeons; Small pieces of gillnets deployed on a rope and lifted when entangled fish are visually detected ('TV nets')

fires. For example, in 2006 and 2007 substantial areas of the floodplain within the Nature Park were locally burned (Fig. 7.11; the Nature Park 'Volga-Akhtuba Floodplain'). When such large areas are exposed to fire, the availability of structural habitat elements, such as tree trunks, and large plant stems will be severely reduced, which may affect habitat suitability for fish spawning and fish nurseries. Burning may also affect water quality, for instance increase the availability of nutrients, dissolve inorganic carbon and alter the pH (Battle & Golladay, 2009). As a result productivity and food availability for (aquatic) consumers might be increased, as was shown for wildfires (Dunham *et al.*, 2007; Koetsier, Tuckett & White, 2007). The effects of fires on aquatic ecosystems are variable and depend on the severity of the fires, but severe fires may have long-lasting effects on the functioning of wetland ecosystems (Koetsier *et al.*, 2007; Malison & Baxter, 2010).

In addition to the effects of habitat alteration, native fish populations are also affected by the introduction of non-native species such as gibel carp which can reach high abundances (Chapter 2). Early maturation, high fecundity and batch spawning are life-history traits making gibel carp very successful in the variable floodplain environment, especially during extreme conditions. Due to its hypoxia tolerance (Lushchak *et al.*, 2001; Roesner *et al.*, 2008), it can take advantage of habitats avoided by other species (Chapter 4 and 5).

The aforementioned direct alterations of the floodplain may be superimposed on the potential increase in atmospheric temperatures and changes in the water cycle because of climate change (Stocker & Raible, 2005). Higher air temperatures will likely lead to earlier snowmelt and to a lower proportion of precipitation falling as snow (Barnett, Adam & Lettenmaier, 2005). In watersheds which are mainly fed by snowmelt, such as the Volga River, this can lead to elevated winter peak flows and decreased spring flows (Barnett *et al.*, 2005; Stewart, Cayan & Dettinger, 2004). Various effects of these changes for fish recruitment in the floodplain can be hypothesized. Reduced flooding will likely decrease the amount of available fish spawning and nursery habitats and lead to higher probabilities of low water levels. This will lead, in turn, to an increased probability of hypoxia and desiccation of water bodies, which may favour hypoxia-tolerant species such as non-native gibel carp. A reduced magnitude and duration as well as a shifted timing of floods may decrease the probability to co-occur with temperatures suitable for spawning and YOY growth and thus reduce the duration of opportunity

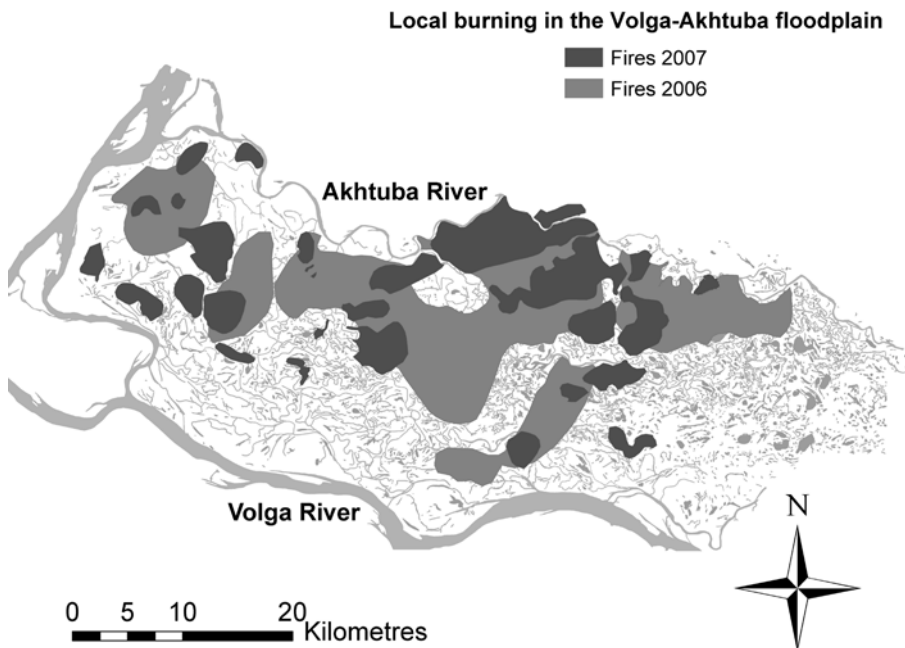


Figure 7.11 Burned floodplain area (top) and map showing the extent of local burning in the floodplain in 2006 and 2007

windows for fish recruitment (Chapter 5). However, the atmospheric temperatures are predicted to increase too, which will also affect the timing of spawning and the duration of opportunity windows. Earlier flooding might favour species that spawn in lower temperatures. Or perhaps more unpredictable flooding will favour more opportunistic species spawning multiple times within a year. How this will affect food availability for young fish and growing opportunity windows still remains an open question.

Furthermore, increased human population growth may lead to increased water withdrawal for human uses (Vörösmarty *et al.*, 2000). This may be accelerated by the current fast economic growth of the Russian Federation. An increased water withdrawal will further reduce the amount of water that is available for spring inundation of the floodplain.

7.7 Implications for floodplain management and restoration

This study confirms that the integrity of the annual flood pulses is very important for fish recruitment in the floodplain systems. Consequently, it implies that it is crucial to preserve the flood pulse because it permits high connectivity and habitat diversity, and as a result of this, high floodplain productivity and diversity.

Attempts to preserve and restore floodplain ecosystems are underway worldwide. Examples are the Danube River, Rhine River (Europe), Kissimmee River (North America), and the Murray River (Australia) (Bernhardt *et al.*, 2005; Hein *et al.*, 1999; Jensen, 2002; Nienhuis *et al.*, 2002). However, to improve the success of these attempts, an understanding of the relationship between fish recruitment and the physical environment of the floodplain is important. Multiple human-induced impacts work in concert to alter diversity and productivity of floodplains. Hence, these factors need to be considered simultaneously when developing management concepts. Future management strategies should carefully take the dependence of fish recruitment on the flood pulse into consideration. Moreover, management goals of floodplain ecosystems are complex and often conflicting. This study suggests that a crucial factor for preserving fish recruitment success is the maintenance of spatio-temporal opportunity windows for spawning and growth of fish species. Even under changing environmental and social

circumstances such opportunity windows should be preserved to save fish recruitment and diversity in the floodplain. Careful discharge management, aiming at a prolonged flood pulse and increasing the probability of the co-occurrence of habitat availability and suitable temperatures is essential to optimize the benefits for fish production and fisheries in the floodplain (Opperman *et al.*, 2009). The Volga-Akhtuba floodplain appears to be a nested system with diverse functional units with various flood pulses from floodplain channels to lakes, resulting in diverse habitats. The diversity of these units, which is essential for fish diversity and resilience of the floodplain, needs to be preserved in order to maintain full ecological functioning of the floodplain. Post-damming changes in floodplain geomorphology (Chapter 2) may require additional management actions to preserve floodplain diversity and productivity.

7.8 Future perspectives

This study addresses some of the knowledge gaps regarding the various factors that govern fish recruitment in large river floodplains. However, more knowledge needs to be acquired to achieve a comprehensible understanding of the complex floodplain processes controlling the productivity and diversity of these systems.

In recent years, advanced models to simulate 2D hydraulics of water flow over floodplains became available (Horritt & Bates, 2002). Until now, they have been mainly applied to assess flood damage or to study overbank deposition. It would be very interesting to apply these hydraulic models also to quantitatively predict responses of various ecological processes and floodplain fish recruitment to different flooding scenarios. Such models may be useful to indicate possible responses of fish recruitment, and other ecological processes operating within the floodplain ecosystem, to various environmental (such as climate change) and management scenarios. Modelling various scenarios may help to elucidate how sensitive the different habitat types are to environmental changes, which may help in making better management decisions.

This study indicates the complex structure of large-scale floodplain systems. Various functional units nested within the Volga-Akhtuba floodplain system experience different flood pulse variation. The diversity of these

units is essential for the distribution and abundance of fish species (Chapter 6) and the resilience of the floodplain to extremes. However, the processes which control the functional linkages between these floodplain units need more quantification. For example, the scale and frequency of occurrence of within-floodplain fish movements for spawning or dispersal; or the transportation of nutrients and food organisms between functional units; or the dynamics of naturally (by flood duration) or human-induced (by burning) water quality alterations.

The quantification of the processes that control fish meta-populations that inhabit floodplains is challenging, but deserves further research. For example, what is the significance of different habitat patches for populations of the various fish species that constitute the floodplain meta-community and dispersal of fish along different spatial and temporal scales? This may help to understand the impact of reduced habitat complexity and connectivity (due to human impact) on the ecological integrity of floodplain systems. Novel genetic and chemical (such as otolith microchemistry) methods may help to unravel some of these processes (Woods *et al.*, 2010; Zeigler & Whitley, 2010).

Finally, comprehensive floodplain knowledge enables the development of sustainable management strategies. The number of stakeholders involved with floodplains is high which potentially leads to more conflicts such as an increased water demand for domestic use, agriculture and hydropower. At the same time, floodplains contain unique nature values that deserve conservation or rehabilitation. Finding a balance between these conflicting needs and pressures are great challenges for the future management of floodplain ecosystems. Therefore the development of suitable decision making and communication tools needs to be addressed (Poff *et al.*, 2003).

7.9 References

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8

Lastly



8.1 Summary

Natural river floodplains are among the most diverse and productive ecosystems on Earth. Fisheries in large rivers and their associated floodplains provide a major source of food, employment and income which is crucial to sustain the livelihoods of multitudes of people. In addition, floodplains play a role in retaining water, mitigating floods, and breaking down pollutants. Periodic flooding (flood pulse) plays a principal role in the ecological processes in floodplain systems. Natural variations in the magnitude, duration and timing of the flood pulse drive high habitat complexity, which in turn results in high biodiversity and productivity.

Recruitment is a crucial component of population dynamics. It plays an essential role in the life history of fish, because the survival of juveniles largely determines the size of adult populations. Floodplains play a key-role in the life cycle of many fish species, especially in relation to recruitment. Therefore fish faunas of large rivers are highly adapted to the natural hydrological regime, i.e. the timing and duration of floodplain inundation.

The *Flood Pulse Concept* (FPC) is the main transversal concept in large river ecology, proposing mechanisms governing the functioning of floodplains and their role for river ecosystems. The FPC states that temporary flooding of the aquatic-terrestrial transition zones bordering the rivers (the flood pulse) is the main determinant of floodplain habitat heterogeneity, plant and animal recruitment, as well as ecosystem productivity. However, little progress has been made in exploring the FPC over larger spatial scales due to the lack of empirical data. To make rational decisions about the quality and extent of river rehabilitation in relation to fish biodiversity and production, it is essential to understand the ecological functioning of floodplains and the relationship between fish recruitment and the characteristics of the flood pulse.

The objective of this thesis was to reveal mechanisms governing fish recruitment in a large-scale temperate floodplain in relation to flooding and temperature dynamics, and thus provide a generic understanding of the relation between the flood pulse and fish recruitment dynamics in floodplains. The study aimed at testing the FPC in a large-scale semi-natural floodplain by (1) analyzing flood pulse dynamics in response to changes in river flow regime at various spatial and temporal scales; (2) relating these dynamics

to recruitment success of riverine fish species that use the floodplain and (3) identifying the hydro-geomorphic variables that are most involved in shaping abundance and distribution of fish in the floodplain.

The central hypothesis of the study was that: **'The characteristics of the flow regime ('the flood pulse') determine the recruitment of fish populations that use the floodplains. Thus, there is a quantitative and causal relationship between flood pulse characteristics and fish recruitment.'**

The study was executed in the Volga-Akhtuba floodplain (lower Volga, Russian Federation), one of the few remaining naturally functioning, large-scale floodplains (it is 10-30 km wide, extends over a length of 300 km and accommodates thousands of lakes and residual floodplain channels) in the temperate zone. The study constitutes of five interrelated parts (Chapters 2-6).

In **Chapter 2**, the characteristics of the annual flood pulse of the lower Volga and its effect on the commercial fish catches in the area are analyzed. The results of these analyses demonstrate that the flood pulse magnitude in the Volga-Akhtuba floodplain has noticeably decreased due to construction of the Volgograd Reservoir, directly upstream of the floodplain, in 1960. Still, in spite of this hydrological control, considerable year-to-year variation in flood magnitude and timing has remained. Flood control is geared to maintain and regulate hydropower production and improve navigation, but fisheries benefits are also considered. As a result, discharge management still provides significant spring flooding. This yearly flooding preserves the eco-hydrological functioning of the floodplain and fish populations in the Volga-Akhtuba floodplain can still depend on annual variations in the year-to-year flow regime. In addition, a strong correlation was found between commercial fish catch in the floodplain and year to year variations in flood magnitude.

In **Chapter 3**, the role of the flood pulse on the spawning of fishes in the floodplain is evaluated. We found that only the spawning of rheophilic species, that released their eggs in the floodplain, coincided with the flood. In contrast, the timing of spawning by eurytopic and limnophilic species was unrelated to flooding. In addition, the populations of resident fish were

shown to be the main source of the spawning stocks in the Volga-Akhtuba floodplain. The main river channels act as the main source of *water* for the floodplain, but not of spawning fish. Instead, the majority of the spawning stocks originate from the floodplain water bodies. The main river channels, however, possibly act as a source for re-colonisation of fish when extreme environmental conditions, such as freezing or desiccation cause extinctions of local populations.

In **Chapter 4**, the habitat use of fish larvae in relation to the flooding is examined. In the Volga-Akhtuba floodplain during the flood, larvae of most fish species were dwelling in the shoreline regions of *permanent* water bodies and hardly used flooded terrestrial habitats. Possibly as a result from a trade-off between food availability and mortality risk due to desiccation, hypoxia and predation, which are supposed to be higher in the flooded areas. Flooded terrestrial habitats produce food organisms that are conveyed with the flood water back towards the main water bodies when water levels retreat after the flood pulse and can then be utilized by fish fry. Thus, the flooded areas appear to function more as an indirect food source for fish larvae than a direct nursery.

In **Chapter 5**, the effects of the extent, timing and duration of flooding and temperature variability on the recruitment success of young fish (YOY) at the end of the growing season are reported. This recruitment appeared to be primarily controlled by spring temperature and its coupling with flooding. Floodplain areas with a large extent and longer duration of flooding accommodated significantly higher densities of young fish, especially species characterized by periodic life history traits (large body size, delayed maturation, high fecundity and low parental investment) such as pike *Esox lucius*, roach *Rutilus rutilus* and ide *Leuciscus idus*. This confirmed that extended inundation improves the recruitment of fish in the floodplain. Gibel carp *Carassius gibelio*, a species tolerant to high temperatures and hypoxia, did especially well in small water bodies in the driest parts of the floodplain. In addition, fish recruitment of some species was also related to long-term characteristics of the water bodies within the floodplain e.g. water body size (bleak *Alburnus alburnus*) and macrophyte cover (rudd *Scardinius erythrophthalmus*).

In Chapter 6, the effects of flood variability and geomorphology of floodplain water bodies on fish abundance and distribution are analyzed. It was

found that the Volga-Akhtuba floodplain accommodated relatively stable fish communities, associated with different parts of the floodplain, despite of its great dynamics. We found that species distributions were strongly associated with large scale hydro-geomorphology of the floodplain, whereas abundance was strongly influenced by both local geomorphology of water bodies and inter-annual flood variability.

In conclusion, this study confirms that the integrity of the annual flood pulses is very important for fish recruitment in the temperate floodplain systems. The match between species-specific environmental requirements for spawning and growing with the environmental conditions occurring during a specific year in terms of timing, duration and height of the flood pulse and water temperature, results in 'opportunity windows' which are suitable for the spawning or growth of young fish of a particular species. Consequently, a crucial factor for fish recruitment in floodplain systems is the maintenance of these spatio-temporal opportunity windows for spawning and growth of fish. Even under changing environmental and social circumstances such opportunity windows should be preserved to maintain fish recruitment and diversity in large floodplains.

8.2 Аннотация

Ненарушенные поймы рек относятся к наиболее разнообразным и продуктивным экосистемам на Земле. Рыболовство на крупных реках и в связанных с ними поймах является важным источником пищи, занятости населения и дохода, что является ключевым фактором в устойчивости жизни для множества людей. Кроме того, поймы аккумулируют воду, играют роль в снижении угрозы затопления во время половодья и очищают загрязнения. Периодическое затопление (flood pulse) играет ведущую роль в экологических процессах, протекающих в пойменных системах. Естественные изменения в амплитуде, продолжительности и времени наступления половодья влекут за собой разнообразие местообитаний, что, в свою очередь, обуславливает высокие биоразнообразие и продуктивность.

Пополнение является решающим компонентом динамики популяций. Оно играет существенную роль в истории жизни рыб, поскольку выживание молоди во многом определяется количеством взрослых особей в популяции. Поймы играют ключевую роль в жизненных циклах многих видов рыб, особенно по отношению к воспроизводству. Поэтому ихтиофауна больших рек высоко адаптирована к естественному гидрологическому режиму, то есть времени и продолжительности затопления поймы.

Концепция пульса половодий - *The Flood Pulse Concept (FPC)* - есть главная всеобъемлющая концепция в экологии крупных рек, в рамках которой предложены механизмы управляющие функционированием пойм и объяснена их роль в экосистеме реки. FPC устанавливает, что временное затопление водно-наземных переходных зон, граничащих с реками (the flood pulse), есть главный определяющий фактор многообразия пойменных местообитаний, воспроизводства растений и животных, а также продуктивности экосистемы. Однако недостаточно полно выяснена работа FPC на больших пространствах из-за недостатка эмпирических данных. Чтобы принимать рациональные решения по поводу качества и масштаба восстановления реки относительно биоразнообразия и продуктивности рыб, очень важно понимать экологическое функционирование пойм и связь между воспроизводством рыбы и характеристиками половодий.

Цель данного диссертационного исследования заключается в выявлении механизмов управляющих пополнением запасов рыб в пойме крупной реки умеренного климата в связи с динамикой затопления и температурного режима воды и, таким образом, в общем понимании связи между периодичностью половодий и динамикой воспроизводства рыбы в поймах. Целью исследования было тестирование концепции FPC в полустественной пойме крупной реки путем: (1) анализа динамики периодичности половодий как результата изменения режима течения реки в различных пространственных и временных масштабах; (2) увязки этой динамики с успешностью воспроизводства речных видов рыб, использующих пойму для нереста и (3) идентификации гидро-геоморфологических переменных, которые наиболее существенно влияют на формирование численности рыб и на ее распределение в пойме.

Центральная гипотеза исследования заключается в следующем: **«Характеристики режима течений («периодичности половодий») определяют воспроизводство популяций рыб, использующих поймы для нереста. Таким образом, существует количественная и причинно-следственная связь между характеристиками периодических половодий и воспроизводством рыбы».**

Исследование проводилось в Волго-Ахтубинской пойме (Нижняя Волга, Российская Федерация), одной из немногих крупномасштабных (распространяется на длину 300 км и ширину 10-30 км) пойм умеренного климата, сохранившихся в естественном состоянии. Работа состоит из пяти взаимосвязанных частей (Главы 2-6).

В **главе 2** анализируются характеристики ежегодных периодических половодий на Нижней Волге и их влияния на коммерческое рыболовство. Результаты этого анализа показывают, что масштаб половодий в Волго-Ахтубинской пойме существенно сократился после сооружения в 1960 году Волгоградского водохранилища выше поймы по течению. Однако, несмотря на регулирование стока, значительные межгодовые колебания уровня и изменения времени наступления половодья сохранились. Контроль стока направлен на выработку и регулирование электроэнергии и улучшение условий навигации, но интересы

рыболовства также учитываются. В итоге регулирование расходов через плотину Волжской ГЭС все еще обеспечивает существенное затопление поймы во время весеннего половодья. Ежегодные половодья сохраняют эко-гидрологическое функционирование поймы и популяции рыб в Волго-Ахтубинской пойме, как и раньше, зависят от межгодовых вариаций режима стока. Кроме того, была обнаружена тесная связь между объемами коммерческих выловов и межгодовых изменений амплитуды половодий.

Третья глава посвящена оценке влияния «пульса половодий» на нерест рыб в пойме. Мы обнаружили, что нерест только реофильных видов, которые мечут икру в пойме, совпадает с половодьем. Наоборот, время нереста эвритопных и лимнофильных видов не было связано с затоплением поймы. Кроме того, популяции рыб, постоянно живущих в пойме, составляют большую часть нерестовых стад в Волго-Ахтубинской пойме. Основные реки и ерики выступают источниками воды в пойме, но не источниками нерестящейся рыбы. Большинство рыб выходит на нерест из водных объектов внутри поймы. Основные реки, однако, могут служить источниками заселения поймы рыбой в случае наступления экстремальных условий среды, таких как промерзание или пересыхание, влекущих за собой сокращение локальных популяций.

В **главе 4** исследуется заселение местообитаний поймы личинками рыб в зависимости от половодья и его характеристик. В Волго-Ахтубинской пойме во время половодья личинки большинства видов рыб держатся у берегов *постоянных* водных объектов, но не на периодически затапливаемых местообитаниях. Вероятно, это результат поиска равновесия между доступностью пищи и риском гибели от пересыхания, гипоксии и хищничества, которые предположительно выше на затапливаемых территориях. Периодически затапливаемые территории поставляют пищу для мальков в основные водоемы на спаде половодья. Таким образом, периодически затапливаемые территории являются косвенным источником пищи для личинок рыб, но не основной средой, в которой происходит рост рыбы.

В **пятой главе** описывается влияние масштаба, времени наступления и продолжительности половодья и динамики температурного режима воды на успех воспроизводства сеголеток в конце сезона.

Выяснилось, что это воспроизводство в первую очередь зависит от весеннего температурного режима и взаимосвязи температуры воды и затопления. Те районы поймы, в которых воды во время половодья больше и задерживается она дольше, сосредотачивают значительно большее количество молоди рыб, особенно тех видов, которые характеризуются четко выраженными жизненными циклами (большие размеры тела, позднее созревание, высокая плодовитость и незначительный родительский уход за потомством). К ним относятся щука *Esox lucius*, плотва *Rutilus rutilus* и язь *Leuciscus idus*. Это подтверждает тот факт, что большее по масштабам половодье улучшает воспроизводство рыбы в пойме. Серебряный карась *Carassius gibelio* – вид, толерантный к высоким температурам и гипоксии, хорошо себя чувствовал в небольших водоемах поймы в наиболее засушливых ее участках. Кроме того, воспроизводство некоторых видов рыб было связано с долгосрочными характеристиками водных объектов внутри поймы, например, с размером водоема (уклейка *Alburnus alburnus*) и наличие высшей водной растительности (красноперка *Scardinius erythrophthalmus*)

В **шестой главе** анализируется влияние изменчивости затопления поймы и геоморфологии пойменных водоемов на численность рыбы и ее пространственное размещение. Выяснено, что в Волго-Ахтубинской пойме обитают относительно стабильные сообщества рыб, приуроченные к различным участкам поймы, несмотря на большую динамичность системы. Мы определили, что распределение видов было в значительной степени связано с крупномасштабными гидро-геоморфологическими процессами в пойме, в то время как обилие рыбы в большой мере определялось как микрорельефом водных объектов, так и межгодовыми колебаниями уровня воды.

В заключении, настоящее исследование подтверждает, что сохранившееся постоянство ежегодных затоплений очень важно для воспроизводства рыбы в пойменных системах умеренного климата. Соответствие между видоспецифичными требованиями для нереста и роста с условиями окружающей среды, возникающими в определенные годы по началу, продолжительности, высоте паводка и температуры воды выражается в наличии «окон благоприятствования», которые являют собой сочетание подходящих условий для нереста или роста молоди рыб определенного вида. Следовательно, важнейшим

условием для воспроизводства рыбы в пойменных системах является обеспечение таких пространственно-временных окон благоприятствования для нереста и роста рыб. Даже под воздействием изменения окружающей среды и социальных условий такие окна благоприятствования обязательно должны быть сохранены для обеспечения воспроизводства рыбы и сохранения ее разнообразия в поймах крупных рек.

8.3 Samenvatting

Riviervloedvlaktes in hun natuurlijke staat behoren tot de meest diverse en productiefste ecosystemen ter wereld. Visserij in grote rivieren en hun vloedvlaktes levert voedsel, werkgelegenheid en inkomen op die cruciaal zijn voor het levensonderhoud voor grote aantallen mensen. Bovendien spelen vloedvlaktes een rol in het vasthouden van water, het verminderen van extreme waterstanden en de afbraak van verontreinigingen. Periodieke overstromingen (de zogenaamde overstromingspuls, beter bekend onder de Engelse benaming 'flood pulse') spelen een belangrijke rol in ecologische processen van vloedvlaktesystemen. Natuurlijke variatie in de hoogte, duur en timing van de overstromingspuls zorgt voor een grote habitatcomplexiteit, die op haar beurt resulteert in hoge biodiversiteit en productiviteit.

Rekrutering van jonge vis is een cruciaal onderdeel van populatiedynamica van visbestanden. Het speelt een essentiële rol in de levenscyclus van vis, want de overleving van jonge vis bepaalt grotendeels de omvang van de populaties volwassen vissen. Vloedvlaktes spelen een sleutelrol in de levenscyclus van vele vissoorten, vooral in relatie tot rekrutering. De visfauna is daarom sterk aangepast aan het natuurlijke hydrologische regime, d.w.z. aan de timing en duur van overstroming van de vloedvlakte.

Het *Overstromingspulsconcept* ('Flood Pulse Concept' –FPC – in het Engels) is het belangrijkste transversale concept in de ecologie van grote rivieren. Het FPC veronderstelt mechanismen die het functioneren van vloedvlaktes en hun rol in rivierecosystemen bepalen. Het FPC stelt dat de tijdelijke overstroming van de aquatisch-terrestrische zone langs de randen van rivieren (overstromingspuls) in belangrijke mate zowel de habitatheterogeniteit van de vloedvlakte, de rekrutering van planten en dieren als de productiviteit van het ecosysteem bepaalt. Er is echter weinig voortgang geboekt in het onderzoeken van het FPC door een gebrek aan empirische data. Om rationale beslissingen te kunnen nemen over herstel van rivieren in relatie tot biodiversiteit van vis en productie, is het essentieel om het ecologische functioneren van vloedvlakten en de relatie tussen visrekrutering en de karakteristieken van de overstromingspuls te begrijpen.

Het doel van dit proefschrift was om mechanismen bloot te leggen die de visrekrutering in een grootschalige, gematigde vloedvlakte bepalen in relatie tot overstromings- en temperatuurdynamiek. Dit zou tot een beter generiek begrip kunnen leiden van de relatie tussen de overstromingspuls en de dynamiek van visrekrutering in vloedvlaktes. Dit onderzoek beoogde het FPC te testen in een grootschalige vloedvlakte door (1) de overstromingsdynamiek te relateren aan veranderingen in het afvoerregime van de Wolga op verschillende ruimtelijke en tijdschalen, (2) de overstromingsdynamiek te relateren aan het rekruteringssucces van riviervis die de vloedvlakte gebruikt, (3) identificeren van de hydro-geomorfologische variabelen die bepalend zijn voor de talrijkheid en verspreiding van vis in de vloedvlakte.

De centrale hypothese van dit onderzoek was dan ook: **'De karakteristieken van het afvoerregime (overstromingspuls) bepalen de rekrutering van vispopulaties die de vloedvlakte gebruiken. Er is daardoor een kwantitatief en oorzakelijk verband tussen de overstromingspuls-karakteristieken en de rekrutering van vis.'**

Dit onderzoek is uitgevoerd in de Wolga-Akhtuba vloedvlakte (Beneden-Wolga, Russische Federatie), één van de weinige overgebleven natuurlijk functionerende vloedvlaktes (10-30 bij 300 km groot en met duizenden meertjes en strangen) in de gematigde zone. Het onderzoek bestaat uit vijf onderling gerelateerde onderdelen (Hoofdstukken 2-6).

In **Hoofdstuk 2** worden de karakteristieken van de jaarlijkse overstroming (overstromingspuls) in de Beneden-Wolga en de effecten hiervan op de commerciële visvangsten in het gebied geanalyseerd. De resultaten van deze analyses laten zien dat de hoogte van de overstromingspuls in de Wolga-Akhtuba vloedvlakte merkbaar lager is geworden door de aanleg van het, direct stroomopwaarts van de vloedvlakte gelegen, Wolgograd reservoir in 1960. Maar ondanks deze hydrologische ingreep varieert de hoeveelheid water waaruit de overstromingspuls bestaat nog steeds van jaar tot jaar, evenals de precieze begin- en einddatum. Het beheer van de rivierafvoer is afgestemd op de waterkrachtwinning en scheepvaart, maar ook de benedenstroomse visserijbelangen worden meegenomen. Hierdoor vindt er in het voorjaar nog steeds een aanmerkelijke overstroming van de Beneden-Wolga plaats. Deze jaarlijkse overstroming houdt het ecohydrologische functioneren van de vloedvlakte in stand en de vispopulaties in de Wolga-Akhtuba-vloedvlakte kunnen nog steeds 'rekenen' op de

jaarlijkse variaties in het afvoerregime. Bovendien is een sterke relatie gevonden tussen de commerciële visvangsten en de jaar op jaar variatie in de hoogte van de vloed.

In **Hoofdstuk 3** is de rol die de overstromingspuls heeft op het paaien van vis in de vloedvlakte geëvalueerd. We vonden dat alleen het paaien van de rheofiele soorten die hun eieren afzetten in de vloedvlakte, samenviel met de vloed. De timing van het paaien door eurytope en limnofiele soorten was daarentegen gerelateerd aan de overstroming. Bovendien bleek dat het merendeel van de paaibestanden afkomstig was van lokale vispopulaties. De hoofdstromen van de rivieren fungeren als belangrijkste bron van *water*, maar niet van paaierende vis. In tegendeel, het grootste deel van de paaibestanden was afkomstig van wateren in de vloedvlakte zelf. De hoofdstromen van de rivieren zouden wel een rol kunnen spelen als bron voor herkolonisatie van vis na lokale uitsterfing door extreme omstandigheden als langdurige bevroering of uitdroging van wateren in de vloedvlakte.

In **Hoofdstuk 4** is onderzocht hoe het habitatgebruik van vislarven is gerelateerd aan het overstromen van de vloedvlakte. In de Wolga-Akhtubavloedvlakte gebruikten de meeste vislarven de oeverzones van *permanente* wateren tijdens de overstroming en nauwelijks de tijdelijk overstromde terrestrische habitats. Mogelijk is dit het gevolg van een afweging tussen enerzijds voedselbeschikbaarheid en anderzijds het sterfterisico door uitdroging, zuurstofloosheid en predatie, die waarschijnlijk hoger zijn in de overstromde delen. Overstromde terrestrische habitats produceren voedselorganismen die met het terugtrekkende water na de vloed worden meegevoerd naar wateren in de vloedvlakte en aldaar benut kunnen worden door vislarven. De overstromde gebieden lijken daardoor eerder te functioneren als een indirecte voedselbron voor vislarven dan als een direct opgroeigebied.

In **Hoofdstuk 5** zijn de effecten weergegeven die de uitgestrektheid, timing en duur van de overstroming en variatie in temperatuur hebben op de rekrutering van eerstejaars vis aan het einde van het groeiseizoen. Deze rekrutering leek voornamelijk te worden bepaald door de voorjaarstemperatuur en de koppeling met de overstroming. Vloedvlaktegebieden met een relatief uitgestrekte en lange overstroming huisvesten significant hogere dichtheden aan jonge vis, vooral van soorten met een 'periodieke' levenscyclus (grote lichaamsgrootte, late volwassenheid, hoge vruchtbaarheid

en geringe ouderzorg) zoals snoek *Esox lucius*, blankvoorn *Rutilus rutilus* en winde *Leuciscus idus*. Dit bevestigde dat uitgestrekte overstromingen de rekrutering van vis verbetert. Giebel *Carassius gibelio*, een soort die bestand is tegen hoge temperasturen en lage zuurstofgehalten, deed het vooral goed in kleine wateren in de 'droogste' delen van de vloedvlakte. Daarnaast was de rekrutering van sommige vissoorten gerelateerd aan lange-termijn kenmerken van de wateren in de vloedvlakte zoals omvang van het waterlichaam (alver *Alburnus alburnus*) en waterplantenbedekking (ruisvoorn *Scardinius erythrophthalmus*).

In **Hoofdstuk 6** zijn de effecten van geomorfologie van wateren in de vloedvlakte en variatie in de overstromingspuls op de verspreiding en talrijkheid van vis geanalyseerd. Het bleek dat de Wolga-Akhtuba-vloedvlakte, ondanks de grote dynamiek, relatief stabiele visgemeenschappen huisvestte, die samenhangen met verschillende delen van de vloedvlakte. We vonden dat de verspreiding van soorten sterk samenhang met de grootschalige Hydro-geomorfologie van de vloedvlakte, terwijl talrijkheid sterk werd beïnvloed door zowel locale geomorfologie als tussenjaarlijkse variatie in de vloed.

Concluderend bevestigt dit onderzoek dat de aanwezigheid van jaarlijkse overstromingspulsen erg belangrijk is voor de rekrutering van vis in vloedvlaktes van rivieren in de gematigde zone. Het overeenkomen van soortspecifieke behoeftes aan milieuomstandigheden voor paai en opgroei met de milieuomstandigheden zoals die in een specifiek jaar voorkomen voor wat betreft timing, duur en hoogte van de overstromingspuls en watertemperatuur, resulteert in 'gelegenheidsvensters' die geschikt zijn voor de paai en opgroei van een bepaalde vissoort. Als gevolg hiervan is het behoud van de spatio-temporele gelegenheidsvensters voor paai en opgroei van vis cruciaal voor de rekrutering van vis in vloedvlaktesystemen. Zelfs onder veranderende milieu- en socio-economische omstandigheden zouden deze gelegenheidsvensters behouden moeten worden om de rekrutering van vis en diversiteit in grote vloedvlaktes van rivieren veilig te stellen.

8.4 Streszczenie

Naturalne obszary zalewowe rzek należą do najbardziej zróżnicowanych i produktywnych ekosystemów na Ziemi. Rybactwo w dużych rzekach i związanych z nimi obszarach zalewowych stanowią ważne źródło pożywienia, zatrudnienia i dochodów dla wielu ludzi. Ponadto, obszary zalewowe odgrywają rolę w retencji wody, zmniejszaniu ryzyka powodzi, i biologicznej utylizacji zanieczyszczeń. Okresowe powodzie (impulsy powodzi, flood pulses) odgrywają bardzo istotną rolę w procesach ekologicznych ekosystemów zalewowych. Naturalne różnice w wielkości, czasie trwania i czasie występowania tych impulsów powodzi kształtują wysoką złożoność siedlisk, co wiąże się z dużą różnorodnością biologiczną i produktywnością. Rekrutacja nowych osobników jest zasadniczym elementem dynamiki populacji. Odgrywa istotną rolę także w życiu ryb, ponieważ wielkość populacji dorosłych zależy w znacznej mierze od przetrwania młodych osobników. Obszary zalewowe odgrywają kluczową rolę w cyklu życiowym wielu gatunków ryb, szczególnie w odniesieniu do rekrutacji. Dlatego ichtiofauna dużych rzek jest przystosowana do naturalnego reżimu hydrologicznego, czyli terminów i długości zalewania terenów zalewowych.

Flood Pulse Concept (Koncept Impulsu Powodzi, FPC) jest w ekologii główną teorią opisującą poprzeczne zależności w wielkich rzekach i proponuje mechanizmy regulujące funkcjonowanie obszarów zalewowych i ich rolę w ekosystemach rzecznych. Według FPC czasowe zalanie wodno-łądowego przejścia granicznej strefy rzeki (impuls powodzi) jest głównym wyznacznikiem różnorodności zwierząt i roślin siedlisk zalewowych, rekrutacji, jak również produktywności tych ekosystemów. Jakkolwiek niewielkie postępy poczyniono w badaniu FPC na większych skalach przestrzennych ze względu na brak danych empirycznych. Przy podejmowaniu racjonalnych decyzji, co do sposobu i zakresu rehabilitacji rzek w odniesieniu do bioróżnorodności ichtiofauny i produkcji ryb, istotne jest, aby zrozumieć ekologiczne funkcjonowanie obszarów zalewowych oraz stosunki między rekrutacją ryb i charakterystyką impulsów powodzi.

Celem niniejszej pracy było poznanie mechanizmów rządzących rekrutacją ryb w dużych zalewowych rzekach klimatu umiarkowanego, w nawiązaniu do dynamiki powodzi i temperatury, a tym samym wyjaśnienie relacji między impulsami powodzi i dynamiką rekrutacji ryb na obszarach zalewowych. Przetestowano teorie FPC na terenach zalewowych dużych, na-

turalnie funkcjonujących rzek poprzez (1) analizę dynamiki impulsów powodzi w związku ze zmianami przepływu wody w głównym korycie rzeki, w różnych skalach przestrzennych i czasowych, (2) odniesiono tę dynamikę do dynamiki sukcesu rekrutacji rzecznych gatunków ryb, które korzystają z obszarów zalewowych oraz (3) określono jakie warunki hydro-geomorfologiczne są najbardziej zaangażowane w kształtowanie i rozmieszczenia ryb w rozlewiskach.

Główna hipoteza badań była następująca: **“Właściwości systemu przepływu wody (‘the flood pulse’, ‘impuls powodzi’) reguluje rekrutację populacji ryb, które korzystają z terenów zalewowych. Tak więc występuje ilościowy i przyczynowy związek między cechami impulsów powodzi i rekrutacją ryb.”**

Badanie zostało zrealizowane w rozlewisku Wołga-Ahtuba (dolna Wołga, Federacja Rosyjska), jednym z niewielu wielkich (około 300 km długości, 10-30 szerokości), zachowanych, naturalnie funkcjonujących obszarów zalewowych w klimacie umiarkowanym. Badanie zostało podzielone na pięć połączonych ze sobą części (rozdziały 2-6).

W **rozdziale 2** zostały przeanalizowane cechy rocznych impulsów powodzi dolnej Wołgi i ich wpływ na komercyjne połowy ryb w tej strefie. Wyniki analiz wskazują, że wielkość impulsów powodzi w rozlewisku Wołga-Ahtuba znacznie spadła z powodu budowy w 1960 roku zbiornika ‘Wołgograd’ powyżej obszarów zalewowych. Głównym zadaniem zbiornika jest kontrola przepływu wody w rzece, produkcji energii elektrycznej oraz poprawa żeglugi. Nie mniej jednak zarządzanie przepływem wody uwzględnia również interesy rybactwa. Zrzuty wody nadal wywołują lokalne wiosenne powodzie. Coroczne powodzie zachowują ekohydrologiczne powiązania terenów zalewowych z rzeką a populacje ryb nadal mogą wykorzystywać pozytywny wpływ powodzi. Ponadto stwierdzono silny związek między komercyjnymi połowami ryb w rozlewisku i corocznymi zmianami w wielkości powodzi.

W **rozdziale 3** oceniane jest oddziaływanie impulsu powodzi na tarło ryb w rozlewisku. Okazało się, że tylko tarło ryb reofilnych, które składają ikrę w rozlewiskach, zbiega się z czasem powodzi. Tarło gatunków eurytopowych i limnofilnych nie miało związku z powodzią. Ponadto populacje ryb zamieszkujące jeziora i strumienie rozlewisk okazały się głównym

źródłem stad tarłowych w rozlewisku Wołga-Ahtuba. Sama rzeka działa głównie jako źródło wody dla terenów zalewowych, a nie tarlaków. Rzeka, jednak prawdopodobnie stanowi zasób tarlaków przy rekolonizacji tych terenów w ekstremalnych warunkach środowiskowych, takich jak całkowite zamrożenie lub wysychanie, które może być przyczyną wymierania lokalnych populacji.

W **rozdziale 4** opisano wyniki badań dotyczących wykorzystywania siedlisk przez larwy ryb w odniesieniu do powodzi. W rozlewisku Wołga-Ahtuba podczas powodzi, larwy większości gatunków ryb przebywają na płycznach stałych zbiorników wodnych i prawie nie wykorzystują zalanych siedlisk. Prawdopodobnie jest to w wyniku kompromisu między dostępnością żywności oraz ryzykiem wysuszenia, niedotlenienia czy presji drapieżników, które prawdopodobnie są wyższe w zalanych obszarach. Zalane tereny są źródłem pokarmu, który może być wykorzystywany przez narybek, gdy poziom wody opada po powodzi, a wraz z cofającą się wodą do głównych zbiorników wodnych spływają różnego rodzaju organizmy pokarmowe. W związku z tym obszary zalewowe wydają się raczej funkcjonować, jako pośrednie źródło pokarmu dla narybku, niż bezpośrednie siedliska.

W **rozdziale 5** opisano wyniki dotyczące skutków czasu wystąpienia powodzi oraz zmian temperatury na sukces rekrutacji młodych ryb (YOY) na koniec okresu wegetacji. Rekrutacja wydaje się być przede wszystkim kontrolowana przez temperaturę wiosną i jej zintegrowanie z powodzią. Obszary zalane w większym stopniu i na dłuższy czas, cechowała znacznie większą gęstość młodych ryb, zwłaszcza gatunków charakteryzujących się dużymi rozmiarami ciała, późną dojrzałością płciową, wysoką płodnością oraz brakiem opieki nad potomstwem takimi jak szczupak *Esox lucius*, płoć *Rutilus rutilus* oraz jaź *Leuciscus idus*. Potwierdza to, że przedłużony czas zalania zwiększa rekrutację ryb w rozlewiskach. Srebrny karaś *Carassius gibelio*, gatunek odporny na wysokie temperatury i niedotlenienie, radził sobie szczególnie dobrze w małych zbiornikach wodnych, podatnych na wysychanie. Ponadto rekrutacja niektórych gatunków ryb związana była również z długoterminowymi właściwościami zbiorników w rozlewiskach np. wielkością zbiornika (ukleja *Alburnus alburnus*) czy pokryciem roślinami wodnymi (wzdręga *Scardinius erythrophthalmus*).

W **rozdziale 6** analizowano skutki powodzi i geomorfologii zbiorników terenów zalewowych na bogactwo i dystrybucję ryb. Stwierdzono, że tereny

zalewowe Wołga – Ahtuba zamieszkują stosunkowo stabilne zespoły ryb, związane z bardzo różnorodnymi terenami zalewowymi. Rozmieszczenie gatunków ryb było ściśle związane z geomorfologią tych terenów w skali makro, podczas gdy liczebność zależała głównie od lokalnych warunków hydrogeomorfologicznych i rocznej zmienności skali powodzi.

Podsumowując, niniejsze badania potwierdziły wpływ różnic wielkości powodzi (impulsów powodzi) na rekrutację nowych roczników ryb na terenach zalewowych rzek klimatu umiarkowanego. Warunkiem sukcesu jest zaistnienie swoistych, czasoprzestrzennych „okien możliwości”, w których wymagania poszczególnych gatunków odnośnie tarła i wzrostu narybku są zgodne z czasem, długością i zakresem impulsu powodziowego oraz termiką wody. Takie „okna możliwości” powinny być zagwarantowane zespołom ryb, pomimo stale zmieniających się uwarunkowań społecznych czy środowiskowych w celu zachowania możliwości rekrutacji i różnorodności ichtiofauny obszarów zalewowych rzek.

8.5 Affiliations

| Affiliations of co-authors | |
|--|---|
| L.A.J. Nagelkerke J.A.J. Verreth K.E. van de Wolfshaar | Aquaculture and Fisheries group, Wageningen University, Wageningen, the Netherlands |
| A.D. Buijse | Deltares, Department of Freshwater Ecology & Water Quality, Utrecht, the Netherlands |
| L.V. van den Bosch H. Middelkoop | Department of Physical Geography, Utrecht University, Utrecht, the Netherlands |
| A.E. Minin | GosNIORKH State Institute for Lake and River Fisheries, Nizhny Novgorod Laboratory, Nizhny Novgorod, Russian Federation |
| V.S. Boldyrev V.V. Khoruzhaya D.A. Vekhov S.V. Yakovlev | GosNIORKH State Institute for Lake and River Fisheries, Volgograd Division, Volgograd, Russian Federation |
| J.J. de Leeuw H.V. Winter | IMARES, Institute for Marine Resources and Ecosystem Studies, Wageningen University and Research, IJmuiden, the Netherlands |
| O.V. Filipov D.V. Zolotarev | Volzhsky Institute of Humanities (branch) Volgograd State University, Volzhsky, Russian Federation |

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8.7 About the Author

Konrad Górski was born on August 28, 1981 in Ostrowiec Świętokrzyski, Poland. After the completion of his high school education in 2000, he undertook a 5 year degree in Biology at Warsaw University of Life Sciences (SGGW). During this study he took part in European student exchange programme in 2003-2004 at the University of Groningen in the Netherlands. In addition as a part of his Msc study, in 2005 he completed a thesis 'Physiological adaptation of bivalves to tropical and temperate climate' at the Royal Netherlands Institute for Sea Research, Texel, the Netherlands. He concluded his study at Warsaw University of Life Sciences and obtained an Msc degree specializing in Biological Basis for Environmental Protection in 2005. In 2006 he started his PhD research at the Aquaculture and Fisheries Group, Wageningen University, the Netherlands (in cooperation with Wageningen IMARES, Utrecht University, Moscow State University and Volgograd State Fisheries Institute), which resulted in this thesis. Continuing with his interest in the ecology of flowing waters, he is currently employed by the University of Waikato in Hamilton, New Zealand, where his research concentrates on the ecological modelling of the Waikato River.

GorskiKE@gmail.com

| Training and Supervision Plan | Graduate School WIAS |
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| | |
|------------------|--|
| Name PhD student | Konrad Górski |
| Project title | Floods and Fish; Recruitment and distribution of fish in the Volga River floodplain |
| Group | Aquaculture and Fisheries |



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| Youth and Progress of Biology, Lviv, Ukraine, 21-24 March 2006 | 2006 | |
| 3rd International Symposium on Riverine Landscapes: Global change and river-floodplain ecosystems, South Stradbroke Island, Australia | 2007 | |
| 10th International RiverSymposium and Environmental Flows Conference, Brisbane, Australia | 2007 | |
| The 7th International Symposium on Ecohydraulics, Concepcion, Chile | 2009 | |
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