

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

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SUMMARY

1. Large river floodplains are considered key nursery habitats for many species of riverine fish. 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 floodplain rivers.
2. We examined the interannual variability in recruitment success of young-of-the-year (YOY) fish in the lower Volga floodplain in relation to flood pulse characteristics and rising water temperatures in the spring. We sampled four areas with different flooding regimes, in three consecutive years (2006–2008).
3. Extensive areas with a long duration of flooding accommodated high densities of young fish. This suggests that extended inundation improves the recruitment success of river fish. In areas with extensive flooding, the biomass of YOY of most fish species was about three times higher in 2006 and 2007 than in 2008. We hypothesise that low spring temperatures in 2008 may have caused this reduced recruitment and that a flood synchronised with rising temperature enhances recruitment success.
4. Extensive flooding was particularly favourable for species characterised by large body size, delayed maturation, high fecundity and low parental investment, such as pike *Esox lucius*, roach *Rutilus rutilus* and ide *Leuciscus idus*. Gibel carp *Carassius gibelio*, a species tolerant of high temperature and hypoxia, did particularly well in small waterbodies in the driest parts of the floodplain.
5. Structural characteristics of floodplain waterbodies explained much of YOY fish density. These species–environment associations varied from year to year, but some species such as common bream *Abramis brama*, roach and gibel carp showed consistent relationships with structural habitat characteristics in all years, despite large interannual fluctuations in flood pulse and spring temperature.

Keywords: flood pulse, inundation, life history, river, seasonal dynamics, Volga river

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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 the temporary inundation of terrestrial habitats. This inundation leads to mineralisation and mobilisation of 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 disturbance in turn result in high biodiversity and production of plants and animals inhabiting the floodplains, as envisaged in the Flood Pulse Concept (FPC) (Lowe-McConnell, 1964; Junk, Bayley & Sparks, 1989; Tockner, Malard & Ward, 2000; Junk & Wantzen, 2004). 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 (Holland & Huston, 1985; Poizat & Crivelli, 1997; Baber *et al.*, 2002; Balcombe *et al.*, 2007). 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, 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: (i) predictability of flooding; (ii) rate of rise and fall in the water level; (iii) extent of inundated area; (iv) duration of inundation; and (v) degree of coupling of flooding and changes in temperature (Trifonova, 1982; King, Humphries & Lake, 2003). After the water recedes, the carrying capacity of permanent waterbodies and competition for food as well as predation and hypoxia 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 species with delayed maturation, high fecundity and low parental investment), such as common bream *Abramis brama* (Linnaeus, 1758), ide *Leuciscus idus* (Linnaeus, 1758) or pike *Esox lucius* Linnaeus, 1758, are adapted to seasonal and large-scale spatial variation in environmental conditions. These species would possibly depend on, but also benefit most from, predictable seasonal dynamics. Opportunistic species, such as sunbleak *Leucaspis delineatus* (Heckel, 1843) and gibel carp *Carassius gibelio* (Bloch, 1783), are more flexible and characterised by early maturation, continuous spawning and a particular ability to colonise 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 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 (Halyk & Balon, 1983; Holland & Huston, 1985; Copp, 1989), 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 Europe's few remaining naturally functioning floodplains (Górski *et al.*, 2010), and it therefore provides a very unusual opportunity to study fish recruitment in such systems that were formerly widespread. Our main objectives were:

1. To assess the interannual variation in recruitment success of fish species in the floodplain and relate these to differences in the yearly flood pulse and between areas within the floodplain that have different flooding characteristics.

2. To assess whether interannual recruitment variability differs among fish species with different life-history strategies. We expect species adapted to seasonality or large-scale spatial variation (periodic strategists) and flexible, fast colonisers (opportunistic strategists) to be most successful in the floodplain environment.

3. To assess to what extent recruitment success of fish species in the floodplain is affected by structural characteristics of waterbodies and whether this effect of waterbody characteristics is similar in years with different flood pulses.

Methods

Study area

The Volga River (Russian Federation), (length 3690 km, mean annual discharge $8103 \text{ m}^3 \text{ s}^{-1}$) 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, have moderately altered the flow regime of the Lower Volga downstream of Volgograd (Mordukhai-Boltovskoi, 1979; Middelkoop *et al.*, 2005). 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. 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 *c.* 2 weeks. To analyse fish recruitment patterns, 12 floodplain waterbodies in four areas (three in each area) with different hydrological characteristics were chosen (Fig. 1).

Data collection

Water level and temperature were recorded at 1-h intervals in one waterbody in each area using automatic data loggers (Diver[®] Water Pressure Logger; Schlumberger Water Services, Sugar Land, TX, U.S.A.; UA-002-64 HOBO[®]; Onset Computer Corporation, Bourne, MA, U.S.A.) in 2007. Daily discharge of the Volga and air temperature at Volgograd were available for 1997–2008 and obtained from the Volgograd Centre of Hydrometeorology and Environmental Monitoring.

For all floodplain waterbodies, surface area, perimeter and distance between the waterbody and the nearest channel connection to the main river channel (Volga or Akhtuba) were estimated from available

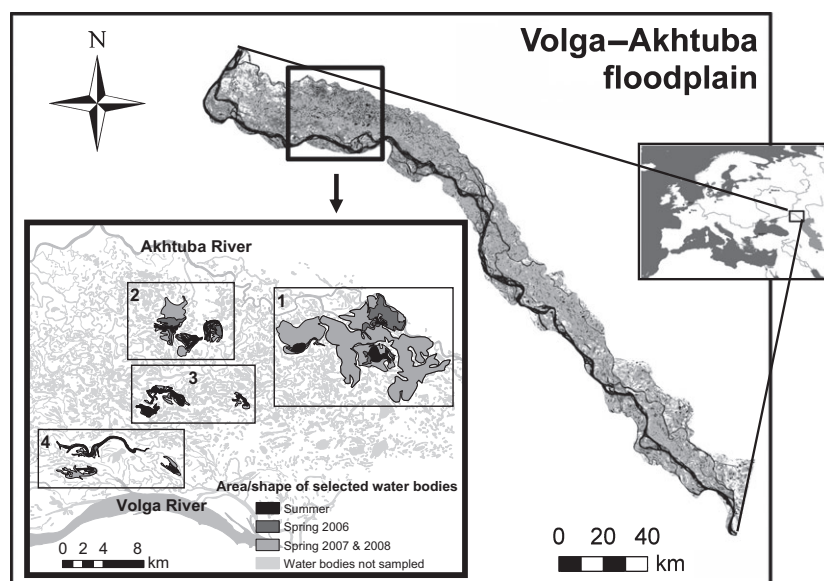


Fig. 1 The Volga–Akhtuba floodplain and the study area, indicating sampled waterbodies in four areas with different hydrological regimes.

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 flooded area of each lake was calculated from the Volga Floodplain Ecological Map (Losev *et al.*, 2004). Average depth of waterbodies 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 and 2008), fish were sampled in the same 12 waterbodies from the end of August to the end of September. On average, three (range from two to five) samples were collected in each waterbody using a beach seine (30-m long, 1.5-m deep, 10-mm stretched mesh size). For each sample, fish were identified to species based on morphological features and pigmentation (Koblitskaya, 1981) and fish were counted and length frequency distributions of (sub-)samples were determined, based on standard length to the nearest mm. To ensure that our length frequency distributions represented the actual size distribution of the population as well as possible, we measured at least 100 individuals if they were available. For the less-abundant fish, all individuals were measured. In each waterbody, 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 the life-history parameters of fish inhabiting the Volga-Akh-tuba floodplain. Most of the 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 (Table 1). Data were obtained for the following life-history traits: (i) maximum length, (ii) age at maturation, (iii) egg size, (iv) length of breeding season (in months), (v) spawning mode categorised as: score 1, single spawning per year; score 2, from two to four spawning events per year, (vi) fecundity as the average number of oocytes of mature females in a single spawning season and (vii) 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 (with a score of 1).

Data analysis

Young-of-the-year 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 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 terms of numbers and biomass were calculated for each species for each waterbody in each year. Overall CPUE (g m^{-2}) values of YOY including all species were compared between different years and areas with analysis of variance (ANOVA). The data used in the analysis were \log_{10} -transformed to achieve an approximately normal distribution.

Density data of YOY fish for each of the 11 most-abundant species were not normally distributed. Since we wanted to analyse the effects of year and area as well as their interaction, we applied Blom's transformation on the ranked data. This transformation adjusts rank scores to achieve an approximately normal distribution (Blom, 1958), which allows for the use of standard two-way ANOVA, including the analysis of interactions. Following ANOVA, we performed pairwise 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 each category

Table 1 Abbreviations, scientific and common names, numbers of fish species caught, as well as some of the life-history characteristics derived from Krizhanovski (1953) and Reshetnikov (2002)

Abbrev	Scientific name	Common name	Total no. of YOY caught	% of total YOY caught	No. of waterbodies 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>	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)	Crustian carp	24	0.016	2	50	4	218	1	2
Cagi	<i>Carassius gibelio</i>	Gibel carp	1513	1.014	11	45	2	215	1	2
Cota	<i>Cobitis taenia</i> (Linnaeus, 1758)	Spined loach	425	0.285	10	20	4	0.3	1	1
Cyca	<i>Cyprinus carpio</i> Linnaeus, 1758	Carp	12	0.008	3	100	3	948	1	1
Eslu	<i>Esox lucius</i>	Pike	662	0.444	12	150	2	118	1	1
Gyce	<i>Gymnocephalus cernua</i> (Linnaeus, 1758)	Ruffe	1693	1.135	8	18.5	2	53	1	2
Lede	<i>Leucaspis delineatus</i>	Sunbleak	4978	3.337	5	9	2	1.4	3	2
Leid	<i>Leuciscus idus</i>	Ide	1022	0.685	10	100	4	76	1	1
Mifo	<i>Misgurnus fossilis</i> (Linnaeus, 1758)	Weatherfish	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
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
Titl	<i>Tinca tinca</i> (Linnaeus, 1758)	Tench	82	0.055	8	63	3	565	1	2

Abbreviated names of the 11 most-abundant species are shown in boldface.

YOY, young-of-the-year; Parental care: 1, non-nesting species with spawning habitat selection; 3, nesting species; Spawning mode: 1, single spawning per year; 2, from two to four spawning events per year.

Table 2 Relationships between life-history traits and how they affect different life-history strategies

	Age at maturity	Fecundity	Survival (large egg size and/or parental care)
Opportunistic	-1	0	-1
Equilibrium	1	-1	1
Periodic	1	1	-1

-1, negative; 0, neutral; 1, positive relationship between size of the life-history trait and the life-history strategy.

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 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 waterbody characteristics (Table 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).

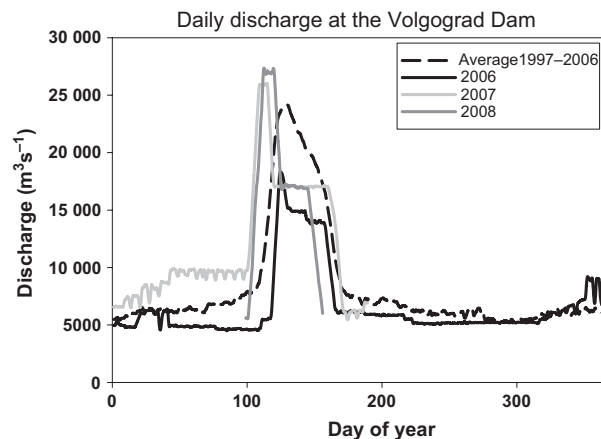
Results

Annual and spatial variation in flood characteristics

Compared with 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 than average ($26\text{--}27 \times 10^3 \text{ m}^3 \text{ s}^{-1}$) (Fig. 2). A conspicuously larger fraction of the floodplain was inundated in 2007 and 2008 than in 2006 (Fig. 1). Peak flow in 2007 lasted about 3 weeks longer than in 2008. The growing season was

Table 3 Environmental variables for the waterbodies sampled, 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 waterbody 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 waterbody)
Depth	Average depth
Forest	Percentage of forests in the flooded area around waterbody (arcsine-transformed)
Grasslands	Percentage of grasslands in the flooded area around waterbody (arcsine-transformed)
Helophytes	Percentage of helophytes in the flooded area around waterbody (arcsine-transformed)
Submerged	Percentage of submerged macrophytes in the waterbody (arcsine-transformed)
MCD	Distance to the main channel (km)

**Fig. 2** Daily discharge of Volga River during sampling years and the average discharge calculated for the years 1997–2006.

the warmest in 2007 (1560 cumulative degree-days (dd) above 12°C air temperature), followed by 2006 (1387 dd) and 2008 (1236 dd).

The dynamics of flooding differed between different areas in the floodplain. Areas 1 and 2 (Fig. 1) were characterised by a similar rapid rise (*c.* 2 weeks from onset of the flood until maximum water level) and large magnitude (*c.* 3 m) of the flood, followed by a stable inundation of about 7 weeks and then a fall for about 2 weeks (Fig. 3). The total area inundated around the sampled waterbodies was significantly

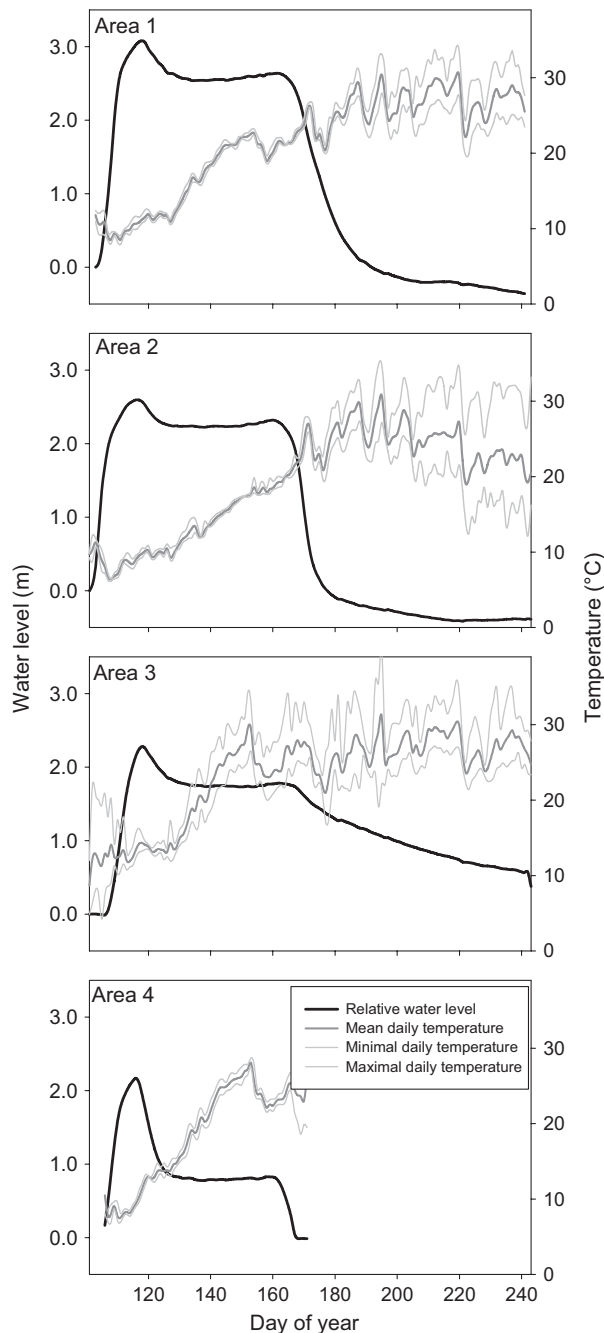


Fig. 3 Water levels and temperature dynamics in different sampling areas in 2007.

greater in Area 1 than in Area 2 (Fig. 1). In Area 3, the rise of the flood was also rapid (c. 2 weeks as in Areas 1 and 2, and the magnitude was about 2 m), but the decline was slow and prolonged (c. 12 weeks) (Fig. 3). In Area 4, a rapid rise (c. 2 weeks) to a maximum level of about 2 m was followed by two stages of rapid

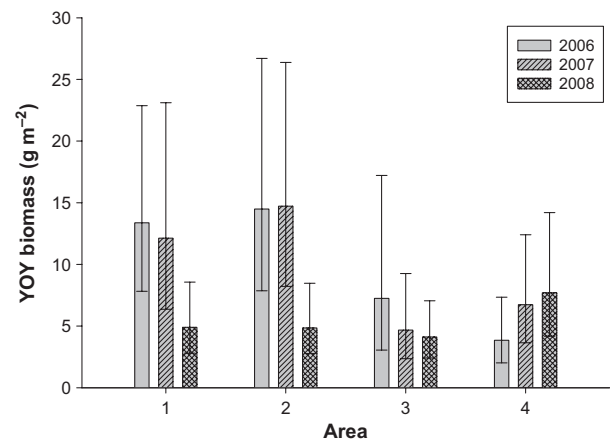


Fig. 4 Comparison of the total biomass of young-of-the-year (mean and 95% confidence limits as estimated by the statistical model) in different years and areas. ANOVA of \log_{10} -transformed catch per unit effort showed significant effects of year ($F = 4.07$, $P = 0.02$), area ($F = 3.46$, $P = 0.02$) and year*area ($F = 2.3$, $P = 0.04$).

decline, the first (of about 1.5 m) just after 2 weeks from the initial rise and the second at the same time as in other areas (Fig. 3).

Overall production of recruits

We recorded the highest overall CPUE biomass of YOY in Areas 1 and 2 in 2006 and 2007 ($12\text{--}14 \text{ g m}^{-2}$; Fig. 4), while that in Areas 3 and 4 was lower in all 3 years ($4\text{--}7 \text{ g m}^{-2}$). In 2008, CPUE in Areas 1 and 2 was much lower ($4\text{--}5 \text{ g m}^{-2}$) than in previous years. CPUE of YOY was highest in Area 4 (c. 7 g m^{-2}) in 2008, while in Area 3, it ranged between c. 4 (2007 and 2008) and 7 g m^{-2} (2006).

Recruitment of different species

For the 11 most-abundant species, comparisons of abundance (CPUE in numbers m^{-2}) and mean length between different years and areas were made (Figs 5 & 6). 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 effects of area or year for common bream, white bream, perch, sunbleak, ruffe or rudd (Table S1). We found a significant effect of year for bleak ($F = 6.60$, $P = 0.004$) and gibel carp ($F = 17.46$, $P < 0.001$), with the highest CPUE in 2006 and the lowest in 2008 for

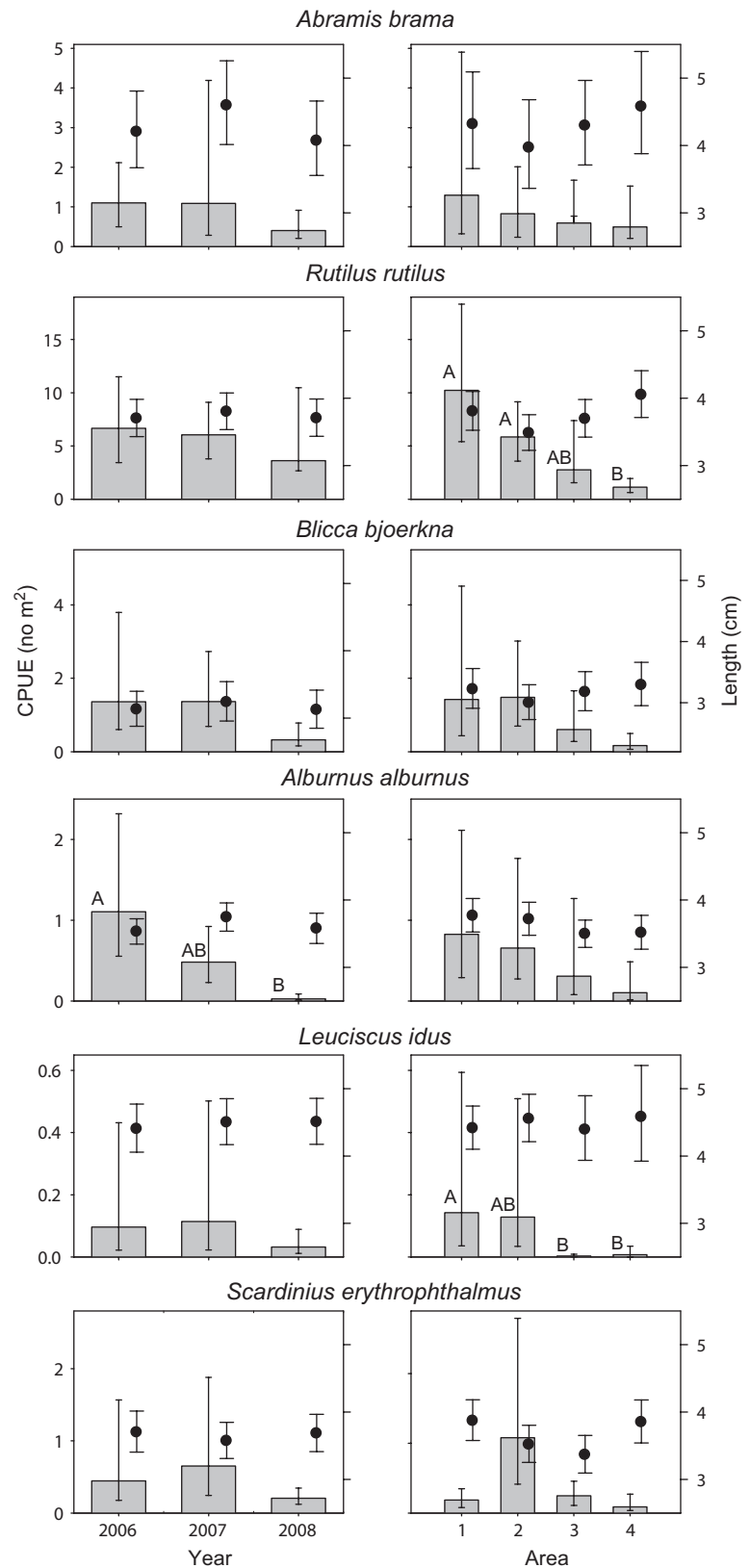


Fig. 5 Comparison of densities (bars) and length (points) of young-of-the-year in different years and areas. Bars with different letters indicate significant differences in catch per unit effort based on Tukey's multiple comparison test.

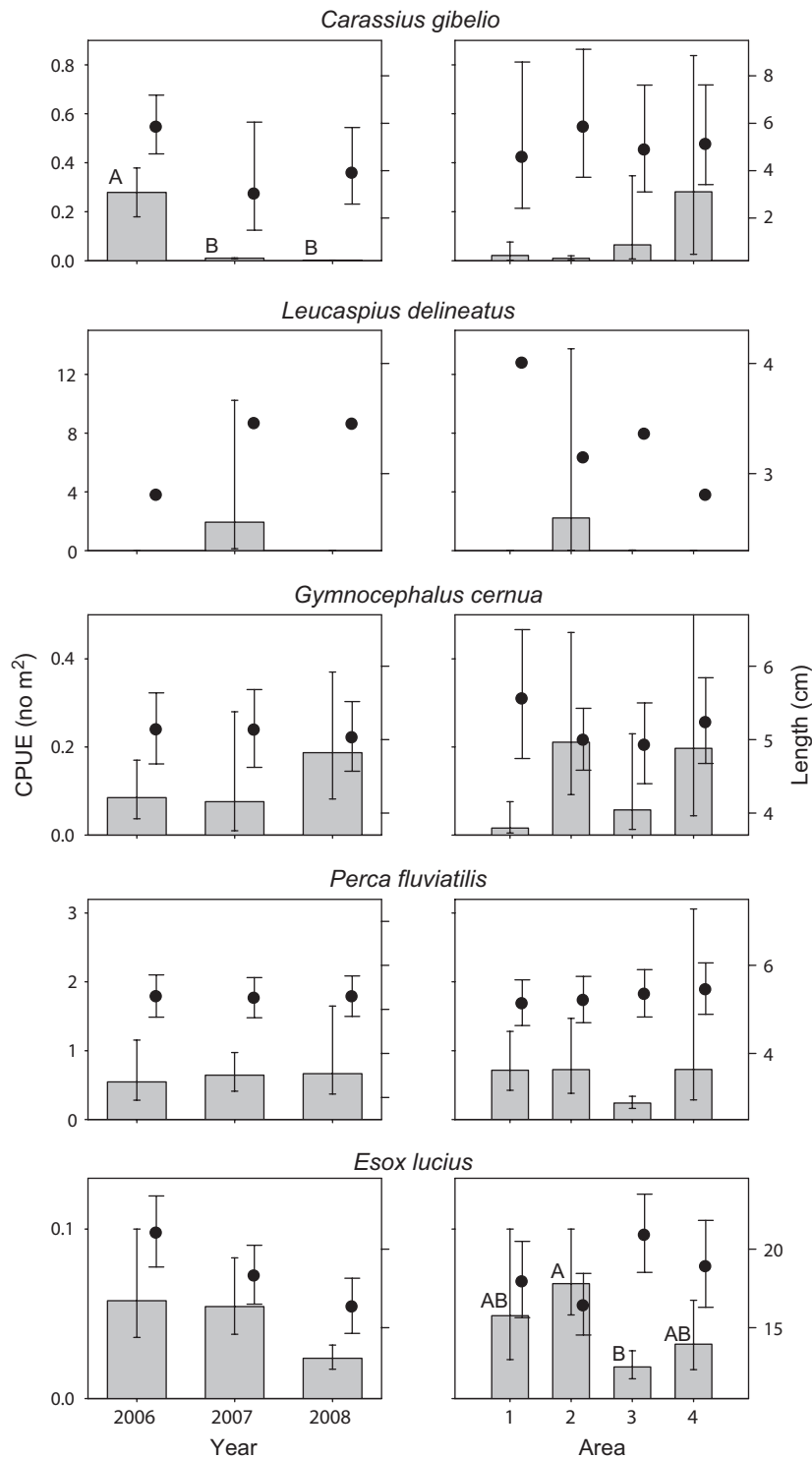


Fig. 6 Comparison of densities (bars) and length (points) of young-of-the-year in different years and areas. Bars with different letters indicate significant differences in catch per unit effort based on Tukey's multiple comparison test.

both species (Figs 5 & 6). For bleak, CPUE in 2007 was less than half that in 2006, while in 2008, it was negligible (c. 2% of its abundance in 2006). For gibel carp, CPUE was <4% in 2007 and <1% in 2008 compared with 2006. Also sunbleak, another opportu-

nistic species, showed a large variability in density with highest values in 2007 and Area 2, while in other years and areas, only a few individuals were found. For the more periodic species pike, ide and roach, there was a significant effect of area ($F = 3.42$,

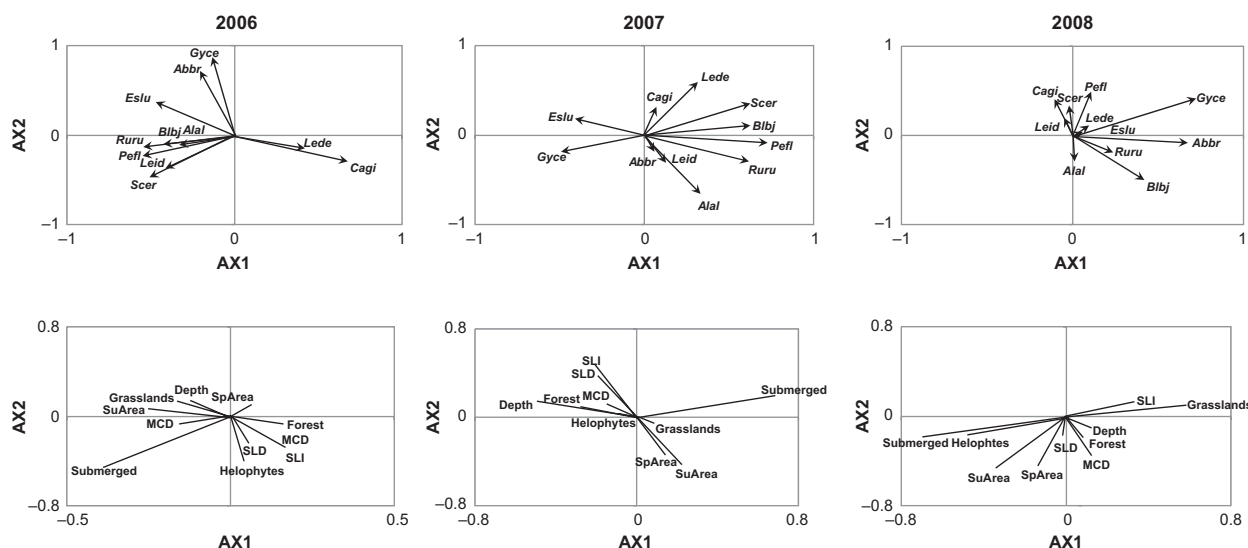


Fig. 7 Redundancy analyses of young-of-the-year fish densities of different species explained by geomorphology, connectivity and vegetation characteristics of waterbodies in the floodplain in 2006–2008. The greater the similarity in size and direction of the vectors of species (upper panels) and waterbody characteristics (lower panels), the stronger the association between the relative abundance of that species and the waterbody characteristic. Abbreviations of species can be found in Table 1 and abbreviations of waterbody characteristics in Table 3.

$P = 0.029$; $F = 6.90$, $P = 0.001$; $F = 6.25$, $P = 0.002$, respectively). Pike had the highest CPUE 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 20 times greater than in Areas 3 and 4 (Figs 5 & 6). Roach showed the lowest CPUE in Area 4 (Fig. 5).

For most of the species, neither area nor year had a significant effect on YOY length. Exceptions were bleak, pike and rudd (Table S2). 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 analysed (c. 50%), whereas opportunistic and equilibrium traits both ranged between 21 and 27%. There were no consistent differences between years and areas in the proportional representation of different strategies, with the exception of Area 4, in which opportunistic traits were slightly, though consistently, more abundant (27% in Area 4, compared to 21–23% in the other areas, with no overlap in the ranges). This larger proportion of opportunistic traits was mostly due to the higher abundance of gibel carp in Area 4 (Fig. 6).

Results of the redundancy analyses showed that environmental variables explained much of the variation in YOY fish abundance in each year sampled (Table S3). In each year, waterbody area in summer, submerged macrophyte cover and shore length index (SLI) were important explanatory variables (Fig. 7). In addition to these three, the cover of shoreline vegetation was also an important explanatory variable in 2006. In 2007, waterbody depth and 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, emphasising the influence of variability between years on recruitment. However, we also observed some consistent patterns. Common bream consistently showed positive correlations with waterbody 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 waterbody area in summer. Roach also correlated positively with summer area. Gibel carp and sunbleak correlated negatively with the extent of grassland and waterbody area in spring. Rudd correlated positively with submerged macrophyte cover in all years.

Discussion

Differences in YOY production between areas and years

Our results indicate that there can be large interannual differences in the overall biomass of YOY fish in some areas of the floodplain, but not in others (Fig. 4). In Areas 1 and 2, much of which is flooded, the biomass of YOY fish was about three times higher in 2006 and 2007 than in 2008. In Areas 3 and 4, however, with a smaller flooded area, no such difference was found. Moreover, YOY biomass in Areas 3 and 4 was, on average, less than half that in Areas 1 and 2 (though not in 2008). Both the higher YOY biomass and interannual variability in Areas 1 and 2 suggest that fish recruitment here was more strongly influenced by the annual flood pulse than those in Areas 3 and 4. This is in accordance with the hypothesis that the flood pulse immediately affects productivity in floodplains (Welcomme, 1985) and the importance of highly productive flooded terrestrial habitats for fish production (Herwig *et al.*, 2004).

The three sampling years differed in the characteristics of the flood, which varied in volume, amplitude, onset and duration (Fig. 2), as well as in the temperature of the growing season, with 2008 being the coldest year. Nunn *et al.* (2003) suggested that discharge rather than spring temperature may be the key factor in the recruitment of young fish in some temperate lowland rivers, but their conclusions were based on a study of a smaller, more severely altered, river. Similarly, in arid African floodplains,

large floods were associated with a high abundance of young fish (Lindholm *et al.*, 2007). Our findings did not show a relationship between flood discharge and biomass of YOY fish, however, since the year with the smallest flood discharge (2006) produced about the same biomass as the year with the highest discharge (2007). Also Balcombe *et al.* (2007) found some indications that there is no relationship between flood discharge and fish biomass in an arid Australian river, although their study was limited to 2 years. On the other hand, factors in addition to discharge, such as temperature and food availability, have been found, in experimental studies, to be highly important for exogenous feeding fish fry (Schiemer, Keckeis & Kamler, 2002). Since we found that YOY biomass in Areas 1 and 2 was more than three times lower in the coldest year 2008 than in the warmer years 2006 and 2007, we postulate that the flood must be coupled with suitably high water temperatures for successful fish recruitment in a temperate floodplain. Of course, our data are from only 3 years and we cannot be sure how general the pattern is, but it is corroborated by other studies (Trifonova, 1982; King *et al.*, 2003).

Temperature in the growing season cannot be the complete explanation for the differences in recruitment success between the years, because we found no marked differences in YOY biomass between 2006 and 2007, despite the lower temperatures and lower flood amplitude and duration in 2006. This could be partly explained by a possible overestimation of YOY biomass in 2006, compared with that in 2007 and 2008, because the lower peak discharge in 2006 resulted in a lower mean depth and volume of waterbodies at the end of summer. However, based on a mean decrease in water depth of 0.2 m in waterbodies of, on average, 1.5 m deep, this could produce overestimate of biomass of *c.* 15% only. Overall high recruitment in 2006 could also partly be attributed to the high abundance of gibel carp. This high recruitment is likely to be a direct effect of the very low flood pulse in that year, which resulted in a reduced water volume of some of the floodplain waterbodies, favouring this species which is known for its tolerance of high water temperature 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 has been shown not to be strong in cyprinid and percid fishes, to which almost all species in this study belong (Mooij, 1996).

Our results suggest that the differences in YOY fish biomass between 2007 and 2008 could not be attributed to differences in the onset of the flood pulse or peak discharge, because both were similar in these years. However, flood duration in 2008 was about 4 weeks shorter than in 2007. This resulted in an earlier decrease in the extent of flooded terrestrial habitat and therefore probably in a decrease in productivity, possibly negatively affecting recruitment. Considering that the flood pulse now occurs earlier and is shorter than before the regulation of the Upper Volga (Mordukhai-Boltovskoi, 1979), this increases the probability that temperatures would be low at the onset of flooding and that the time window in which flooding provides a suitable habitat at suitable water temperatures will be smaller. Potentially, this could lead to a long-term decrease in recruitment success.

In addition to the extent 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 waterbodies did not dry up, nor were there any signs of extensive anoxia (although locally this may have played a role). It is more likely, therefore, that the temperature conditions that we report actually enhanced the effect of (un)successful spawning. For instance, the low summer temperatures of 2008 may 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.

There is no direct evidence that the effects of flooding and temperature on the recruitment of YOY fish also affect the abundance of adult floodplain fishes. However, historical data show that catches are usually higher in years following years with large

floods (Górski *et al.*, 2011). This could be an indication that YOY fish that recruited in years of large floods showed high survival and/or somatic growth, resulting in a higher catchable biomass in the following years.

Recruitment of different species and life-history strategies

Areas 1 and 2 accommodated significantly higher densities of young fish than areas 3 and 4, particularly of species with more periodic characteristics such as common bream and roach. This is consistent with findings that extensive 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 that are suitable prey for young pike. Moreover, the extended and prolonged connectivity of Areas 1 and 2 with the main channel could have made these areas a more suitable nursery habitat for the periodic ide, which is the most rheophilic of the fish species analysed. 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 of the species, especially of periodic strategists. The more opportunistic gibel carp, also known for its high temperature and hypoxia tolerance, showed high recruitment success here (Lushchak *et al.*, 2001; Roesner *et al.*, 2008).

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 and species with specific environmental adaptations such as hypoxia tolerance might be at an advantage, as shown for Area 4. This is in accordance with reports from African and Australian dryland rivers, which have less predictable flood pulses and where more opportunistic or physiologically tolerant species dominate (Merron, Bruton & De Lalouviere, 1993; Balcombe *et al.*, 2006, 2007). Therefore, further

alterations in the flood pulse might result in a shift of the fish community towards more opportunistic strategists.

Role of permanent waterbody characteristics

Even though there is significant interannual variability in fish recruitment in the Volga-Akhtuba floodplain, we found that more permanent characteristics of the waterbodies 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 the ability of this species to render growth conditions unsuitable for aquatic macrophytes (Scheffer, 1998). The pelagic bleak was associated with larger waterbodies with a low shoreline index, which is in line with its open-water habitat preference. As expected, the 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). The hypoxia-tolerant gibel carp was the only species surviving in drying waterbodies, which become progressively smaller, thereby showing negative correlations with size and extent of flooded grasslands.

In conclusion, fish recruitment in the lower Volga floodplain varies among different areas that are differentially influenced by the spring flood pulse. Differences in hydrology between years interact with these spatial differences. These interannual differences could be caused by the characteristics of the flood pulse, such as its onset, peak discharge and duration, although our results also suggest that temperature in the growing season could have an important effect. We hypothesise that a suitably high spring temperature needs to coincide with the flood for successful YOY fish recruitment. A mismatch between flood timing and high temperature could reduce recruitment success of all species, especially periodic strategists (Cushing, 1990). The shorter flood duration caused by the regulation of the Volga River increases 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 waterbodies within the floodplain, especially related to their morphology, hydrology and vegetation, also explain a large part of the variation in fish recruitment.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. ANOVA of the CPUE (numbers m^{-2}) of YOY fish of the most abundant species.

Table S2. ANOVA of \log_{10} -transformed lengths of YOY fish of the most abundant species that showed at least one significant effect.

Table S3. Redundancy analyses of the environmental variables explaining the abundance of YOY fish.

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