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River discharge drives recruitment success of the European bitterling *Rhodeus amarus* in a regulated river in central Europe

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A 15 year data set revealed that the abundance of 0+ year *Rhodeus amarus* in a regulated river was negatively associated with mean river discharge, while mean standard length was positively related to the cumulative number of degree-days $\geq 10°$ C. Results are discussed in the context of the recent invasion success of *R. amarus*.

Key words: interannual variation; invasive species; juvenile growth; long-term data set; water temperature; young-of-the-year fish.

Several freshwater fish species have undergone abrupt increases in range, size and abundance of local populations within the last few decades. While some are directly linked to human activity, such as intentional or unintentional stocking outside a species' native range, others may be facilitated by human alteration of habitats such as river regulation and river channelization (Marchetti *et al.*, 2004; Olden *et al.*, 2006). Finally, some changes in freshwater fish distribution have been linked to changes in ambient temperature (Daufresne *et al.*, 2003; Van Damme *et al.*, 2007), which is a crucial environmental variable that can limit species' ranges (Gaston, 2003). When range size increases by continuous spreading rather than large distance dispersal, it is typically coupled with an increase in the abundance of local populations and associated colonization of new habitats (Hanski, 1991).

Recruitment success in source populations is central to the understanding of colonization success (Hanski, 1991). Recruitment describes the input of new individuals into a breeding population (Wootton, 1998), and in annual species, it can be approximated by the abundance of 0+ year individuals at the end of the first growing season (Jurajda, 1995). The abundance of 0+ year individuals is

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strongly affected by environmental variables that, directly or indirectly, act on adult spawning success, embryonic and juvenile mortality and the condition of juveniles (Mills & Mann, 1985; Schlosser, 1985; Townsend, 1989). Hence, interannual variation in environmental factors may predict interannual variation in recruitment (Rose, 2000; Grenouillet *et al.*, 2001*a*; Nunn *et al.*, 2003). For many riverine fish populations, river discharge and water temperature are the key triggers for reproductive activity and strongly affect survival, growth rate and the length of the growing period for juveniles (Durham & Wilde, 2006; Gillet & Dubois, 2007; Wolter, 2007). In riverine cyprinids, strong year-classes are often correlated with high water temperature during the first summer of life (Nunn *et al.*, 2003). Furthermore, biotic factors such as competition, predation or population demography may affect year-class strength (Wootton, 1998).

One species that is currently extending its range size and increasing its relative abundance (Kozhara *et al.*, 2007; Van Damme *et al.*, 2007) is the European bitterling *Rhodeus amarus* (Bloch), a small cyprinid fish (subfamily Acheilognathinae) that inhabits lotic and lentic habitats throughout Europe. *Rhodeus amarus* populations decreased considerably during the 1970s and 1980s, especially in western Europe, and were included in most European conservation lists, including EC Habitat Directive (Lelek, 1987; European Commission, 2002). The trend recently, however, appears to have reversed; *R. amarus* population numbers have increased throughout Europe, and the extent of its distribution now exceeds its former range (Kottelat & Freyhof, 2007). The expansion of *R. amarus* appears largely a result of natural dispersal into new habitats (Kozhara *et al.*, 2007; Van Damme *et al.*, 2007). *Rhodeus amarus* spawns inside the gill cavity of unionid mussels where embryos reside for *c.* 1 month before starting their independent life at a standard length (L_S) of 7·5–9·5 mm. The spawning season is initiated by an increase in water temperature >12° C and typically lasts from mid-April to late June. After emergence from mussels, larvae enter shallow, vegetated margins that serve as nursery areas up to late autumn (Jurajda, 1999; Przybylski & Zięba, 2000; Reichard *et al.*, 2002*a*, 2004; Smith *et al.*, 2004). Sexual maturity is achieved after their first winter. *Rhodeus amarus* is reported to live up to 5 years, but the study population consists mainly of 1 year-old fish (Smith *et al.*, 2000; unpubl. data) and is principally annual.

The present study used a 15 year data set on recruitment of *R. amarus* from a lowland regulated river in central Europe to investigate the influence of river discharge and water temperature on the abundance and growth of young-of-the-year fish measured at the end of the first growing season. The prediction was that the abundance of 0+ year *R. amarus* and L_S would be positively related to water temperature in a given year, while river discharge was predicted to be negatively related to 0 + *R. amarus* abundance.

The study was carried out in the lower reaches of the River Morava (Danube basin, Czech Republic) (river km 69·4–92·8) between the village of Moravská Nová Ves (48°46′51″ N; 17°04′20″ E) and the River Morava's confluence with the River Dyje (48°36′59″ N; 16°56′21″ E). This stretch is 50–60 m wide, regulated by five weirs, with a maximum depth of at least 1 m above weirs even during periods of the lowest discharge. The daily discharge varied between 2·5 and 850·0 $m^3 s^{-1}$ during the study, and mean annual discharge was 14–148 (mean 47) $m^3 s^{-1}$. A detailed description of the study stretch is given in Jurajda

(1999). Sampling was undertaken annually from 1991 to 2005 in August, except for 1991 and 1997 (sampling in October). A DC electroshocker (ML3; www.r-bednar.cz) (years 1991–1999) and backpack electroshocker (Lena; www.r-bedner.cz) (years 2000–2005) were used; the two electroshockers provide concordant results for 0+ year fish point abundance sampling (M. Janáč, unpubl. data). Point abundance sampling was used at 15 localities in 1991, 21 localities in 1992–1999 (except in 1996 when 17 localities were sampled for logistical reasons) and 20 localities from 2000 to 2005. Localities were distributed along the whole-study stretch and were chosen to represent typical habitats of the study stretch area. The relative proportion of habitats was maintained. Each locality was *c.* 80–200 m long and consisted of 20 sampling points chosen haphazardly within a selected stretch (Jurajda, 1999). Sampling lasted 2–7 days. Captured 0+ year fish were killed in a lethal dose of anaesthetic and stored in 4% formaldehyde, and their L_S was measured in the laboratory using digital callipers to the nearest 0·01 mm ($n = 10094$ fish across 15 years). Abundance was expressed as catch per unit effort (CPUE) and calculated as the number of *R. amarus* captured per 100 sampling points.

Daily water temperature and river discharge data were obtained from the nearest station of the Czech Hydrometeorological Institute (located 42 km upstream). Mean values and variation in water temperature and river discharge data were calculated from annual data sets that were adjusted for the start (the first day with water temperature $\geq 10°$ C) and end (median sampling date for a given year) of the season. The temperature of 10° C was chosen since the gauging station measures temperature in the main channel and water temperatures tends to be *c.* 2° C higher in nearshore areas where *R. amarus* spawning occurs. Given that *R. amarus* embryos reside inside the mussel for at least 25 days and, therefore, are not affected by river discharge during this part of their development, variables related to river discharge data were calculated from a truncated data series (start 25 days after $\geq 10°$ C). The 0+ year *R. amarus* abundance in the preceding year was included as an explanatory variable in the analysis of juvenile abundance as temporal autocorrelation. Cumulative numbers of degree-days $\geq 10°$ C were included in the analyses of mean L_S and its variability to account for length of the growing season. For analyses of L_S, the years 1991 and 1997 were excluded (sampling in October and, in 1997, only two 0+ year *R. amarus* were captured after a large flood), and for abundance analysis, the year 1991 was excluded given the lack of juvenile abundance data from previous year.

Spearman rank correlations and multiple regression analysis were used to investigate the relationship between juvenile abundance (CPUE), mean L_S and variability in L_S (measured as range interval, *i.e.* maximum minus minimum L_S). Mean and variation in water temperature and river discharge were always entered into saturated regression models. All saturated models had five explanatory variables. Stepwise removal of redundant variables based on Akaike information criterion (AIC) was used in R statistics (R 2.0.4) (R Core Development Team, 2007; www.r-project.org/). All candidate models were compared on the basis of their AIC value, difference in AIC (DAIC) value, Akaike weight (wi) and relative fit (åwi). Standard stepwise regressions may provide biased parameter estimates (Whittingham *et al.*, 2006), and this can be overcome by model selection based on AIC. It was apparent that this approach (when no null model was evaluated and no synthetic model was build) could not overcome several shortcomings associated with stepwise regressions (Whittingham *et al.*, 2006), but the approach was imposed by the limited size of the data set.

The abundance of juvenile *R. amarus* in August was significantly related to river discharge (Fig. 1). There was a negative correlation with mean river discharge (D_{m}) ($r_{\mathrm{s}} = -0{\cdot}53$, $P < 0{\cdot}05$) and with variation in river discharge (D_{var}) ($r_{\mathrm{s}} = -0{\cdot}57$, $P < 0{\cdot}05$). The regression analysis identified mean discharge as the

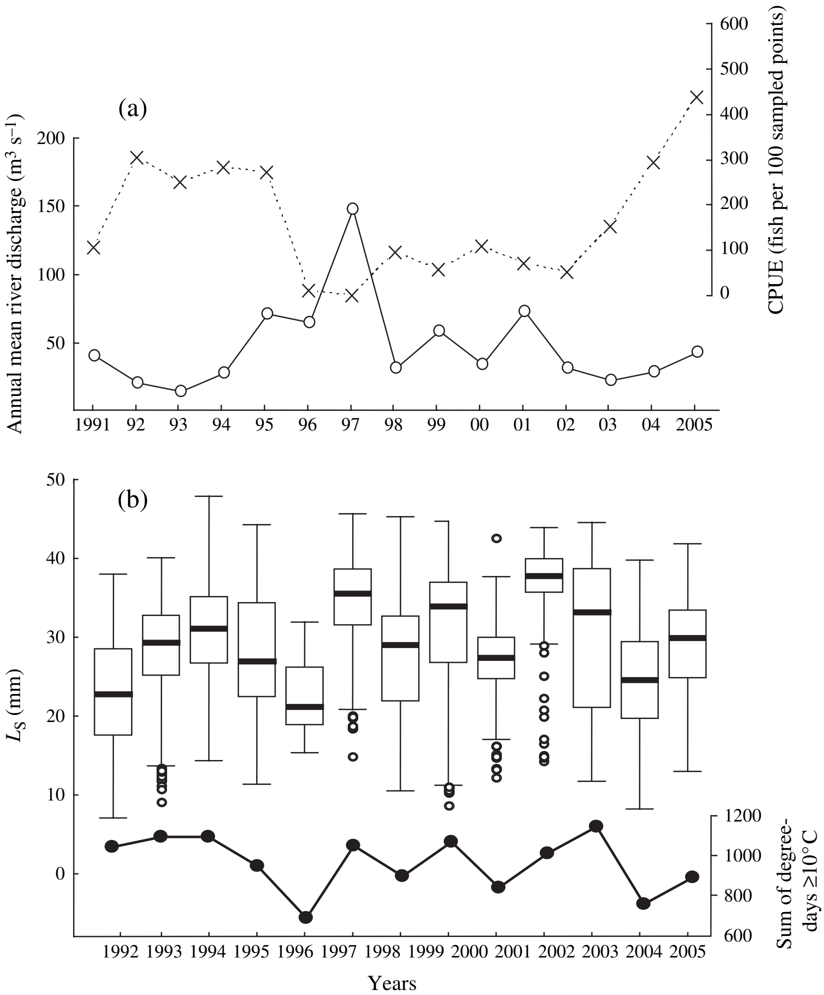

FIG. 1. Interannual variation in juvenile *Rhodeus amarus* demographic variables and environmental data. (a) Mean river discharge (calculated from the data set relevant to *R. amarus* reproductive and growing period) for the period between 1991 and 2005 (–○–) and abundance of 0+ year *R. amarus* in autumn (CPUE; ··×··). (b) Median standard length (L_{S}) of 0+ year *R. amarus* over the study period (with interquartile range and outliers indicated as boxes and dots, respectively) and cumulative number of degree-days ≥10° C for the period between 1991 and 2005, excluding the years 1991 and 1997 where sampling was conducted 2 months later that in other years.

most powerful predictor of 0+ year *R. amarus* abundance. The best model also included temporal autocorrelation structure and variance in water temperature, with 0+ year abundance in a particular year positively related to the 0+ year abundance in the preceding year (C_{P-1}) and increasing variance in temperature (T_{var}) (final model: $F_{3,10}$, $P = 0{\cdot}001$, adjusted $r^2 = 0{\cdot}71$; Table I). The mean L_S of juvenile *R. amarus* was positively correlated with the cumulative number of degree-days ≥10° C (D_{d10}) ($r_s = 0{\cdot}59$, $P < 0{\cdot}05$), and the best regression model included only D_{d10} (final model $F_{1,11}$, $P < 0{\cdot}05$, adjusted $r^2 = 0{\cdot}27$; Table I). There was no direct correlation between the variability in L_S and the measured environmental variables (all $P > 0{\cdot}05$), and there was no regression model that significantly fitted these data (all $P > 0{\cdot}05$; Table I). The frequency distribution of *R. amarus* at the end of the first growing seasons is shown in Fig. 1(b).

Results did not support the prediction that water temperature had the most significant influence on the abundance of 0+ year *R. amarus* at the end of the growing season. Instead, river discharge was the most important factor

TABLE I. Results of multiple regression analysis using Akaike information criterion (AIC) for best model selection. Values of AIC, variation in difference in AIC between each model and the model with the lowest AIC (DAIC), Akaike weights (wi) and the relative fit of the model compared to the best model (åwi) are indicated for each model considered during stepwise removal of potentially redundant variables. The best models for 0+ year abundance and mean standard length (L_S) are indicated (*) and their summaries are shown on the right panel. No candidate model significantly explained variability in L_S

Models considered					Best model summary		
Model	AIC	DAIC	wi	åwi	Predictor	Estimate (S.E.)	*P*
0+ year abundance							
I_m, T_{var}, D_m, D_{var}, C_{P-1}	21·30	3·99	0·05	0·14	Intercept	1·623 ± 0·482	<0·01
T_{var}, D_m, D_{var}, C_{P-1}	19·30	1·99	0·14	0·37	T_{var}	0·033 ± 0·018	>0·05
*T_{var}, D_m, C_{P-1}	17·31	0·00	0·37	1·00	D_m	−0·014 ± 0·003	0·001
T_{var}, D_m	17·95	0·64	0·27	0·73	C_{P-1}	0·285 ± 0·161	>0·05
D_m	18·92	1·61	0·17	0·45			
Mean L_S							
T_m, T_{var}, D_m, D_{var}, D_{d10}	81·00	7·06	0·02	0·03	Intercept	11·362 ± 7·576	>0·05
T_{var}, D_m, D_{var}, D_{d10}	79·00	5·06	0·04	0·08	D_{d10}	0·019 ± 0·008	<0·05
D_m, D_{var}, D_{d10}	77·03	3·09	0·12	0·21			
D_m, D_{d10}	75·49	1·55	0·26	0·46			
*D_{d10}	73·94	0·00	0·56	1·00			
Variability in L_S							
T_m, T_{var}, D_m, D_{var}, D_{d10}	−4·14	2·24	0·13	0·32			
T_m, T_{var}, D_m, D_{var}	−5·75	0·63	0·28	0·73			
T_{var}, D_m, D_{var}	−6·38	0·00	0·39	1·00			
D_m, D_{var}	−3·52	2·87	0·09	0·24			
D_m	−3·75	2·63	0·10	0·27			

C_{P-1}, 0+ year *Rhodeus amarus* abundance in previous autumn; D_{d10}, cumulative number of degree-days ≥10° C; D_m, mean river discharge; D_{var}, variation in mean river discharge; T_m, mean water temperature; T_{var}, variation in water temperature.

affecting *R. amarus* recruitment success. This is an important finding for the understanding of the invasive success of *R. amarus* in recent decades because the increase in *R. amarus* abundance, and its colonization of new areas in northern and eastern Europe (*e.g.* Denmark, upper Ural River, drainages of the Volga and Kuban Rivers) (Møller & Menne, 1998; Kozhara *et al.*, 2007) has been linked to an increase in global temperature (Van Damme *et al.*, 2007). The present data showed that, for populations of *R. amarus* in regulated rivers, high discharge conditions can considerably limit the abundance of 0+ year fish. This effect arises because juvenile fish have no protection from strong water currents in the River Morava and other similar regulated rivers without any connection to the former flood plain (Reichard *et al.*, 2001), while habitat complexity and the capacity of nursery areas are considerably increased at low river discharge (Jurajda, 1999; Nunn *et al.*, 2007*a*). It should further be noted that there is an association between high temperatures and low precipitation in central Europe (Pal *et al.*, 2004), which is mirrored by a significant negative correlation between mean river discharge and mean water temperature ($r_s = 0{\cdot}67$, $P < 0{\cdot}05$) in the present data set. The effect of temporal autocorrelation indicates that recruitment success was also related to the abundance of the adult population and that a failure in recruitment in 1 year may severely affect population size in subsequent years [Fig. 1(a)].

The occurrence of *R. amarus* is primarily controlled by presence of unionid mussels that are used as a spawning substratum. There is no direct link, however, between the abundance of mussels and the *R. amarus* recruitment success (Smith *et al.*, 2000). Juvenile *R. amarus* inhabit shallow, vegetated areas with a minimal water velocity (Reichard *et al.*, 2004), where they are safe from fish predators such as perch, *Perca fluviatilis* L. (Smith *et al.*, 2000). The present sampling design did not allow the extent of nursery habitats to the estimated directly, but there is clear relationship between low river discharge and availability of shallow patches in the River Morava (Jurajda, 1995, 1999). High discharge conditions can further increase unintentional downstream drift of 0+ year *R. amarus* (Reichard *et al.*, 2001) that is associated with high mortality rates (Reichard *et al.*, 2002*b*). Therefore, it is likely that high river discharge increases mortality of 0+ year *R. amarus* through a combination of direct effects of the river flow (drift) and indirect effects mediated by a lack of suitable nursery areas (predation and reduced food availability).

Water temperature may still be an important direct factor determining the success of new *R. amarus* populations to establish themselves at the periphery of their current range, especially at its northern limit. The present analysis showed that the sum of degree-days $\geq 10°$ C was the most important variable for mean L_S (Table I) and hence for juvenile growth. Over-winter survival was positively related to L_S of 0+ year juvenile fish at the end of the growing season (Kirjasniemi & Valtonen, 1997). Large size interval between the smallest and the largest 0+ year fish would suggest a longer reproductive season, but variables used in the analysis failed to predict any significant association between range in L_S and environmental conditions. Interannual differences in mean L_S and its close association with water temperature have already been reported for other European cyprinids, including roach *Rutilus rutilus* (L.), chub *Leuciscus cephalus* (L.) and dace *Leuciscus leuciscus* (L.) from the Yorkshire River

Ouse (Nunn *et al.*, 2003) and for *R. rutilus*, silver bream *Abramis bjoerkna* (L.) and bleak *Alburnus alburnus* (L.) in the lower River Oder (Wolter, 2007) and appears to be widespread. Increased ambient temperature may also improve over winter survival of *R. amarus*, a member of a primarily subtropical subfamily (Smith *et al.*, 2004), but this has not been investigated.

River regulation strongly affects fish assemblage structure (Aarts *et al.*, 2004). Some species suffer significant decreases in their relative abundance from habitat alteration; this may be especially the case for species that use specific spawning substrata (*e.g.* phytophilic species) that may become unavailable after river channelization (Jurajda, 1995). Other species may suffer from population fragmentation when weirs present a barrier to annual migration to spawning grounds (Lucas & Baras, 2001). Other species, however, may benefit from river regulation, for example when artificial embankments provide substrata for spawning or juvenile survival (Wolter & Vilcinskas, 1997; Aarts *et al.*, 2004). Finally, some species may profit from reduced competition with adversely affected species. Notably, most cyprinids use the same food resources during the first months of their lives (Garner, 1996; Grenouillet *et al.*, 2001*b*; Nunn *et al.*, 2007*b*). *Rhodeus amarus* does not appear to be directly affected by river regulation and channelization (Reichard, 1998), and the species is commonly found in regulated rivers (Kozhara *et al.*, 2007). River regulation stabilizes river discharge and eliminates extreme discharge conditions (Magilligan *et al.*, 2003). Hence, it may be speculated that, in general, *R. amarus* invasion is facilitated by river regulation and alteration of natural habitats (perhaps by reducing the frequency of high discharge conditions) and associated with an increase in ambient temperatures (Kozhara *et al.*, 2007; Van Damme *et al.*, 2007).

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References

Aarts, B. G. W., Van den Brink, F. W. B. & Nienhuis, P. H. (2004). Habitat loss as the main cause of the slow recovery of fish faunas of regulated large rivers in Europe: the transversal floodplain gradient. *River Research and Applications* **20,** 3–23.

Daufresne, M., Roger, M. C., Capra, H. & Lamoroux, N. (2003). Long-term changes within the invertebrate and fish communities of the Upper Rhône River: effects of climatic factors. *Global Change Biology* **10,** 124–140.

Durham, B. W. & Wilde, G. R. (2006). Influence of stream discharge on reproductive success of a prairie stream fish assemblage. *Transactions of the American Fisheries Society* **135,** 1644 –1653.

Garner, P. (1996). Microhabitat use and diet of 0+ cyprinid fishes in a lentic, regulated reach of the River Great Ouse, England. *Journal of Fish Biology* **48,** 367–382.

Gaston, K. J. (2003). *The Structure and Dynamics of Geographic Ranges*. Oxford: Oxford University Press.

Gillet, C. & Dubois, J. P. (2007). Effect of water temperature and size of females on the timing of spawning of perch *Perca fluviatilis* L. in Lake Geneva from 1984 to 2003. *Journal of Fish Biology* **70,** 1001–1014.

Grenouillet, G., Hugueny, B., Carrel, G. A., Olivier, M. & Pont, D. (2001*a*). Large-scale synchrony and inter-annual variability in roach recruitment in the Rhône River: the relative role of climatic factors and density-dependent processes. *Freshwater Biology* **46,** 11–26.

Grenouillet, G., Pont, D. & Olivier, J. M. (2001*b*). Linking zooplankton and juvenile fish assemblages in a large lowland river: influence of submerged macrophytes. *Archiv für Hydrobiologie* **151,** 383–404.

Hanski, I. (1991). Single-species metapopulation dynamics-concepts, models and observations. *Biological Journal of the Linnean Society* **42,** 17–38.

Jurajda, P. (1995). Effect of channelization and regulation on fish recruitment in a floodplain river. *Regulated Rivers: Research & Management* **10,** 207–215.

Jurajda, P. (1999). Comparative nursery habitat use by 0+ fish in a modified lowland river. *Regulated Rivers: Research & Management* **15,** 113–124.

Kirjasniemi, M. & Valtonen, T. (1997). Winter mortality of young-of-the-year pikeperch *Stizostedion lucioperca*. *Ecology of Freshwater Fish* **6,** 155–160.

Kottelat, M. & Freyhof, J. (2007): *Handbook of European Freshwater Fishes*. Cornol: Publications Kottelat.

Kozhara, A. V., Zhulidov, A. V., Gollasch, S., Przybylski, M., Poznyak, V. G., Zhulidov, D. A. & Gurtovaya, T. Yu. (2007). Range extension and conservation status of the bitterling, *Rhodeus sericeus amarus* in Russia and adjacent countries. *Folia Zoologica* **56,** 97–108.

Lelek, A. (1987). *Threatened Fishes of Europe*. Wiesbaden: Aula-Verlag.

Lucas, M. C. & Baras, E. (2001). *Migration of Freshwater Fishes*. Oxford: Blackwell.

Magilligan, F. J., Nislow, K. H. & Graber, B. E. (2003) Scale-independent assessment of discharge reduction and riparian disconnectivity following flow regulation by dams. *Geology* **31,** 569–572.

Marchetti, M. P., Light, T., Moyle, P. B. & Viers, J. H. (2004). Fish invasions in California watersheds: testing hypotheses using landscape patterns. *Ecological Applications* **14,** 1507–1525.

Mills, C. A. & Mann, R. H. K. (1985). Environmentally induced fluctuations in year class strength and their implications for management. *Journal of Fish Biology* **27,** 209–226.

Møller, P. R. & Menne, T. (1998). Bitterling *Rhodeus sericeus* (Pallas, 1776) – first record from Denmark. *Flora og Fauna* **104,** 29–34.

Nunn, A. D., Cowx, I. G., Frear, P. A. & Harvey, J. P. (2003). Is water temperature an adequate predictor of recruitment success in cyprinid fish populations in lowland rivers? *Freshwater Biology* **48,** 579–588.

Nunn, A. D., Harvey, J. P., Britton, J. R., Frear, P. A. & Cowx, I. G. (2007*a*). Fish, climate and the Gulf Stream: the influence of abiotic factors on the recruitment success of cyprinid fishes in lowland rivers. *Freshwater Biology* **52,** 1576–1586.

Nunn, A. D., Harvey, J. P. & Cowx, I. G. (2007*b*). The food and feeding relationships of larval and 0+ year juvenile fishes in lowland rivers and connected waterbodies. I. Ontogenetic shifts and interspecific diet similarity. *Journal of Fish Biology* **70,** 726–742.

Olden, J. D., Poff, N. L. & Bestgen, K. R. (2006). Life-history strategies predict fish invasions and extirpations in the Colorado River Basin. *Ecological Monographs* **76,** 25–40.

Pal, J. S., Giorgi, F. & Bi, X. Q. (2004). Consistency of recent European summer precipitation trends and extremes with future regional climate projections. *Geophysical Research Letters* **31,** L13202.

Przybylski, M. & Zięba, G. (2000). Microhabitat preference of European bitterling, *Rhodeus sericeus*, in the Drzewiczka River (Pilica basin). *Polish Archives of Hydrobiology* **47,** 99–114.

Reichard, M. (1998). Biology of bitterling (*Rhodeus sericeus*) in atypical conditions in a regulated lowland river. MSc Thesis, Masaryk University, Brno, Czech Republic.

Reichard, M., Jurajda, P. & Václavík, R. (2001). Drift of larval and juvenile fishes: a comparison between small and large lowland rivers. *Archiv für Hydrobiologie* (Suppl.) **135**, 373–389.

Reichard, M., Jurajda, P., Šimková, M. & Matějusová, I. (2002*a*). Size-related habitat use by bitterling (*Rhodeus sericeus*) in a regulated lowland river. *Ecology of Freshwater Fish* **11,** 112–122.

Reichard, M., Jurajda, P. & Ondračková, M. (2002*b*). Interannual variability in seasonal dynamics and species composition of drifting young-of-the-year fishes in two European lowland rivers. *Journal of Fish Biology* **60,** 87–101.

Reichard, M., Jurajda, P. & Smith, C. (2004). Spatial distribution of drifting cyprinid fishes in a shallow lowland river. *Archiv für Hydrobiologie* **159,** 395–407.

Rose, K. A. (2000). Why are quantitative relationships between environmental quality and fish population so elusive? *Ecological Applications* **10,** 367–385.

Schlosser, I. J. (1985). Flow regime, juvenile abundance, and the assemblage structure of stream fishes. *Ecology* **66,** 1484–1490.

Smith, C., Reynolds, D. C., Sutherland, W. J. & Jurajda, P. (2000). Adaptive host choice and avoidance of superparasitism in the spawning decisions of bitterling (*Rhodeus sericeus*). *Behavioral Ecology and Sociobiology* **48,** 29–35.

Smith, C., Reichard, M., Jurajda, P. & Przybylski, M. (2004). The reproductive ecology of the European bitterling (*Rhodeus sericeus*). *Journal of Zoology* **26,** 107–124.

Townsend, C. R. (1989). Population cycles in freshwater fish. *Journal of Fish Biology* **35** (Suppl. A), 125–131.

Van Damme, D., Bogutskaya, N., Hoffmann, R. C. & Smith, C. (2007). The introduction of the European bitterling *Rhodeus amarus* to west and central Europe. *Fish and Fisheries* **8,** 79–106.

Whittingham, M. J., Stephens, P. A., Bradbury, R. B. & Freckleton, R. P. (2006). Why do we still use stepwise modelling in ecology and behaviour? *Journal of Animal Ecology* **75,** 1182–1189.

Wolter, C. (2007). Temperature influence on the fish assemblage structure in a large lowland river, the lower Oder River, Germany. *Ecology of Freshwater Fish* **16,** 493–503.

Wolter, C. & Vilcinskas, A. (1997). Perch (*Perca fluviatilis*) as an indicator species for structural degradation in regulated rivers and canals in the lowlands of Germany. *Ecology of Freshwater Fish* **6,** 174–181.

Wootton, R. J. (1998). *Ecology of Teleost Fish*. Dordrecht: Kluwer.

Electronic Reference

European Commission (2002). *Reference List of Habitat Types and Species Present in the Continental Region*. Available at http://biodiversity.eionet.europa.eu/activities/Natura_2000/Ref-con