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FISH AND DIADROMY IN EUROPE

Does global warming impact on migration patterns and recruitment of Allis shad (*Alosa alosa* L.) young of the year in the Loire River, France?

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Abstract The hydrological and thermal changes in the Loire River were investigated to test the influence of climatic changes on a short freshwater stage anadromous fish species, Allis shad, for the 1995–2004 period. The mean water temperatures during the adult migration and juvenile growth phases showed significant increase, and mean water flow during these two phases decreased significantly. The period below the threshold of 18°C shortened, and the period between 18°C and the maximum lengthened, while the temperature amounts (number of degree-days) received by aquatic organisms between 18 and 24°C showed an increase. The pattern of young-of-the-year downstream migration was modified. The first day when the juvenile catches reached 5% occurred 17 days earlier at the end of the 1995–2004 period than at the beginning. The first day when the juvenile catches reached 50% was related to the 18°C threshold (reproductive threshold) and the temperature amounts accumulated between the 18 and 20°C thresholds. The year-on-year levels of young-of-the-year abundance showed wide variations, which were not explained by environmental parameters, probably because of the long distance between the study site and the spawning grounds.

Keywords Water temperature · Hydrology · Trends · Migration pattern · Abundance · Allis shad

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Introduction

The oldest daily air temperature records in Europe date back to the nineteenth century, but this type of records is very rare for water temperatures (Webb & Nobilis, 1994). During the twentieth century, the water temperature in the Danube in Austria has shown a significant increase in monthly mean water temperatures of 0.8°C, varying from 0.66 to 2.0°C. Severe low water levels and human activities are accelerating this process (Webb & Nobilis, 1994, 1995). In the upper Rhône River (France), between 1979 and 1999, the average water temperature rose by about 1.5°C due to atmospheric warming, and the flow rates fluctuated around the annual mean without showing any particular trends (Daufresne et al., 2003). Linear regression models based on monthly air temperature and flow rate data were used to reconstruct the temperatures for the period 1881–2003 in the middle section of the Loire River (France). The rapid rise in water temperatures observed since 1976 is part of a general trend over the century, marked by other warm periods around 1900 and 1950 (Moatar & Gailhard, 2006). The mean annual water temperatures increased by 1.6°C between 1976 and 2003.

The Allis shad (*Alosa alosa*) is an anadromous Clupeid historically ranging from south Morocco to north Germany (Baglinière, 2000). This species frequents the Loire watershed where spawning grounds are located about 550–750 km from the sea (Boisneau et al., 1990). As there are no stocking phenomena, this species provides an interesting model for assessing the impacts of global changes. The freshwater stage is very short, ranging from 3 to 6 months. The juveniles migrate downstream to the sea during the summer and early autumn (Taverny et al., 2000).

The global warming of rivers in temperate zones is likely to affect ectothermic aquatic organisms. Flow and water temperature exercise fundamental control over these ecosystems and their communities (Ward, 1992). Although density-dependent processes interact with environmental factors to determine recruitment levels and variability, water temperature and flow are two important factors that affect freshwater fish dynamics (Schlosser & Angermeier, 1990; Cattaneo et al., 2001, 2002). Water temperature controls physiology and influences phenology, while survival of fish during their early life may be affected by water temperature and water flow rates. This can lead to earlier maturity, change the population age breakdown and generate year class fluctuations (Mann, 1991; Elliott et al., 2000; Davidson et al., 2006).

As climatic factors are known to influence freshwater fish abundance, our question in this article is whether these factors influence an anadromous species with a short freshwater stage. Especially, we address the following questions: (1) What are the hydrological and thermal changes in the middle section of the Loire River during Allis shad freshwater phases? What are the consequences of these changes? (2) For the migration pattern of young of the year, and (3) On their inter-annual abundance?

Methods

Study sites

The Loire River runs over a 1,000-km course from the centre of France and drains an area of about 117,000 km ^{2}. The study site where fish were caught is located 250 km from the sea and 300 km downstream from the spawning grounds (Fig. 1). The annual mean flow at the study site is 364 m^3/s. (1863–2004).

Temperature and flow data

Daily flow rate data were taken from the HYDRO national database managed by the French Department of the Environment for the nearest site. Daily temperature data were recorded by Electricité de France upstream from the Chinon-Avoine nuclear power plant, the nearest spot where water temperatures are recorded (Fig. 1). The levels of thermal waste flow into the Loire are very low, with a median rise of 0.1°C (Moatar et al., 2006) and they do not interfere with anadromous fish migration.

To evaluate the effects of hydrological and thermal changes on Allis shad, the freshwater stage was divided into two periods, adult upstream migration and spawning from 15/03 to 15/06, and the young of

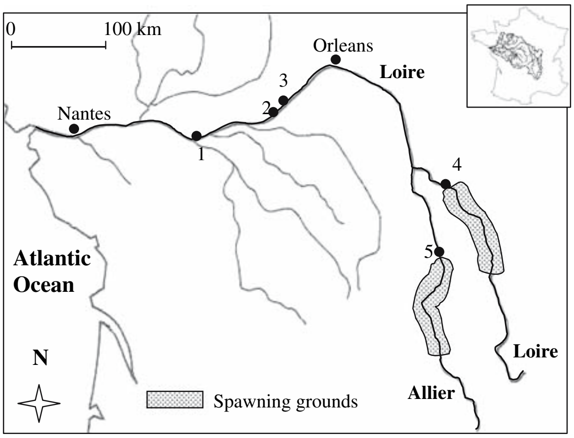

Fig. 1 Location of the temperature recording site, Avoine (1), the fish sampling site (2), the flow rate recording site (3) and Allis shad adult control stations (4–5)

the year (YOY) early growth and downstream migration, from 15/06 to 15/10. Several hydroclimatic variables were used (Carrel, unpublished data). They were calculated from daily data, for each year, from 1976 to 2004:

- The number of days (Julian calendar) between 1 January and the date of exceeding a given threshold. This shows whether the temperature rise phase occurs late or early. The thresholds adopted were 16, 18, 20, 24°C and the maximum. The temperature range chosen covers the adult migration period, the egg incubation period and the initial live stage (Roule, 1923; Hoestlandt, 1958). The variables are called C16, C18, C20, C24 and Cmax.
- The duration, in days, between the two thermal thresholds, between 16 and 18°C (D16–18), between 18 and 20°C (D18–20) and between 20 and 24°C (D20–24). This expresses the variations in length of the periods between two thresholds.
- The sum of daily thermal differences between the annual curve and an inter-annual smoothed curve (1976–2004) for the period between two thresholds, 16 and 18°C (S16–18), 18 and 20°C (S18–20), 20 and 24°C (S20–24). This is the equivalent of a degree-day amount as compared with the inter-annual curve. It quantifies temperature increases or decreases.
- The average conditions of seasonal water flow and temperature were estimated from the mean water temperature, the mean water flow rate and the median daily flow rate (Q50) over each migration season.
- The high and low flow level events were described with the 0.1, 0.2, 0.8, 0.9 percentiles of water flow expressed as Q10, Q20, Q80 and Q90 for the two periods of shad migration.
- Flow rate variability was expressed as the ratio Q10/Q90.

Fish data

Downstream migrating juvenile were intercepted with a beach seine, because Allis shad juveniles are near the bank (Taverny et al., 2000) (location 2, Fig. 1). The mesh size was 10 mm. The water depth ranged from 0.5 to 1.2 m and the water flow speed varied from 0.3 to 0.8 m/s. The substrate was sand and gravel. Sampling was carried out from Mondays to Fridays, from mid-June to mid-October, and from 1995 to 2004. The water flow rate ranged from 55 to 254 m^3/s. The fish were measured (fork length) to the nearest millimetre.

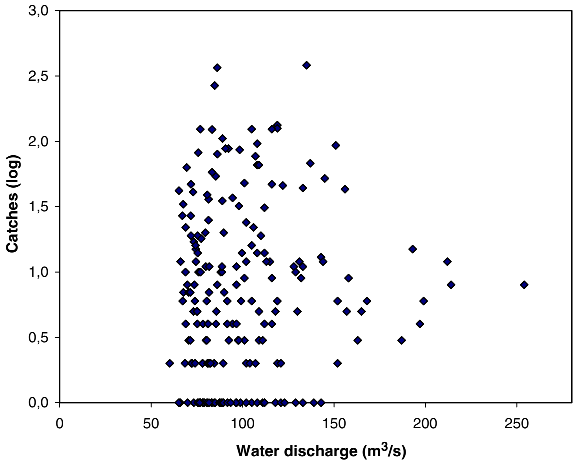

Fig. 2 Relationship between catches of Allis shad YOY and water flow rate during fish sampling

The links between YOY catches and effort were checked for each year. They showed no relationship except for 2001, which accounted for 6.3% of catches over the entire series. Catches and effort were still considered as independent. The links between catches and water flow were also checked for each year and did not show any relationship ($P >> 0.05$, Fig. 2). The YOY abundance was expressed as catch per unit effort (CPUE), calculated for each year, as a ratio of the total number of catches to the total effort.

The pattern of juvenile migration was determined by the days (Julian calendar) when the 0.05, 0.5 and 0.95 percentile of catches occurred. The durations, in days, between two of these dates (days when 0.05 and 0.5 of the catches occurred; days when 0.5 and 0.95 of the catches occurred) were calculated. This expresses the variations in the length of the migrating period.

The numbers of adults reaching the main spawning grounds in the watershed were obtained from fish control stations managed by LOGRAMI[1], since 1998, the starting date for data collection. They were expressed as the total number of adults getting over

[1] LOGRAMI is an NGO bringing together recreational and commercial fishermen from the Loire River watershed. It provides assistance for diadromous fish management.

the fish pass on the Loire and the Allier Rivers (Fig. 1, locations 4 and 5), over a period ranging from 14 April to 3 July.

Data analysis

In order to detect trend over time for thermal and hydrological parameters and in migration patterns, we used a non-parametric seasonal Kendall test and seasonal Kendall slope estimator. This non-parametric test (based on ranks) seeks trend once autocorrelation effects are removed (Webb & Nobilis, 1994).

The influence of flow and thermal changes on the migration pattern for YOY was tested with a Spearman rank correlation between the days of 0.05 and 0.5 percentile of catches and the environmental variables that showed significant prior trends.

Spearman rank correlations were used to test the potential relationship between YOY abundance and some selected environmental variables that showed significant prior trends, and between YOY abundance and the number of adults reaching the main spawning grounds.

Results

Temperature and flow rate data

The mean water temperature during the two periods of shad migration showed a significant increase of 2.5°C for the adult upstream migration period and 2.0°C for the YOY downstream migration period, between 1976 and 2004 (Table 1). The numbers of days before the thermal thresholds (Ci) showed significant decrease for the 18, 20 and 24°C levels, but not for the maximum (Table 1). The duration, in days, between the thresholds (Di) remained unchanged, but the increase in the heat amount (Si) between 18 and 20°C and 20 and 24°C was significant (Table 1).

The mean water flow rate during the two periods of shad migration showed a significant decrease (Table 2). These seasonal flow rate falls were part of a general trend over the entire year. The annual mean flow rate was 469 m^3/s in 1976 and 264 m^3/s in 2004 ($r_k = -0.547$, $P = 0.002$), the decrease is around 40%. The mean water flow rate during adult upstream migration was 626 m^3/s in 1976 and 298 m^3/s in 2004, and the mean water flow rate during YOY downstream migration was 218 m^3/s in 1976 and 98 m^3/s in 2004 (Table 2). The high flow levels for each migration season showed significant falls, though the low flow levels only dropped during the adult upstream migration (Table 2). Flow rate variability increased significantly during the juvenile downstream migration.

None of these trends were sensitive to extreme years; they remained significant at the 0.05 confidence level when we removed the hot years 1976 and 2003.

Fish data

Allis shad juveniles are very difficult to catch, and it was the first time in France that they has been successfully sampled over a 10-year period (1995–2004). 4,613 young Allis shad were sampled, with an absence of catches in 1996. The mean length was

Table 1 Trends in thermal variables of the median part of the Loire River between 1976 and 2004

Parameter	Slope of linear trend	Significance of trend (*P*)	Change over the study period Data for 1976 and 2004
C18 (Julian day for threshold 18°C)	−0.56	0.041	Day 140–day 124
C20 (Julian day for threshold 20°C)	−0.83	0.010	Day 159–day 135
C24 (Julian day for threshold 24°C)	−1.3	0.001	Day 198–day 161
S18–20 (temperature increase)	1.64	0.021	46°C. day
S20–24 (temperature increase)	5.31	0.000	102°C. day
Mean water temperature during adult upstream migration (15/03–15/06)	0.09	0.000	13.3–15.8°C
Mean water temperature during YOY downstream migration (15/06–15/10)	0.07	0.001	19.3–21.3°C

Only variables showing significant trends are shown

Table 2 Trends in the Loire River flow rate variables between 1976 and 2004

Parameter	Slope of trend	Significance of trend (*P*)	Change over the study period Data for 1976 and 2004
River flow rate during adult upstream migration			
Q20 (percentile 0.2)	−6.72	0.046	372–183 m^3/s
Q50 (percentile 0.5)	−9.94	0.048	538–260 m^3/s
Q80 (percentile 0.8)	−15.68	0.039	826–387 m^3/s
Q90 (percentile 0.9)	−21.37	0.036	1087–489 m^3/s
Mean river flow rate	−11.7	0.036	626–298 m^3/s
River flow rate during YOY downstream migration			
Q50 (percentile 0.5)	−3.36	0.038	172–78 m^3/s
Q80 (percentile 0.8)	−6.4	0.041	306–128 m^3/s
Q90 (percentile 0.9)	−9.36	0.047	417–155 m^3/s
Flow rate variability (Q10/90)	0.07	0.029	0.266–0.468
Mean river flow rate	−4.299	0.039	218–98 m^3/s

Only variables showing significant trends are shown

58 mm (standard deviation: 11 mm) with extremes ranging from 45 to 76 mm.

YOY were intercepted between 28 June and 15 October. The starting date for their downstream migration was 17 days earlier at the end of the time lapse than at the beginning (Fig. 3). The days when 50% and 95% of the catches occurred did not show any significant trend. This means that the duration of the first half of the migration period is lengthening.

No significant relationships were found between environmental variables and the day when 5% of catches of YOY occurred, but significant relationships were found between the day when 50% of catches occurred and the 18°C threshold ($r_s = 0.745$, $P = 0.012$), and the number of degree days between 18 and 20°C ($r_s = 0.745$, $P = 0.012$).

The year-on-year changes in abundance of YOY showed considerable variability, with very low levels in 1996, 1999, 2000 and 2003, and a very high level in 2004 (Fig. 4), but no links were found between juveniles abundance and adult abundance, thermal variables or river flow rates (Table 3).

Discussion

Temperature and flow rate data

The rise in water temperatures observed for the Loire River is consistent with the changes occurring in other European rivers, despite differences in their hydrological regime (Daufresne et al., 2003; Davidson et al., 2006; Mouthon & Daufresne, 2006; Webb & Nobilis, 1995). For the Loire, the water temperatures show significant increases in the spring, summer and winter (Moatar & Gailhard, 2006). During the spring and summer, the 18, 20 and 24°C thresholds are reached earlier, but the day when the maximum is reached does not show any significant trends. The period before the 18°C threshold has shortened, and the period between 18°C and the maximum has lengthened accordingly, while the temperature amount received by aquatic organisms between 18 and 24°C has increased.

In contrast with the trends noted concerning water flow rates in the Rhône and Saône Rivers (Daufresne et al 2003; Mouthon & Daufresne, 2006), the mean annual flow rate of the Loire is decreasing. This is also observed for the flow rate parameters, Q50, Q80 and Q90 for spring and summer. The maximum flow rate and flow rate variability (Q10/Q90) during the adult migration period do not show any trends. On the other hand, flow rate variability during the juveniles migration is increasing. We can assume that species spawning or/and having their larval development during spring and early summer probably emerge earlier and grow faster. This could be accelerated by lower water flow rates and lower levels of variability.

YOY of Allis shad

Climatic conditions during the larval period generally determine the survival rate of the fish during their

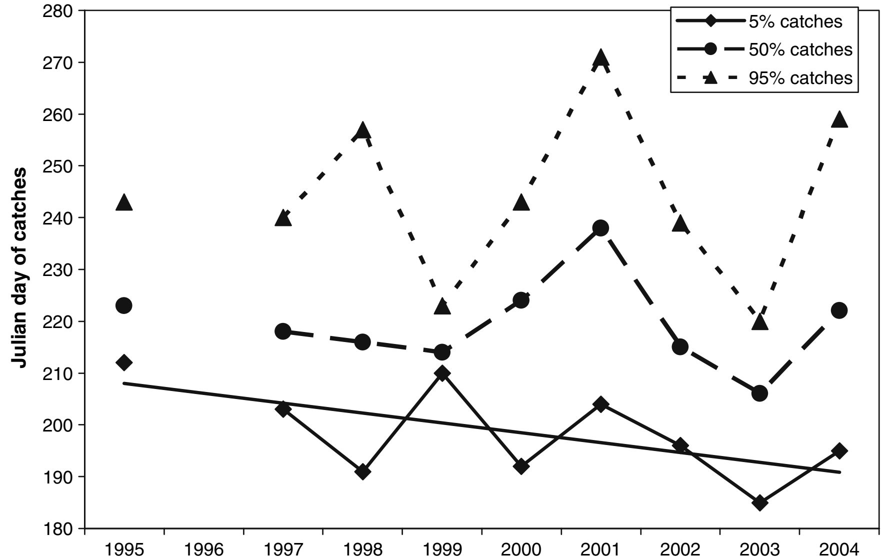

Fig. 3 Temporal evolution of the Julian days when 0.05, 05 and 0.95 percentile of YOY of Allis shad catches occurred. Only significant trends are shown. 5% of catches (seasonal Kendall test, $r_k = -0.700$, $P = 0.03$; 50% of catches, $r_k = -0.367$, $P = 0.09$; 95% of catches, $r_k = 0.112$, $P = 0.327$)

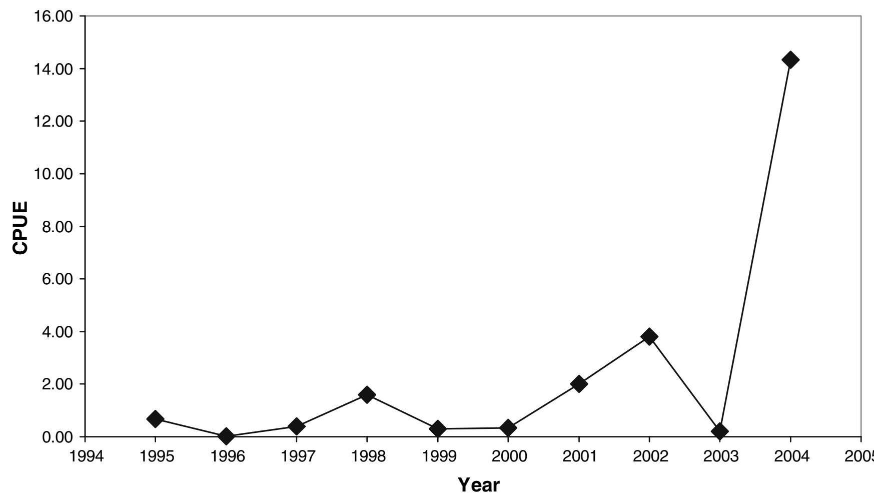

Fig. 4 Temporal evolution in abundance of Allis shad YOY

Table 3 Relationship between Allis shad YOY abundance and environmental parameters (1995–2004)

Parameter	Correlation (r_s)	Probability level (P)
Mean water temperature during adult upstream migration (15/03–15/06)	−0.479	0.16
Mean water temperature during YOY downstream migration (15/06–15/10)	−0.333	0.217
C18 (Julian day for threshold 18°C)	0.033	0.463
C20 (Julian day for threshold 20°C)	−490	0.15
C24 (Julian day for threshold 24°C)	0.382	0.138
S18–20 (temperature increase)	−0.261	0.191
S20–24 (temperature increase)	−0.127	0.36
Mean water flow during adult upstream migration (15/03–15/06)	0.406	0.122
Mean water flow during YOY downstream migration (15/06–15/10)	0.539	0.054
Number of adults reaching the main spawning grounds	0.464	0.147

initial life, and their abundance in small or large rivers (Cattaneo et al., 2001, 2002; Elliott et al., 2000; Daufresne, 2003; Grenouillet et al, 2001). Annual juveniles abundance shows strong fluctuations, without any apparent relationship with environmental variables. If the fishing effort is constant in terms of time and surface when the flow rate increases, the relative proportion of sampled habitat is reduced. This could account for the absence of links between YOY abundance and summer water flow rate. The distance between the study site and the spawning grounds is another possible explanation for the absence of links between YOY abundance and hydroclimatic variables. The spawning grounds are located 300 km upstream from the sampling site, and the environmental parameters are probably different. It was not possible to test the impact on the YOY survival rate of flows and temperatures during incubation and the early stages of life in the spawning grounds.

There are positive relationships between the day when 50% of the juveniles catches occurred and the 18°C threshold and the number of degree-days between 18 and 24°C. As is the case for other fish species, the durations of egg and larval development are related to temperatures, and especially to the temperature for adult reproduction, 18°C being the median temperature value when spawning occurs (Hoestlandt, 1958).

The day when the 0.05 percentile of catches was reached, occurred earlier (27 July in 1995 and 10 July in 2004). The downstream migration now starts earlier than the mid-August date given for the Garonne and Loire rivers (Taverny et al., 2000).

The absence of a relationship between the day for the 0.05 percentile of YOY catches and the environmental variables could be explained by the location of the sampling site; but according to Bernard & Larinier, (1988) water temperature and water flow rate are not at the origin of juveniles migration on the Garonne River. It could be the same on the Loire River; certain biological and physiological parameters (length and hormone concentration) could be involved in the downstream departure process, as is shown for twaite shad (*Alosa fallax*) (Aprahamian, 1988) and *Alosa sapidissima* (Limburg, 1996).

To conclude, our results indicate impacts of climatic change in the Loire River either in the thermal or the hydrological regime for the 1976–1995 period. This influences the departure of YOY Allis shad on their downstream migration, but not their annual abundance. This strongly suggests the need to take into account the impact of climatic change in anadromous fish monitoring programs.

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