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## Differences in sensitivity of native and exotic fish species to changes in river temperature

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**Abstract** This paper describes the effects that temperature changes in the Rhine river distributaries have on native and exotic fish diversity. Site-specific potentially affected fractions (PAFs) of the regional fish species pool were derived using species sensitivity distributions (SSDs) for water temperature. The number of fish species in the river distributaries has changed remarkably over the last century. The number of native rheophilous species declined up until 1980 due to anthropogenic disturbances such as commercial fishing, river regulation, migration barriers, habitat deterioration and water pollution. In spite of progress in river rehabilitation, the native rheophilous fish fauna has only partially recovered thus far. The total number of species has strongly increased due to the appearance of more exotic species. After the opening of the Rhine-Main-Danube waterway in 1992, many fish species originating from the Ponto-Caspian area colonized the Rhine basin. The yearly minimum and maximum river temperatures at Lobith have increased by circa 4 °C over the period 1908–2010. Exotic species show lower PAFs than native species at both ends of the temperature range. The interspecific variation in the temperature tolerance of exotic fish species was found to be large. Using temporal trends in river temperature allowed past predictions of PAFs to demonstrate that the increase in maximum river temperature negatively affected a higher percentage of native fish species than exotic species. Our results support the hypothesis that alterations of the river Rhine's temperature regime caused by thermal pollution and global warming limit the full recovery of native fish fauna and facilitate the establishment of exotic species which thereby increases competition between native and exotic species. Thermal refuges are important for the survival of native fish species under extreme summer or winter temperature conditions [*Current Zoology* 57 (6): 852–862, 2011].

**Keywords** Aquatic invaders, Global warming, Heat discharges, Lethal temperature, River Rhine, Thermal heterogeneity

Water temperature is one of the most important environmental factors in the lives of freshwater fish (Rahel and Olden, 2008; Webb et al., 2008). Fish species are poikilotherm organisms whose physiology, energetics and behaviour are strongly influenced by external temperature. Alterations of a river's thermal regime can also affect invasion stages of exotic species, thereby mediating the impact of invaders on native species (Hellmann et al., 2008; Rahel and Olden, 2008). Native fish species and exotic invaders could therefore have differing responses to river temperature alterations.

The number of exotic species has increased in many river basins due to the unintentional and deliberate introduction of species and the facilitation of species dispersal by the construction of waterway networks as well

as navigation and habitat modification (Van der Velde et al., 2002; Leprieur et al., 2008; Rahel and Olden, 2008; Leuven et al., 2009). The temperature regimes of rivers are changing all over the world due to influences of global warming, both directly and indirectly associated with human alterations of their catchments and thermal pollution (Webb et al., 2008; Milner et al., 2009).

A good understanding of the influences of thermal regime changes on the survival of native and exotic fish species is essential in order to effectively predict the effects of global warming and biological invasions on species diversity in river basins (Hellmann et al., 2008; Rahel and Olden, 2008; Bomford et al., 2010). The effects of biological invasions and climate change on biodiversity have usually been assessed independently

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(Walther et al., 2009).

The diversity of the fish fauna is a suitable indicator for describing the ecological condition of a river because fish are relatively abundant in rivers as well as diverse, displaying a high but species-dependent sensitivity to changing environmental conditions such as toxic stress (Posthuma and De Zwart, 2006) and river discharge (Xenopoulos et al., 2005). The composition of fish fauna is also one of the biological quality elements for the ecological status classification of rivers, as prescribed by the European Water Framework Directive (European Council, 2000). To assign a good ecological status to a river, the fish diversity may only slightly differ from the type-specific community attributable to anthropogenic impacts on physico-chemical properties such as water temperature conditions.

This paper describes the effects that changes in river temperature have on fish diversity using species sensitivity distributions (SSDs) to derive the potentially affected fraction (PAF) of native and exotic fish species in the river Rhine. We hypothesize that native fish species exhibit a higher sensitivity to rising water

temperature than exotic species, and that global warming and thermal pollution both limit the full recovery of native fish fauna. We aim to answer the following research questions:

1. What are the temporal trends of the minimum and maximum river temperature?
2. Which native and exotic fish species have been recorded in the tributaries of the river Rhine and what is their temperature tolerance?
3. Do the potentially affected fractions of native and exotic fish species differ with changes in the thermal regime of the river?

The implications of our results for fish conservation and management of exotic invaders will be discussed.

## 1 Material and Methods

### 1.1 Framework

We retrieved data for river temperature conditions, species occurrence and the temperature tolerance of fish species to analyze the fraction of native and exotic fish groups affected by thermal regime changes in the river Rhine (Fig. 1).

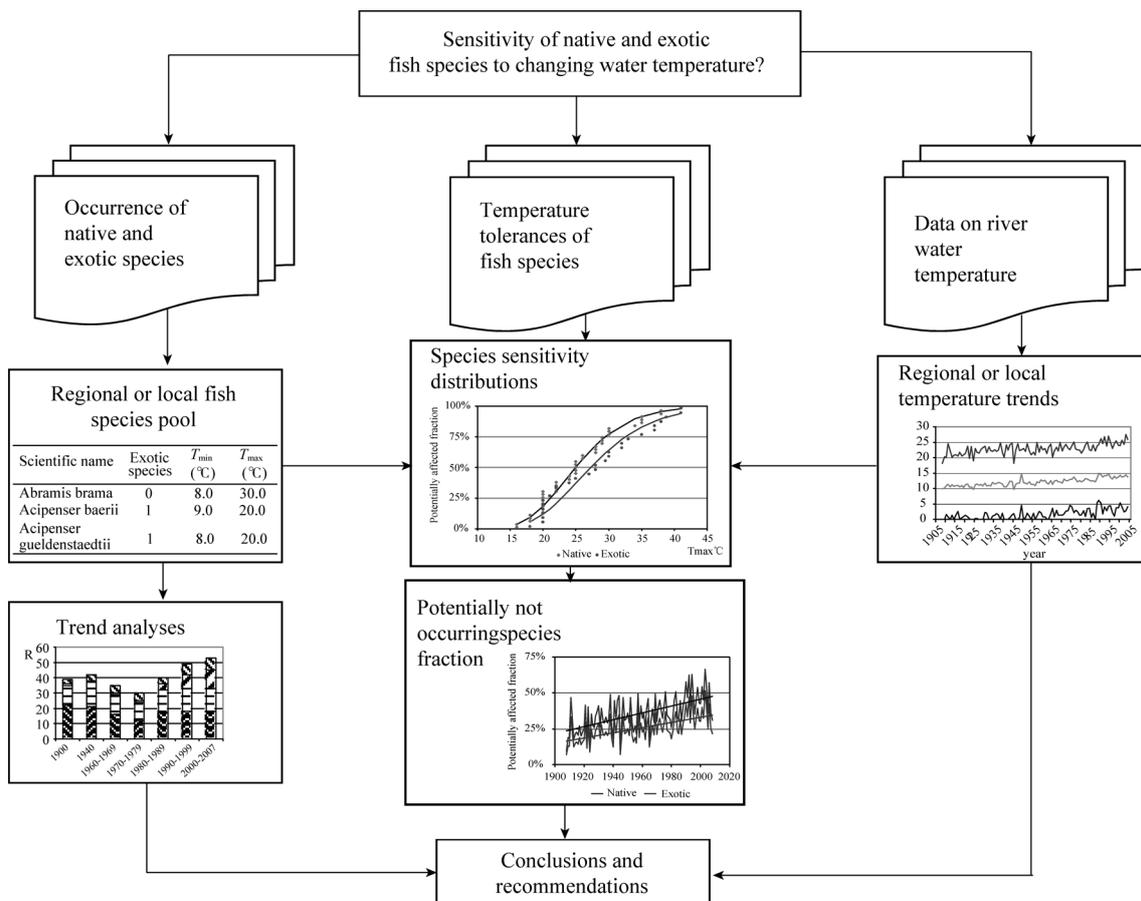


Fig. 1 Assessment framework to analyse the potentially affected fractions of fish species due to changes in the water temperature regime

SSDs were constructed to analyse the sensitivity of fish species to changes in the thermal regime of a river, such as alterations in the minimum or maximum water temperature. An SSD is a statistical distribution that describes the cumulative fraction of a particular population or species group potentially affected (PAF) as a function of the exposure to a specific environmental stressor (Aldenberg et al., 2002; Posthuma et al., 2002; Van Zelm et al., 2007; Smit et al., 2008; De Vries et al., 2009; Struijs et al., 2011). This distribution reflects the interspecies variation in sensitivity to an environmental stressor. The SSD-PAF approach has been widely used for generic risk assessment (Posthuma et al., 2002) and also allows location-specific risk assessments (Smit et al., 2008; De Vries et al., 2009).

In the present study the PAFs were used to represent the fraction of each regional fish species pool potentially affected due to lethal effects of the minimum and maximum water temperature at a particular river location (i.e. gauging station). Normal distributions were

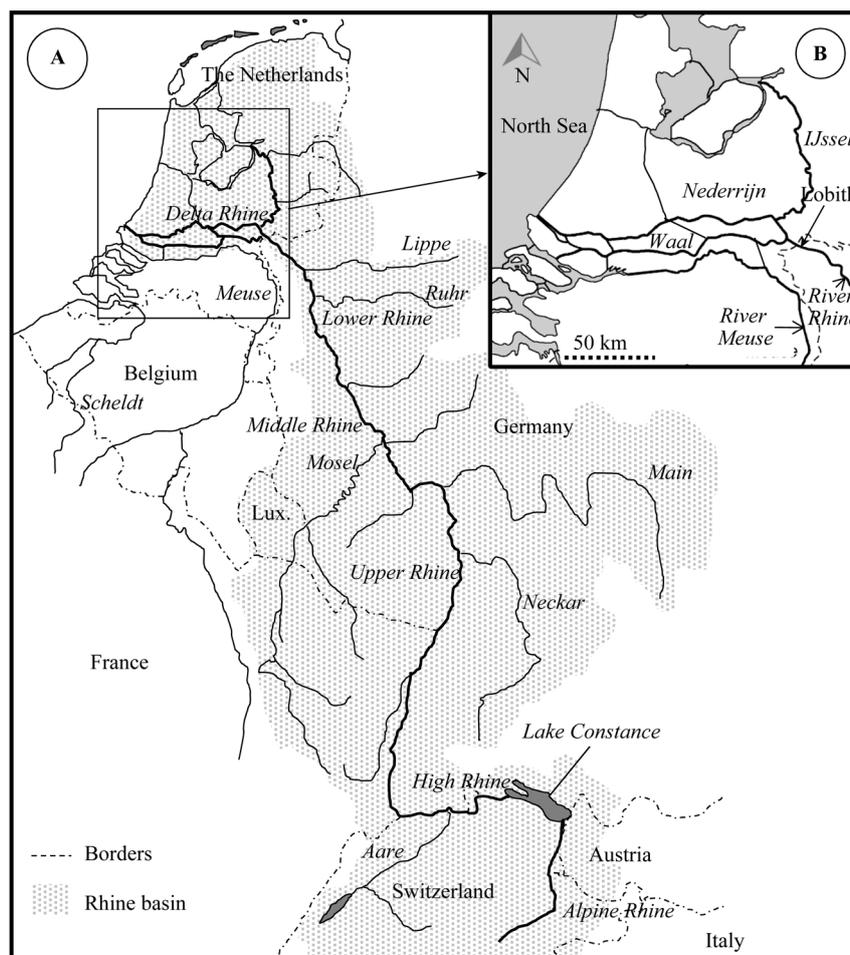
used to derive SSDs for the native and exotic fish species pool, following the method described by De Vries et al. (2009). The mean value of the SSD ( $\mu$ ) represents the minimum or maximum temperature that is lethal for 50% of the species, whereas the standard deviation ( $\sigma$ ) reflects the variation in sensitivity among species in the native or exotic species pool.

Data on the species pool composition and long-term records of river temperature facilitate predictions of past trends in PAFs for a specific location. This elucidates the importance of historical changes in thermal conditions for fish diversity.

## 1.2 Case study

The SSDs for minimum and maximum temperature were derived separately for the native and exotic fish species pools that exist in the freshwater sections of the Rhine distributaries in the Netherlands (Delta Rhine), i.e. the main and side channels of the rivers Waal, Nederrijn and IJssel (Fig. 2).

An existing database of Van den Brink et al. (1990)



**Fig. 2** Geographical location of the river Rhine in north-western Europe

A. The river basin and sections. B. The distributaries Waal, Nederrijn and IJssel of the Delta Rhine and the gauging station Lobith near the Dutch-German border.

on the distribution of fish species in the Rhine distributaries was updated using data from recent fish surveys (Admiraal et al., 1993; Raat, 2001; Aarts and Nienhuis, 2003; Aarts et al., 2004; De Leeuw et al., 2007; Dorenbosch et al., 2011). The nomenclature of fish species was adopted from Kottelat and Freyhof (2007). Rheophilous and non-rheophilous fish species were classified according to Aarts et al. (2004). Climate in the native region was based on distribution maps of fish species (Kottelat and Freyhof, 2007).

The fish database was completed using data on the tolerance of fish species to extremes in river temperature. We applied the minimum and maximum temperature that a given species can withstand derived during short term exposure (mainly 8-96 h duration). The temperature tolerance data was obtained from FishBase Consortium (2007) and updated when recent scientific literature referred to lower or higher tolerance values than those of FishBase (e.g., Hokanson, 1977; Luczynski, 1991; Fredrich, 2003; Van Emmerik and De Nie, 2006).

Equations assuming normal distributions for temperature sensitivity of fish species were applied to calculate the temporal trend in PAF of both the native and exotic species pool at a specific river location in the river Rhine. The yearly minimum and maximum temperature of river water were used for these calculations (temperature data and SSDs were summarized in Figs. 4 and 5). Gauging station Lobith (coordinates 51° 51' N, 6° 08' E) was selected for this case study because of the availability of long-term data. The river temperature was measured daily in the upper water layer (depth: 0.5 m; time of measurement: 8.00-12.00 h). Data on the yearly minimum and maximum temperature over the period 1908-2010 were retrieved from the public database Waterbase, containing validated measurements from the Dutch Ministry of Infrastructure and Environment (2011). The minimum and maximum temperatures were defined as the lowest and highest readings in the data base for each calendar year. Temporal trends of PAFs of the native and exotic fish species pool for both the yearly minimum and maximum river temperatures were derived.

Potential differences in sensitivity between the native and exotic species groups were investigated by comparing the mean ( $\mu$ ) and variance ( $\sigma$ ) values of their minimum and maximum temperature tolerances. The mean values were compared with an independent *t*-test assuming equal variances, as values from both groups of species were normally distributed according to the

Kolmogorov-Smirnov tests. The Levene's test was used to compare the equality of variance values. Statistical significance was tested at a critical P value of 0.05. All statistical tests and linear regression analyses for the trends of river temperatures and PAFs were performed with SPSS 15.0 for Windows®.

## 2 Results

In total, 61 fish species were recorded in the Rhine distributaries from the beginning of the 20<sup>th</sup> century onwards, 37 of which were native species and the other 24 were exotic species (Table 1). The richness and composition of the fish fauna have changed remarkably over the last century (Fig. 3). The number of native rheophilous species greatly declined in the period between 1900–1979 and partially recovered in recent decades. Several locally extinct species were able to re-colonize the river, or were reintroduced after environmental rehabilitation (such as the Atlantic salmon *Salmo salar* or houting *Coregonus oxyrinchus*). The Atlantic sturgeon *Acipenser sturio* is now extinct in the river Rhine. The number of native non-rheophilous fish species (i.e., stagnophilous and euryoecious species) showed a mild decrease until 1980 and increased again after the environmental rehabilitation of the river. The number of exotic species slightly increased over the period 1900–1980, but showed a steep rise after 1990. Many Ponto-Caspian fish species colonized the Rhine river basin, especially after the opening of the Rhine-Main-Danube waterway in 1992. This includes several rheophilous gobiid species such as the Western tubenose goby *Proterorhinus semilunaris* since 2002, round goby *Neogobius melanostomus* since 2004, big-head goby *Neogobius kessleri* since 2007 and Pontian monkey goby *Neogobius fluviatilis* since 2009.

In the period between 1908–2010, both the yearly minimum and maximum water temperature of the river Rhine at Lobith have significantly increased by 0.4 °C per decade (Fig. 4).

There was available data to construct SSDs for both the minimum and maximum temperature tolerance of 35 native and 22 exotic fish species (Table 1). The normal distributions differed remarkably between the native and exotic species pool (Fig. 5). The SSDs for the maximum temperature showed that the temperature tolerance of the exotic species pool was consistently  $2.4 \pm 1.8$  °C higher than that of the native species pool, indicating that the exotic species represented are better adapted to warm water conditions than the native species pool. However, the mean values ( $\mu$ ) of the minimum and

**Table 1** Minimum and maximum temperature tolerances of native and exotic fish species occurring in main and side channels of the Rhine river distributaries

Scientific name	Exotic species	Rheophilous species	Climate in region of origin	Minimum temperature (°C)	Maximum temperature (°C)
<i>Abramis brama</i>	0	0	T, C	8.0	30.0
<i>Acipenser baerii</i>	1	1	B, C	9.0	20.0
<i>Acipenser gueldenstaedtii</i>	1	1	C	8.0	20.0
<i>Acipenser ruthenus</i>	1	1	C	9.0	20.0
<i>Acipenser stellatus</i>	1	1	C	2.4	29.5
<i>Acipenser sturio</i>	0	1	B, T, S	10.0	18.0
<i>Alburnoides bipunctatus</i>	0	1	T, C, S	10.0	18.0
<i>Alburnus alburnus</i>	0	1	B, T, C	10.0	26.0
<i>Alosa alosa</i>	0	1	T, C, S	na	na
<i>Alosa fallax</i>	0	1	T, S	na	na
<i>Ameiurus melas</i> ( <i>Ictalurus melas</i> )	1	0	C, S	8.0	30.0
<i>Ameiurus nebulosus</i> ( <i>Ictalurus nebulosus</i> )	1	0	C, S	0.5	37.0
<i>Anguilla anguilla</i>	0	0	B, T, C, S	4.0	35.0
<i>Aspius aspius</i>	1	1	T, C	4.0	20.0
<i>Ballerus sapa</i> ( <i>Abramis sapa</i> )	1	1	C, (T)	8.0	33.0
<i>Barbatula barbatula</i> ( <i>Noemacheilus barbatulus</i> )	0	1	B, T, C	14.0	25.0
<i>Barbus barbus</i>	0	1	T, C	10.0	28.0
<i>Blicca bjoerkna</i> ( <i>Abramis bjoerkna</i> )	0	0	B, T, C	4.0	29.0
<i>Carassius carassius</i>	0	0	T, C	2.0	38.0
<i>Carassius gibelio</i> ( <i>Carassius auratus</i> )	1	0	B, T, C	0.5	41.0
<i>Chondrostoma nasus</i>	0	1	T, S	8.0	29.0
<i>Cobitis taenia</i>	0	1	T, C	6.0	25.0
<i>Coregonus albula</i>	0	0	T, C	4.0	16.0
<i>Coregonus oxyrinchus</i>	0	1	T	4.0	20.0
<i>Cottus gobio</i> s.l.	0	1	T	1.0	20.0
<i>Ctenopharyngodon idella</i>	1	1	B, C, S	0.5	38.0
<i>Cyprinus carpio</i>	1	0	T, S	3.0	32.0
<i>Esox lucius</i>	0	0	B, T, C, S	3.0	29.0
<i>Gasterosteus aculeatus</i> s.l.	0	0	B, T, C, S	4.0	20.0
<i>Gobio gobio</i>	0	1	T, C	4.0	28.0
<i>Gymnocephalus cernua</i>	0	0	B, T, C	10.0	20.0
<i>Hypophthalmichthys molitrix</i> ( <i>Aristichthys molitrix</i> )	1	1	B, C, S	6.0	28.0
<i>Lampetra fluviatilis</i>	0	1	T, C, S	5.0	18.0
<i>Leuciscus idus</i>	0	1	B, T, C	4.0	35.0
<i>Leuciscus leuciscus</i>	0	1	B, T, C	4.0	28.0
<i>Lota lota</i>	0	1	B, T, C	4.0	20.0
<i>Micropterus salmoides</i>	1	0	C, S	5.0	37.0
<i>Misgurnus fossilis</i>	0	0	T, C	4.0	25.0

(to be continued on the next page)

Table 1 (Continued)

Scientific name	Exotic species	Rheophilous species	Climate in region of origin	Minimum temperature (°C)	Maximum temperature (°C)
<i>Neogobius fluviatilis</i>	1	1	C	na	Na
<i>Neogobius kessleri</i>	1	1	C	na	na
<i>Neogobius melanostomus</i>	1	1	C	4.0	30.0
<i>Oncorhynchus mykiss</i>	1	1	B, T, S	10.0	24.0
<i>Osmerus eperlanus</i>	0	1	B, T	4.0	20.0
<i>Perca fluviatilis</i>	0	0	B, T, C, (S)	7.0	22.0
<i>Petromyzon marinus</i>	0	1	T, C, S	5.0	22.0
<i>Platichthys flesus</i>	0	1	B, T, S	5.0	25.0
<i>Poecilia reticulata</i>	1	0	Trop.	18.0	28.0
<i>Proterorhinus semilunaris</i>	1	1	C	4.0	18.0
<i>Pseudorasbora parva</i>	1	0	B, C, S	5.0	22.0
<i>Pungitius pungitius</i> s.l.	0	0	B, T	5.0	26.0
<i>Rhodeus amarus</i> ( <i>Rhodeus sericeus</i> )	1	0	T, C	14.0	21.0
<i>Romanogobio belingi</i> ( <i>Gobio albipinatus</i> )	1	0	T, C	8.0	30.0
<i>Rutilus rutilus</i>	0	0	B, T, C	10.0	22.0
<i>Salmo salar</i>	0	1	B, T	2.0	20.0
<i>Salmo trutta</i>	0	1	B, T, C, (S)	5.0	24.0
<i>Sander lucioperca</i> ( <i>Stizostedion lucioperca</i> )	1	0	T, C, (S)	6.0	32.0
<i>Scardinius erythrophthalmus</i> ( <i>Rutilus erythrophthalmus</i> )	0	0	T, C	2.0	35.0
<i>Silurus glanis</i>	0	0	T, C	4.0	20.0
<i>Squalius cephalus</i> ( <i>Leuciscus cephalus</i> )	0	1	T, C	4.0	34.0
<i>Tinca tinca</i>	0	0	T, C, S	4.0	38.0
<i>Vimba vimba</i>	1	1	T, C	10.0	20.0

Synonyms of scientific names of fish species are given in brackets. Climate in region of origin: B: boreal or subarctic, T: Atlantic maritime and temperate; C: continental; S: subtropical; Trop.: tropical climate; climate region in brackets: species is introduced in that climate zone.

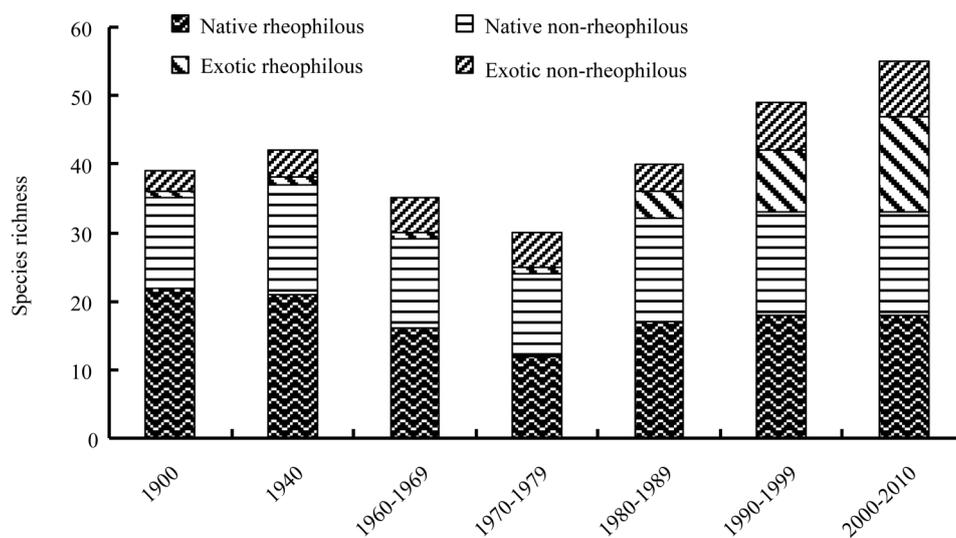
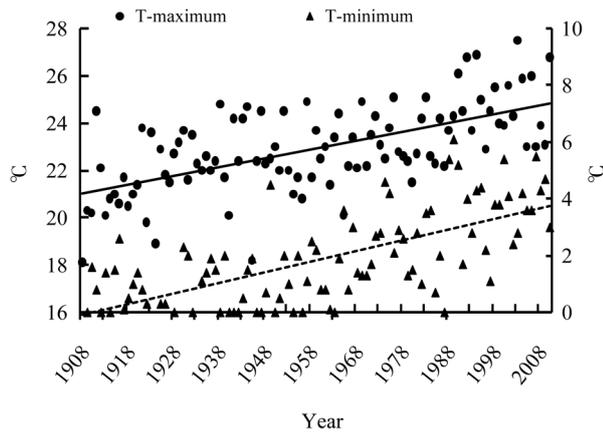


Fig. 3 Contribution of native and exotic species to the total fish species richness in the freshwater sections of the Rhine distributaries (Delta Rhine) for various periods

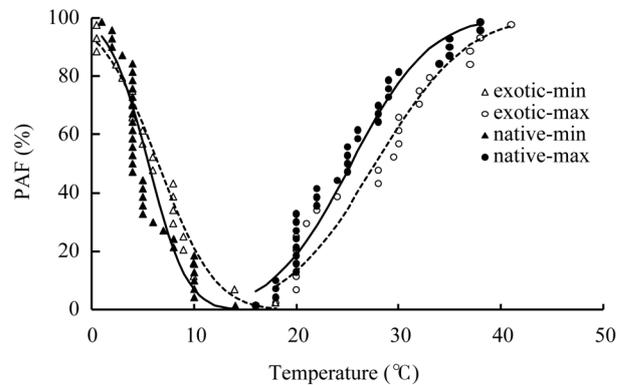


**Fig. 4** Yearly minimum and maximum water temperature of the river Rhine at Lobith in the Netherlands

Measured in upper water layer; linear regression lines:  $T_{\max} = 0.04X + 21.01$ ,  $R^2 = 0.36$ ,  $P < 0.001$  and  $T_{\min} = 0.04X - 0.15$ ,  $R^2 = 0.47$ ,  $P < 0.001$ , with  $X$  = number of years elapsed since 1908 and  $T_{\min}$  and  $T_{\max}$  in  $^{\circ}\text{C}$ ; Data: www.waterbase.nl.

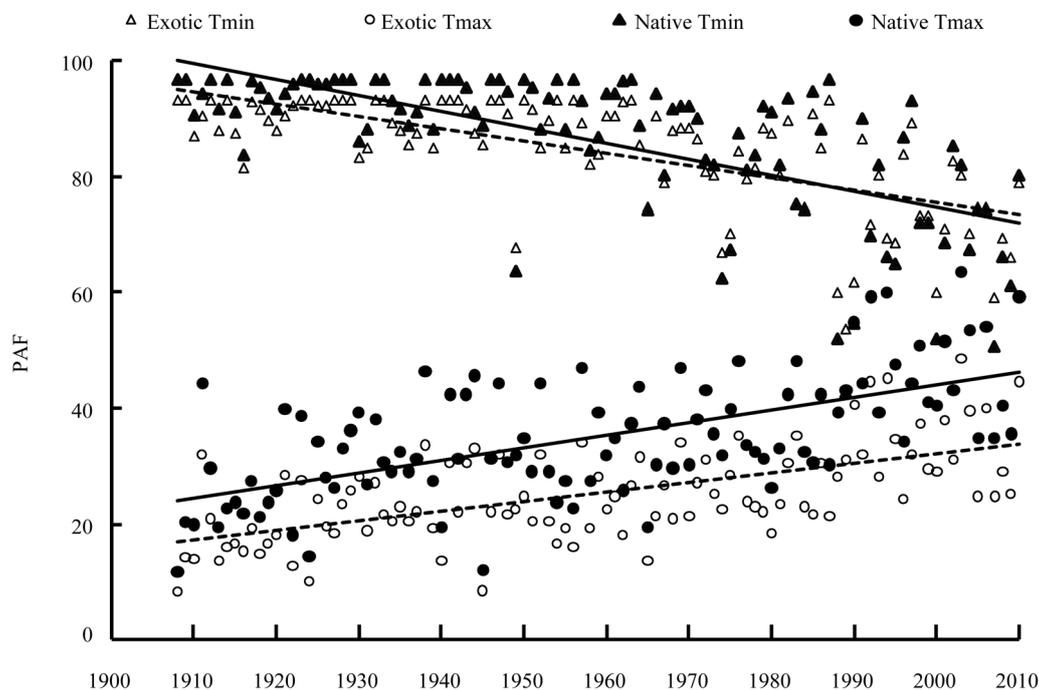
maximum temperature tolerances did not differ significantly between the native and exotic species groups because of the relatively small sample size and high variability in temperature tolerance ( $t$ -tests for equality of means of the minimum and maximum temperature tolerances, equal variances assumed based on Levene's test:  $P = 0.35$  and  $P = 0.18$ , respectively). The slopes of

the lines for minimum temperature tolerance differed for both species pools, indicating that some exotic species were better adapted to coldwater conditions and others were more sensitive than native species.



**Fig. 5** Temperature sensitivity distributions for native and exotic fish species occurring in the Rhine river distributaries

PAF: Potentially affected fraction of species. Curves represent normal distributions based on averages and standard deviations of Hazen plotting positions for individual species' tolerances (minimum temperature tolerance of native species:  $n = 35$ ,  $\mu = 5.5$   $^{\circ}\text{C}$ ,  $\sigma = 3.0$   $^{\circ}\text{C}$ ; exotic species:  $n = 22$ ;  $\mu = 6.5$   $^{\circ}\text{C}$ ,  $\sigma = 4.3$   $^{\circ}\text{C}$ ; Maximum temperature tolerance of native species:  $n = 35$ ,  $\mu = 25.4$   $^{\circ}\text{C}$ ,  $\sigma = 6.1$   $^{\circ}\text{C}$ ; exotic species:  $n = 22$ ,  $\mu = 27.8$   $^{\circ}\text{C}$ ,  $\sigma = 7.0$   $^{\circ}\text{C}$ ); The fish species and their temperature tolerance ranges are summarized in Table 1.



**Fig. 6** Potentially affected fraction (PAF) of the native and exotic fish species pool in relation to yearly minimum and maximum temperature in the upper water layer of the river Rhine at Lobith for the period 1908–2010

Statistical specifications of linear regressions  $\text{PAF} = a \text{ year} + b$ : Exotic species -  $T_{\text{minimum}}$   $a = -0.21$ ,  $b = 501.2$ ,  $r^2 = 0.474$ ,  $P < 0.001$ ; Exotic species -  $T_{\text{maximum}}$   $a = 0.17$ ,  $b = -299.4$ ,  $r^2 = 0.374$ ,  $P < 0.001$ ; Native species -  $T_{\text{minimum}}$   $a = -0.28$ ,  $b = 626.0$ ,  $r^2 = 0.404$ ,  $P < 0.001$ ; Native species -  $T_{\text{maximum}}$   $a = 0.22$ ,  $b = -391.0$ ,  $r^2 = 0.376$ ,  $P < 0.001$ .

The PAFs of the native and exotic fish species pools in relation to the yearly maximum temperature in the upper water layer of the river showed a significant linear increase over the period 1908–2010 (Fig. 6). The increase in PAF over time for  $T_{max}$  means that the maximum summer temperatures exceeded the upper temperature limits for increasing fractions of the species pool for both native and exotic species. The fraction of the species pool affected by unsuitable summer temperatures was generally greater for native species, indicating that they were under more thermal stress than most exotic species.

The PAFs corresponding to the yearly minimum water temperature showed a significant linear decrease (Fig 6.). The exotic species overall appeared to be less affected than the native fish fauna at lower as well as upper temperature extremes.

### 3 Discussion

The characteristics of the fish fauna in the Rhine distributaries have changed remarkably over the last century. Rheophilous species appear to have been the first group to suffer a strong decline in diversity. Important causes for this decline included the closing of the river mouths by dams and sluices, deterioration of spawning and nursery habitats, river regulation for shipping, migration obstacles such as hydropower stations and weirs, organic pollution and commercial fishing (Admiraal et al., 1993; De Groot, 2002; Aarts and Nienhuis, 2003; Aarts et al., 2004). In the period between 1960–1980, severe water pollution also caused a decline in the number of non-rheophilous species (Van den Brink et al., 1990; Admiraal et al., 1993; Aarts and Nienhuis, 2003).

The communal, industrial and agricultural discharges of nutrients and toxic substances in the river Rhine have decreased since 1980 by 50–90 percent, resulting in a strong increase in the river water's oxygen content (Nienhuis et al., 2002; Bij de Vaate et al., 2006). In spite of recent improvements in water quality, extensive habitat restoration, construction of fish passages, river rehabilitation and abandonment of fisheries, native biodiversity has yet to completely recover (Admiraal et al., 1993; Nienhuis et al., 2002), a situation also reflected by the composition of the native fish fauna in our study. In contrast, the number of exotic species has undergone a consistent increase over the last century. Most exotic fish species that were already present in the Rhine distributaries before 1980 were deliberately or accidentally introduced. These species predominantly origi-

nated from fish restocking or escapes (Van der Velde et al., 2002). In contrast to earlier settlement patterns of exotic fish species, the majority of recent invaders colonized the river through the network of artificial waterways that exist in Europe, especially from the river Danube through the Main-Danube canal to the river Rhine (Southern invasion corridor: see Leuven et al., 2009). The egg capsules of gobiid species may also be transported when attached to the hulls of ships sailing on inland waterways, or by transport in the ballast water of seagoing ships (Van Kessel et al., 2011). The Main-Danube canal connects the North Sea and Atlantic Ocean to the Black Sea, creating a navigable artery between the Rhine delta and the Danube Delta in eastern Romania. The present canal was completed in 1992 and is 171 km long. Ponto-Caspian species have to pass through a coldwater habitat filter in the Main-Danube canal because the crest altitude of the canal is 406 m above sea level and 175 m above the river Main. The temperature regime of the canal does not appear to limit the dispersal of Ponto-Caspian invaders (*cf.* Kley and Maier, 2006).

Established populations of exotic species can alter the spatial patterns of fish diversity through various processes such as changes in food availability, increased competition or pathogen transfer (Leprieur et al., 2008; Leuven et al., 2009; Blanchet et al. 2010). These processes may limit the recovery of the native species pool in the river Rhine. Thermal discharges, climate change and their interaction strongly affect the river's temperature regime and can also have direct or indirect consequences on native fish diversity. Both the yearly minimum and maximum river temperatures have increased by 4 °C at Lobith over the past century. About 2/3 of this increase in river temperature was attributed to thermal discharges in the Rhine basin while 1/3 was attributed to climate change (Ligtvoet et al., 2006).

Analyses of a worldwide dataset on fish species in river basins show that exotic fish species are a non-random subset of the worldwide set of fish species (Blanchet et al., 2010). According to Blanchet et al. (2010) the median body size of fish increases due to introductions of exotic species and that the shifts in body size are related to climate factors such as temperature and the percentage of maximum glacier coverage for each river basin. Our study reveals that the mean values for minimum and maximum water temperature tolerances do not significantly differ between the native and exotic species pools in the river Rhine. The SSD for the maximum temperature tolerance of the

exotic species pool appears to be consistently higher compared to that of the native species pool. Differences in tolerances can be explained by distinct phylogenetic positions and specific adaptations to the climate in regions of origin. Several exotic species originate from regions with a continental climate, e.g. the Ponto-Caspian area (Table 1). Water temperature ranges in these regions are more extreme than in maritime climate zones. Fish species originating from continental climate zones will thus be better adapted to extreme winter and summer temperatures. Other invaders originated from the subtropical and tropical regions (Table 1). These species are adapted to warm water conditions and can only survive severe winter conditions at locations with thermal discharges.

The SSDs of native and exotic species reveal that rising water temperature will affect species pools both in summer and winter. The PAFs based on maximum temperatures of exotic species are lower than those of native fish species especially. The differences in species sensitivity and trends of PAFs support our hypothesis that full recovery of native fish fauna may be limited by current water temperature conditions. Further increases in river temperature due to climate change will negatively influence a higher percentage of native fish species rather than exotic ones. Differences in temperature sensitivity of species under the changing thermal regimes of rivers also indirectly affect competitive ability and habitat choice, with potential consequences for their thermal distribution. Such competition for shelter caused by invasive exotic gobiids in the river Rhine appears to be a realistic threat to small native benthic fish species (Van Kessel et al., 2010).

Over the 102 year period of analysis, the ranges of PAFs for native and exotic fish species combined were quite broad for both minimum (42.6%–96.8%) and maximum river temperatures (8.3%–63.6%) (Fig. 5). The very high PAFs for minimum temperature in particular may raise the question of how it was possible for native fish species to survive the extreme winter temperatures in the Rhine distributaries. The PAFs in our study were only derived for temperature conditions in the upper water layer of the river Rhine at Lobith (depth of measurement: 0.5 m). Thermal heterogeneity of rivers has been recognized as an important factor for shaping river habitat conditions (Webb et al., 2008). Longitudinal, lateral and vertical heterogeneity in water temperature of rivers is considerable, due to thermal stratification, lateral inflow of groundwater, tide and influences of thermal discharges. In comparison with

temperature records of downstream and upstream gauging stations, at Lobith highest maximum water temperatures and relatively low minimum values were recorded (Boderie et al., 2006; Uehlinger et al., 2009). The upwelling and lateral inflow of groundwater provide thermal refuges with relatively constant cool water conditions, such as in the Rhine delta area, where the minimum temperature of groundwater at a depth > 1 m is always above 7.5 °C (cf. Bense and Kooi, 2004; Kooi, 2008), corresponding with a PAF value of 1.2% for the native fish species pool. A study on the water temperature regime in the rivers Rhine and Meuse within the years 2001-2004 also confirmed that vertical heterogeneity in water temperature was significant at several locations (Boderie et al., 2006). The temperature near the bottom of the water was up to 3 °C higher in winter periods and up to 4.5 °C cooler during summer periods. Lateral variations in water temperature conditions of side channels and floodplain lakes along the river Danube were found to be as wide as 16 °C (Ward et al., 2001). Ecologically meaningful effect assessments of changes in thermal regimes on biological diversity in river ecosystems will thus require more detailed information on the spatial and temporal variability of water temperature than the information used in our case study. Our results clearly demonstrate the importance of thermal heterogeneity for the survival of native fish species under extreme summer and winter conditions. As it appears to be impossible to counteract global warming in the short term, the protection and maintenance of cool water refuges and the reduction or relocation of heat discharges during periods of extreme summer temperatures are relevant management options for fish conservation in lowland rivers.

In this study, the SSD-PAF approach was used for a location-specific assessment of fish diversity in relation to river temperature conditions, but can also be applied to other types of ecosystems, taxa or groups of species varying in life history strategies. The effects of thermal pollution and global warming often coincide with additional stressors such as hypoxia, salinity or water pollution (Webb et al., 2008). Such situations may require a multiple stress approach, integrating risks for stressors in one overall indicator, instead of evaluating all risks separately (De Zwart and Posthuma, 2005; De Vries et al., 2009). This will be feasible when sufficient data on species sensitivity to multiple stressors or modes of stressor interaction are available, and remains one of the major challenges for environmental impact assessments.

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