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Sensitivity of native and non-native mollusc species to changing river water temperature and salinity

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Abstract Climate change may strongly affect the abiotic conditions in riverine ecosystems, for example by changing water temperature regimes and salinisation due to sea water intrusion and evaporation. We analysed the effects of changes in water temperature and salinity on the species pool of freshwater molluscs in the river Rhine. Species sensitivity distributions (SSDs) for maximum temperature and salinity tolerance were constructed for native and non-native species that are currently present in the river Rhine. The maximum temperature tolerance was significantly higher for non-native mollusc species than native ones. For salinity tolerance, no significant difference was found between the two groups. The SSDs were used to determine the potentially not occurring fractions (PNOFs) of each species group corresponding with the yearly maximum water temperature and salinity levels recorded in (1) different river sections for the extreme warm and dry year 2003, and (2) the river Rhine at Lobith (The Netherlands) over the period 1960–2009. Changing temperature and salinity conditions in the river Rhine over the past 50 years corresponded with a net increase in PNOF for native species. This was mainly due to rising river water temperatures, which had a larger influence than decreasing salinity levels. For non-native species no change in PNOF was found, indicating that future temperature rise will disproportionally affect native mollusc species. Validation of the PNOF estimated for Lobith with the not occurring fraction (NOF) of mollusc species derived from monitoring data revealed similar trends for native as well as non-native mollusc species richness. The increase in the PNOF accounted for 14% of the increase in the NOF. The construction and application of SSDs appeared a promising approach to address the separate and combined effects of changing abiotic conditions on native and non-native species pools.

Keywords Aquatic invaders · Climate change · Macroinvertebrates · Multiple stressors · Potentially not occurring fraction · Species sensitivity distribution

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Introduction

Physiological responses to environmental conditions may differ between native and non-native freshwater

species, which may influence establishment of non-native species and interspecific competition (Karatayev et al. 2009; Leuven et al. 2007, 2011). Climate change may affect environmental conditions, and subsequently bioinvasions, by altering the pool of potential invaders and influencing the chance that non-native species will establish (Rahel and Olden 2008). Studies on the effects of climate change in lake and river systems have shown changes in freshwater species composition and diversity for fish (Buisson et al. 2008; Daufresne and Boet 2007) and macroinvertebrates (Burgmer et al. 2007; Chessman 2009; Daufresne et al. 2004; Mouthon and Daufresne 2006). Abiotic changes in river systems typically include increases in water temperature, river dynamics and salinity (Gornitz 1991; Webb 1996). So far, however, most research has focused on water temperature effects on fish species (Chu et al. 2005; Jackson and Mandrak 2002; Lehtonen 1996; Leuven et al. 2007, 2011). Responses of macroinvertebrate species to climate change are difficult to predict due to a lack of knowledge on species-specific physiological tolerances (Heino et al. 2009). Rising water temperatures may lead to replacement of coldwater mollusc species by more thermophilic ones (Daufresne et al. 2004), but the mechanisms that may explain this shift are not yet understood. As molluscs constitute a large share of the group of macroinvertebrate invaders (Karatayev et al. 2009; Leuven et al. 2009) and invasive, fouling molluscs have serious economic and ecological impacts (Connelly et al. 2007; Pimentel et al. 2005; Strayer 2010; Vanderploeg et al. 2002), there is a particular need for knowledge on physiological tolerances of these species. Knowledge on facilitating or limiting factors for the establishment of non-native mollusc species could be helpful to predict future species replacements and to derive management options for invasive species.

The aim of this study was to identify differences in maximum temperature and salinity tolerance between native and non-native mollusc species and to assess the impact of changes in water temperature and salinity on the occurrence of both species groups in the river Rhine. To this end, we first analysed which mollusc species are currently present in the river Rhine. Next, we constructed species sensitivity distributions (SSDs) with regard to temperature and salinity tolerance and used these relations to analyse differences in sensitivity between native and non-native mollusc species. We applied the SSDs to assess the

potentially not occurring fraction (PNOF) of species in various sections of the river Rhine using temperature and salinity data obtained during the heat wave in the year 2003. Further, we analysed the separate and combined effects of changes in water temperature and salinity on the potential occurrence of mollusc species in the river Rhine at Lobith over a period of 50 years (i.e., 1960–2009). Finally, we compared the temporal trends in PNOF to the actual not occurring fraction (NOF) of mollusc species using monitoring data obtained at Lobith from 1988 through 2003.

Materials and methods

Species sensitivity distributions

In order to assess the differences in sensitivity to thermal and saline stress, SSDs were constructed for native as well as non-native mollusc species. A SSD is a statistical distribution that describes the variation between species in sensitivity to an environmental stressor (Leuven et al. 2007, 2011; Posthuma et al. 2002; Smit et al. 2008). In our study, the calculated fraction of species affected is addressed as the potentially not occurring fraction (PNOF) (van Zelm et al. 2007), representing the fraction of mollusc species potentially excluded from the river Rhine because of water temperature and salinity limitations. Various distribution curves can be used to describe a SSD, because there are no theoretical grounds to favour a particular distribution function. In this study, the logistic distribution was used, as outlined by Aldenberg and Slob (1993) and recently used by De Zwart (2005). In a logistic distribution, the PNOF is determined by the location parameter alpha (α) and the scale parameter beta (β) (Eq. 1).

$$PNOF = \frac{1}{1 + e^{-\left(\frac{x-\alpha}{\beta}\right)}} \tag{1}$$

where x represents the environmental stressor (temperature in °C or salinity in ‰). The location parameter α equals the sample mean of the species-specific upper tolerance values. The scale parameter β of the logistic distribution depends on the sample standard deviation (SD) of the upper tolerance values (Aldenberg and Slob 1993). Assuming independent action, the combined effect of temperature ($PNOF_T$) and salinity ($PNOF_S$) on the occurrence of species can be calculated (Eq. 2) (Traas et al. 2002).

$$PNOF_{TS} = 1 - (1 - PNOF_T) \times (1 - PNOF_S) \quad (2)$$

Parameterization and comparison

A list of freshwater mollusc species present in the river Rhine was compiled based on the results of a large-scale international survey of macroinvertebrate species conducted in 2000 (IKSR 2002) and a more recent study on macroinvertebrate invaders by Leuven et al. (2009). Next, a database of upper tolerance values was set up with data from the literature (Table 1). Data were obtained from scientific articles and a survey of freshwater molluscs of the Netherlands (Gittenberger et al. 1998) (see Table 1 for references). Upper tolerance values represent the maximum temperature (T_{max}; °C) or salinity (S_{max}; ‰) at which individuals were recorded in the field. If the upper tolerance value for a species was given as a range or if more than one value was found in the literature, the highest value was added to the database. If available, we also included the temperature and salinity ranges measured over the sites investigated, as this may confirm the absence of species at environmental conditions exceeding their maximum tolerance levels. Next, we tested the reliability of the field-derived maximum tolerance levels by a comparison with lethal temperature and salinity levels for 50% of the species based on laboratory tests, which have been reported for a few of the species. A paired-samples t test was used for the comparison (SPSS 15.0). Field-derived tolerance levels did not significantly differ from LC/LT_{50} values reported from available laboratory tests for salinity (n = 10; $P = 0.71$) and temperature (n = 6; $P = 0.22$) (unpublished data).

The salinity tolerance data were log-transformed, because of their skewed distribution. The temperature tolerance data were within one order of magnitude, obviating the need for log-transformation. Differences in upper tolerance limits between the two species groups were tested with independent-samples t tests (SPSS 15.0) and were considered to be statistically significant at $P < 0.05$.

River Rhine case study and comparison with survey data

The SSDs for native and non-native molluscs for the two stressors were used to calculate the PNOFs of each group corresponding with water temperatures and salinity levels recorded in the river Rhine. The river Rhine is one of the large rivers in Europe, rising in the Swiss and Austrian Alps and flowing through Germany, France and the Netherlands to the North Sea, and is characterized by a high richness and abundance of non-native species (Arbačiauskas et al. 2008; Bij de Vaate et al. 2002; Leuven et al. 2009; Panov et al. 2009).

To obtain insight into spatial differences along the river, PNOFs were calculated for various river sections based on temperature and salinity data from seven water quality measurement stations. These data were obtained from the International Commission for the Protection of the Rhine (IKSR), the Directorate-General for Public Works and Water Management (2009) and Uehlinger et al. (2009) for the year 2003 (i.e., an extreme dry and warm year). Potential influences of temporal changes in water temperature and salinity were assessed based on measurements conducted in the surface water layer of the main river channel near the Dutch-German border at Lobith. Data were obtained from a web-based portal (www.waterbase.nl) and covered the period 1960–2009 (Directorate-General for Public Works and Water Management 2009). Water temperature values from the Directorate-General for Public Works and Water Management (2009) were obtained as daily measurements with an accuracy of 0.1°C. Water temperature data from the IKSR portal were available as maximum water temperatures of 2-week periods from continuous measurements (IKSR 2011). The salt content of the river Rhine was expressed as conductivity (in mS/m or μS/cm) which was typically measured twice a month. Conductivity values were transformed to salinity units, using the method described by Grabowski et al. (2009). Yearly maximum water temperatures (°C) and salinities (‰) were used to calculate the PNOFs. Linear regression confidence intervals (95%) were calculated to reveal whether temporal trends in PNOF at Lobith were significant.

We compared the PNOFs calculated for Lobith with the actual not occurring fraction (NOF) of mollusc species derived from survey data (Eq. 3).

$$NOF = 1 - R/R_{max} \quad (3)$$

in which R is the number of species found at Lobith and R_{max} the total species pool of the river Rhine (i.e., the same number of species used for calculating the

Table 1 Maximum temperature and salinity at which native and non-native mollusc species were observed in the field. Ranges in environmental conditions of sampling sites are given in brackets

Species	Abbreviations	S_{max} (‰)	References	T_{max} (°C)	References
Native species					
Acroloxus lacustris (Linnaeus, 1758)	Al	3	*8*	30 (0–33)	*9;15*
Ancylus fluviatilis (Müller, 1774)	Af	4	*8*	30 (0–33)	*9;15;35*
Anodonta anatina (Linnaeus, 1758)	Aa	3	*8*	24	*1;24*
Anodonta cygnea (Linnaeus, 1758)	Ac	2	*8*	28 (0–32)	*1;15;24;29*
Bathyomphalus contortus (Linnaeus, 1758)	Bc	8.5 (0–33.5)	*5;8*		
Bithynia leachii (Sheppard, 1823)	Bl	6	*8*	25 (0–32)	*15*
Bithynia tentaculata (Linnaeus, 1758)	Bt	12 (0–33.5)	*5;8*	30 (0–32)	*15*
Galba truncatula (Müller, 1774)	Gt	19 (0–33.5)	*5;8*	25	*8*
Gyraulus albus (Müller, 1774)	Ga	5	*8*	30 (0–32)	*15*
Lymnaea stagnalis (Linnaeus, 1758)	Ls	7	*8*		
Mercuria anatina (Poirot, 1801)[a]	Mc	5.5	*8*		
Physa fontinalis (Linnaeus, 1758)	Pf	11 (0–33.5)	*5;8*	25 (0–32)	*15*
Pisidium amnicum (Müller, 1774)	Pam	0.5	*8*	29.5 (0–32)	*15;23*
Pisidium casertanum (Poli, 1791)	Pcm	3	*14*		
Pisidium henslowanum (Sheppard, 1823)	Ph	1.5	*8*		
Pisidium moitessierianum Paladilhe, 1866	Pm	0.5	*8*		
Pisidium nitidum Jenyns, 1832	Pn	3.5	*14*		
Pisidium supinum Schmidt, 1851	Ps	0.5	*14*		
Planorbis carinatus (Müller, 1774)	Pcs	3	*8*		
Planorbis planorbis (Linnaeus, 1758)	Pp	11 (0–33.5)	*5;8*	29 (0–29)	*4*
Pseudanodonta complanata (Rossmässler, 1835)	Pca	0.5	*8*	24 (0–24)	*1*
Radix auricularia (Linnaeus, 1758)	Ra	6 (0–33.5)	*5;8;28*	25 (0–32)	*15;30*
Radix balthica (Linnaeus, 1758)[b]	Rb	14 (0–33.5)	*5;8*	32 (0–32)	*13;15*
Sphaerium corneum (Linnaeus, 1758)	Sc	5	*8*		
Sphaerium rivicola (Lamarck, 1818)	Sr	2	*8*		
Sphaerium solidum (Normand, 1844)	Ss	2	*8*		
Stagnicola corvus (Gmelin, 1791)	–				
Theodoxus fluviatilis (Linnaeus, 1758)	Tf	18	*8;10;28*		
Unio crassus (Philipsson, 1788)[c]	Uc	0.5	*8*		
Unio pictorum (Linnaeus, 1758)	Up	3	*8*	28 (0–32)	*1;15;24*
Unio tumidus Philipsson, 1788	Ut	3	*8*	24 (0–24)	*1*
Valvata cristata Müller, 1774	Vc	5 (0–33.5)	*5;8*		
Valvata piscinalis (Müller, 1774)	Vp	5	*8*	29.5 (0–29.5)	*23*
Viviparus viviparus (Linnaeus, 1758)[d]	Vv	3	*8*	25 (0–32)	*15*
Non-native species					
Corbicula fluminalis (Müller, 1774)	Cfs	27 (0–34.5)	*8;20;21*		
Corbicula fluminea (Müller, 1774)	Cfa	17 (0–34.5)	*8;12;21*	37 (0–42)	*3;6;17;19*
Dreissena polymorpha (Pallas, 1771)	Dp	6	*8;11;16;33*	34	*11;15;18;26*
Dreissena rostriformis bugensis Andrusov, 1897	Dr	5 (0–33.5)	*11;12;27*	34	*11;32*
Ferrissia wauteri (Mirolli 1960)[e]	Fw	1	*8*	33 (0–33)	*9;31*
Lithoglyphus naticoides (Pfeiffer, 1828)	Ln	3	*8*	29.5 (0–29.5)	*22*
Menetus dilatatus (Gould, 1841)	Md			32	*2;25*

Table 1 continued

Species	Abbreviations	S_{max} (‰)	References	T_{max} (°C)	References
Musculium transversum (Say, 1829)	–				
Physella acuta (Draparnaud, 1805)[f]	Pac	8 (0–33.5)	5;8	35 (7–44)	7;8;15
Potamopyrgus antipodarum (Gray, 1843)[g]	Pan	28 (0–33.5)	5;8	30 (0–34)	8;15;34

References to studies with highest reported tolerance value for a species are italicized. References included: 1: Aldridge (1999); 2: Berger and Dzięczkowski (1979) 3: Britton and Morton (1982); 4: Costil and Daguzan (1995); 5: reviewed in Costil et al. (2001); 6: Dreier and Tranquilli (1981); 7: Forcart (1948); 8: reviewed in Gittenberger et al. (1998); 9: Hadderingh et al. (1987); 10: Kangas and Skoog (1978); 11: reviewed in Karatayev et al. (1998); 12: reviewed in Karatayev et al. (2007); 13: Krkac (1979); 14: reviewed in Kuiper and Wolff (1970); 15: Langford (1971); 16: McMahon (1996); 17: McMahon and Williams (1986); 18: Mihuc et al. (1999); 19: Morgan et al. (2003); 20: Morton (1986); 21: Morton and Tong (1985); 22: Mouthon (2007); 23: Mouthon and Daufresne (2008); 24: Müller and Patzner (1996) 25: Müller et al. (2005); 26: Orlova (2002); 27: Orlova et al. (2005); 28: reviewed in Perez-Quintero (2007); 29: Ricken et al. (2003); 30: Rossetti et al. (1989); 31: Van der Velde (1991); 32: reviewed in Van der Velde et al. (2010); 33: Walton (1996); 34: Winterbourn (1969); 35: Wulfhorst (1991)

[a] Synonymous with *Mercuria confusa*

[b] Synonymous with *Radix peregra/ovata*

[c] Probably extinct

[d] Species is regarded as non-native in Germany and the Upper Rhine (Kinzelbach 1995; Bernauer and Jansen 2006) however the non-native status is disputed for the Dutch part of the river Rhine as fossil remnants of this species have been found (Gittenberger et al. 1998)

[e] Synonymous with *Ferrissia clessiniana*; taxonomic status uncertain, possibly *Ferrissia fragilis* (Walther et al. 2006)

[f] Synonymous with *Physa acuta*, *Haitia acuta*, *Physella costatella* and *Physella heterostropha* (Dillon et al. 2002)

[g] Synonymous with *Potamopyrgus jenkinsi*

PNOF). Monitoring data on molluscs in the river Rhine at Lobith were obtained from Limnodata Neerlandica of the Dutch Foundation for Applied Water Research STOWA (www.limnodata.nl). These data originated from monitoring activities over the period 1988–2003, including sampling of hard substrates (groyne stones, rip rap, large woody debris), sediment (core and Van Veen samplers), artificial substrates (marbles), and other microhabitats (dip nets). All available survey data were pooled per year and regression lines were fitted through the resulting NOFs in order to facilitate comparison with the PNOFs. All (P)NOFs were expressed as percentages.

Results

Species sensitivity distributions

In total 34 native and 10 non-native mollusc species were recorded in the river Rhine. The non-native species originate from North America (n = 4), the Ponto-Caspian Area (n = 3), Asia (n = 2) and New Zealand (n = 1). The non-native status of one species is still ambiguous (i.e., *Ferrissia wautieri*). Temperature tolerance data were found for 18 native and 8 non-native species, accounting for 53% and 80% of their species pools in the river Rhine, respectively. The maximum temperature tolerance of native species ranged from 24.0 to 32.0°C. For non-native species this range was 29.5–37.0°C (Fig. 1). The maximum temperature tolerance was significantly higher for non-native than for native species ($P < 0.01$).

The SSDs for salinity were based on data for 33 native and 8 non-native species, constituting 97% and 80% of their species pools in the river Rhine, respectively. For native species the maximum salinity tolerance ranged from 0.5 to 19.0‰, while for non-native species this range was 1.0–28.0‰. The mean maximum salinity tolerance was not significantly different between native and non-native species ($P = 0.08$), although all data points belonging to the non-native species sensitivity curve were below the native species curve. Two non-native species (*Corbicula fluminalis* and *Potamopyrgus antipodarum*) showed a considerably higher salinity tolerance than all native species (Fig. 2).
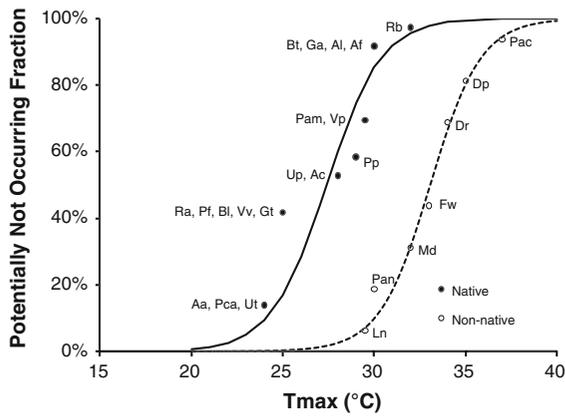
Fig. 1 Species sensitivity distributions for maximum temperature tolerances of native and non-native molluscs of the river Rhine. The data points represent individual species' tolerances based on Hazen plotting positions (Native: n = 18; α = 27.39, β = 1.49; Non-native: n = 8; α = 33.06, β = 1.39). Full species names can be found in Table 1
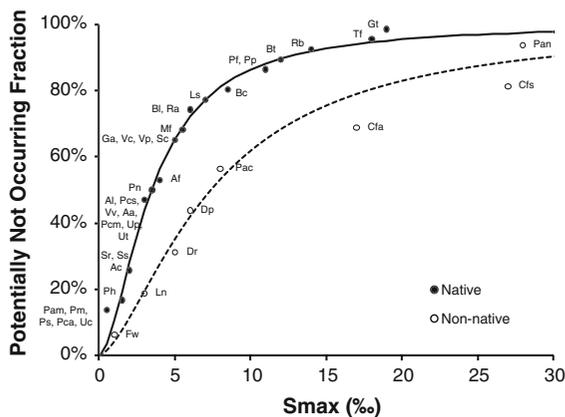

Fig. 2 Species sensitivity distributions for maximum salinity tolerances of native and non-native molluscs of the river Rhine. The data points represent individual species' tolerances based on Hazen plotting positions (Native: n = 33; α = 0.54, β = 0.25; Non-native: n = 8; α = 0.87, β = 0.27). Full species names can be found in Table 1

River Rhine case study and comparison with survey data

In the summer of 2003, potential salinity effects were minimal in nearly the entire river Rhine, except for the coastal region where the PNOFs for native as well as non-native species were high (Table 2). Temperature data yielded higher PNOFs for the Lower and Middle Rhine sections, whereas for the other sections the

Table 2 Potentially not occurring fractions (PNOFs; in percentages) of native and non-native mollusc species in different river sections of the river Rhine for the extreme warm and dry year 2003

Station	River section	Salinity		Temperature	
		Native	Non-native	Native	Non-native
Maassluis	DR	78.8	49.6	14.9	0.3
Lobith	DR/LR	1.8	0.8	61.7	2.7
Koblenz	MR	1.4	0.6	69.3	3.8
Lauterborg	UR	1.0	0.4	40.2	1.1
Wheil am Rhein	UR/HR	0.8	0.3	32.5	0.8
Reckingen	HR	0.7	0.3	32.5	0.8
Diepoldsau	AR	0.7	0.3	0.1	0.0

Data on temperature and salinity of the river sections from the International Commission for the Protection of the Rhine (IKSR 2011), with the exception of Maassluis (temperature data from www.waterbase.nl) and Diepoldsau (data derived from Uehlinger et al. 2009). DR: Delta Rhine; LR: Lower Rhine; MR: Middle Rhine; UR: Upper Rhine; HR: High Rhine; AR: Alpine Rhine

potential effects were less pronounced. In addition, the PNOFs found for native species were higher than for non-native species, except in the Alpine Rhine where the occurrence of both species groups appeared not to be limited by maximum water temperature.

The yearly maximum water temperature of the river Rhine at Lobith increased 2.5°C over the period 1960–2009 (Fig. 3). The maximum salinity showed an increase over the period 1960–1985 and a steep decline from 0.6 to 0.4‰ since the mid 1980s, as a
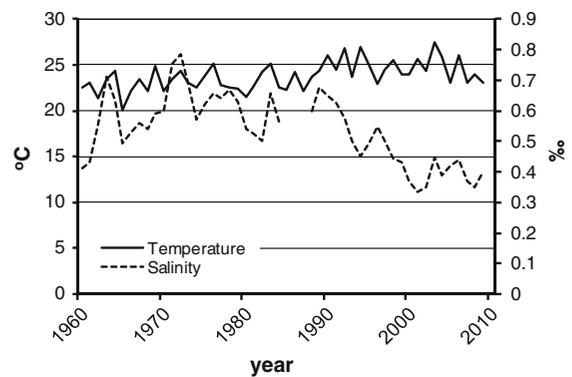

Fig. 3 Maximum water temperature and salinity of the river Rhine at Lobith (salinity measurements for the years 1985–1987 were not available)

Table 3 Slope (a), intercept (b), statistical probability (*P*-value) and explained variance (r²) of trends in potentially not occurring fractions (PNOF) and not occurring fractions (NOF) of native and non-native mollusc species

	Slope (a)	Intercept (b)	r²	*P*-value
PNOF-temperature				
Native (1960–2009)	3.29E−03	ns	0.19	<0.01
Non-native (1960–2009)	8.65E−05	ns	0.15	<0.01
PNOF-salinity				
Native (1960–1976)	1.43E−04	ns	0.31	<0.05
Non-native (1960–1976)	5.39E−04	ns	0.31	<0.05
Native (1977–2009)	−9.98E−04	6.84E−02	0.65	<0.01
Non-native (1977–2009)	−3.78E−04	2.68E−02	0.65	<0.01
PNOF-temperature and salinity				
Native (1960–2009)	2.75E−03	8.48E−02	0.15	<0.01
Non-native (1960–2009)	ns	2.05E−02	0.08	>0.05
NOF (field monitoring data)				
Native (1988–2003)	2.01E−02	6.50E−01	0.65	<0.01
Non-native (1988–2003)	ns	5.50E−01	0.004	>0.05

ns not significant

result of effective water pollution control (i.e., international treaties concerned with a reduction in salt load of the river Rhine in 1976). The PNOFs of native and non-native species with regard to water temperatures significantly increased over the period 1960–2009 (*P* < 0.01; Table 3). For native species, however, the total increase was higher due to lower maximum tolerance levels (Fig. 4a). The trends of the PNOFs for salinity stress include a turning point. After the initiation of international treaties in 1976, the PNOFs of both species groups at Lobith have significantly declined (*P* < 0.01; Table 3), and PNOFs for both native and non-native species are currently lower than in 1960 (Fig. 4b). As the effects of temperature are considerably stronger than the salinity effects, the trend lines for the combined effects of these stressors largely resemble the trend lines for temperature effects (Fig. 4c). For native species, a statistically significant increase in PNOF was found (*P* < 0.01; Table 3). For non-native species no significant change was found (*P* > 0.05; Table 3).

Monitoring data on macroinvertebrates allowed for trend analysis of the mollusc species richness for the period 1988–2003 in the river Rhine at Lobith. The NOF of non-native species remained fairly constant over this period, while the NOF of native species showed an increase, which indicates a gradual decrease in species richness (*P* < 0.01; Fig. 5). These trends agree well with the trends in PNOF for both non-native and native species (Fig. 4c), although the increase in the PNOF of native mollusc species is less pronounced than the increase in the NOF (Table 3). A comparison of the slopes of the regression lines (Table 3) suggests that the increase in PNOF accounts on average for 14% of the increase in the NOF.

Discussion

Species sensitivity distributions

Based on field-derived maximum tolerance levels for water temperature and salinity, we constructed SSDs for native and non-native mollusc species in the river Rhine. The species included currently occur in this river, which increases the applicability of our SSDs in site-specific assessments (De Vries et al. 2008). Input data for the SSDs comprised maximum tolerance levels derived from field observations. The use of field observations to derive tolerance levels is open to debate (Von Stackelberg and Menzie 2002), as it cannot be ruled out that the species included are able to live in warmer or more saline waters than indicated by the field observations. For both temperature and salinity, a comparison of field-based maximum tolerance levels with LC_{50} values reported from laboratory
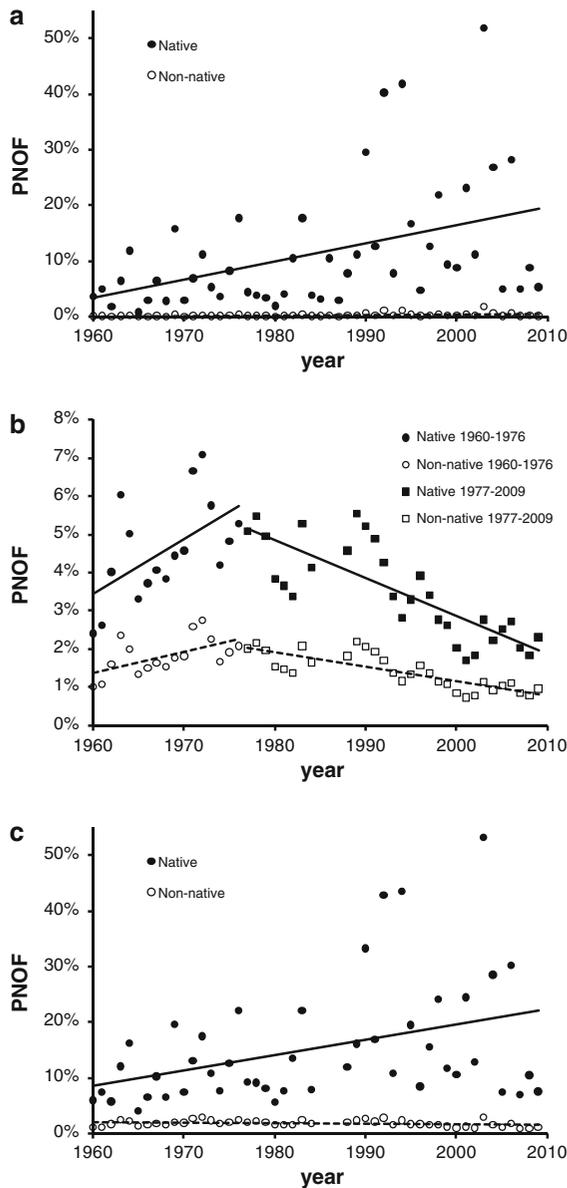
Fig. 4 Potentially not occurring fraction (PNOF) of native and non-native molluscs at Lobith in relation to yearly maximum water temperature conditions (**a**), yearly maximum salinity conditions (**b**) and both stressors combined under the assumption of additive effects (**c**) for the period 1960–2009

Fig. 5 Not occurring fraction (NOF) of native and non-native molluscs at Lobith derived from monitoring data for the period 1988–2003

2007; Kefford et al. 2004). Moreover, for 15 species the field-based maximum temperature tolerance was derived from occurrence data of surveys that also include water bodies with a wider temperature range (Table 1); for maximum salinity this holds for 13 species. This supports that our field-based SSDs indeed reflect maximum temperature and salinity tolerances. Unfortunately, for the remaining species data on temperature and salinity ranges of water bodies were not reported. We chose to accept the limitations of field data for reasons of data availability, as laboratory data for temperature tolerance were available for only six mollusc species and several species groups (e.g., Sphaeriidae and Unionidae) are only rarely the subject of physiological research. Moreover, other authors suggest that tolerance levels derived from field data may be more environmentally relevant and realistic than reference levels obtained in laboratory tests (Kwok et al. 2008; Leung et al. 2005; Struijs et al. 2011).

Our results showed that non-native mollusc species in the river Rhine have a higher maximum temperature tolerance than native species. This agrees with other studies on temperature tolerance of aquatic species. For example, non-native fish species can tolerate higher maximum temperatures than native fish species (Leuven et al. 2007, 2011). Higher tolerance levels of non-native mollusc species also explain their high abundance at sites with elevated temperature (Langford 1971; Müller et al. 2005). The difference between native and non-native species can be explained by the origin of species, as previous studies found

tests revealed no significant difference. This corresponds with findings in previous studies, where comparisons of laboratory- and field-derived salinity tolerance data revealed that salinities lethal to 50% of individuals (LC_{50}) were correlated with the maximum salinity at which a species had been collected in the field, both at family and species level (Horrigan et al.
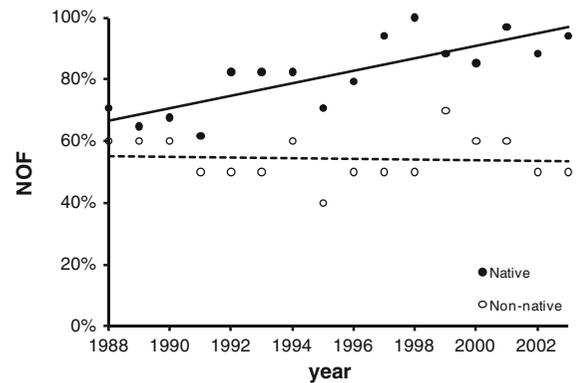
significantly higher temperature tolerances for (sub)tropical than for temperate species (De Vries et al. 2008).

Salinity tolerances of native and non-native species were not significantly different, which agrees with other recent studies on salinity tolerance of native and non-native macroinvertebrates (Piscart et al. 2011; Van de Meutter et al. 2010). However, our results also show that some non-native species can tolerate considerably higher salinities than native species. Two examples are *Corbicula fluminalis* and *Potamopyrgus antipodarum*. These species originate from Asia and New Zealand and started their colonisation in the estuaries and dispersed upstream. Their main vector of intercontinental dispersal is ballast water (Leuven et al. 2009; Nehring 2002), which acts as a strong filter in favour of species with high salinity tolerances. This is, again, consistent with Piscart et al. (2005, 2011), who also found higher tolerance levels for non-native species from outside Eurasia.

River Rhine case study and comparison with survey data

Based on the SSDs, we calculated the potentially not occurring fractions (PNOFs) of native and non-native mollusc species corresponding with maximum water temperature and salinity levels recorded in the river Rhine (1) for different river sections in 2003, and (2) at Lobith over the period 1960–2009. Whereas daily measurement data were available for temperature, salinity was measured at 2-week intervals, so peak values could have been missed. In comparison with maximum salinity values derived from daily (24 h) averaged measurements, which were available for a shorter time span (from 1979 onwards), daily values indeed resulted in maximum salinity values exceeding ours with a maximum of 0.8‰. Hence, the PNOFs for maximum salinity conditions calculated in this study are underestimated compared to PNOFs that would be based on daily salinity measurements. However, we preferred the 2-week interval data because of the longer time span covered. Moreover, the implications for the overall combined impact of both stressors are minimal in the freshwater sections of the river Rhine, as salinity is a less important stressor than temperature (Table 2, Fig. 4a, b).

As the PNOFs were derived from yearly maximum values obtained from one location, the resulting

patterns and trends should be interpreted with care. Possibly, short term maximum temperature and salinity conditions might be insufficient to induce significant effects on molluscs, indicating that the use of single maximum values may result in overestimated PNOFs. Effects could also be overestimated due to spatial variation in abiotic conditions. In the upper water layer of the main river channel, where measurements are commonly conducted, water temperatures may be higher than in deeper water layers that receive inflowing ground water. Indeed, water temperatures measured at the channel floor in the rivers Rhine and Meuse throughout the year were up to 4.5°C lower than in the upper water layer, confirming that vertical heterogeneity in water temperature may be large (Boderie et al. 2006). Such heterogeneity may create thermal refugia and thus mitigate potential negative temperature effects on organisms.

Although it is possible to compare SSDs with actual species richness in a river system (Kefford et al. 2006), validation using species survey data is not straightforward. Our SSD predictions do not account for spatial variability in species richness and additional factors that play a role in determining field species' distributions (Kefford et al. 2011a, b). Besides maximum temperature and salinity, other factors may influence the occurrence of mollusc species in the river Rhine, including, for example, wave conditions (Gabel et al. 2011) or minimum temperature (Weitere et al. 2009). In addition, a proper validation requires extensive sampling of species, preferably along an environmental gradient with limited and well documented environmental conditions (Kefford et al. 2006, 2010). As the mollusc survey data used to calculate the NOFs were not specifically obtained for the yearly maximum temperature and salinity values used to calculate the PNOFs, the PNOFs cannot be validated for single years. Yet, although the increase in the PNOF of native mollusc species was less pronounced than the increase in the NOF, our results showed similar temporal trends in empirical and modelled (P)NOF for native as well as non-native mollusc species (Table 3). This suggests that comparison with survey data helps to confirm and interpret general trends in species loss predicted with SSDs.

Despite the uncertainties associated with the PNOFs, the trends and patterns presented here can be qualitatively evaluated and interpreted. Increasing PNOFs were found in relation to temperature changes

from 1960 through 2009, reflecting rising river water temperatures due to thermal pollution and, in particular, global warming (Uehlinger et al. 2009). PNOFs were higher in river sections with higher water temperatures due to large cooling water discharges of power plants and effluents of industrial and communal water treatment facilities, i.e., in the Lower and Middle Rhine (Table 2). For salinity, we found a net decrease in PNOF at Lobith for native as well as non-native species, reflecting a reduction of salt water effluents from kali mines following the 1976 Rhine Salt Treaty (Dieperink 2000). In the delta region, however, extreme salinities may occur, which potentially have considerable impact on both native and non-native mollusc species (Table 2). Previous research has shown that rising sea water levels and increased evaporation due to climate change may result in higher salinity levels (Bonte and Zwolsman 2010). Therefore, in ecological impact assessments special attention should be paid to areas that are more susceptible to climate change and where effects may be more pronounced.

Interpretation of the results from the multiple stressor analysis has to be done carefully. We assumed an additive effect of temperature and salinity, whereas previous research has suggested that the interaction between temperature and salinity is complex (Bradley 1975; Brenko and Calabrese 1969; Verween et al. 2007; Wright et al. 1996). Temperature can either modify the effects of salinity, thereby changing the salinity tolerance range of mollusc species, or vice versa, whereby interactions between salinity and temperature can be species-specific (Browne and Wanigasekera 2000; Kefford et al. 2007). Irrespective of possible interactions, however, effects of salinity in the river Rhine were small relative to temperature effects, reflected by a net increase in PNOF for native species from 1960 to 2009 when both stressors were combined (Fig. 4c). Combined salinity and temperature changes had no significant effect on non-native species, mainly due to their higher maximum temperature tolerance. Thus, the results of our study indicate that future temperature rise as a result of climate change will disproportionally affect native mollusc species. This corresponds with the findings of Mouthon and Daufresne (2006), who studied the effects of heatwaves on mollusc species. They found that both native species and invaders appear to be struck by heatwaves, but that invaders are able to recover remarkably well. Non-native species like dreissenids and corbiculids are well adapted to unstable habitats, thanks to their high fecundity, fast growth and early maturity allowing rapid (re)colonization (Van der Velde et al. 2010).

SSDs based on generic species pools show systematic differences in sensitivity among species from different regions and taxonomic groups (De Vries et al. 2008). By using a river basin specific species pool from one taxonomic group, our SSDs account for these differences. Constructing and applying river basin specific SSDs for native as well as non-native species appeared a promising approach for quantifying and comparing tolerance levels and for assessing separate and combined effects of changing abiotic parameters. In addition to conventional methods for expressing upper tolerance levels of species (i.e., classification of physiological tolerances) our SSD-PNOF approach also allows for prediction of changes in mollusc communities in response to future environmental conditions. More data on species tolerances for various abiotic stressors would facilitate the construction of SSDs, whereas long term surveys of actual species distributions will be helpful to validate the PNOFs. Especially measurements of species richness along environmental gradients and mesocosm studies are required for further validation of PNOFs derived from SSDs.

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