

# Consequences of climatic change for water temperature and brown trout populations in Alpine rivers and streams

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## Abstract

Twenty-five years of extensive water temperature data show regionally coherent warming to have occurred in Alpine rivers and streams at all altitudes, reflecting changes in regional air temperature. Much of this warming occurred abruptly in 1987/1988. For brown trout populations, the warming resulted in an upward shift in thermal habitat that was accelerated by an increase in the incidence of temperature-dependent Proliferative Kidney Disease at the habitat's lower boundary. Because physical barriers restrict longitudinal migration in mountain regions, an upward habitat shift in effect implies habitat reduction, suggesting the likelihood of an overall population decrease. Extensive brown trout catch data documenting an altitudinally dependent decline indicate that such a climate-related population decrease has in fact occurred. Our analysis employs a quantitatively defined reference optimum temperature range for brown trout, based on the sinusoidal regression of seasonally varying field data.

*Keywords:* Alpine rivers and streams, altitude dependence, brown trout, climatic change, habitat shift, optimum temperature, Proliferative Kidney Disease, regional coherence, sinusoidal regression, water temperature

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## Introduction

In the 1990s, an alarming decline in the catch of brown trout in Western European rivers and streams occurred (European Inland Fisheries Advisory Commission, 2002), the cause of which is still largely unknown. During the same time period, Northern Hemisphere air temperatures are likely to have been the highest of the entire previous millennium (Folland *et al.*, 2001), suggesting the possibility of a causal link between the two phenomena. Here, we investigate the likelihood of such a link.

From 1976 to 2000, the mean Northern Hemisphere air temperature rose by 0.24 °C per decade on average, with warming over the land surface being even more intense (Folland *et al.*, 2001). Over the same period, air temperatures in Switzerland increased much more rapidly: the mean air temperature at Zurich and Basle, for instance, increased by 0.57 °C per decade. Stream temperatures follow ambient air temperatures closely (e.g. Webb & Walling, 1997; Mohseni & Stefan, 1999), and

modelling studies confirm that air temperature is a major determinant of the heat balance of Swiss lakes (Peeters *et al.*, 2002) and streams (Meier *et al.*, 2003). Consequently, the rising air temperatures of the last few decades of the 20th century have been reflected in rising water temperatures in Swiss lakes (Peeters *et al.*, 2002; Livingstone, 2003) and rivers (Jakob *et al.*, 1996; Hari & Zobrist, 2003).

Various studies have shown that lake surface water temperatures, because they are driven by regionally coherent meteorological driving variables, also exhibit a high degree of regional coherence (e.g. Magnuson *et al.*, 1990; Baines *et al.*, 2000; Benson *et al.*, 2000). In the specific case of the mountain areas of central Europe, air temperatures are known to fluctuate synchronously over large areas (Weber *et al.*, 1997), eliciting a regionally coherent response in the surface water temperatures of lakes in Switzerland and Austria (Livingstone & Lotter, 1998; Livingstone *et al.*, 1999, 2005; Livingstone & Dokulil, 2001). During the winter half-year, the North Atlantic Oscillation (NAO) dictates much of the variability in air temperature in the Northern Hemisphere in general (e.g. Hurrell, 1995; Hurrell *et al.*, 2003) and in

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Switzerland in particular (Beniston & Jungo, 2002). The NAO, therefore, has a large synchronizing influence not only on the surface temperatures of central European lakes (Livingstone & Dokulil, 2001), but also on their entire ecosystems (e.g. Straile *et al.*, 2003). However, while lakes are confined to one well-defined altitude, rivers and streams may behave differently because they span a range of altitudes, so that their heat balance is influenced by a corresponding range of altitudinally dependent air temperatures and other climatic drivers. The important question that therefore arises is whether river and stream water temperatures (henceforth: RWTs) also exhibit large-scale regional coherence with a temporal pattern that is capable of interpretation in terms of large-scale climatic forcing, which would allow general conclusions to be drawn about the effects of large-scale climatic forcing on riverine fish habitats.

The brown trout (*Salmo trutta fario* L.) is the most important fish for hobby anglers in Swiss rivers. Catches of brown trout, which are registered and fiscally controlled by government agencies, have declined by approximately 50% over the last 15 years. Of the many hypotheses that have been advanced to explain this decline (Burkhardt-Holm *et al.*, 2002), one of the most important is that it is the result of increasing water temperatures. Here, we assess the plausibility of this hypothesis. A quantitative analysis of the effect of observed increases in RWT on brown trout populations is possible because their physiological temperature dependence is quite well known. Maximum growth rates occur at 13.1–13.9 °C, while growth ceases below 2.9–3.6 °C and above 18.7–19.5 °C (Elliott & Hurley, 2001). A diverse river morphology is crucial if brown trout are to outlive short-term RWT peaks (Peter, 1998; McCullough, 1999; Elliott, 2000; Schmutz *et al.*, 2000). During summer droughts, brown trout have been reported to have survived in pools, with a preference for RWTs below  $24.7 \pm 0.5$  °C (Elliott, 2000). This is essentially the incipient lethal temperature (survival for 7 days) established in the laboratory; the ultimate lethal temperature (survival for 10 min) is  $29.7 \pm 0.36$  °C (Elliott, 1981). Brown trout mortality is highest in spring, when sensitive juvenile life stages occur. As the carrying capacity of a stream or river is predetermined, the establishment of a feeding territory in May and June represents a bottleneck in development (Milner *et al.*, 2003). An important temperature-dependent factor known to influence populations of brown trout is the occurrence of Proliferative Kidney Disease (PKD), a serious infectious disease causing high mortality, with clinical symptoms occurring above 15–16 °C (Gay *et al.*, 2001; Chiltonczyk *et al.*, 2002; Wahli *et al.*, 2002).

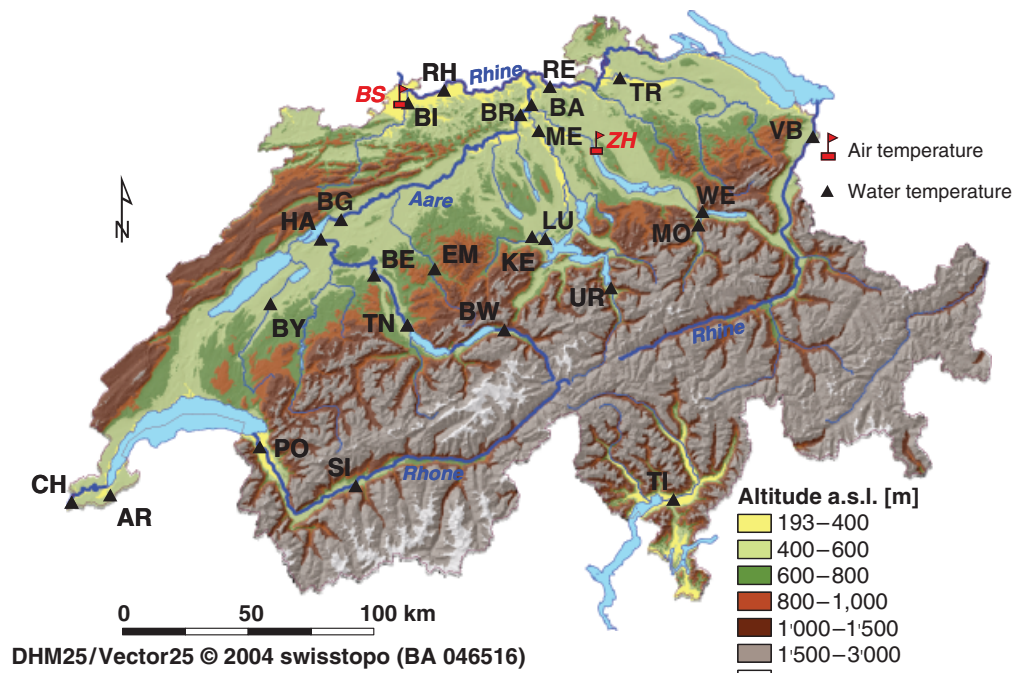
Stream warming can be assumed to affect cold-water fish populations negatively at the warmer boundaries of

their habitat, and positively at the cooler boundaries (Matthews & Zimmerman, 1990; Rahel *et al.*, 1996; O'Brien *et al.*, 2000; Reid *et al.*, 2001). The effects on fish of changes in RWT in the field can be expected to be most pronounced at these boundaries, which, geographically, can be defined either in terms of latitude or altitude. Switzerland's mountainous terrain, which spans more than 4000 m of altitude, contains both the warmer and cooler brown trout habitat boundaries and is ideal for such a study.

## Data

Since the 1960s, RWTs at sites distributed throughout Switzerland have been measured automatically at 1-min intervals using platinum resistance thermometers (de Montmollin & Parodi, 1990; Jakob *et al.*, 1996). Here, daily, monthly, seasonal and annual mean RWTs computed from the original measurements at 95 sampling stations are employed. The data were obtained partly from the Swiss Federal Office for Water and Geology and partly from a publication by the Wasser- und Energiewirtschaftsamt des Kantons Bern (2002). Attention is focused on the data from 25 of these stations (Fig. 1, Table 1), where RWT data are available uninterruptedly during the entire 25-year period from 1978 to 2002. These 25 sampling stations span a catchment area altitude range of 4607 m. All lie on the north side of the main Alpine chain except one (station TI), which lies on the south side. Daily mean discharge data (*Q*) from 24 of the 25 stations were also available for the same 25-year period. For one station (HA), measured data on *Q* were available only from 1984 to 2002; the missing data for this station were estimated by linear regression based on the measured data from station BE, 50 km up-river from HA (Fig. 1). Using GIS techniques, the mean altitude of the catchment area of each measuring station (Table 1) was computed up-river as far as the next large lake (>3 km<sup>2</sup>), which was considered to buffer the influence of ambient air temperature on the RWT of its outlet. Other physical data employed included meteorological data from the meteorological stations of Zurich and Basle that also cover the period 1978–2002. For the purposes of this paper, the regional air temperature pattern in Switzerland is assumed to be given by the mean of the air temperatures at these two stations. Air temperatures throughout Switzerland are highly coherent, so that measurements from very few stations on the Swiss Plateau suffice to capture the temporal structure of the regional air temperature (Livingstone & Lotter, 1998), even at altitudes >2000 m a.s.l. (Livingstone *et al.*, 1999, 2005).

A matrix of brown trout catch data, expressed in terms of the annual number of individuals per km



**Fig. 1** Map of Switzerland showing the 25 river and stream monitoring stations with long-term time-series data (see Table 1 for details), the meteorological stations at Basle (BS) and Zurich (ZH), and the main rivers and lakes. The altitude classes illustrated are those used in the analyses of Proliferative Kidney Disease (PKD), thermal habitat and catch data (Figs 8 and 9).

(ind  $\text{km}^{-1}$ ) caught by rod and line, were available from 413 river sections throughout Switzerland (E. Staub, personal communication; Staub *et al.*, 2003), spanning an altitude range from 193 to 3029 m a.s.l. Here, we employ two separate data sets derived from the original catch matrix: a long data set (L, 1978–2001) with relatively few catch sections (87) and a short data set (S, 1989–2001) with correspondingly more catch sections (254). All 87 catch sections of data set L are included in data set S. For the purposes of this paper, the catch data were binned into five altitude classes: 200–400, 400–600, 600–800, 800–1000 and 1000–1500 m a.s.l. The locations of these altitude classes within Switzerland are illustrated in Fig. 1.

Data on the occurrence of PKD in Swiss rivers and streams were available from various studies conducted from 1997 to 2001 (e.g. Wahli *et al.*, 2002). Included in the present study are the results of tests for PKD conducted on a total of 9435 brown trout from 352 sites in Switzerland that span an altitude range from 247 to 1759 m a.s.l.

## Methods

### Regional coherence

Month by month, the degree of regional coherence (i.e. spatial autocorrelation) exhibited at each measuring

station with regard to its RWT and discharge ( $Q$ ) was estimated as the proportion of variance shared pairwise between the linearly detrended time series of RWT (or  $Q$ ) at that station and the linearly detrended mean of the 24 remaining time series (method of Livingstone & Dokulil, 2001). Linear detrending involved computing a linear regression of each time series on time, and subtracting the regression line thus obtained to leave a time series of residuals. In Fourier terms, linear detrending removes the zero-frequency (infinite-period) component from the time series, leaving the finite-frequency fluctuations.

### Sinusoidal regression

To facilitate making quantitative comparisons between different years or different rivers (Table 1), sinusoidal regressions were computed (Güttinger, 1980), thus allowing the essential properties of the seasonal variation in RWT to be expressed in terms of only three parameters,  $T_s$ ,  $A$  and  $M$ , as follows:

$$T(t) = T_s + A \cos \omega(t - M), \quad (1)$$

where  $t$  is time, in Julian days: e.g. 5 March =  $(31 + 28 + 5) \text{ d} = 64 \text{ d}$ ;  $T(t)$  is the RWT at time  $t$  ( $^{\circ}\text{C}$ );  $T_s$  is the mean of the sinusoid ( $^{\circ}\text{C}$ );  $A$  is the amplitude of the sinusoid ( $^{\circ}\text{C}$ );  $\omega$  is the frequency =  $2\pi/365.25$

**Table 1** Characteristics of the river monitoring stations of Fig. 1 and their catchment areas, and the parameters of the sinusoidal regression of water temperature data for Subseries I (1978–1987) and II (1988–2002)

River or stream name	Catchment area (up-river to the next lake)				Results of sinusoidal regressions											
	Mean discharge (1978–2002): $Q$ ( $m^3 s^{-1}$ )	Station altitude: $h$ (m a.s.l.)	Mean altitude: $h_m$ (m a.s.l.)	Maximum altitude (m a.s.l.)	Area ( $km^2$ )	% glacier	Parameters 1978–1987			Parameters 1988–2002			Shifts from 1978–1987 to 1988–2002			
							$T_s$ ( $^{\circ}C$ )	$A$ ( $^{\circ}C$ )	$M$ (d)	$T_s$ ( $^{\circ}C$ )	$A$ ( $^{\circ}C$ )	$M$ (d)	$\Delta T_s$ ( $^{\circ}C$ )	$\Delta T_{max}$ ( $^{\circ}C$ )	$\Delta T_{min}$ ( $^{\circ}C$ )	$\Delta M$ (d)
Aare Brugg (BR)*	335	332	654	2197	3487	–	11.0	7.5	218	12.0	7.4	213	1.0	0.9	1.0	–5.5
Emme Emmenmatt (EM)	12.3	638	1069	2197	443	–	7.7	5.6	214	8.4	6.0	208	0.7	1.0	0.3	–6.3
Aare Brügg Ägerten (BG)*	256	428	437	599	53	–	10.9	7.4	225	12.0	7.5	219	1.1	1.2	1.0	–6.1
Broye Payerne (BY)	8.9	441	717	1514	423	–	9.9	7.7	208	10.9	7.9	203	1.1	1.3	0.8	–5.0
Aare Hagneck (HA)*	185	437	1007	3248	2711	–	10.9	6.0	224	11.7	6.2	218	0.8	1.0	0.7	–6.3
Aare Bern (BE)*	126	502	803	2176	539	–	10.1	6.0	225	10.9	6.1	219	0.8	1.0	0.6	–6.1
Aare Thun (TN)*	116	548	571	936	65	–	10.2	5.8	228	10.9	6.1	222	0.7	1.0	0.5	–6.1
Aare Brienzwiler (BW)	37	570	2140	4274	558	19.9	5.7	1.9	214	5.8	2.0	214	0.0	0.1	0.0	0.6
Birs Münchenstein (BI)	16	268	762	1445	966	–	10.3	5.6	209	11.1	5.7	204	0.8	0.9	0.6	–4.9
Rhein Rheinfelden (RH)*	1090	262	645	2502	6052	–	11.3	7.4	219	12.2	7.6	213	0.9	1.2	0.7	–6.1
Rhein Rekingen (RE)*	465	323	628	2502	3775	–	10.8	7.8	221	11.8	8.1	215	1.0	1.3	0.7	–5.8
Thur Andelfingen (TR)	50	356	778	2502	1708	–	9.9	7.4	208	10.7	7.5	204	0.8	0.9	0.7	–4.8
Rhein vor Bodensee (VB)	245	410	1732	3614	6436	1.6	7.5	4.2	211	8.0	4.4	207	0.5	0.7	0.2	–3.8
Limmat Baden (BA)*	104	332	541	1229	443	–	11.4	8.0	221	12.4	8.2	216	1.0	1.2	0.8	–5.3
Linth Weesen (WE)*	54	419	608	1865	33	–	9.7	5.6	229	10.5	5.9	223	0.8	1.2	0.5	–5.8
Linth Mollis (MO)*	34	436	1723	3614	535	4.7	7.1	3.2	215	7.4	3.2	211	0.3	0.3	0.3	–3.7
Reuss Mellingen (ME)*	144	345	738	2350	1051	–	10.9	7.4	217	11.7	7.7	212	0.8	1.1	0.5	–4.4
Kleine Emme Littau (KE)	15.9	431	1050	2350	482	–	8.4	7.2	211	9.0	7.2	206	0.6	0.6	0.6	–5.2
Reuss Luzern (LU)*	112	432	455	1026	124	–	10.8	6.8	221	11.9	7.4	217	1.1	1.6	0.5	–4.9
Reuss Seedorf (UR)	44	438	2012	3630	837	9.5	6.3	3.2	211	6.6	3.5	207	0.3	0.6	0.0	–3.6
Rhône Chancy (CH)*	368	336	1080	4807	2873	3.2	10.8	6.4	222	11.6	6.6	216	0.9	1.0	0.7	–5.6
Arve Genève (AR)	82	380	1362	4807	2000	4.6	7.9	3.8	206	8.4	3.7	201	0.6	0.4	0.7	–4.4
Rhône Porte du Scex (PO)	193	377	2099	4634	5333	13.9	6.8	2.9	198	7.3	2.9	196	0.5	0.4	0.5	–2.7
Rhône Sion (SI)	108	484	2295	4634	3336	18.1	6.7	2.6	191	7.0	2.6	191	0.3	0.3	0.2	–0.3
Ticino Riazzino (TI)	68	200	1649	3383	1609	0.8	8.4	4.2	210	9.1	4.6	208	0.7	1.1	0.4	–2.4
Zurich (air temperature) (ZH)		556					8.5	9.2	203	9.6	8.9	197	1.0	0.7	1.3	–5.6
Basle (air temperature) (BS)		316					9.5	9.0	202	10.7	8.6	197	1.2	0.8	1.6	–4.9

Catchment areas of stations marked with asterisks were measured up-river to the next lake ( $> 3 km^2$ ). The parameters of the sinusoidal regression of river or stream water temperature (RWT) ( $T_s, A, M$ ) are defined in Eqn (1). The shift in mean RWT from Subseries I to II,  $\Delta T_s$ , is defined as  $T_s$  for Subseries II minus  $T_s$  for Subseries I. Summer RWT is estimated by  $T_{max} = T_s + A$ , and winter RWT by  $T_{min} = T_s - A$ ;  $\Delta T_{max}$  is defined as  $T_{max}$  for Subseries II minus  $T_{max}$  for Subseries I;  $\Delta T_{min}$  is defined analogously.



$\text{rad d}^{-1}$ ;  $M$  is the time of the annual maximum (i.e. the phase of the sinusoid), in Julian days.

Additional parameters, such as a meaningful summer RWT ( $T_s + A$ ), phase shifts ( $\Delta M$ ) and differences in growth periods, can be computed as required from  $T_s$ ,  $A$  and  $M$ . Because the maximum summer RWT occurs later in the year at higher altitudes than at lower altitudes, 'summer' for Swiss Alpine streams cannot be meaningfully defined in terms of a fixed time window. This problem was overcome by defining the summer RWT based on the sinusoidal regression as  $T_s + A$ , thus automatically taking account of any altitudinal shift in the phase  $M$ .

*Optimum water temperature range*

RWT and brown trout catch data were available simultaneously for 37 river sections with a wide range of annual mean  $Q$  ( $0.8\text{--}248\text{ m}^3\text{ s}^{-1}$  in 2002). Based on these data, for each day of the year we determined the optimum RWT range  $T_{\text{opt}}$  for brown trout populations. Staub *et al.*, (2003) define the 'recent catch' as the mean of the catches in 2000 and 2001. The median 'recent catch' for all 413 river sections for which catch data were available was  $49.2\text{ ind km}^{-1}$ . A catch exceeding this figure was considered as evidence for the existence of an abundant population at a given river section in a specific year. For the 37 river sections this was the case in a total of 181 years of data.

$T_{\text{opt}}$  was defined operationally as the range of RWTs lying between the sinusoidal representations of the upper and lower bounds of the 95% predictive interval (PI) of the RWTs for all 181 years of data and for each day of the year, assuming a Gaussian distribution (Fig. 2). Sinusoidal regressions of the mean and the upper and lower bounds of the 95% PI yielded the parameters listed in Table 2.

*Altitudinal dependence of water temperature*

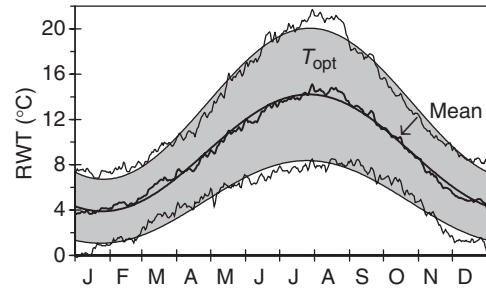
The altitudinal dependence of the summer RWT was calculated by linear regression of  $T_s + A$ , determined for each of the 95 measuring stations in 2002, on altitude  $h$ :

$$T_s + A = 19.6\text{ }^\circ\text{C} - (0.0095\text{ }^\circ\text{C m}^{-1})h \quad (2)$$

( $n = 95$ ,  $P < 0.001$ ,  $r^2 = 0.44$ , standard error =  $s = 2.56$ , 95% PI =  $\pm 5.1\text{ }^\circ\text{C}$ ).

*Thermal habitat*

The probability  $P_i$  of a given altitude slice  $i$  being conducive to brown trout abundance was computed by integrating numerically the normal distribution associated with the linear regression described by Eqn (2),



**Fig. 2** Determination of the optimum river water temperature (RWT) range for brown trout ( $T_{\text{opt}}$ ), based on daily water temperature and data on catch abundance.  $T_{\text{opt}}$  is defined for each day of the year as the range within the 95% predictive interval (fine black 'noisy' curves), assuming a normal distribution. The parameters of the equivalent sinusoidal regression curves are listed in Table 2.

**Table 2** Parameters of the optimum river water temperature range for brown trout,  $T_{\text{opt}}$ , determined by sinusoidal regression (see Fig. 2)

	$T_s$ ( $^\circ\text{C}$ )	$A$ ( $^\circ\text{C}$ )	$M$ (d)	$T_s + A$ (summer) ( $^\circ\text{C}$ )	$T_s - A$ (winter) ( $^\circ\text{C}$ )	$M$ (summer) (date)	
Upper bound of 95% PI	13.4	6.7	208	20.0	6.7	27 July	
Mean		9.1	5.2	207	14.2	3.9	26 July
Lower bound of 95% PI	4.7	3.7	205	8.4	1.1	24 July	

$T_s$ ,  $A$  and  $M$  are defined as in Eqn (1).

PI, predictive interval, assuming the daily mean water temperatures of different streams to be normally distributed about the mean.

d, Julian days.

taking into account the limitation imposed by  $T_{\text{opt}}$  in summer (Fig. 3):

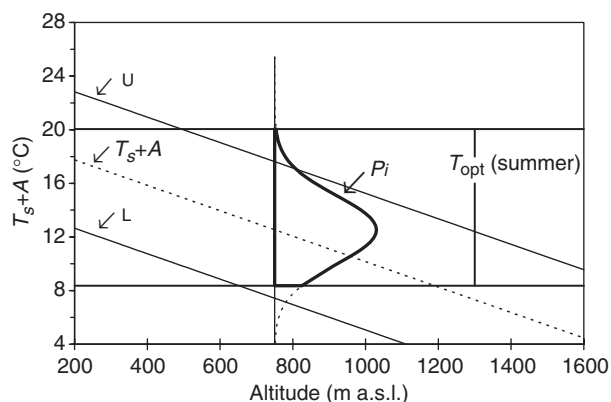
$$P_i = \frac{1}{\sqrt{2\pi}} \int_a^b e^{-\frac{z^2}{2}} dz, \quad (3)$$

where  $a$  ( $= 8.4\text{ }^\circ\text{C}$ ) and  $b$  ( $= 20.0\text{ }^\circ\text{C}$ ) are the lower and upper limits, respectively, of  $T_{\text{opt}}$ ;  $z = (x - \mu) / \sigma$ ;  $\mu = (T_s + A) = 19.6\text{ }^\circ\text{C} - (0.0095\text{ }^\circ\text{C m}^{-1})h$ ; and  $\sigma = s = 2.56$ .

The probability of thermal conduciveness of a given altitude class  $c$ ,  $P_c$ , is then given as the arithmetic mean of  $P_i$  for all altitude slices  $i$  within altitude class  $c$ . If the total length of the streams and rivers located in altitude class  $c$  is  $L_c$ , then the thermal habitat within altitude class  $c$ , expressed in km, is  $P_c L_c$ .

*Date of emergence and duration of growth period*

The estimated date of emergence of brown trout fry from their gravel nest (50% eggs hatched) was



**Fig. 3** Probability of thermal conduciveness of one altitude slice ( $P_i$ ), here for the example of 750 m a.s.l., defined as that part of the normally distributed summer water temperature ( $T_s + A$ ) that lies within the range of  $T_{opt}$  in summer (8.4–20.0 °C). Also shown are the altitudinal dependence of  $T_s + A$  and the upper (U) and lower (L) bounds of its 95% predictive interval.

calculated using the equation of Elliott & Hurley (1998):

$$E_{50} = C_{50}(T_1 - T)(T - T_0), \quad (4)$$

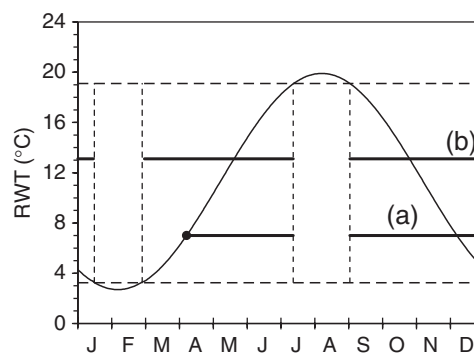
where  $C_{50} = 76.21 \text{ d } ^\circ\text{C}^{-2}$ ,  $T_1 = 22.0^\circ\text{C}$ ,  $T_0 = -2.8^\circ\text{C}$  and  $T$  is the mean ambient RWT between the fertilization date of the eggs (15 November in Switzerland: A. Peter, personal communication) and  $E_{50}$ .

For brown trout, the lower RWT limit for growth lies between 2.9 and 3.6 °C and the upper limit between 18.7 and 19.5 °C (Elliott & Hurley, 2001). The duration of the growth period was computed as the number of days per calendar year during which the RWT, as estimated by sinusoidal regression, lay between the respective mean values of 3.25 and 19.1 °C. For yearlings, the calculation began on the estimated date of emergence (Fig. 4).

## Results

### *Regional coherence in water temperature*

From Fig. 5a, it is apparent that the RWTs, in addition to showing a general decrease with increasing altitude, also show a high degree of regional coherence. The existence of this coherence, coupled with the general similarity shown by the temporal structure of the RWTs (Fig. 5a) to that of the regional air temperature and to that of Hurrell's (1995) index of the NAO in winter,  $NAO_{win}$  (Fig. 5b), implies that the RWTs are exhibiting a common response to regional climatic forcing. The degree of regional coherence is shown for each river and for each season in Fig. 6a. With respect not only to RWT, but also to  $Q$ , the degree of regional coherence in all seasons is very high on the Swiss Plateau and in the foothills of the Alps ( $r^2 > 0.5$ ;  $P < 0.001$ ), but decreases as

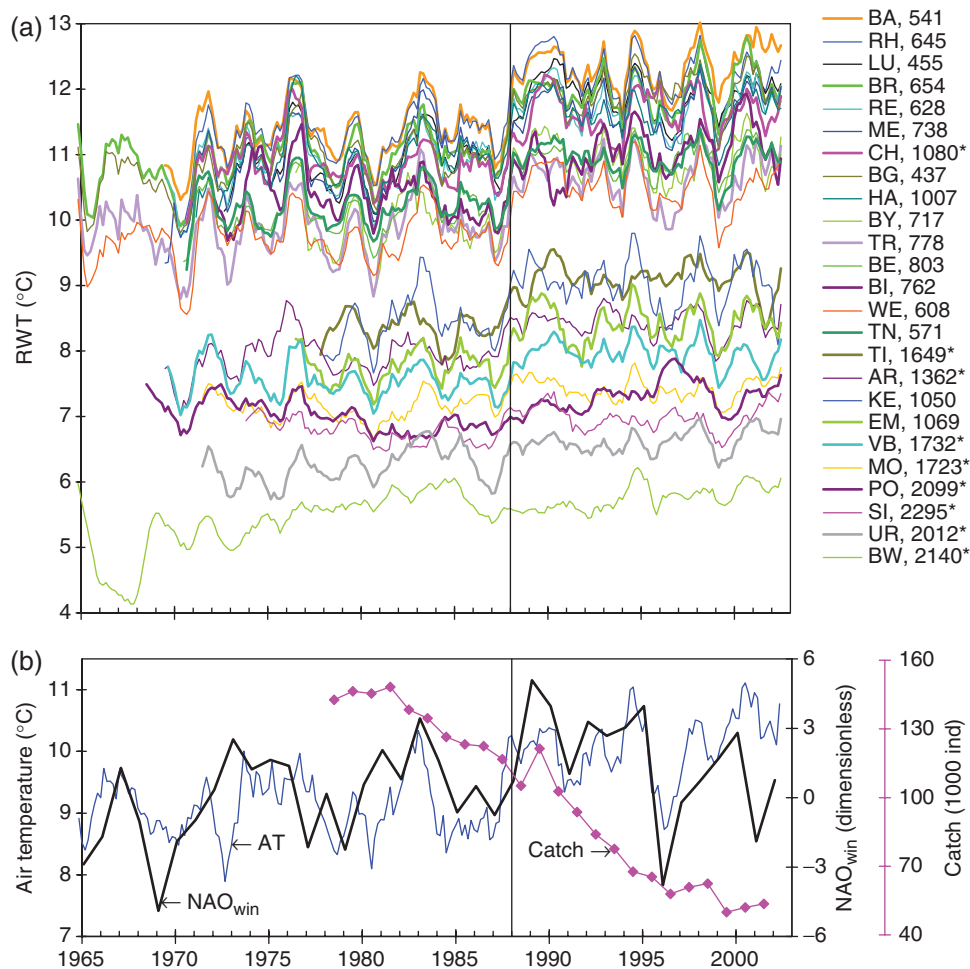


**Fig. 4** Calculation of the period of growth for brown trout for the first year (solid line a), defined as the period from the date of emergence of the fry from their gravel nest (black dot) to 31 December, and for the second and subsequent years (solid line b), defined as the period from 1 January subsequent to emergence to the following 31 December. The river water temperature (RWT) range within which growth can occur is defined as that between 3.25 and 19.1 °C (dashed horizontal lines), following Elliott & Hurley (2001). When RWT (sinusoid) lies below this range (January and February) or above this range (July and August), the period of growth is interrupted.

the mean altitude of the catchment area of the sampling station increases.

Coherence tends to be disproportionately low when glaciers or hydro-electric power stations are present in the catchment area of the sampling station, because both meltwater from glaciers and deep-water from reservoirs depress RWTs and partially decouple the streams from regional climatic forcing. Streams with no glaciers in their catchment areas show a high degree of regional coherence at all times of the year ( $P < 0.001$  in all months), whereas, in the case of streams with partially glaciated catchment areas, the coherence in summer and autumn is lowered by inflowing glacial meltwater. The catchment areas of the three sampling sites with the lowest coherence (PO, SI, BW; Table 1, for locations see Fig. 1) each contain over 14% glaciers and several hydro-power stations; the sampling site BW with the lowest coherence has the highest percentage of glacier cover in its catchment area and the highest hydro-electric power production rate.

Leaving out sites PO, SI and BW, the regional coherence of RWT at each of the 22 remaining sampling stations is significant at the  $P < 0.01$  level in all seasons. Interestingly, this is the case even for station TI, the only sampling station located south of the Alpine mountain barrier, in the Mediterranean climate regime (Fig. 6a). The Alps, therefore, reduce, but do not eliminate, regional coherence in RWT. The regional coherence of  $Q$  is comparable with that of RWT, but in the case of TI it is significant at a slightly lower level ( $P < 0.05$ ) in winter and spring.

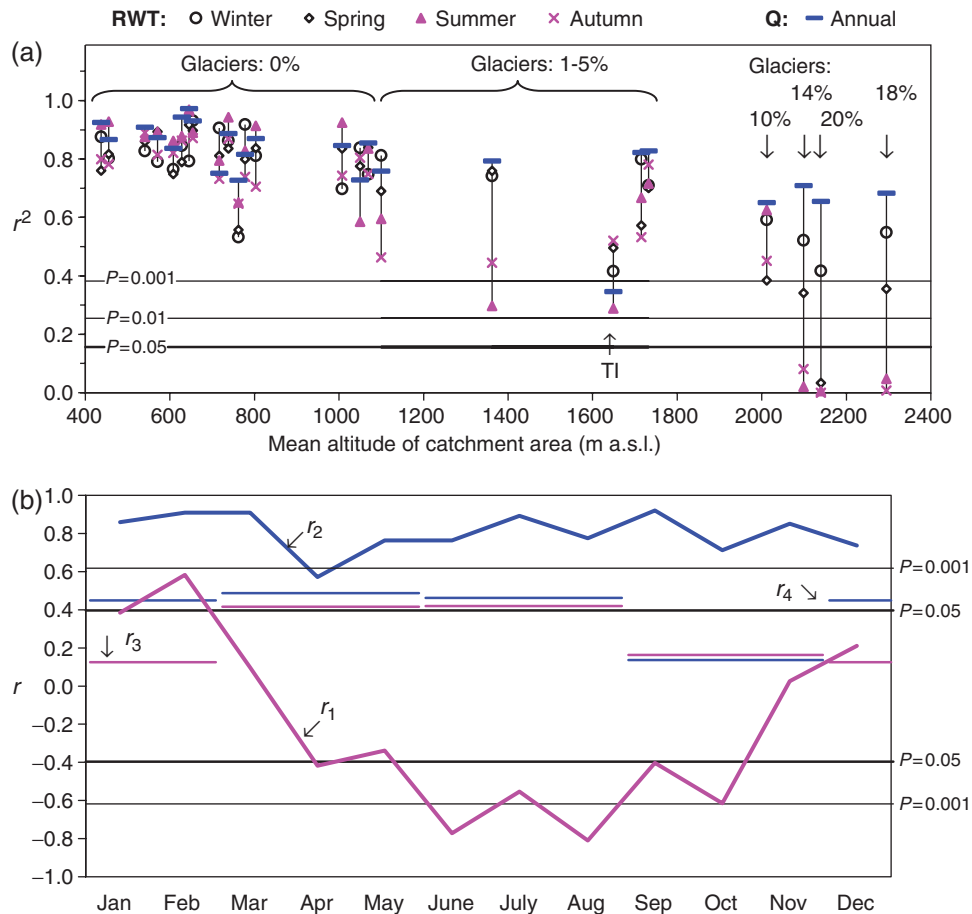


**Fig. 5** Time series. (a) River and stream water temperatures (RWT) measured in Switzerland from 1965 to 2002, 12-month running means of 1-min measurements (1969–2002) or daily measurements (1965–1968). The measuring stations are listed to the right in descending order of the mean annual water temperature in 2002 (see Table 1 for an explanation of the two-letter abbreviations and Fig. 1 for the station locations); the mean altitude of the catchment area up-river to the next lake (m.a.s.l.) is also listed. Asterisks denote the presence of glaciers in the catchment area. (b) Air temperature in Switzerland (AT, mean of measurements at Zurich and Basle), Hurrell's (1995) winter NAO index ( $NAO_{win}$ ) and the brown trout catch in the 87 river sections with uninterrupted data covering 1978–2001 (described as data set L in the text). The vertical lines indicate the abrupt 1987/1988 shift in water and air temperatures mentioned in the text.

The correlations between the mean RWT of the 25 sampling sites and both regional air temperature and  $NAO_{win}$  were also determined (Fig. 6b). The RWTs at the various sampling sites are highly correlated not only with each other, but also with the regional air temperature during most of the year. Only in April does the significance of this latter correlation dip temporarily below  $P < 0.001$  (because of the effect of snowmelt). The regional air temperature is significantly ( $P < 0.05$ ) correlated with  $NAO_{win}$  in winter, spring and (surprisingly) summer. The regional RWTs, however, exhibit a significant correlation with  $NAO_{win}$  only in spring and summer. This is firstly because RWTs cannot follow the air temperature below  $0^\circ\text{C}$  in winter,

and secondly because RWT tends to lag air temperature in its response to climatic forcing. Although the correlation of regional air temperature and RWT with  $NAO_{win}$  is significant on a seasonal basis, this is not the case for monthly data.

Of ecological importance is the seasonally dependent relationship that appears to exist between RWT and  $Q$  (Fig. 6b). In winter, the mean RWT and mean  $Q$  (of all 25 rivers) show a significant positive correlation ( $P < 0.05$ ). Thus, in winter, high  $Q$  appears to buffer cooling. There is no significant correlation in spring, but in summer an extremely high negative correlation exists ( $P < 0.001$ ) that continues, albeit more weakly, into autumn ( $P < 0.05$ ). Thus, in summer and autumn, high  $Q$



**Fig. 6** Coherent climatic influence on the water temperature and discharge measurements conducted at the 25 Swiss river and stream sampling stations of Table 1 and Fig. 1. (a) Coherence of seasonal mean water temperature (RWT) as a function of the mean altitude of the station's catchment area up-river to the next lake, computed as the proportion of variance ( $r^2$ ) shared pairwise between the RWT time series for each station and the mean of the 24 remaining RWT time series. The coherence of the annual mean discharge (Q) was computed analogously. The proportion of each station catchment area covered by glaciers is also indicated. All stations are located north of the main Alpine chain except TI, which is located south of the Alps. (b) Monthly correlation coefficient between the mean RWT of all 25 stations and the mean Q of all 25 stations ( $r_1$ ), and between the mean RWT of all 25 stations and the mean air temperature measured at Zurich and Basle ( $r_2$ ). Seasonal correlation coefficient between the mean RWT of all 25 stations and Hurrell's (1995) winter NAO index ( $r_3$ ), and between the mean air temperature measured at Zurich and Basle and Hurrell's (1995) winter NAO index ( $r_4$ ). Note the significant negative correlation between RWT and Q in summer and autumn. All time series cover the period 1978–2002 and were linearly detrended prior to computing  $r$ . Significance levels ( $P = 0.001, 0.01, 0.05$ ) are shown as horizontal lines.

appears to buffer heating. As a corollary to this, however, high RWTs tend to be associated with low Q, resulting in a scarcity of refuge from the high RWTs for brown trout populations and causing them additional stress. The most likely mechanism underlying these correlations is the direct effect of variations in Q on the heat balance of the rivers and streams concerned. However, other mechanisms, such as the dependence of the amount of precipitation stored as snow on air temperature in winter, or the dependence of evapotranspiration rates on air temperature in summer, might also play a role.

#### *Changes in stream and river water temperature*

Because RWTs respond coherently to regional climatic forcing, any changes in this forcing are also likely to elicit a coherent change in response. From Fig. 5a, it is apparent not only that RWTs at all altitudes have risen over the last few decades, but also that a coherent, abrupt increase in the late 1980s is responsible for much of this rise. Application of the Mann–Kendall test verified the presence of a monotonic trend in annual mean RWT and spring RWT (March–May) at all 25 sampling sites and in summer (June–August) at 24 of



**Table 3** Altitudinal dependence of the 1987/1988 shift in the parameters of the sinusoidal regression (Table 1), computed from linear regressions of the parameters on the mean altitude  $h_m$  of the catchment area (up-river to the next lake)

	<i>s</i>	<i>r</i> <sup>2</sup>
$\Delta T_s$ (°C) = $1.18\text{ }^\circ\text{C} - 0.00042\text{ }^\circ\text{C m}^{-1} (h_m)$	0.124	0.81
$\Delta T_{\max}$ (°C) = $1.47\text{ }^\circ\text{C} - 0.00052\text{ }^\circ\text{C m}^{-1} (h_m)$	0.212	0.69
$\Delta T_{\min}$ (°C) = $0.90\text{ }^\circ\text{C} - 0.00032\text{ }^\circ\text{C m}^{-1} (h_m)$	0.170	0.57
$\Delta M$ (d) = $-7.3\text{ d} + 0.0025\text{ d m}^{-1} (h_m)$	1.02	0.69
$\Delta E_{50}$ (d) = $-17.7\text{ d} + 0.0059\text{ d m}^{-1} (h_m)$	2.37	0.69

Each linear regression is based on 25 data points and is significant at the  $P < 0.001$  level. The standard error of the regression (*s*) and the coefficient of determination ( $r^2$ ) are also listed. The emergence date  $E_{50}$  is defined as the date by which 50% of the alevins have become emerging fry.  $E_{50}$  occurs  $\Delta E_{50}$  days earlier in Subseries II (1988–2002) than in Subseries I (1978–1987) (Table 5).

these sites. No monotonic trend in RWT was found in autumn (September–November) or winter (December–February). Application of the Pettitt change-point test (Pettitt, 1979) and the computation of cumulative *z*-scores (e.g. Assel & Robertson, 1995; Gerten & Adrian, 2000) confirmed that this trend was the result of an abrupt increase in RWT from 1987 to 1988 in the annual means (at 24 sites), in spring (at 24 sites), and in summer (at 22 sites). The same tests revealed a similar abrupt increase in regional air temperature (Fig. 5b), but no abrupt change in either *Q*, precipitation, cloud cover or air pressure, suggesting that the shift in RWT occurred primarily in response to regional air temperature forcing. The abrupt increase was detected in the daily minimum, daily mean and daily maximum air temperature measured at Zurich in winter, spring and summer, and in the annual mean. With the exception of the daily minimum air temperature in winter, the same results were obtained for Basle.

The existence of the shift allowed us to divide the RWT time series at each sampling site into two subseries, Subseries I (1978–1987) and Subseries II (1988–2002) (cf. Gerten & Adrian, 2000). For 49 of the 50 resulting subseries, no significant trend in the annual mean was found. Each subseries can therefore be considered to be stationary, allowing all further analyses to be based on a comparison of two stationary subseries separated by an abrupt shift in the mean. For each river and for each subseries, the arithmetic mean RWT computed directly from the data was identical (within measurement error) to the mean RWT obtained from the sinusoidal regression ( $T_s$  in Table 1); for the purposes of this study, the sinusoidal

regression parameters were used throughout to characterize the shift.

The magnitude of the shift ( $\Delta T_s$  in Table 1) varies between 0.1 and 1.1 °C. It decreases significantly ( $P < 0.001$ ) as the mean altitude of the catchment area increases (Fig. 7a, Table 3). The shift in mean RWT was accompanied by a simultaneous shift in seasonality, expressed as a shift in the phase *M* of the sinusoid (Fig. 7a). Figure 7b illustrates the employment of Eqn (1) to describe Subseries I and II for one particular river (BI) as an example. The mean seasonal variability of each subseries is represented by one sinusoid from January to December. The differences between the two subseries with respect to their summer maxima ( $\Delta T_{\max}$ ) and winter minima ( $\Delta T_{\min}$ ), and with respect to the timing of their annual extrema ( $\Delta M$ ), for all 25 rivers (Table 1) are presented as a function of altitude in Fig. 7a, and the equations representing their altitudinal dependence are listed in Table 3. A comparison of Subseries I with the time series of the previous 10 years of RWT data (1968–1977) revealed essentially no difference between them at any time of the year, emphasizing the uniqueness of the event that occurred in 1987/1988. In all rivers, changes in seasonality involve a shift towards an earlier spring coupled with higher summer RWTs.

#### *Optimum water temperature for brown trout*

The seasonally varying optimum RWT range  $T_{\text{opt}}$  for brown trout populations, calculated as described in the Methods section, is illustrated in Fig. 2 and the parameters defining it are listed in Table 2. The practical applicability of our definition of  $T_{\text{opt}}$  is supported by the fact that its summer maximum (20.0 °C) lies close to the upper temperature growth limit for brown trout (18.7–19.5 °C) determined in the laboratory by Elliott & Hurley (2001), and its summer mean (14.2 °C) agrees very well with the optimum growth temperature (13.1–13.9 °C) determined by the same authors. The slightly higher values found in the field compared with the laboratory values can be accounted for by the presence of cooler niches in streams (Elliott, 2000).

Here, we use this definition of  $T_{\text{opt}}$  as a benchmark to assess the adequacy of given thermal conditions in a stream or river section for brown trout populations and to predict the possible consequences of RWT changes. In Fig. 7c, d, positive and negative consequences of the 1987/1988 RWT shift are illustrated using two different rivers as examples. The river BI, which was already relatively warm before the shift, moved out of the  $T_{\text{opt}}$  range and experienced a declining fish catch. The river UR, however, which was relatively cold before the shift, moved further into the  $T_{\text{opt}}$  range and experienced an enhanced catch.

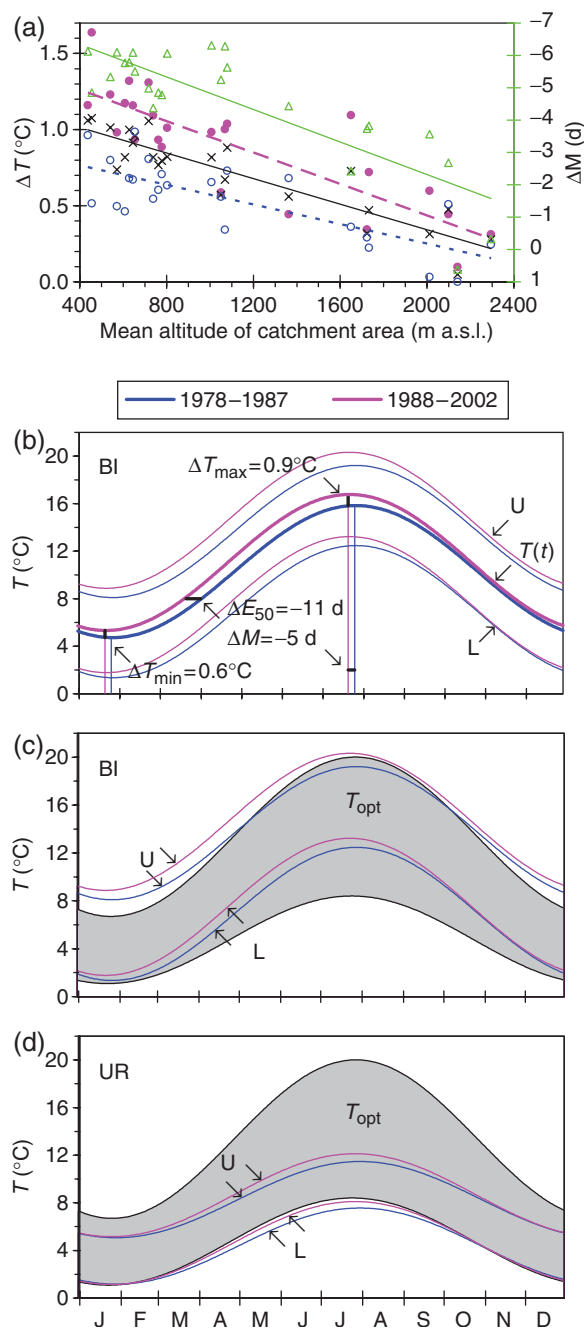
## Consequences for brown trout populations

In the 87 river sections from which data were available from 1978 to 2001 (data set L), the brown trout catch declined by 66.4% (Fig. 5b). Expecting adverse effects of an RWT increase in already warm regions (low altitudes) coupled with beneficial effects in colder regions (high altitudes), we focus here on the two most important temperature-related factors influencing the altitudinal dependence of brown trout occurrence – PKD (Gay *et al.*, 2001; Chilmonczyk *et al.*, 2002; Wahli *et al.*,

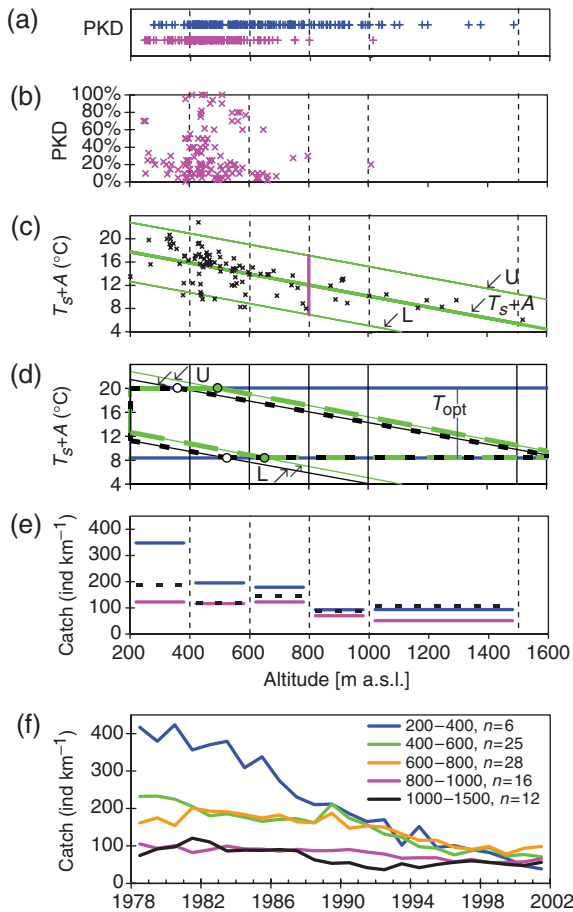
2002) and thermal habitat (Matthews & Zimmerman, 1990; Rahel *et al.*, 1996) – and relate these factors to the observed catch data.

**PKD.** In the Swiss PKD studies, when one trout at a particular site tested positive, the site was considered infected. Of the 352 sites tested, 158 were found to be infected. Although noninfected sites are found at all altitudes in the Alps, 157 of the 158 infected sites were found to lie below 800 m a.s.l. (Fig. 8a), demonstrating that the incidence of PKD is clearly higher at low (warmer) altitudes than at high (colder) altitudes. At the 121 sites at which 10 or more trout were tested, the percentage of PKD-positive individuals per site was calculated (Fig. 8b), allowing the altitudinal distribution of PKD-positive trout to be determined. Below 400 m a.s.l., 73% of the sites were infected, with a mean of 27% infected trout per site; between 400 and 600 m a.s.l., 52% of the sites were infected, with a mean of 36% infected trout per site; between 600 and 800 m a.s.l., 23% of the sites were infected, with a mean of 14% infected trout per site (Fig. 8b). Mortality as a result of PKD is not included in these results as dead fish were not counted. However, PKD mortality is suspected to be high below 400 m a.s.l. as the kinetics of the parasite multiplication are temperature dependent (Gay *et al.*, 2001).

The dependence of PKD on RWT was determined by combining the altitudinal dependence of PKD with the



**Fig. 7** Altitudinal and seasonal dependence of the shift in mean water temperature in Swiss rivers and streams from Subseries I (1978–1987) to II (1988–2002), and a comparison with the optimum water temperature range ( $T_{opt}$ ) for brown trout. (a) Mean shift in annual mean water temperature ( $\Delta T_s$ , black), annual maximum water temperature ( $\Delta T_{max}$ , red), annual minimum water temperature ( $\Delta T_{min}$ , blue) and phase ( $\Delta M$ , green) from Subseries I to II, expressed as linear functions of the mean altitude of the catchment area of the measuring station (up-river to the next lake). All linear regressions are significant at the  $P < 0.001$  level (Table 3). (b) Example of the shift in the seasonal cycle of water temperature ( $T$ ) from Subseries I to II in a representative river (BI). The seasonal cycle is expressed as a sinusoid (bold), the parameters of which were obtained by sinusoidal regression (Eqn (1)). The upper (U) and lower (L) bounds of the 95% predictive interval (PI) of the sinusoidal regression are shown as fine lines (also in (c) and (d)).  $\Delta T_{max}$ ,  $\Delta T_{min}$  and  $\Delta M$  are as in (a);  $\Delta E_{50}$  is the shift in the estimated date of emergence of brown trout fry from their gravel nest (Table 5). (c) The shift in water temperature ( $T$ ) from Subseries I to II for river BI, located close to the upper boundary of  $T_{opt}$ . After the shift, the water temperature of river BI exceeds  $T_{opt}$  by more than before the shift. (d) The shift in water temperature ( $T$ ) from Subseries I to II for river UR, located close to the lower boundary of  $T_{opt}$ . After the shift, the water temperature of river UR lies closer to  $T_{opt}$  than it did before the shift.



**Fig. 8** Altitude-dependent temperature effects on brown trout in Switzerland. (a) Incidence of temperature-dependent Proliferative Kidney Disease (PKD) as a function of altitude. Sampling sites with PKD (158 sites, red) and without PKD (194 sites, blue). (b) Percentage of PKD-infected trout per sampling site (only for sites with  $n \geq 10$  tested trout). (c) Altitudinal dependence of summer water temperature ( $T_s + A$ , from Eqn (2) with the upper (U) and lower (L) bounds of the 95% PI, also in (d)) for Subseries II (1988–2002), showing the summer water temperature range corresponding to the PKD altitude threshold at 800 m a.s.l. ( $12.1 \pm 5.1$  °C, red). (d) Shift in brown trout thermal habitat (dashed polygons) from Subseries I (1978–1987, black) to II (1988–2002, green). The polygons are defined by the intersection of  $T_{opt}$  in summer (range 8.4–20.0 °C, from Fig. 2 and Table 2; blue) with the summer water temperature range illustrated by the 95% PI of  $T_s + A$ . The altitudinal shift in habitat is given by the altitudinal shift in the points of intersection (open circles). (e) Mean observed brown trout catch for Subseries I (blue) and II (red), and the catch estimate for Subseries II (black dashed) based on the effects of PKD, thermal habitat shift and angler activity, by altitude class. (f) Time series of brown trout catch (data set L) for each altitude class, with the number of catch sections ( $n$ ) per altitude class. The locations of the altitude classes within Switzerland are illustrated in Fig. 1.

altitudinal dependence of summer RWT (Eqn (2)). In terms of summer RWT, the 800 m a.s.l. PKD threshold translates empirically to  $T_s + A = 12.1 \pm 5.1$  °C (Fig. 8c).

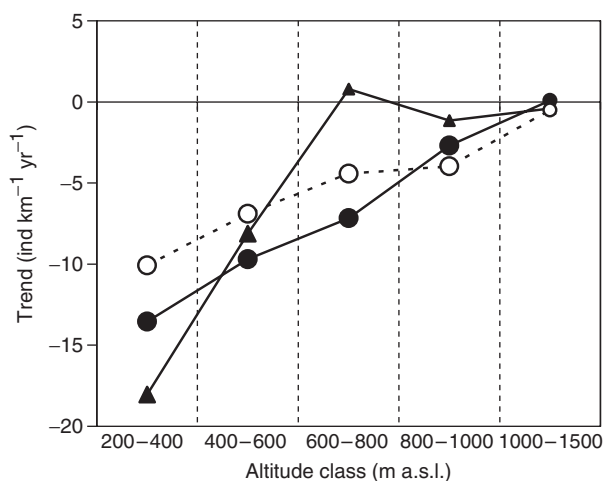
**Thermal habitat.** To quantify the possible loss or gain of thermal habitat, we combined two variables that together determine the extent of brown trout habitat in summer: viz. the band of  $T_{opt}$  in summer (8.4–20.0 °C) (Table 2, Fig. 2) and the band of altitudinally decreasing summer RWT (Fig. 8c). As a simplification we regard here only the situation in summer. For each of Subseries I and II, the polygon defined by the intersection of  $T_{opt}$  with the respective summer RWT band represents the available thermal habitat (Fig. 8d), which can be seen to decrease in extent with increasing altitude. As a result of the 1987/1988 RWT shift, this thermal habitat shifted upwards by  $\sim 130$  m, worsening the situation for brown trout at low altitudes but potentially improving it at high altitudes.

Assuming summer RWT to be normally distributed, the polygon areas can be weighted accordingly. The probability  $P_c$  that the thermal habitat was conducive to brown trout abundance was computed as described in the Methods section for the five altitude classes 200–400, 400–600, 600–800, 800–1000 and 1000–1500 m a.s.l. (for the locations of the altitude classes see Fig. 1). For a given altitude class, the change in  $P_c$  computed before and after the 1987/1988 shift, multiplied by the total length  $L_c$  of the streams and rivers in that class, yields an estimate of the change in habitat that resulted from the 1987/1988 shift. The results (Table 4) show that a net loss in potential thermal habitat resulted below 600 m a.s.l., whereas a net gain resulted above 600 m a.s.l.

**Catch data.** The catch data of data sets L and S were binned into the same five altitude classes. Only set L, which covers Subseries I and most of Subseries II, is suitable for comparison with the thermal habitat calculated in this study (Fig. 8e, f), but set S covers most of Subseries II. Both data sets show very clearly, in terms of both linear trend (Fig. 9) and percentage decline, that the decline in catch diminishes with increasing altitude, supporting the hypothesis of an upward shift in thermal habitat. Focusing on the possible consequences of the 1987/1988 shift, Fig. 9 shows that prior to the shift (first part of data set L) no significant decline occurred above 600 m a.s.l., implying that the population there was stationary. After the shift (second part of data set L and the whole of data set S), the population was stationary only above 1000 m a.s.l. Taking into account that equilibration of the ecosystems after the 1987/1988 shift may well have lasted several years, these results

**Table 4** Change in extent of thermal habitat ( $P_cL_c$ ) per altitude class from Subseries I (1978–1987) to II (1988–2002). The gain or loss is also expressed as a percentage of the thermal habitat in 1978–1987. See Fig. 1 for the locations of the altitude classes listed

Altitude class (m a.s.l.)	All rivers (km)	$P_cL_c$	$P_cL_c$	$\Delta P_cL_c$	
		(1978–1987) (km)	(1988–2002) (km)	(km)	(%)
200–400	2216	2115	1968	–147	–6.9
400–600	12 221	11 868	11 827	–41	–0.3
600–800	8477	7713	8119	406	5.3
800–1000	7164	5335	6102	767	14.4
1000–1500	13 246	4118	5586	1468	35.7
200–1500	43 325	31 158	33 626	2468	7.9

**Fig. 9** Long-term change in brown trout catch before and after the 1987/1988 shift as a function of altitude. Black triangles: linear trend from 1978 to 1987, based on data set L (87 stations). Black circles: linear trend from 1988 to 2001, also based on data set L. White circles: linear trend from 1989 to 2001, based on data set S (254 stations). Large symbols: trends significant at the  $P < 0.05$  level. Small symbols: trends not significant at the  $P < 0.05$  level. The altitude classes given are the same as in Fig. 8; for their locations within Switzerland see Fig. 1.

also agree with the hypothesis of an upward shift in thermal habitat.

*Thermally related factors affecting the brown trout catch.* The effects of PKD and thermal habitat shift on the brown trout populations within each altitude class were estimated quantitatively from the results illustrated in Fig. 8b and Table 4. Both population and catch are additionally affected by angler activity, which declined by 20% from 1980 to 2000 (Mosler *et al.*, 2002). Taking all three factors into account, the brown trout catch in the three classes covering the range 400–1000 m a.s.l. can be explained very well (Fig. 8e). In the lowest and the highest altitude classes, however,

discrepancies exist. Below 400 m a.s.l., at the warm boundary of the thermal habitat, the most severe catch decline is likely to result from enhanced PKD mortality at high RWT exacerbated by the extremely steep reduction in the ratio of growth to food intake that occurs at RWTs exceeding 13 °C (Elliott & Hurley, 2001). Above 1000 m a.s.l., additional factors, such as competition between individuals because of overstocking (Milner *et al.*, 2003) and lack of stream connectivity (Peter, 1998), may play a comparatively more important role.

## Discussion

### *Coherent response to climatic forcing*

Within the time-window 1978–2002, the detrended time series of monthly mean RWT exhibited a high degree of coherence, as did the detrended time series of monthly mean  $Q$ . Correlations were also significant pairwise between RWT and air temperature, and in part with  $NAO_{win}$ . This coherent response of streams and rivers to climatic forcing, which enormously simplifies the investigation of the effects of large-scale climatic forcing on riverine fish habitats because of the generalization it makes possible, is perhaps surprising in a heterogeneous mountainous area exceeding 40 000 km<sup>2</sup> with over 4000 m altitude difference between the highest catchment area and the lowest river station. In fact, RWTs behave even more coherently than the surface water temperatures of lakes (Livingstone & Dokulil, 2001), because the greater degree of turbulence in rivers accelerates water temperature equilibration.

### *Warmer summers and earlier springs after 1987/1988*

After a long period of stationarity previous to 1987, RWTs in winter, spring and summer underwent a significant, simultaneous, abrupt increase to a higher mean level, at which they have since remained. As



**Table 5** Calculated emergence date ( $E_{50}$ ) of brown trout (assuming the fertilization date to be 15 November) and period of growth (number of days with water temperature between 3.25 and 19.1 °C; see Fig. 4) for each river for Subseries I (1978–1987) and II (1988–2002), arranged in increasing order of the mean altitude of the catchment area  $h_m$  (up-river to the next large lake). The significance levels associated with the linear regression of each dependent variable on the mean altitude of the catchment area ( $P < 0.05$ ,  $P < 0.01$ ,  $P < 0.001$ ) are shown for each result column (NS, not significant at the  $P < 0.05$  level)

$h_m$	River or stream name	Subseries (I or II)		$P <$	Emergence date ( $E_{50}$ )		Mean RWT from fertilization to emergence		Difference		No. of days of growth in the first year		Difference		No. of days of growth in the second and subsequent years		Difference	
		I	II		I	II	I	II	I	II	I	II	I	II	I	II	I	II
		0.01	0.001		0.001	0.001	0.001	0.001	0.01	0.001	0.001	0.001	0.05	NS	0.05	NS	0.05	NS
	Mean at low altitudes (<700 m a.s.l.)	10 Apr	27 Mar		-14	5.8	6.4	0.6	261	244	-16	355	331	-24				
	Mean at high altitudes (>1200 m a.s.l.)	5 May	28 Apr		-7	4.9	5.1	0.2	240	247	7	359	360	1				
437	Aare Brügg-Ägerten (BG)	13 Apr	26 Mar		-19	5.6	6.4	0.8	261	244	-17	365	329	-36				
455	Reuss Luzern (LU)	6 Apr	25 Mar		-13	5.9	6.5	0.5	268	252	-16	365	336	-29				
541	Limmat Baden (BA)	13 Apr	28 Mar		-16	5.7	6.3	0.7	233	207	-26	336	294	-42				
571	Aare Thun (TN)	1 Apr	21 Mar		-11	6.1	6.6	0.5	273	284	11	365	365	0				
608	Linth Weesen (WE)	7 Apr	26 Mar		-12	5.9	6.4	0.5	268	279	12	365	365	0				
628	Rhein Rekingen (RE)	22 Apr	8 Apr		-14	5.3	5.9	0.5	253	216	-37	313	314	1				
645	Rhein Rheinfelden (RH)	7 Apr	24 Mar		-14	5.9	6.5	0.6	268	229	-39	365	313	-52				
654	Aare Brügg (BR)	14 Apr	27 Mar		-17	5.6	6.3	0.7	261	244	-16	365	331	-34				
717	Broye Payerne (BY)	5 May	20 Apr		-15	4.9	5.4	0.5	234	255	20	304	331	27				
738	Reuss Mellingen (ME)	15 Apr	4 Apr		-11	5.6	6.0	0.4	259	235	-24	365	330	-35				
762	Birs Münchenstein (BI)	3 Apr	23 Mar		-11	6.1	6.6	0.5	272	283	11	365	365	0				
778	Thur Andelfingen (TR)	3 May	20 Apr		-12	5.0	5.4	0.4	240	254	14	310	334	24				
803	Aare Bern (BE)	8 Apr	26 Mar		-14	5.8	6.4	0.6	266	280	14	365	365	0				
1007	Aare Hagneck (HA)	27 Mar	14 Mar		-13	6.3	6.9	0.6	279	291	13	365	365	0				
1050	Kleine Emme Littau (KE)	25 May	14 May		-11	4.3	4.6	0.3	203	216	13	276	290	14				
1069	Emme Emmenmatt (EM)	23 May	13 May		-11	4.4	4.7	0.3	215	226	12	290	304	14				
1080	Rhône Chancy (CH)	3 Apr	20 Mar		-14	6.1	6.7	0.6	272	286	14	365	365	0				
1362	Arve Genève (AR)	26 Apr	13 Apr		-13	5.2	5.6	0.5	249	261	13	365	365	0				
1649	Ticino Riazзино (TI)	20 Apr	10 Apr		-10	5.4	5.8	0.4	254	264	10	365	365	0				
1723	Linth Mollis (MO)	4 May	26 Apr		-7	4.9	5.2	0.2	241	248	7	365	365	0				
1732	Rhein vor Bodensee (VB)	7 May	1 May		-7	4.8	5.0	0.2	237	244	7	365	365	0				
2012	Reuss Seedorf (UR)	21 May	17 May		-4	4.4	4.5	0.1	223	228	4	320	326	6				
2099	Rhône Porte du Scex (PO)	3 May	23 Apr		-10	5.0	5.3	0.3	242	251	10	365	365	0				
2140	Aare Brienzwiler (BW)	18 May	18 May		0	4.5	4.5	0.0	227	227	0	365	365	0				
2295	Rhône Sion (SI)	29 Apr	25 Apr		-5	5.1	5.2	0.1	245	250	5	365	365	0				

RWT, river or stream water temperature.

RWTs in autumn did not undergo this increase, the result was an 'earlier spring' in addition to the higher RWTs in summer. These last 15 years of stationary, high RWTs in probably the warmest decade of the last millennium (Folland *et al.*, 2001) are presumably associated with the unusual duration of the present positive phase of the NAO (Hurrell *et al.*, 2003), possibly stabilized by global warming (Paeth *et al.*, 1999). Other studies confirm that the unique climatic event of 1987/1988 was not confined to Swiss rivers and streams, but also manifested itself, for instance, in abrupt changes in lake phytoplankton in northern Germany (Gerten & Adrian, 2000) and Switzerland (Anneville *et al.*, 2004). An analysis of terrestrial plant phenology in Switzerland also indicates a shift towards an earlier spring after 1988 (Studer *et al.*, in press).

The 1987/1988 shifts in both magnitude and phase of RWT are significantly less pronounced at higher than at lower altitudes, because an increase in altitude is accompanied by a decrease in air temperature and an increase in the effect of meltwater on RWT. Perhaps unexpectedly, in view of the emphasis that has been put on the effects of recent winter warming in Europe, the RWT shift in summer ( $\Delta T_{\max}$ ) is actually slightly higher than that in winter ( $\Delta T_{\min}$ ) (Fig. 7a).

#### *Shift of brown trout habitat up-river*

Although fish catch depends on several variables, a significant part of the reported drastic decline in the Swiss brown trout catch reflects an actual population decline, as opposed, for instance, to a change in angler behaviour (Mosler *et al.*, 2002). Brown trout populations on the Swiss Plateau live at the upper limit of their temperature tolerance range, so that even modest warming leads to additional stress, resulting in an advantage for competing species such as grayling. Warming results in potential brown trout habitats being pushed up-river to cooler altitudes. In mountain regions, however, the upward migration of fish is often impeded by numerous natural and artificial physical barriers. In Swiss streams on average, approximately 1–2 barriers with a vertical drop of 15 cm or more exist per 100 m stream reach (Peter, 1998), many of which present insurmountable obstacles to the upstream movement of fish, thus severely limiting their ability to seek refuge upstream from adverse environmental conditions of any kind. Thus, a climatically driven upward habitat shift in fact implies habitat reduction, indicating the likelihood of an overall population decrease (which might be combated to some extent by artificial stocking).

Based on the 87 catch time series of data set L, the brown trout catch in Switzerland decreased from a mean of 907 ind km<sup>-1</sup> before the 1987/1988 shift to a

mean of 484 ind km<sup>-1</sup> afterwards. Because of the temperature effects described above, we would expect an altitudinal dependence to manifest itself in the catch data, with the greatest decreases occurring at lower altitudes, and possibly even increases at higher altitudes (although the effect of the physical barriers makes this unlikely). Although our data show catch reductions at all altitudes, decreases at lower altitudes substantially exceeded those at higher altitudes, with the greatest reduction occurring within the 200–400 m a.s.l. altitude class (Figs 8e, f and 9). Thus, it is likely that the increase in RWT exacerbated the decline in catch at low altitudes, while mitigating it at higher altitudes. Along with the upward shift of the brown trout thermal habitat, mortality because of PKD is certain to play a dominant role in translating the RWT increase into a decrease in catch by amplifying the negative effects of increasing RWT, particularly at the lower boundary of the habitat.

The probable establishment of PKD at the end of the 1970s, and its increased incidence thereafter (Wahli *et al.*, 2002), may also provide an explanation for the fact that the brown trout catch began to decrease in the early 1980s, before the abrupt increase in RWT could have affected fish populations. This early decrease in the brown trout catch (Fig. 5b) occurred only in the warmer rivers and streams below 400 m a.s.l., where conditions for the transmission of PKD would have been most suitable, but was weak or nonexistent in cooler, higher-altitude streams (Fig. 8f). Other factors possibly contributing to this early decrease in the brown trout catch at low altitudes include anthropogenic alterations to the physical and chemical characteristics of the low-altitude rivers and streams that are most immediately influenced by human settlements, and the effect of the early decline in angler activity.

In North America, it is thought that an increase in RWT of 3–4 °C in the Great Plains would probably extinguish several fish species because migration to the north is blocked (Matthews & Zimmerman, 1990). In the Rocky Mountains, an increase of 1 °C in mean July air temperature would result in a loss of thermal habitat for brown trout (and other fish species) equivalent to 7.5% of total river length, based on an assumed upper tolerance limit for air temperature of 22 °C (Rahel *et al.*, 1996). This present study has attempted to present a more realistic picture of the temperature dependence of a fish species by basing it on ambient RWT rather than air temperature and by establishing an altitudinally dependent and seasonally varying optimum RWT range ( $T_{\text{opt}}$ ) that characterizes the thermal habitat of the fish by including both a lower (warm) and an upper (cold) boundary. The upper boundary of this thermal habitat is extended upwards by climatic warming,

implying a potential habitat gain at high altitudes that might counterbalance to some extent the loss of thermal habitat at low altitudes. The comparison of available catch data with the calculated thermal habitat provides partial support for these expectations.

#### *Effects on biological timing*

Any shift in the seasonal variability of RWT is likely to be crucial for the survival of fish populations, both because of the possibility of disturbance during especially sensitive life stages and because of its effect on the general ecological balance. The abrupt shift in the phase *M* of RWT from Subseries I to II (Fig. 7a, b and Table 3) implies an earlier onset of spring in terms of RWT, but in terms of brown trout development it also implies that brown trout fry will emerge earlier from their gravel nest. The estimated date of emergence of the fry ( $E_{50}$ ) was calculated for each river and each year. For Subseries I, fry in rivers or streams at low altitudes (mean altitude of the catchment area <700 m a.s.l.) were predicted to emerge on average on 10 April, and for Subseries II 14 days earlier. At high altitudes (mean altitude >1200 m a.s.l.), the equivalent times were 5 May and 7 days earlier, respectively (Table 5). Thus, for brown trout in Switzerland, this suggests a regional advance in the timing of spring by 2.8–5.6 d per decade. Phenological data from many species indicate that spring is advancing at a global mean rate of 2.3 d per decade (Parmesan & Yohe, 2003). Therefore, as might be expected from the fact that regional warming rates in Switzerland greatly exceed global warming rates (Beniston *et al.*, 1994; Lister *et al.*, 1998), our data suggest that the regional rate of spring advancement in Switzerland is also much higher than the global rate.

Assuming RWT growth limits of 3.25 and 19.1 °C (Elliott & Hurley, 2001), at low altitudes the estimated time available for growth decreased from Subseries I to II by 24 days on average, whereas at high altitudes there was essentially no difference. Although emergence occurs earlier in the year, the estimated time available for the growth of yearlings decreased by 16 days at low altitudes, because there RWT exceeds the upper limit; at high altitudes however, it increased by 7 days (Table 5). In addition to the effects on growth, increased RWTs increase the probability of lethal RWTs (>24.7 °C) being attained.

Although the observed annual increase in RWT lies well within the range of natural fluctuation to which the fish are adapted, it does result in a systematic shift in habitat conditions, thus exerting a selective pressure towards more tolerant individuals (or even species) and disturbing established balances in the ecosystems affected. Additionally, temporal effects, such as the accel-

eration of egg, alevin and fry development, may result in mismatching problems that are more dramatic than the RWT increase itself (Visser & Holleman, 2001).

#### Conclusions

Based on 25 years of high-resolution data, we have shown that the temperatures of rivers and streams in Switzerland respond coherently to regional climatic forcing at all altitudes. During the last quarter of the 20th century, substantial stream warming occurred, most of which can be attributed to an abrupt increase in temperature located fairly precisely at 1987/1988 and which is possibly associated with a shift in the NAO to its present generally highly positive phase. Based on calculations of the seasonally varying thermal habitat available to brown trout populations at different altitudes, we offer a plausible explanation for the well-documented long-term decline in the catch of brown trout. A reduction in thermal habitat and an increase in the frequency of occurrence of PKD result in population decline at low altitudes. At higher altitudes, the presence of physical barriers to longitudinal migration prevents the trout from exploiting the potential thermal habitat that would otherwise become available to them upstream.

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