Vital rates, source-sink dynamics, and type of competition in congeneric species

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Table S1. Topological characteristics of Upper Volaja. Stream altitude is between 725 (Sector 4) and 683 (Sector 1) m.

Sector	Length (m)	Area (m^2)	Slope	Number of pools	Pool area (m2)
1	44.52	136.57	13%	5	65.59
2	78.53	254.59	17%	5	88.55
3	47.72	134.57	16%	3	43.46
4	93.87	220.54	15%	4	60.74
Total	264.64	746.27	15% (avg)	17	258.34

Table S2. Symbols and abbreviations used in the main text.

Symbol or Abbreviation	*Explanation*
GDDs	Growing degree-days
D_{0+}	Density of age-0+ fish
$D_{>0+}$	Density of fish older than 0+
L_{0+}, $\bar{L}_{0+}$	Length and mean length of fish at age 0+
vBGF	Von Bertalanffy growth function
L_{∞}	Asymptotic size in the vBGF
k	Growth coefficient in the vBGF
t_0	Age at which size is equal to 0 in the vBGF
u	Individual random effect for vBGF's k
v	Individual random effect for vBGF's L_{∞}
σ_u	Standard deviation of the distribution of individual random effect for vBGF's k
σ_v	Standard deviation of the distribution of individual random effect for vBGF's L_{∞}

x_{ij}	Continuous predictor of vBGF's parameters for individual *i* in group *j*
ε_{ij}	Error term of the vBGF for individual *i* in group *j*
σ_{ε}^{2}	Variance of the error term for the vBGF
α, β	Categorical predictors of vBGF's parameters for individual *i* in group *j*
$D_{>0+,born}$	Density of fish older than 0+ when the fish/cohort was born
$D_{>0+,m}$	Mean of $D_{>0+}$ at year *t* in September and *t*+1 in June
Cohort	Year-class
Data_{W}	Whole dataset
Data_{S}	Dataset including (a) trout that were sampled once at age 1+, and (b) trout that were sampled multiple times in the same sector and were sampled for the first time at age 1+
Data_{D}	Dataset including all cohorts for which density and water temperature in the first year of life are known
G_d	Daily growth in size
Season	Sampling season: June-September (*Summer*), September-June (*Winter*)
$D_{s,t}$	Density of spawners at yeat *t*
R_t	Recruitment (density of age-0+ in September) at year *t*
GAM	Generalized Additive Model

GAMM	Generalized Additive Mixed-Model
$\bar{T}$	Mean temperature during a *Season*
Time	Sampling occasion in the model of survival
ϕ	Apparent survival
p	Probability of capture in the model of survival
CJS	Cormack-Jolly-Seber model of survival
σ_{0+}	Apparent survival of fish from age 0+ to age 1+

Table S3. Estimated number of fish (N_est±Std.est) alive in each *Year* and *Season* for fish aged 0+ (0) or 1+ (1) and older. LCI and UCI are 95% CI for number (N_) and density (D_) of fish. p.capt and std.p.capt are point estimate and standard error of probability of capture at a single pass. There was complete recruitment failure in 2014. Density is in fish ha^{-1}.

Year	Sampling	N_est	Std.est	p.capt	Std.p.capt	N_LCI	NUCI	Dest	DLCI	DUCI	Age
2004	Sept	59	0.70	0.92	0.04	57.62	60.38	790.60	772.11	809.09	0
2005	Sept	60	1.00	0.90	0.05	58.03	61.97	804.00	777.64	830.36	0
2006	Sept	30	0.39	0.94	0.05	29.24	30.76	402.00	391.79	412.21	0
2007	Sept	38	0.91	0.88	0.06	36.21	39.79	509.20	485.26	533.14	0
2008	Sept	33	2.96	0.72	0.12	27.19	38.81	442.20	364.41	519.99	0
2009	Sept	15	0.27	0.94	0.07	14.46	15.54	201.00	193.78	208.22	0
2010	Sept	8	0.87	0.80	0.19	6.30	9.70	107.20	84.46	129.94	0
2011	Sept	17	1.18	0.81	0.13	14.69	19.31	227.80	196.90	258.70	0
2012	Sept	53	1.08	0.88	0.05	50.88	55.12	710.20	681.81	738.59	0
2013	Sept	24	1.89	0.77	0.13	20.29	27.71	321.60	271.93	371.27	0
2014	Sept	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0
2015	Sept	65	1.44	0.86	0.05	62.17	67.83	871.00	833.10	908.90	0
2004	Sept	548	2.86	0.90	0.01	542.40	553.60	7343.20	7268.13	7418.27	1
2005	June	468	2.63	0.90	0.02	462.85	473.15	6271.20	6202.23	6340.17	1
2005	Sept	503	1.22	0.95	0.01	500.61	505.39	6740.20	6708.15	6772.25	1
2006	June	388	2.19	0.91	0.02	383.71	392.29	5199.20	5141.73	5256.67	1
2006	Sept	374	1.38	0.94	0.01	371.29	376.71	5011.60	4975.35	5047.85	1

2007	June	390	1.76	0.92	0.02	386.55	393.45	5226.00	5179.83	5272.17	1
2007	Sept	391	1.46	0.94	0.01	388.14	393.86	5239.40	5201.04	5277.76	1
2008	June	413	2.71	0.89	0.02	407.69	418.31	5534.20	5463.01	5605.39	1
2008	Sept	422	1.91	0.92	0.01	418.26	425.74	5654.80	5604.75	5704.85	1
2009	June	335	3.39	0.86	0.02	328.35	341.65	4489.00	4399.96	4578.04	1
2009	Sept	366	2.14	0.91	0.02	361.81	370.19	4904.40	4848.21	4960.59	1
2010	June	400	1.44	0.94	0.01	397.17	402.83	5360.00	5322.13	5397.87	1
2010	Sept	337	2.18	0.90	0.02	332.72	341.28	4515.80	4458.51	4573.09	1
2011	June	323	2.31	0.90	0.02	318.48	327.52	4328.20	4267.64	4388.76	1
2011	Sept	371	1.81	0.92	0.02	367.45	374.55	4971.40	4923.88	5018.92	1
2012	June	326	2.23	0.90	0.02	321.64	330.36	4368.40	4309.95	4426.85	1
2012	Sept	357	1.79	0.92	0.02	353.50	360.50	4783.80	4736.84	4830.76	1
2013	June	379	2.22	0.91	0.02	374.65	383.35	5078.60	5020.32	5136.88	1
2013	Sept	338	2.24	0.90	0.02	333.60	342.40	4529.20	4470.27	4588.13	1
2014	June	419	2.51	0.90	0.02	414.08	423.92	5614.60	5548.74	5680.46	1
2014	Sept	435	2.33	0.91	0.02	430.43	439.57	5829.00	5767.79	5890.21	1
2015	June	331	0.98	0.95	0.01	329.08	332.92	4435.40	4409.63	4461.17	1
2015	Sept	327	1.88	0.91	0.02	323.31	330.69	4381.80	4332.37	4431.23	1

Table S4. Proportion of "late incomers" present in the population each year in September. We applied the same ratio of "late incomers" to total number of fish found for cohorts born after the start of sampling to cohorts born before the start of sampling (from 2000 to 2003). Early.inc = "early incomers", i.e. fish that were either born in Upper Volaja or came into Upper Volaja before age 1+ in September. FP_Coh = number of fish from cohorts born before the start of sampling. N.tot = total number of fish aged 1+ or older sampled each Septebmer. Late.inc = "late incomers", i.e. fish that were born in AW and came into Upper Volaja when 1+ in September or older. Prop.late.inc = proportion of "late incomers" in Upper Volaja each year in September.

Year	Early.inc	FP_Coh	N.tot	Late.inc	Prop.late.inc
2010	198	13	334	128	0.38
2011	216	8	369	148	0.40
2012	208	6	355	143	0.40
2013	226	5	335	106	0.32
2014	293	6	432	135	0.31
2015	225	1	325	99	0.30

Table S5. Predictors of vBGF's parameters L_∞ and k (*Constant* = no predictors except for individual random effects), number of parameters, and AIC of the tested growth models (dataset $Data_W$; only September data).

L_∞	*k*	*npar*	*AIC*
Cohort	*Cohort*	*32*	40608.0
Constant	*Cohort*	19	40736.2
Cohort	*Constant*	19	40831.2
Constant	*Constant*	6	41687.4

Table S6. Cohort-specific point estimates and 95% CI of vBGF's parameters, number of data points (DP), predicted (P_L) and observed (O_L) mean size at age 1+ to 3+. NA means data not available. Avg is for parameters, predictions for the model with no predictors (and observations for all brown trout in the dataset).

Cohort	Linf	Linf _lcl	Linf _ucl	k	k_lcl	k_ucl	t_0	t_0_lcl	t_0_ucl	DP	P_L1	P_L2	P_L3	O_L1	O_L2	O_L3
C00	279.46	241.27	317.65	0.51	0.05	0.98	-1.61	-1.72	-1.51	10	206.37	235.71	253.27	NA	NA	NA
C01	246.44	234.25	258.63	0.60	0.43	0.78	-1.61	-1.72	-1.51	58	195.73	218.74	231.32	NA	NA	232.79
C02	228.55	223.00	234.10	0.50	0.45	0.54	-1.61	-1.72	-1.51	382	165.91	190.37	205.29	NA	191.17	203.45
C03	240.28	234.26	246.30	0.33	0.30	0.35	-1.61	-1.72	-1.51	721	137.80	166.31	186.89	137.56	164.39	184.74
C04	227.04	221.41	232.67	0.34	0.32	0.37	-1.61	-1.72	-1.51	501	134.15	161.05	180.17	131.20	162.88	183.16
C05	227.11	221.55	232.67	0.33	0.30	0.35	-1.61	-1.72	-1.51	548	130.35	157.30	176.75	130.10	158.45	177.78
C06	229.34	223.62	235.06	0.32	0.30	0.34	-1.61	-1.72	-1.51	461	129.53	156.74	176.53	130.54	155.82	174.78
C07	226.24	219.47	233.01	0.32	0.29	0.34	-1.61	-1.72	-1.51	322	127.98	154.83	174.34	126.97	156.38	172.34
C08	225.68	218.99	232.37	0.32	0.30	0.35	-1.61	-1.72	-1.51	353	128.61	155.40	174.79	128.95	153.12	172.64
C09	236.13	228.22	244.04	0.29	0.27	0.32	-1.61	-1.72	-1.51	336	126.87	154.78	175.55	125.12	155.80	176.32
C10	252.69	240.26	265.12	0.27	0.24	0.30	-1.61	-1.72	-1.51	258	126.86	156.32	178.89	126.35	154.69	178.09
C11	244.56	229.16	259.96	0.30	0.26	0.34	-1.61	-1.72	-1.51	153	132.05	160.97	182.45	128.38	160.89	185.60
C12	314.89	282.84	346.94	0.21	0.17	0.24	-1.61	-1.72	-1.51	277	130.89	165.08	192.92	128.87	168.43	192.29
C13	258.97	235.52	282.42	0.29	0.24	0.34	-1.61	-1.72	-1.51	210	137.58	168.13	191.00	136.31	170.46	NA
Avg	224.87	222.21	227.53	0.41	0.39	0.43	-1.25	-1.34	-1.17	4590	134.99	165.06	185.07	131.98	165.91	184.49

Table S7. Sector-specific point estimates and 95% CI of vBGF's parameters, number of data points (DP), predicted (P_L) and observed (O_L) mean size at age 1+ to 3+.

Sector	Linf	Linf _lcl	Linf _ucl	k	k_lcl	k_ucl	t_0	t_0_lcl	t_0_ucl	DP	P_L1	P_L2	P_L3	O_L1	O_L2	O_L3
1	213.29	204.93	221.65	0.41	0.37	0.46	-1.27	-1.42	-1.11	328	129.69	158.00	176.73	130.53	157.59	175.70
2	213.10	205.55	220.65	0.42	0.37	0.47	-1.27	-1.42	-1.11	611	130.81	159.03	177.58	131.03	158.67	177.91
3	220.14	209.58	230.70	0.40	0.35	0.46	-1.27	-1.42	-1.11	322	132.09	161.38	180.93	132.51	161.42	181.00
4	230.64	220.38	240.90	0.39	0.34	0.44	-1.27	-1.42	-1.11	378	134.82	165.62	186.52	134.99	166.85	184.58

Table S8. Recapture models for the "global model" of probability of survival ϕ(*Cohort * Season*). The best recapture model was *p*(*Time*).

Model	npar	AIC	ΔAIC	weight	neg2lnl
ϕ(*Cohort * Season*) *p* (~*Time*)	52	13520.62	0	0.74	13416.62
ϕ (*Cohort * Season*) *p* (~*Season* + *Time*)	53	13522.74	2.12	0.26	13416.74
ϕ (*Cohort * Season*) *p* (~*Season * Time*)	63	13542.74	22.12	1.17E-05	13416.74
ϕ (*Cohort * Season*) *p* (~*Season*)	32	13594.99	74.36	5.28E-17	13530.99
ϕ (*Cohort * Season*) *p* (~bs(*Age*))	34	13597.31	76.68	1.65E-17	13529.31
ϕ (*Cohort * Season*) *p* (~*Age*)	32	13600.42	79.79	3.50E-18	13536.41
ϕ (*Cohort * Season*) *p* (~1)	31	13605.27	84.65	3.08E-19	13543.27
ϕ (*Cohort * Season*) *p* (~*Cohort*)	45	13608.68	88.06	5.60E-20	13518.68

Figure S1

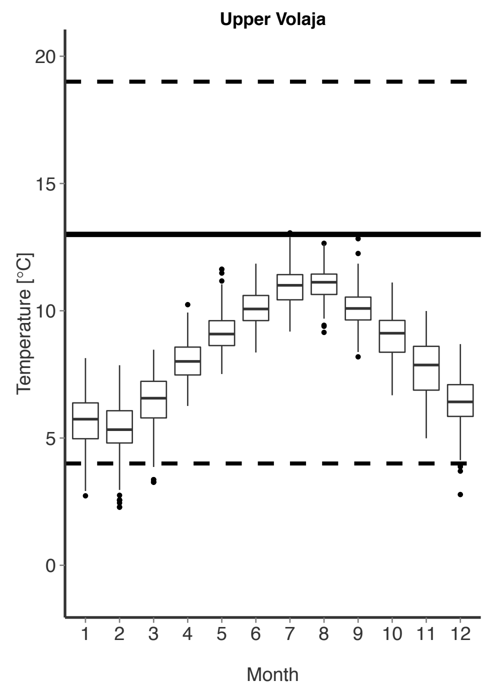

Fig. S1. Boxplots of water temperature recorded (by month) in Upper Volaja between 2004 and 2014. Dashed lines enclose the range of temperatures allowing growth and the thick solid line identifies the temperature for maximum growth according to Elliott et al. (1995).

Figure S2

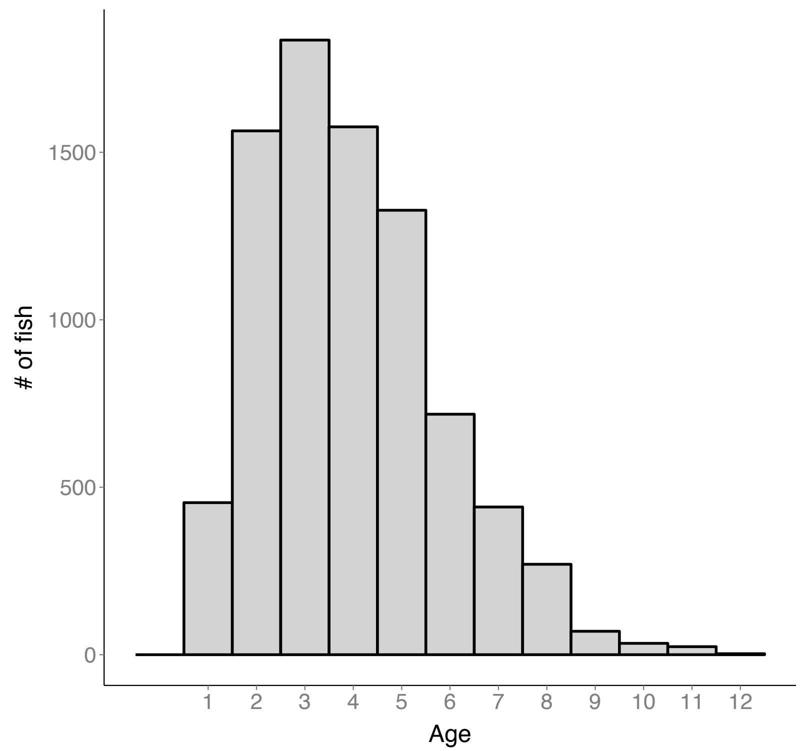

Figure S2. Age at (apparent) death (i.e. maximum age at which the fish was sampled) for tagged brown trout in Upper Volaja. Most fish did not survive past 6 years old.

Figure S3

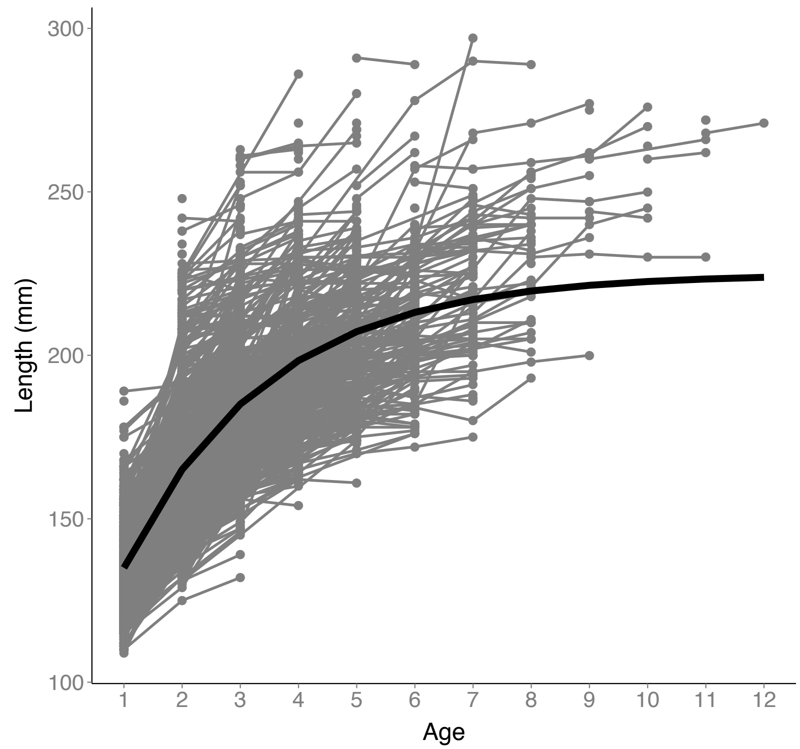

Figure S3. Individual growth trajectories of brown trout and prediction of the growth model of growth trajectory of the average fish in Eqs. (2.2) and (2.3) in the main text (see Avg in Table S6).

Figure S4

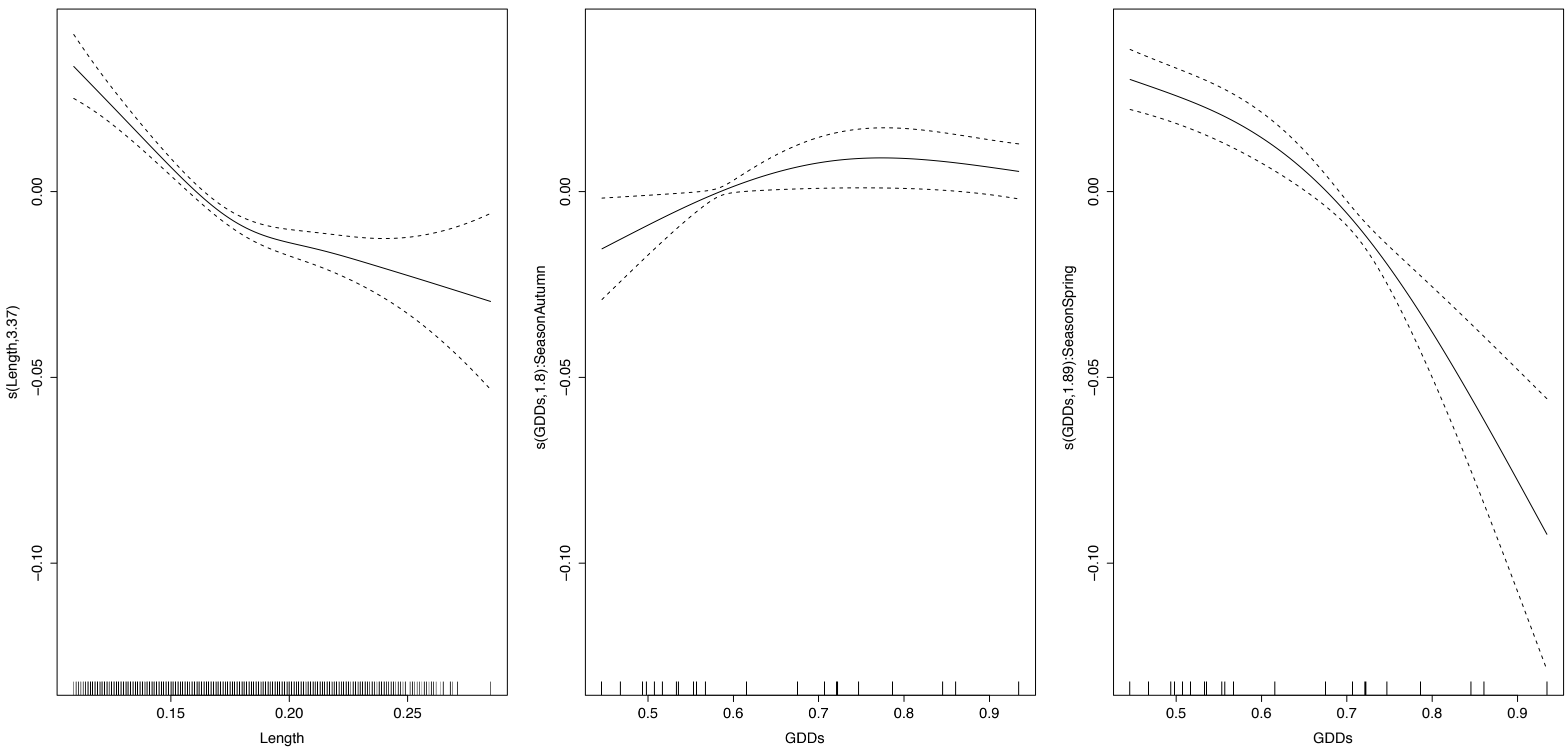

Figure S4. Plots of the effects on the response variable of the non-linear functions (*L* and *GDDs* by Season) of the best GAMM model of daily growth.

Figure S5

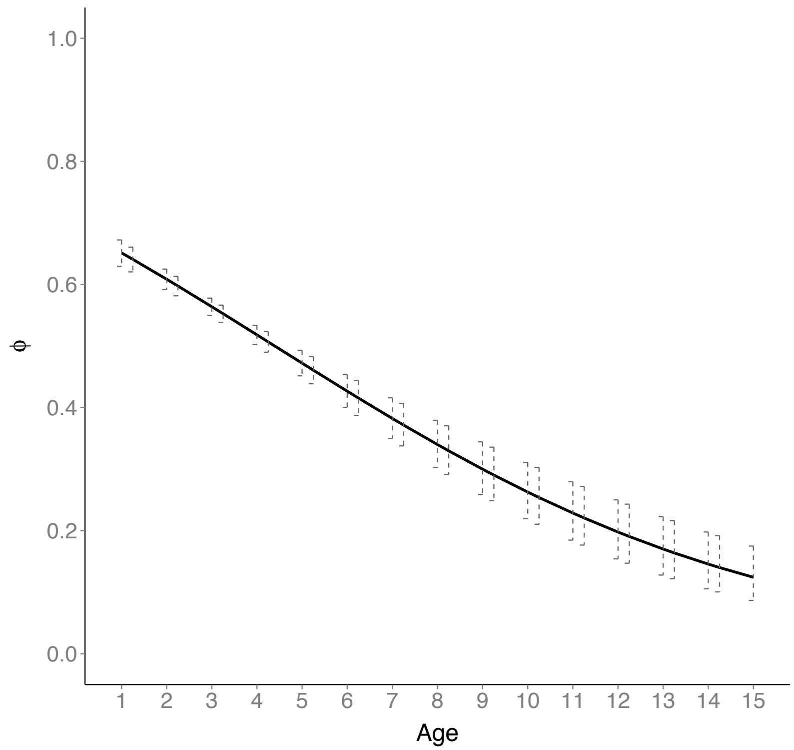

Fig. S5. Point estimates of probability of survival and 95% CI as a non-linear function of *Age* in the population of Upper Volaja (fish are aged 1 in June and 1.25 in September of the second year and so on).

Figure S6

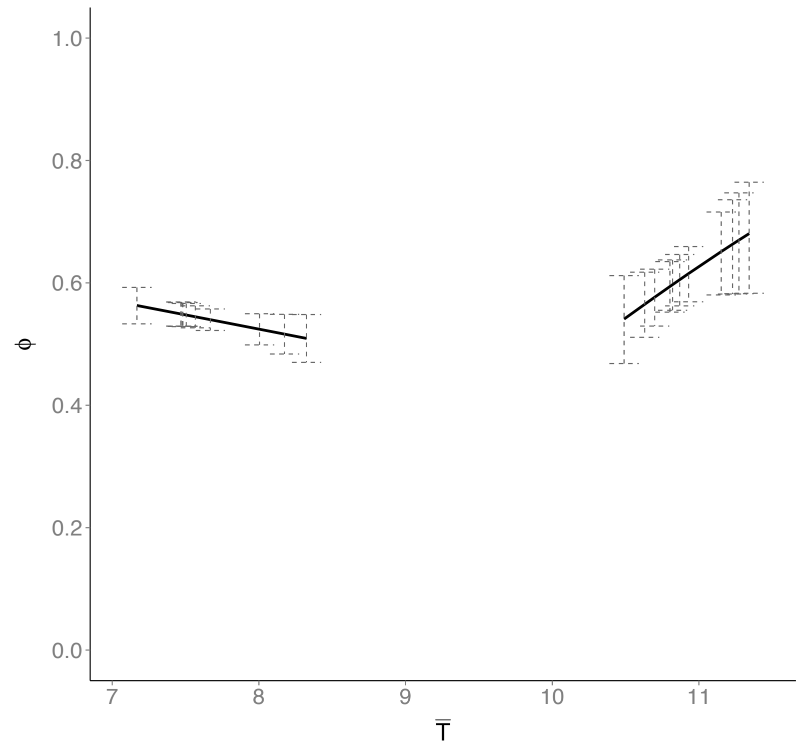

Fig. S6. Point estimates of probability of survival and 95% CI as a function of mean temperature within the sampling interval.

Text S1

When a fish is sampled in September (1+ and older), the following occurrences are possible:

(1) Fish was in Upper Volaja when 0+ (fish born in the stream)

- 1.a fish was sampled when 0+ and the adipose (ad) fin was cut (+)
- 1.b fish was present and not sampled when 0+ (ad not cut)
    - 1.b.1 fish was sampled at 1+ in June, smaller than 115 mm, and the ad was cut (+)
    - 1.b.2 fish was sampled at 1+ in June, bigger than 115 mm (thus getting tagged), and the ad was not cut (-)
    - 1.b.3 fish was not sampled at 1+ in June (missed in two occasions) and the ad was not cut (-)

(2) Fish was in Upper Volaja when 1+ in June but not when 0+

- 2.a fish was sampled when 1+ in June, smaller than 115 mm, and the ad was cut. (+)
- 2.b fish was sampled when 1+ in June, bigger than 115 mm (thus getting tagged), and the ad was not cut. (-)
- 2.c fish was not sampled when 1+ in June (ad was not cut).

(3) Fish was in Upper Volaja when 1+ in September or older, but not when 0+ or 1+ in June.

The two-pass removal and the estimation of capture rates of tagged fish indicate that the probability of sampling a fish when alive and present is between 0.85 and 0.90. Given the very high probability of capturing a fish when present (the point estimate for 0+ is the total number of fish aged 0+ sampled for almost all years), we assumed that 1.b was negligible (see Table S3 for the estimates of density). Since 1+ in June with $L < 115$ had the ad cut and ~43% of 1+ in June had $L < 115$, we cannot tease apart fish that were sampled when 0+ and fish that were sampled when 1+ in June and had $L < 115$ (we cannot tease apart 1.a from 2.a). Therefore, we have to assign fish to "early incoming" group (which includes fish born in the stream and fish migrating from AW when at max aged 1+ in June, that is 1.a + 2.a + 2.b) and "late incoming" group (fish that migrate into the streams when older than age 1+ in June, that is (3)).

Given the high capture rates, we also assumed that 2.c. was negligible (it will tend to slightly increase the proportion of "early incomers").

Text S2

Our goal was to investigate the effects of mean temperature, early density, season, age, sampling occasion, and growth potential on variation in probability of survival of tagged fish using continuous covariates ($D_{>0+}$, mean temperature between sampling intervals $\bar{T}$) at the same time of categorical predictors (*Cohort, Time*, *Season*).

Two probabilities can be estimated from a capture history matrix: ϕ, the probability of apparent survival, and p, the probability that an individual is captured when alive (Thomson et al. 2009). In the following, for ϕ we will simply use the term probability of survival.

We used the Cormack–Jolly–Seber (CJS) model as a starting point for the analyses (Thomson et al. 2009). The global starting model, that is the model with the maximum parameterization for categorical predictors, was different for each population. For both ϕ and p, a multiplicative interaction between *Cohort* and *Time* (i.e. the interval between two consecutive sampling occasions) was included. We could not use the "true" global model of survival with interaction between *Cohort*, *Time*, and *Season* as the model failed to converge.

We tested the goodness-of-fit of the CJS model with the program Release. The global model was a good starting point to model survival and capture probabilities. All other survival models tested were simplified versions of this global starting model, with the potential addition of covariates. We modeled the seasonal effect (*Season*) as a simplification of full time variation, dividing each year in two periods: June to September (*Summer*) and September to June (*Winter*). Since the length of the two intervals (*Summer* and *Winter*) was different, we estimated probability of survival on a common annual scale.

We only tested models with a potential biological interpretation (see Online Code and Results). Normalized Akaike weights (AIC weights) represent the relative probability of a model being closest to the unknown process that generated the data (Burnham and Anderson 2002). From the global model, we first modeled recapture probability by allowing the recapture probability to vary among *Cohort*, *Time*, and *Season*. We then used the recapture model with the lowest AIC to model survival probabilities. Fixing the recapture probability component of the model allowed the survival component of the model to be compared, as any difference in AIC and AIC weight given to individual models would be due to the survival component (McCallum 2000).

Both *Age* and mean temperature between sampling intervals $\bar{T}$ were introduced as either non-linear (as B-splines, Boor 2001) or linear predictors, while $D_{>0+}$ was introduced only as a linear predictor. In addition, we tested whether, after taking account of *Cohort,* probability of survival of trout that was born in AW was different from that of fish born in Upper Volaja. In this case, we used a subset of the whole dataset that included cohorts born between 2004 and 2010 included.

Unless otherwise noted, in this work probability of survival ϕ refers to an annual temporal scale. We use the symbol σ for probability of survival at the population level. We carried out the analysis of probability of survival using the package *marked* (Laake et al. 2013) for R. Tag-loss is not taken into account in *marked*, although the large number of samples and low proportion of fish losing their tag (<10%) should only slightly bias downwards the survival estimates.

Text S3

Because fish were not tagged when 0+, we assumed a binomial process for estimating the probability σ_{0+} of first overwinter survival (0+ to 1+). We estimated survival by dividing the number of 0+ with the adipose fin cut in September by the estimated number of 1+ with the adipose fin cut in June. We did not use density of 0+ and 1+ the following year since newborns (and 1+ fish the following year before June sampling) can enter the sampling section after the September sampling, thus inflating the estimate of apparent survival. The estimate of the number of 1+ with the adipose fin cut ($\hat{A}_{dc}$) is thus $\hat{A}_{dc} = A_{dc} + (1 - p_s)A_{dc}$, where A_{dc} is the sampled number of fish aged 1+ with the adipose fin cut and p_s is the probability of capture at time *t* of fish that were alive at time *t*. We estimated the standard error of the parameter of the binomial distribution using the delta method (Hilborn and Mangel 1997).

Ethics statement

All sampling work was approved by the Ministry of Agriculture, Forestry and Food of Republic of Slovenia and the Fisheries Research Institute of Slovenia. Original title of the Plan: RIBISKO - GOJITVENI NACRT za TOLMINSKI RIBISKI OKOLIS, razen Soce s pritoki od izvira do mosta v Cezsoco in Krnskega jezera, za obdobje 2006–2011. Sampling was supervised by the Tolmin Angling Association (Slovenia).

References

Boor, C. de. 2001. A Practical Guide to Splines. Springer New York.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach. Springer Verlag, New York.

Elliott, J. M., M. A. Hurley, and R. J. Fryer. 1995. A new, improved growth model for brown trout, Salmo trutta. Functional Ecology 9:290–298.

Hilborn, R., and M. Mangel. 1997. The Ecological Detective. Princeton University Press.

Laake, J. L., D. S. Johnson, and P. B. Conn. 2013. marked: An R package for maximum-likelihood and MCMC analysis of capture-recapture data. Methods in Ecology and Evolution 4:885–890.

McCallum, H. 2000. Population Parameters: Estimation for Ecological Models. Blackwell Science, Oxford.

Thomson, D. L., E. G. Cooch, and M. J. Conroy. 2009. Modeling Demographic Processes in Marked Populations. Springer.