

## Research Article

# Status of young-of-the-year brown trout (*Salmo trutta fario*) in Swiss streams: factors influencing YOY trout recruitment

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**Abstract.** As part of the Swiss Fischnetz project (network for declining fish yields in Switzerland) studies were carried out to investigate the decline in catches of brown trout. Insufficient YOY (young-of-the-year) recruitment of brown trout due to different abiotic and/or biotic factors was hypothesized as a potential cause of this decline. Quantitative assessments of fish ecology parameters and habitat measurements were carried out at 97 river sites over a two-year period. The main objectives of this study were to document the occurrence and abundance of naturally reproduced YOY trout and to develop an understanding of environmental factors respon-

sible for the observed YOY density. A general linear model (GLM) was used to analyse the influence of selected environmental abiotic and biotic parameters on YOY density.

Successful recruitment of YOY trout was observed in all but three of the sites studied. Abundance was correlated with abiotic and biotic factors, such as river width, slope, altitude, substratum condition, and the occurrence of proliferative kidney disease (PKD). The results highlight the importance of small streams for natural YOY recruitment of brown trout and their function as a source of individuals for downstream river sections.

**Key words.** Fish catch decline; reproduction; fish habitat; PKD; general linear model.

## Introduction

Catches of brown trout (*Salmo trutta fario*) by anglers in Swiss rivers have been decreasing since 1985 (Burkhardt-Holm et al., 2002). Rivers in Switzerland are detrimentally affected by a variety of factors in varying combinations. Population density on the Swiss central plateau is high (380 inhabitants km<sup>-2</sup>). Here intensive land use, food protection measures, and the production of hydroelectric energy have resulted in river channelization and a substantial decrease in the size of floodplains (>90% of the total area over the past 100 years (Bundesamt für Sta-

tistik, 2002)). Today, most Swiss streams and rivers, as well as their tributaries, are channelized and often characterized by an anthropogenically modified flow regime (Peter et al., 2005). Embankments and other constructions disrupt longitudinal and lateral connectivity of streams and rivers, causing fragmentation. The habitat conditions created by these different factors likely affect trout populations, their migratory patterns and habitat diversity (Peter, 1998).

In the Fischnetz project – a 5-year Switzerland-wide project on fish catch decline – a lack of young-of-the-year (YOY) fish was hypothesized as a key factor responsible for the decline in trout catches in certain rivers and, ultimately, in population abundance (Burkhardt-Holm et al., 2002; Burkhardt-Holm et al., 2007). Brown trout is the most common and commercially most important riv-

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erine fish species in Switzerland. For these reasons, brown trout was targeted in the present study.

The presence and abundance of YOY trout are dependent on various factors. During the incubation period, early life stages are frequently exposed to harsh conditions such as floods, elevated levels of fine sediments in the pore space of river beds and a lack of oxygen supply. Fine sediments negatively impact the survival of eggs and fry (Acornley and Sear, 1999), and a level of >15% fine material was found detrimental to the survival of Atlantic salmon embryos (O'Connor and Andrew, 1998).

Following emergence from the gravel, competition gives rise to mortality that is mainly density-dependent (Elliott, 1994) and regulates the population. After 33–70 days, mortality of young trout is no longer correlated with their density (Elliott, 1994). Thus, the 0+ trout remaining in late summer are individuals that have survived the losses arising from these significant mortality factors. YOY density is further influenced by water quality and physical habitat. Eklöv et al. (1999) showed that the occurrence and density of trout, especially 0+, were largely affected by prevailing oxygen conditions and the presence of medium-sized substrata. They found high YOY densities in narrow shallow streams. River depth and shelter were found to be the two parameters that influenced YOY trout distribution within a river basin (Bagliniere and Maisse, 2002).

Besides abiotic factors and the above mentioned intraspecific competition, YOY trout are affected by additional biotic factors, such as disease or interspecific competition and predation. Proliferative kidney disease (PKD) is widespread in Swiss streams and rivers (Wahli et al., 2007). PKD is a serious, potentially fatal parasitic disease in salmonids that can induce a pronounced inflammatory response in kidney tissue. In Switzerland, it is the most frequently diagnosed disease in wild brown trout (Wahli et al., 2002), due to the fact that clinical symptoms of other diseases are less obvious. YOY fish are particularly vulnerable to PKD when they are exposed to the parasite for the first time. Competition with coexisting species and the presence of predators can also affect YOY trout densities (Eklöv et al., 1999).

As very little information has been published on the abundance and natural reproduction of YOY trout in Swiss streams, quantitative assessments of fish were conducted as part of this study. Besides the results presented for selected objectives, the data may also serve as an important foundation for the future management of rivers and trout.

The principal selected objectives were:

- to confirm or refute that natural reproduction of brown trout occurs in Swiss streams;
- to analyse the status of YOY trout in Swiss streams;
- to identify biotic and abiotic factors influencing YOY density.

## Materials and methods

### Site selection

Most of the selected sampling sites were in trout streams (Huet, 1959) and inhabited mainly by brown trout and typical accompanying species. Streams in the Swiss central plateau were targeted because the largest angler catch decline has been reported there. Stream orders ranged from 1 to 5, with the greatest majority of sites (70%) corresponding to orders 3 and 4. The selection of rivers for sampling was considerably limited as a result of extensive stocking practices in the whole of Switzerland. In most of the selected rivers (N = 64 sites), annual fish stocking was delayed until after our sampling campaign. In the remainder of streams, stocking practices did not take place due to their insignificance in relation to angling activity or because of an ecologically based management (N = 33 sites). As a consequence, it is assumed that the YOY trout caught at all the sites were naturally reproduced.

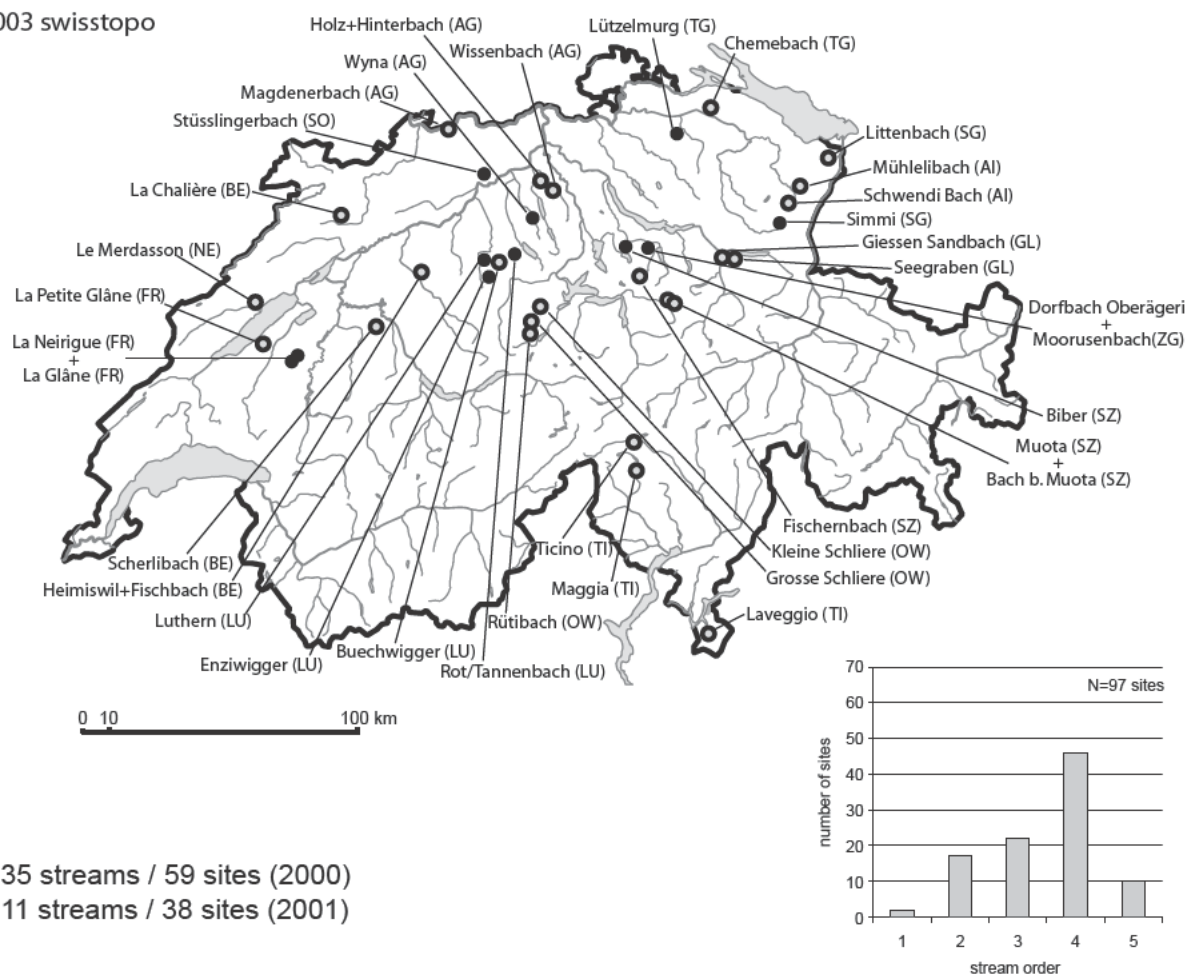
Field surveys were carried out between August and September in 2000 and 2001, resulting in a total of 35 streams and 97 sampling sites. In 2001, 11 of the sampled streams in 2000 were sampled with a greater number of sites per stream (Fig. 1). Thirteen sites were sampled in both years. End of summer 0+ trout are usually large enough to be caught using electrofishing.

### Fish sampling and population estimates

Fish were sampled using quantitative electrofishing (DC generator, 8 kW, 300–600 V). To prevent fish movements during sampling, each 100-m long site was sealed off with nets at the downstream end and with an electric fence at the upstream end. All fish were caught in three consecutive removals, allowing the estimation of fish densities using the removal method (Zippin, 1956). Although trout were of particular interest, all fish species were included in the study. All individuals were anaesthetized using clove oil (0.03 ml/L; Hänseler AG, Switzerland) (Vermeirssen et al., 2005), measured (total length to the nearest mm), and weighed (to the nearest g) before being returned to the river.

Population estimates (density and biomass) were calculated using the Microfish 3.0 software programme (Van Deventer and Platts, 1986) by applying the maximum likelihood estimator. To minimize the known size bias associated with electrofishing, estimates were calculated separately for three different size classes (YOY, >YOY to 220 mm total length, >220 mm). For the other fish species, only total numbers were calculated. Comparison of the different sites was facilitated by standardizing density and biomass to an area of one hectare. Trout were defined as YOY using length-frequency distributions. At most sites the youngest cohort could be visually distinguished relatively clearly (Fig. 2). None-

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**Figure 1.** Location of the 35 rivers (97 sites) sampled in 2000 and 2001 (source of map: Swiss Federal Office of Topography, 2003). Stream orders range from 1 to 5.

**Table 1.** Description of the variables used for statistical analyses.

| Variable                  | Values                                     |
|---------------------------|--|
| Altitude                  | Metres above sea level                     |
| Slope                     | Percent                                    |
| Average width             | Metres                                     |
| Average maximum depth     | Centimetres                                |
| CV average width          | Percent (StD/mean*100)                     |
| CV average maximum depth  | Percent (StD/mean*100)                     |
| Riffles + Glides          | Percent of area sampled                    |
| Shading                   | Percent of area sampled                    |
| Colmation                 | 1 = high, 2 = medium, 3 = low, 4 = none    |
| Embeddedness              | 1 = high, 2 = medium, 3 = low/none         |
| PKD                       | 1 = positive, 0 = negative                 |
| Interspecific competition | 1 = presence of other species, 0 = absence |

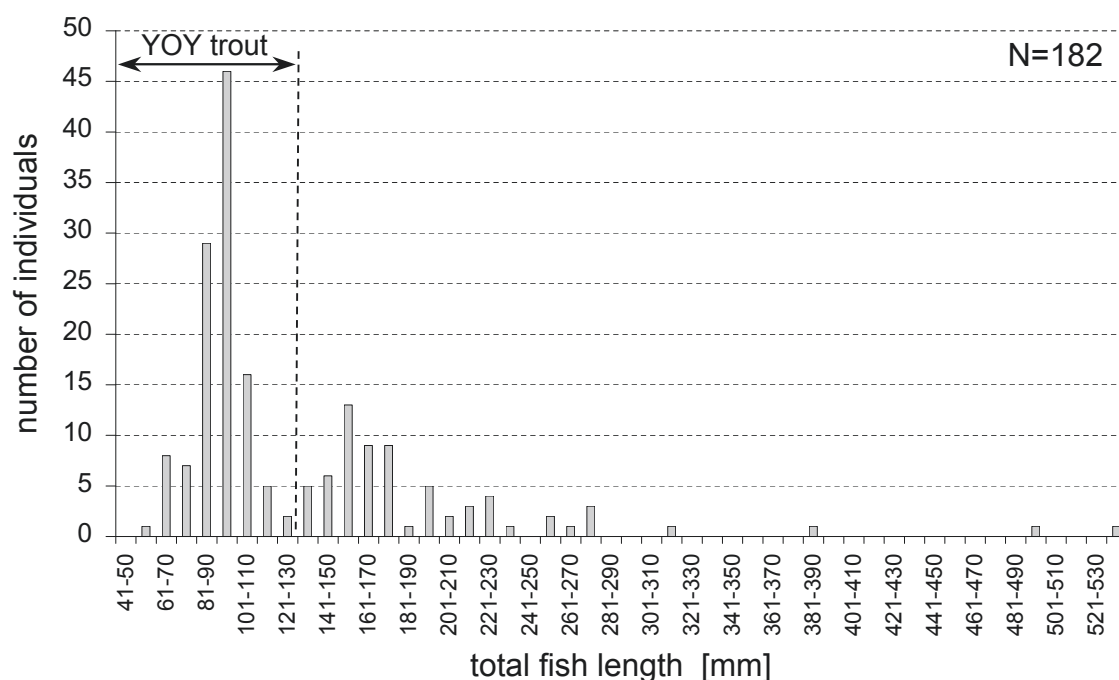
CV: Coefficient of Variance, PKD: proliferative kidney disease

theless, some inaccuracies cannot be excluded due to cohort overlapping.

### Habitat characterization

Each site was characterized using habitat parameters (listed in Table 1) that were assumed to be of importance for YOY trout and could be measured with a level of effort appropriate to the scope of the project. Altitude and slope were derived from topographic maps (1:50,000, Swiss Federal Office of Topography, 2000). Measurements of evenly distributed transects (5 to 10 transects per site) allowed for the calculation of the mean width (m) and mean maximum depth (cm) as well as their coefficients of variance (CV). The corresponding wetted area was used to standardize fish data.

Mesohabitat structure in terms of the presence of different hydraulic units was characterized by the percentage of riffles, glides, and pools (Bisson et al., 1981) in the sampled area. The condition of the substratum was described by two characteristics: colmation and embeddedness. Colmation is the clogging of the top layer of the channel sediments (Brunke and Gonser, 1997), where



**Figure 2.** Example of a length-frequency distribution used as a tool for distinguishing between YOY trout and larger fish in each of the sites sampled.

mainly cohesive particles (<0.06 mm size) are aggregated within the pore space. It was assessed according to the method of Schälchli (2002). Embeddedness is the degree to which large substrate particles are surrounded or covered by fine sediment (<2 mm). Embeddedness was estimated visually. These variables were classified into four and three categories, respectively. Percentage shading was estimated for the whole site as vertical projection.

#### Fish health and Proliferative Kidney Disease (PKD)

Up to 20 individual YOY trout per site were analysed for proliferative kidney disease (PKD). For 23 sites, no PKD data could be derived because there were too few fish or because PKD samples were missing for some sites. Fish used for PKD analysis were killed by using an overdose of MS 222 (tricaine methane-sulfonate Aldrich-Sigma, Milwaukee, USA; 100 mg/L). Pieces of the kidney from each fish were fixed in buffered 4% formalin, embedded in paraffin wax and sectioned according to routine histological protocols. The 5-µm sections were stained with hematoxylin and eosin (HE) and examined for the presence of *Tetracapsuloides bryosalmonae* (Schmidt et al., 2001).

#### Data analyses

General linear modelling was performed using the data from 74 sites. The remaining sites (N = 23) had to be excluded because values were missing for “PKD”.

A general linear model (GLM) was used to analyse the

main effects of abiotic/biotic variables on YOY trout density. The GLM describes the relationship between a dependent variable and N independent variables. The independent variables in the GLM may be numerical as well as categorical. The model for the applied analysis included the four categorical variables colmatation, embeddedness, PKD and interspecific competition (presence/absence of other fish species) as fixed factors. The other eight independent variables were treated as covariates (Table 1). The model was refined by means of repeated backward selection of each variable with the lowest significance level. This procedure produced a final model that only included significant variables (p-values <0.05). Prior to analyses, data were transformed using standard transformations (log, arcsin) according to recommendations in Stahel (1999). Residuals were examined for normality and homogeneity of variance. Analyses were carried out using SPSS 14.0.

## Results

#### Species distribution in the sites sampled

A total of 29,523 individuals belonging to 21 species were caught by electrofishing during the two sampling campaigns. The most dominant species were brown trout and its typical accompanying species bullhead (*Cottus gobio*). Together, they accounted for 81% of the individuals caught. Besides these two species, only stone loach (*Barbatula barbatula*) and minnow (*Phoxinus phoxinus*)



**Table 2.** Species and number of individuals caught at 97 sites during the two sampling campaigns and their percentage of the total catch.

| Species                      | total         | %             |
|------------------------------|---------------|---------------|
| <b>Salmo trutta fario</b>    | 15,548        | <b>53.68</b>  |
| <b>Cottus gobio</b>          | 8,007         | <b>27.12</b>  |
| <b>Barbatula barbatula</b>   | 3,926         | <b>13.30</b>  |
| <b>Phoxinus phoxinus</b>     | 1,358         | <b>4.60</b>   |
| Leuciscus cephalus           | 197           | 0.67          |
| Lampetra planeri             | 54            | 0.18          |
| Alburnoides bipunctatus      | 41            | 0.14          |
| Barbus caninus               | 19            | 0.06          |
| Leuciscus souffia            | 14            | 0.05          |
| Anguilla anguilla            | 11            | 0.04          |
| Salvelinus fontinalis        | 11            | 0.04          |
| Oncorhynchus mykiss          | 9             | 0.03          |
| Barbus barbus                | 8             | 0.03          |
| Lepomis gibbosus             | 7             | 0.02          |
| Gobio gobio                  | 5             | 0.02          |
| Tinca tinca                  | 2             | 0.01          |
| Lota lota                    | 2             | 0.01          |
| Thymallus thymallus          | 1             | 0.00          |
| Perca fluviatilis            | 1             | 0.00          |
| Rutilus rutilus              | 1             | 0.00          |
| Gasterosteus aculeatus       | 1             | 0.00          |
| <b>total no. individuals</b> | <b>29,523</b> | <b>100.00</b> |
| <b>total no. species</b>     | <b>21</b>     |               |

were present at high abundances up to 3,926 and 1,358 individuals, respectively. All other species showed a proportion of <1 % in the species distribution (Table 2).

### YOY trout

YOY trout were present at all sites, with the exception of three sites in the river Ticino in the Southern Alpine region where the trout population consisted of 1+ and older individuals. Values for YOY trout total length were between 30 and 164 mm. Median and mean values for YOY total length were 85 and 84 mm, respectively (Table 3). The smallest YOY fish occurred at sites located at altitudes >1,000 m a.s.l. The largest YOY trout were found in the river Laveggio in southern Switzerland.

### Brown trout density, YOY trout density and biomass

Brown trout densities ranged between 17 and 26,651 ind. ha<sup>-1</sup> (median 2,537 individuals). YOY trout densities

varied significantly between sites and ranged from 10 to 22,589 ind. ha<sup>-1</sup> with a median value of 1,196 (Fig. 3). Values for total trout biomass were between 0.1 and 552 kg ha<sup>-1</sup> (mean 139 kg ha<sup>-1</sup>, median 115 kg ha<sup>-1</sup>). Biomasses >100 kg ha<sup>-1</sup> were recorded at 52 sites (Table 3). Low YOY densities (<500 ind. ha<sup>-1</sup>) were reported for 26 sites. Some of those sites also featured a low total trout density, while in others the population consisted mainly of individuals 1+ and older. In sites with densities >8,000 ind. ha<sup>-1</sup> the 0+ cohort was the strongest (72 % mean proportion of total trout density).

Thirteen sites were sampled in both study years, and differences in YOY abundances were analyzed by one-way-ANOVA. To meet the assumptions of this test, abundances were log-transformed prior to the test. The results showed that YOY abundances did not differ significantly between years (p-value 0.471). It was not possible to identify any patterns between the density of YOY, on the one hand and the density of 1+ and older trout on the other hand.

### YOY densities with respect to locality in the water course

In 2001, a number of sites (2 to 6) were sampled per river. Ten of the 11 rivers sampled had higher YOY densities at sites situated further upstream (Fig. 4). In the river Rot, high YOY densities were documented in all 3 sites sampled, although the site most upstream had the lowest value. The streams Wyna, Lützelburg, Neirigue and Luthern had generally low YOY densities. Discrimination between downstream/upstream sites was based mainly on the distance from source, complemented by average width and/or slope. Nevertheless, all sites but three belonged to the trout zone (Huet, 1959).

### Abiotic and biotic characteristics

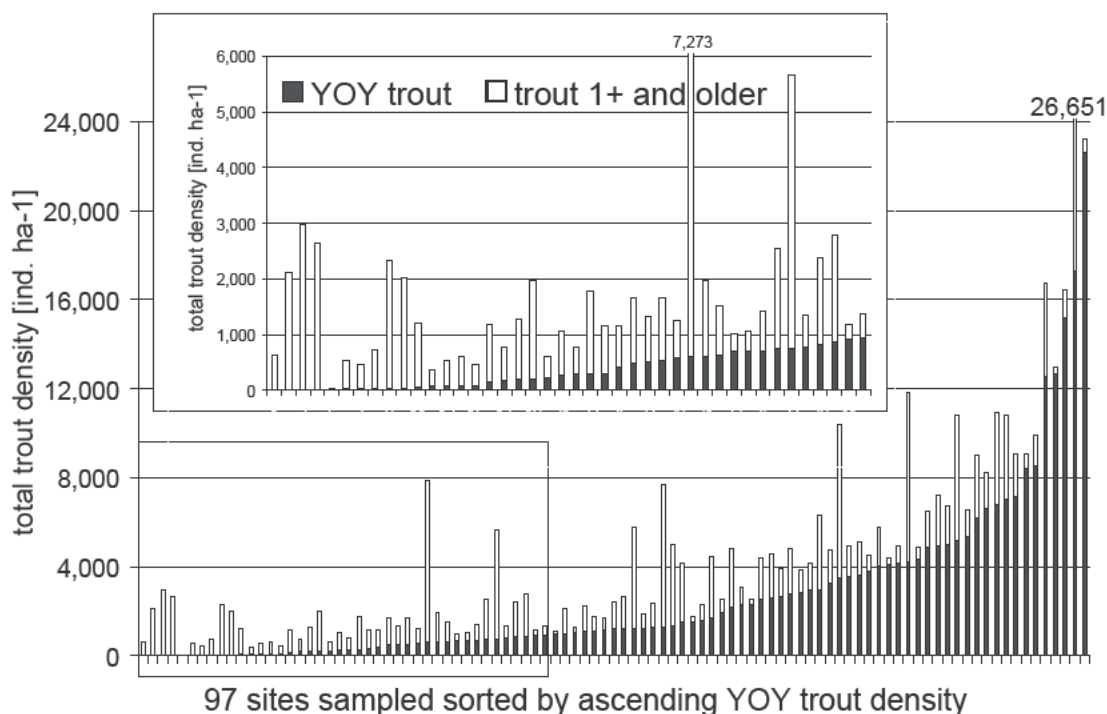
The distribution of the 12 abiotic and biotic environmental variables used for statistical analyses are shown in Table 4. Descriptive statistics for the numerical variables are listed in Table 5.

### YOY trout variability with respect to abiotic and biotic parameters

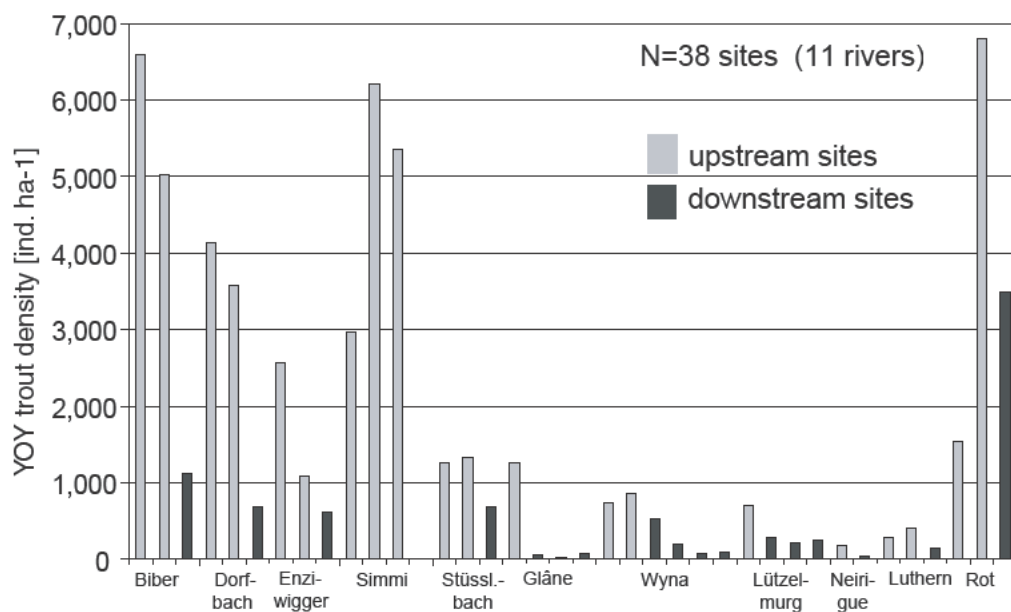
Data analysis by means of a GLM started with a full model with all 12 independent variables. The final reduced model included PKD, average width, colimation,

**Table 3.** Brown trout density, biomass, YOY trout density and YOY trout lengths. N = number of sampling sites (for trout density and biomass) or number of YOY fish (for YOY trout total length).

| Parameter              |                       | N     | Minimum | Maximum | Median | Mean  | St. Deviation |
|------------------------|-----------------------|-------|---------|---------|--------|-------|---------------|
| trout density total    | ind. ha <sup>-1</sup> | 97    | 17.0    | 26,651  | 2,537  | 4,385 | 4,653         |
| trout biomass total    | kg ha <sup>-1</sup>   | 97    | 0.1     | 552     | 115    | 139   | 103           |
| YOY trout density      | ind. ha <sup>-1</sup> | 97    | 0.0     | 22,589  | 1,196  | 2,674 | 3,853         |
| YOY trout total length | mm                    | 8,285 | 30      | 164     | 84     | 85    | 19            |



**Figure 3.** Distribution of trout density among sites sorted by YOY trout density (black columns). Sites with YOY densities <1,000 ind. ha<sup>-1</sup> are shown in the separate rectangle.



**Figure 4.** YOY trout densities in the 11 rivers sampled in 2001. Most of them show a clear declining gradient from the headwater site to the site further downstream.

altitude, slope and CV average width as significant variables. This model accounted for 76 % of the variation in YOY trout density (Table 6). Stream width, variation in the average stream width, altitude, PKD and colmation were negatively correlated with YOY density. In contrast,

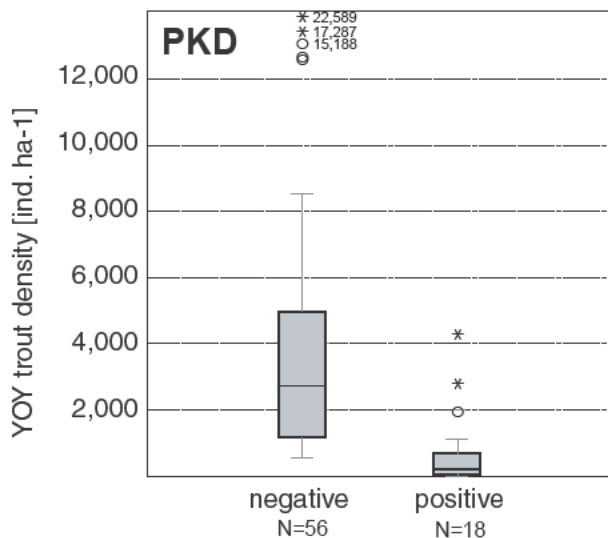
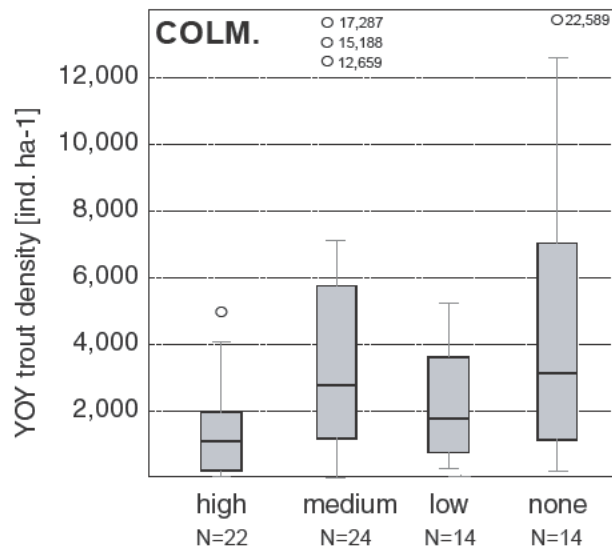
slope was positively correlated. Thus, high 0+ trout densities were found in narrow streams at a lower altitude and with a steeper slope as well as a smaller variation in the average width, where PKD does not occur and the colmation of the river is low.

**Table 4.** Distribution of the 12 abiotic and biotic environmental variables used for statistical analyses.

| Variable                | level     | N total | N* | Variable                  | level       | N total | N* |
|-------------------------|-----------|---------|----|---------------------------|-------------|---------|----|
| Altitude m asl          | ≤300      | 0       | 0  | Riffles + Glides %        | ≤25         | 0       | 0  |
|                         | >300–500  | 27      | 22 |                           | >25–50      | 5       | 5  |
|                         | >500–700  | 35      | 28 |                           | >50–75      | 30      | 30 |
|                         | >700–900  | 18      | 14 |                           | >75         | 61      | 61 |
|                         | >900–1100 | 10      | 10 |                           | NA          | 1       |    |
|                         | >1100     | 7       | 0  |                           |             |         |    |
| Slope %                 | ≤1        | 27      | 22 | Shading %                 | ≤25         | 35      | 35 |
|                         | >1–5      | 52      | 39 |                           | >25–50      | 8       | 8  |
|                         | >5–10     | 16      | 11 |                           | >50–75      | 21      | 21 |
|                         | >10       | 2       | 2  |                           | >75         | 32      | 32 |
|                         |           |         |    |                           | NA          | 1       |    |
| Average width m         | ≤2        | 13      | 13 | Colmation                 | high        | 24      | 24 |
|                         | >2–5      | 43      | 43 |                           | medium      | 30      | 30 |
|                         | >5–10     | 29      | 29 |                           | low         | 18      | 18 |
|                         | >10–15    | 7       | 7  |                           | none        | 24      | 24 |
|                         | >15       | 5       | 5  |                           | NA          | 1       |    |
| Average max. depth cm   | ≤25       | 27      | 27 | Embeddedness              | high        | 34      | 34 |
|                         | >25–50    | 54      | 54 |                           | medium      | 38      | 38 |
|                         | >50–75    | 14      | 14 |                           | low or none | 24      | 24 |
|                         | >75       | 1       | 1  |                           | NA          | 1       |    |
|                         | NA        | 1       |    |                           |             |         |    |
| CV average width %      | ≤10       | 14      | 14 | PKD                       | negative    | 56      |    |
|                         | >10–25    | 52      | 52 |                           | positive    | 18      |    |
|                         | >25–50    | 30      | 30 |                           | NA          | 23      |    |
|                         | >50–75    | 0       | 0  |                           |             |         |    |
|                         | >75       | 0       | 0  |                           |             |         |    |
|                         | NA        | 1       |    |                           |             |         |    |
| CV average max. depth % | ≤10       | 0       | 0  | Interspecific competition | absence     | 43      | 43 |
|                         | >10–25    | 15      | 15 |                           | presence    | 54      | 54 |
|                         | >25–50    | 53      | 53 |                           |             |         |    |
|                         | >50–75    | 24      | 24 |                           |             |         |    |
|                         | >75       | 4       | 4  |                           |             |         |    |
|                         | NA        | 1       |    |                           |             |         |    |

N\*: number of sites used for statistical analyses

NA: number of sites for which no data could be recorded

**Figure 5.** YOY abundance in relation to PKD. YOY abundance is significantly negatively related to PKD (Table 6;  $p < 0.001$ ).**Figure 6.** YOY abundance in relation to colmation. YOY abundance is significantly negatively related to colmation (Table 6;  $p < 0.001$ ).

**Table 5.** Numerical abiotic characteristics in the sites sampled. N = number of sampling sites, for which where data could be derived for the specific parameter.

| Parameter             |                   | N  | Minimum | Maximum | Median | Mean  | St. Deviation |
|-----------------------|-------------------|----|---------|---------|--------|-------|---------------|
| Altitude              | m above sea level | 97 | 310.0   | 1,900.0 | 650.0  | 700.5 | 277.5         |
| Slope                 | %                 | 97 | 0.4     | 12.6    | 1.8    | 2.8   | 2.4           |
| Average width         | m                 | 97 | 0.8     | 19.8    | 4.5    | 5.7   | 4.0           |
| Average max. depth    | cm                | 96 | 12.5    | 80.4    | 34.6   | 35.7  | 15.6          |
| CV average width      | %                 | 96 | 3.0     | 48.6    | 21.1   | 21.5  | 10.4          |
| CV average max. depth | %                 | 96 | 10.7    | 99.9    | 39.4   | 41.3  | 17.6          |
| Riffles + Glides      | %                 | 96 | 26.0    | 100.0   | 80.0   | 79.1  | 15.7          |
| Shading               | %                 | 96 | 0.0     | 100.0   | 60.0   | 49.6  | 36.4          |

CV: Coefficient of Variance

**Table 6.** Results of the general linear model (GLM) for the analysis of the effects of different abiotic and biotic parameters on the YOY trout density. +/- indicate the direction in which YOY abundance is influenced. (SS: sum of squares, df: degrees of freedom, F: ratio between two mean squares; p: probability of error). Only variables with  $p < 0.05$  are interpreted as statistically significant.

| Source of variability |   | SS    | df | F      | P      |
|-----------------------|---|-------|----|--------|--------|
| Average width         | - | 3.699 | 1  | 36.786 | <0.001 |
| PKD                   | - | 2.619 | 1  | 26.044 | <0.001 |
| Colmation             | - | 3.810 | 3  | 12.630 | <0.001 |
| Altitude              | - | 0.747 | 1  | 7.430  | 0.008  |
| CV Average width      | - | 0.736 | 1  | 7.316  | 0.009  |
| Slope                 | + | 0.463 | 1  | 4.604  | 0.036  |

CV: Coefficient of Variance, PKD: proliferative kidney disease  
 $R^2 = 0.756$ ,  $F = 24.460$ ,  $p = <0.001$ 

### YOY trout density in relation to PKD and colmation

Results of the GLM showed that YOY trout density is inversely related to PKD and colmation that are not based on morphology and topography (Table 6,  $p < 0.001$ ). Abundance is significantly lower in sites with PKD infested trout (Fig. 5). Colmation influences YOY abundance negatively, especially if it occurs at a high level (Fig. 6).

## Discussion

Naturally reproduced YOY trout were found in all but three sites in the river Ticino in the Alpine region. The observed YOY densities showed a high variability that, on the one hand, could be linked to the natural variability of sampling locations in terms of stream width, slope and altitude. On the other hand, YOY trout density may also be explained by the negative influences of river bed substrate alteration by colmation of the river bed and infestation with PKD.

The presence of higher YOY densities in small streams predicted in our model highlights their important role in the reproductive cycle of brown trout through the provision of suitable habitats for reproduction and rearing. A correlation between stream width and 0+ trout density was also shown for Swedish streams, where high YOY

densities were reported in narrow shallow streams and high oxygen supply (Eklöv et al., 1999). These findings have also been confirmed for the river Scorff in a comprehensive study carried out by Bagliniere and Maisse (2002). In their study, they detected different recruitment strategies for YOY brown trout, with tributaries and small streams playing a crucial role in that respect. In a study carried out in the French Pyrenean region, Baran et al. (1993) showed that stream width was the only habitat feature related to the abundance of YOY brown trout, confirming the importance of small streams for YOY trout. In this context, we demonstrated higher YOY abundances in headwaters and upstream reaches along the stream courses in our study, which underlines these findings.

The results of the GLM predicted higher YOY densities with decreasing altitude and greater slope of the river bed in the range of the values reported for sites at which YOY trout were caught. This tallies with the topography of Switzerland and the demonstrated importance of stream width - small streams coming from the mountains mostly show a steeper gradient. The negative correlation between altitude and YOY density is assumed to be a consequence of the wide range of altitudes of the sites sampled and the influence of climatic conditions which could limit trout reproduction at sites of greater altitude.

Impacts on the river bed arising from the accumulation of fine sediments in the interstitial pores have negative effects on the survival rate of brown trout eggs and larvae during incubation. The sediment input into Swiss streams from surface runoff is elevated by anthropogenic activities and originates mainly from agriculture and urban development. Between 1970 and 1990, the total agricultural area in Switzerland increased, thereby causing significant soil erosion problems (Mosimann et al., 1990).

Excessive fines can cement the gravel bed: thus, redd construction is inhibited and the permeability of the gravel and flow of oxygenated water are reduced (Crisp, 2000). In addition, the removal of metabolic waste from eggs and alevins is impaired. Low YOY trout densities in sites with extensive river bed clogging are the direct consequence of this. Low egg-to-fry survival of brown trout was correlated with a high percentage of fine sediments in different



studies carried out by Acornley and Sear (1999), Massa et al. (1998) or Rubin and Glimsater (1996). Bagliniere and Maisse (2002) confirmed the low egg-to-fry survival (1.3–14.7%) for the river Scorff, which is suggested to be due to the amount of fines (<2 mm) in the substrate. Embeddedness does not necessarily implicate colmation of the river bed. Colmation is a more static process, where the pore space of the top layer of the river bed is clogged up by cohesive particles and can only be broken up during high floods of a certain magnitude. Embeddedness is a much more dynamic process which occurs naturally in all rivers that transport fine sediments (particles <2 mm). Depending on flow conditions fine sediments are accumulated in or removed from the river bed.

With respect to biotic parameters that may influence 0+ trout density, PKD and interspecific competition were considered in this study. Infection with PKD may result in mortalities of up to 90% in YOY brown trout (Schubiger, 2003; Burki 2006). In general, mortality due to PKD is high where the water temperature exceeds 15 °C for more than 2–4 weeks (Schubiger 2003). In the current study, PKD also emerged as a significant determinant of the YOY trout density in the sites sampled. Densities were significantly lower at sites with PKD-positive fish than at sites without PKD occurrence. This pattern was observed for all sites in rivers in which upstream and downstream sites were sampled, although YOY density was usually higher upstream than downstream. Although PKD and river bed colmation are thought to be responsible for the lower densities at these sites, they may in part also be explained by natural zonation.

Other factors (percentage of riffles, embeddedness, variability of stream depth, shading, interspecific competition) that were assumed to influence YOY density did not have significant effects in our study. However, YOY brown trout were classified as riffle-dwelling in a comprehensive study based on a small catchment analysis (Danehy et al., 1998). Several studies also refer to the presence of riffles and glides as important habitats for YOY trout (Roussel and Bardonnet, 1999; Bagliniere and Maisse, 2002). On the other hand, habitat use is mainly determined by access to food and protection from predators and need not necessarily be associated with the presence of riffles. Sites that fish selectively prefer in streams must satisfy all of the basic requirements for their survival (Bjornn and Reiser, 1991). Moreover, interspecific competition has been reported to affect trout density negatively (Eklöv et al., 1999), although this could not be confirmed in our streams.

## Conclusion

Naturally reproduced brown trout occurred in 94 of the investigated 97 sites in small to medium-sized Swiss rivers. The outcome of our survey, which was carried out over two years, gives an overview of the range of naturally produced trout densities and confirms the importance of small streams as rearing habitat for brown trout. The results provide evidence that natural recruitment of YOY trout is generally not a major problem in the streams sampled. Although we observed low YOY densities in 26 sites, we assume that natural YOY recruitment for small and medium-sized streams in Switzerland is sufficient, at least for streams with similar characteristics to the streams sampled within this study. Observations in additional headwater streams showed that the reproduction capacity in tributaries and headwaters is generally high (Wigger river system, A. Peter, unpublished data).

However, PKD and colmation of the river bed have detrimental effects on YOY trout density and necessitate appropriate remedial actions and measures. A therapy for PKD cannot be administered. The disease could potentially be reduced by strictly avoiding stocking with PKD-infected trout. Enhancement of the river bed sediment must include land use practices and restoration measures (rehabilitation of vegetation buffer strips).

In order to state whether YOY occur in adequate abundances to contribute to stock recruitment, a scientifically sound threshold would be needed for different types of streams. We recommend long-term monitoring studies with a special focus on YOY fish in rivers that are not stocked with trout. A better understanding of the natural contribution to the YOY recruitment is essential to improve the river and trout management in Switzerland.

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