8 Grain size distribution and brown trout life history

Using brown trout, a dominant fish in most Swiss rivers, as a study system, the present chapter focuses on age and sex dependencies in habitat preference and local specificity of life-history traits, including female size at maturity and juvenile traits. The importance of taking these aspects into account when developing strategies to mitigate the impacts of substrate modification on ecologically and economically important species in Swiss rivers is emphasized.

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8.1 Introduction

Of all the environmental components determining habitat quality for organisms, substrate is particularly important for most animals that live within river ecosystems, such as fish, amphibians and aquatic insects. Substrates of a suitable size create shelter, provide quality spawning and nursery habitat, and help support a more dynamic food web and the provision of abundant food resources (Brown 2003; Jonsson and Jonsson 2011). Consequently, any modification to river substrates can impact the animals that are dependent upon them. This consideration is especially important today, as disruption to river substrates is occurring increasingly, in large part due to anthropogenic activities such as the construction of hydropower structures (Baxter 1977; Chen *et al.* 2015). However, in order to effectively establish how the disruption of river substrates can be suitably mitigated, it is imperative that we also investigate how river substrates can affect individual organismal traits (e.g. rates of growth, development and reproduction) and overall river population demographics. In this chapter, using brown trout (*Salmo trutta*) in Swiss rivers as a study system, we present the relationships between substrate structure and demographic and organismal traits.

Brown trout in Swiss rivers serve as an excellent study system to examine the link between substrate structure and life-history traits for multiple reasons. First, their wide distribution across Switzerland means it is possible to study populations originating from habitats with a range of substrate structures. Thus, by investigating how life-history traits vary among populations, we can better understand how substrate structure can affect brown trout ecology. Notably, brown trout is not only widely distributed across Switzerland but also the dominant fish species in most Swiss rivers. For instance, based on the data from the Progetto Fiumi reference collection of Swiss river fish, which was carried out by Eawag in 2013–2018, more than half of the fish that were caught were brown trout in 69% of the rivers sampled across Switzerland (212 out of 308 sampled sites; Brodersen *et al.* 2023). Moreover, brown trout are acknowledged as an ecologically and economically important species (Box 11). Consequently, any changes to brown trout populations can have strong propagating effects on riverine community members. Knowledge on how substrate structure can affect brown trout ecology is therefore essential for predicting how substrate modification, such as compensation for sand and gravel deficit, affects riverine communities in Swiss rivers. In the present chapter, we report results from surveys conducted to examine how substrate can affect trout life-history traits. Specifically, we examine: (i) how habitat (substrate) preference differs depending on trout age and sex and (ii) how female size at maturity differs depending on substrate structure.

8.2 Age- and sex-dependent differences in substrate preference

Substrate structure can affect brown trout spatial distribution, partly because this species is highly dependent on prey items residing on substrate surfaces and in interstitial spaces, and also because it is a substrate-spawning species (Armstrong *et al.* 2003; Jonsson and Jonsson 2011). Notably, as is the case for most animal species (Werner and Gilliam 1984), brown trout individuals exhibit diet shifts during their life span (Jonsson and Jonsson 2011). Moreover, females dig their nests into the substrate when spawning, whereas males are not involved in this activity (Jonsson and Jonsson 2011). It is thus expected that the substrate preference of brown trout differs depending on age and sex. Indeed, age- and sex-dependent differences in substrate preference in salmonid species, including brown trout, are well documented (Armstrong *et al.* 2003; Aas *et al.* 2011; Jonsson and Jonsson 2011). Here, using a brown trout population in the Latrejebach river in the canton of Bern (46°37’18’’N, 7°46’04’’E; Fig. 46), we examined whether age- and sex-dependent substrate preferences similar to those documented in previous studies are also observed in the Swiss river population (Aerne 2020). We assessed the spatial distribution of brown trout in this small river in early October, just a few weeks before spawning started. Specifically, the sampling site had a total length of 210 m along the river, which we split into 14 subsections 11.5–19 m in length. We then measured brown trout density in each subsection. At the same time, we measured abiotic environmental variables in each subsection: mean water depth, width and velocity, and mean grain size. Moreover, we measured prey invertebrate density in each subsection. Then, we explored the links between trout spatial distribution, age, sex, and abiotic and biotic environmental variables.

There were large variations in both brown trout density and focal environmental variables among subsections. Importantly, trout density changed with mean grain size but the relationship differed depending on stage and sex, as expected, although most relationships were only marginally significant because of the small number of replicates (Fig. 47). Specifically, the total density of brown trout declined as mean grain size increased (Fig. 47a). However, our findings suggested that this overall relationship may differ depending on the stage structure and sex ratio of the population. First, total adult density decreased with increasing mean grain size (Fig. 47b), and this negative relationship was stronger in adult females than adult males (Fig. 47c, d). Further analyses demonstrated that the strong negative relationship between adult female density and mean grain size was partly driven by the females’ preference for the river subsection with a higher proportion of substrate theoretically suitable for spawning (<10% female body length; Kondolf and Wolman 1993). In contrast, juvenile density increased with increasing mean grain size (Fig. 47e). Additional analyses indicated that this positive relationship was partially due to the juveniles’ preference for the river subsection with a higher abundance of their food items. These results are generally consistent with findings from previous studies on age and sex dependencies in the habitat preference of brown trout and other salmonid species (Armstrong *et al.* 2003), demonstrating the importance of maintaining spatial habitat (substrate) heterogeneity within a river to conserve fish populations as a whole.

Figure 46

Photograph of the Latrejebach river study site (BE).

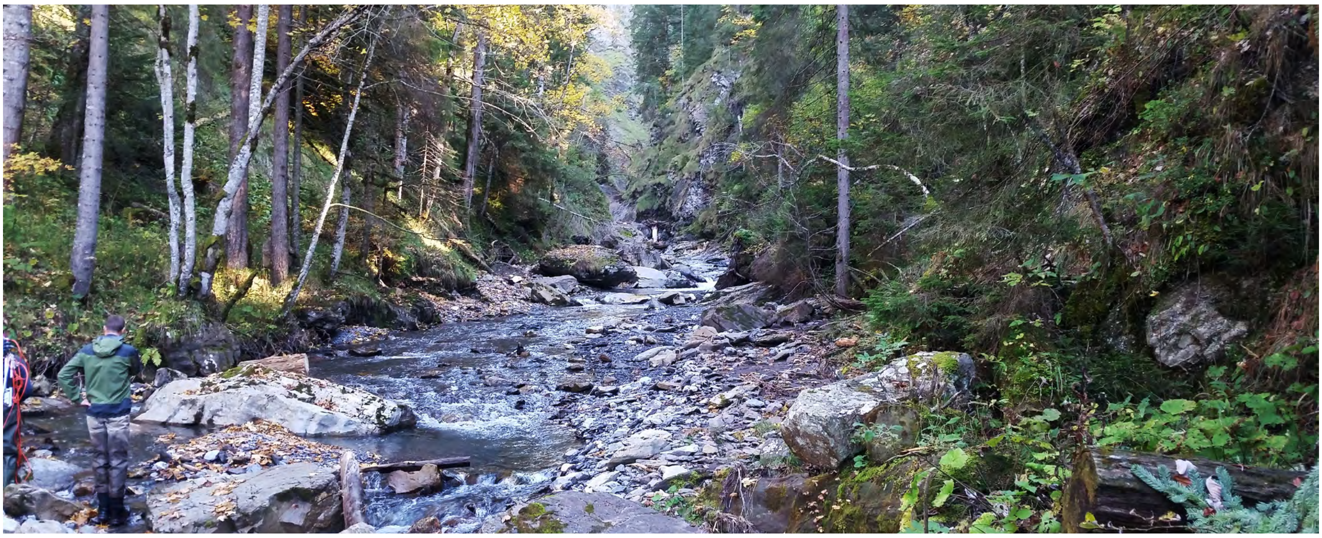
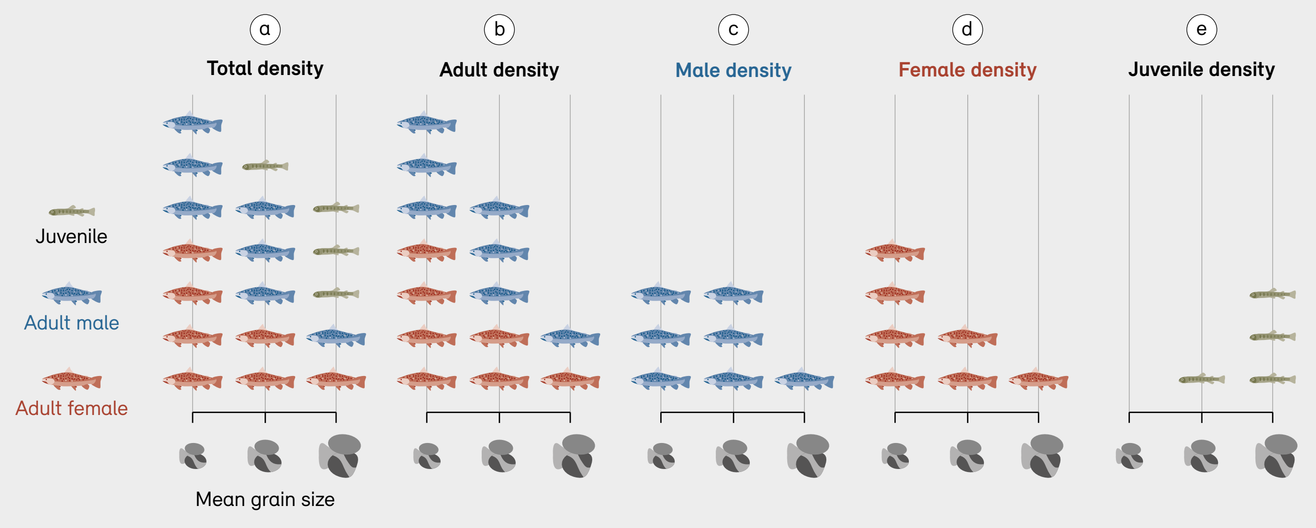


Photo: K. Takatsu

Figure 47

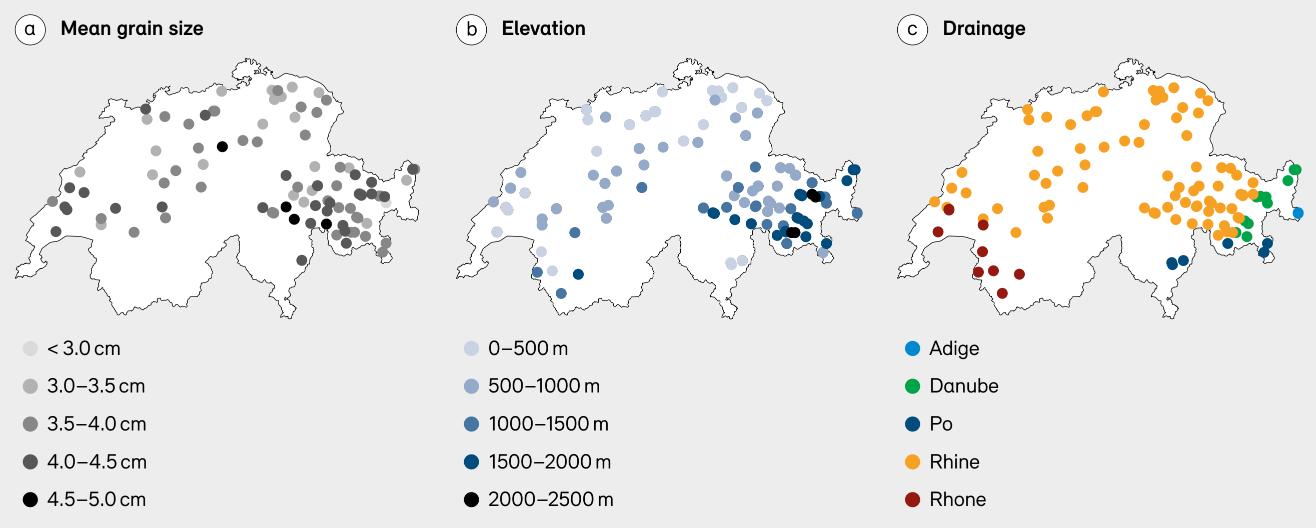
Relationships between mean grain size and (a) total, (b) adult, (c) adult male, (d) adult female, and (e) juvenile brown trout density in the Latrejebach river.



Data source: Aerne (2020)

Figure 48

*Maps of 120 study sites on Swiss rivers. Variation in (a) geometric mean grain size, (b) elevation and (c) drainages. The geometric mean grain size (dg) was calculated using the following equation: dg = (D84) * (D16) $^{0.5}$ (Kondolf and Wolman 1993), where D16 and D84 are 16th and 84th percentile substrate diameters, respectively.*



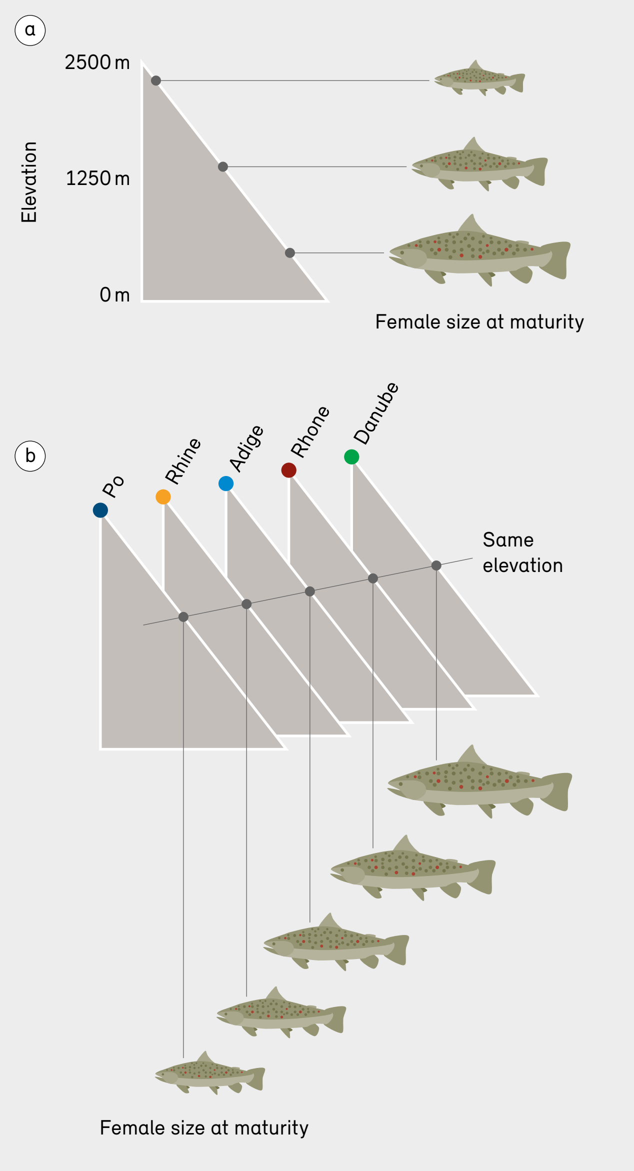
Data source: Progetto Fiumi and Eawag

8.3 Link between female size at maturity and substrate structure

As shown in the study on brown trout in the Latrejebach river described above (Fig. 47), adult female brown trout exhibit a preference for habitat with substrate suitable for spawning, which is partly determined by female body size (Kondolf and Wolman 1993). The females' habitat preference is expected to have been acquired and maintained, probably because occupying a habitat with substrate suitable for spawning can strongly affect their reproductive success. Notably, as well as within-river variability, there is large variation in substrate structure among Swiss mountain rivers (Fig. 48a). For example, in 120 rivers containing brown trout (Progetto Fiumi reference collection of Swiss river fish), the largest mean grain size was about 1.7 times larger than the smallest mean grain size (Fig. 48a). It has therefore been proposed that females mature at a larger size in rivers with a larger mean grain size (Riebe *et al.* 2014). Examining the relationship between female size at maturity and local substrate structure can provide valuable knowledge relevant for fine-tuning strategies for mitigating possible harmful effects of substrate modification on brown trout, such as adding fine/coarse pebbles. In this study, we assessed the body size and maturity status of 562 female brown trout collected from the 120 rivers across Switzerland during the Progetto Fiumi survey (Fig. 48). Specifically, we investigated the link between mean grain size and female size at maturity.

Figure 49

(a) Relationship between elevation and female brown trout size at maturity. (b) Drainage-dependent differences in female size at maturity.



Data source: Progetto Fiumi and Eawag

In general, larger females tended to be assigned as mature regardless of their origin. However, there were differences in maturity status even among same-sized females. Suppose that a larger female size at maturity is favoured in a river with a larger substrate. At a given female size, we would then expect that female trout originating from a river with a larger mean grain size would not be assigned as mature, while female trout originating from a river with a smaller mean grain size would be assigned as mature. Contrary to this expectation, we did not detect a significant relationship between mean grain size and female maturity status. Instead, we found that female maturity status differed with the elevation of the collection sites and across the Swiss drainages (i.e. Adige, Danube, Po, Rhine and Rhone; Fig. 49). First, at a given size, high-elevation female trout were assigned as mature more often than females at lower elevations, meaning that high-elevation female trout exhibit a smaller size at maturity than those at lower elevations (Fig. 49a). Second, at a given size and elevation, the probability of a female trout being assigned as mature differed across the drainages: Po > Rhine > Adige > Rhone > Danube. This indicates that female size at maturity was largest in the Danube and smallest in the Po drainage (Fig. 49b).

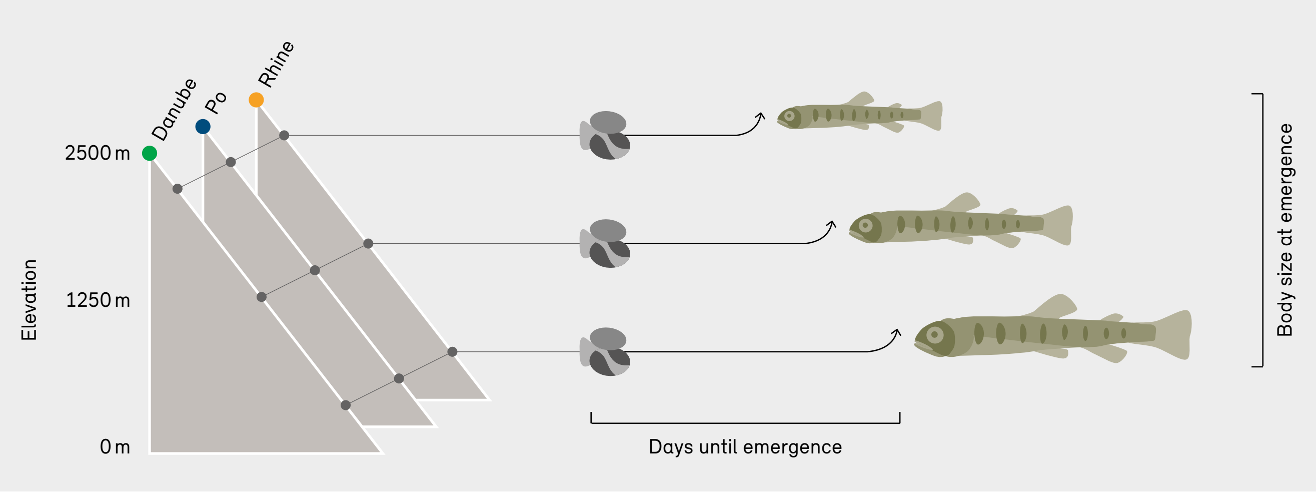
Interestingly, not only female size at maturity but also very early life-history traits, time until emergence, and body size at emergence from the gravel nest differed with the elevation of the collection sites. In an additional study, we reared brown trout embryos from 14 populations from different elevations from three Swiss drainages (Danube, Po, Rhine) in the canton of Grisons. Although we kept the embryos in the same rearing environment (i.e. a common-garden experiment), the time until emergence was shorter and body size was smaller for high-elevation trout than for low-elevation trout (Fig. 50). These differences along the elevation gradient were partly the result of the smaller egg size of high-elevation trout (Fig. 51).

These findings on adult and juvenile trout suggest that environmental factors that vary along an elevation gradient, such as water temperature, conspecific density, predator and prey density, and species composition, could be a critical factor in shaping the whole life history of brown trout. It would be interesting to investigate the adaptive significance of smaller female size at maturity and earlier emergence with smaller body size in high-elevation rivers, and also to determine key environmental factors shaping trait variation along the elevation gradient. Studies exploring mechanisms explaining the drainage specificities in the life-history traits of brown trout would be another interesting next step. It is worth mentioning that intensive stocking activities using several million captive-reared trout could have altered the relationships between elevation, drainage, substrate structure and trout life-history traits in our study (but see Keller *et al.* 2011, 2012). Thus, it would also be useful to examine how stocking history affects female size at maturity and juvenile traits.

Considering the importance of the body size of females in determining their substrate preference (Kondolf and Wolman 1993), the observed variation in female size at maturity is expected to be linked to female substrate preference. For instance, since female size at maturity was found to be smaller for high-elevation trout than for low-elevation trout (Fig. 49a), high-elevation females would be expected to exhibit a stronger preference for smaller substrate. Similarly, since the size at maturity of females from the Po drainage was smallest among the Swiss drainages (Fig. 49b), female trout originating from Po would be expected to exhibit a stronger preference for smaller substrate. Therefore, it could be important to take elevation and drainage specificity into account when fine-tuning substrate modification strategies to benefit brown trout. For instance, the size of fine pebbles used for substrate compensation to improve spawning habitat should be smaller at higher-elevation sites and in the Po drainage than at lower elevation sites and in other drainages.

Figure 50

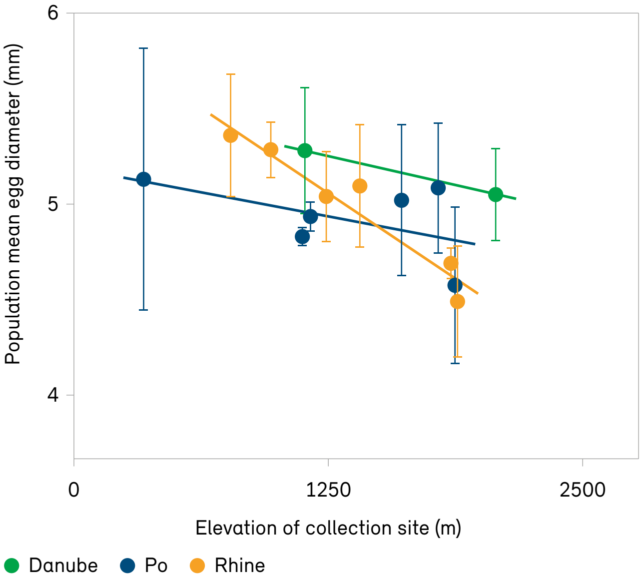
Relationships between elevation of the collection site, drainage, days until emergence, and body size at emergence from the gravel nest. Regardless of the drainage, high-elevation brown trout generally emerged from the gravel nest earlier and with a smaller body size.



Data source: Eawag

Figure 51

Relationships between drainage, elevation of the collection site, and population mean egg diameter of 14 brown trout populations in the canton of Grisons. Error bars denote standard deviation.



Data source: Eawag

8.4 Implications for strategies to support trout populations and improve their habitats

In the present chapter, we report the results from surveys showing: (i) age- and sex-dependent differences in substrate preference (Fig. 47) and (ii) no clear link between female size at maturity and substrate structure, but instead variation in female size at maturity among drainages and across an elevation gradient (Fig. 49). The former results emphasize the importance of maintaining spatial substrate heterogeneity within a river to conserve the important fish species. Considering the female preference for substrate suitable for spawning and the female body size dependency of the substrate preference (Kondolf and Wolman 1993; Riebe *et al.* 2014), the latter results suggest that females' preference for substrate differs depending on the drainage and elevation. Therefore, the drainage and elevation should be considered when fine-tuning strategies for restoring brown trout spawning habitat. For example, while an increase in spatial substrate heterogeneity might improve habitat quality for brown trout overall, sections with relatively small pebbles should be established in the Po drainage, considering the smaller female size at maturity of trout originating there (Fig. 49). However, in our study we did not directly examine how the differences in female size at maturity among drainages and across populations at different elevations are linked to female substrate preference. Therefore, investigating the variation in substrate preference among drainages and across elevations would be an important next step. Moreover, studies on the link between substrate and the ecology of other fish species, particularly species residing in slow-flow rivers (e.g. chub, barbel, stone loach and gudgeon), are needed for a comprehensive understanding of how substrate modification affects the fish community in Swiss rivers.

Moreover, our study provides insight into trout fishery management (Box 11). Female size at maturity differed among drainages and across populations from different elevations (Fig. 49). Similarly, the timing and size at emergence from the nest differed among populations from different elevations (Fig. 50). Suppose that the variation in life-history traits among drainages and across elevations has been shaped and maintained by natural selection associated with environmental variables that vary across the drainages and along the elevation gradient. Implementing uniform fishery management strategies across rivers, including harvest size regulations and stocking strategies, could result in different consequences for the local trout populations, depending on the drainage and elevation.

While fishery management strategies considering the local specificities of trout life-history traits, so-called 'small-scale fisheries management' strategies, have been acknowledged, implementing them is often challenging, as described in Box 11. Further studies on Swiss brown trout ecology are needed to form feasible fishery management strategies. For instance, examining egg size variation across Swiss rivers (e.g. Fig. 51) could provide helpful information for improving stocking strategies. This is because egg size is a key factor determining trout early life-history traits, and eventually growth and survival in later life stages (Einum and Fleming 1999). Suppose that the egg size variation among drainages and elevations observed for Swiss brown trout (Fig. 51) has been shaped and maintained by natural selection acting on the early life stages. Fisheries managers could stock juveniles originating from eggs whose size is similar to that observed in the natural population of a focal stocking site and from the same management unit (individuals within the same unit are assumed to be genetically more similar than those in different units). The phenotypic characters of the stocked juveniles would be then suitable for that site and their genetic characters would be similar to those observed in the wild. Thus, even no changes to the current, relatively coarse management unit (Box 11), fisheries managers could effectively supplement the trout with consideration of local genetic specificity. The accumulation of such knowledge regarding the basic ecology of Swiss brown trout might help set management strategies for this ecologically and economically important fish species while still considering feasibility and genetic integrity.

Box 11: In practice – The challenge of small-scale fishery management

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About one-third of all brown trout catches in Switzerland's rivers are made in the canton of Grisons. Accordingly, angling is of great importance in Grisons. For the past 160 years, the Canton has been the sole holder of fishing rights and has been responsible for fisheries management. For an entire century, river-specific characteristics were only given marginal consideration in fisheries management. There was little differentiation in catch regulations, and management guidelines were geared towards expansion. The function of brown trout as a usable product rather than local, river-specific considerations formed the cornerstones of fisheries management.

Based on the findings from the present study, the previous fisheries management strategy, implemented by the cantonal administrations, would have to be classified as a failure. However, if one takes into account the degeneration of the river habitat, the growing number of anglers, and the lack of knowledge about genetic integrity during the same period, the decisions made at that time are certainly understandable. And where does Canton Grisons stand today in terms of setting goals for fisheries management? The poor condition of the rivers and the high demand for use on the part of fisheries have remained as the boundary conditions. Scientific findings and first-hand experience have led to a new approach to fisheries management over the last 20 years. The limitations and negative effects of 'haphazard' management of brown trout, as well as the problem of poorly differentiated catch size limits, have been recognized. The principle of 'small-scale fisheries management' has been accepted, but it poses considerable challenges to the responsible parties. For example, evaluating the size of brown trout as they enter sexual maturity was possible for only 50 stream segments, within the inventory of 1600 km of rivers and about 2500 m of elevation. Limitations in terms of time, logistics and funding restricted the level of detail at which river-specific catch size limits could be defined. Based on these surveys, 6 minimum catch sizes or catch windows were defined for about 450 river sections, depending on the elevation, river size and fishing pressure. The findings from the study presented here concerning local adaptation of the size of female brown trout at sexual maturity should thus carry more weight in management strategies.

It is particularly difficult to consistently consider local-scale aspects in brown trout management. Until a few years ago, the management units (MUs) were kept large and were based on eight main catchment areas. In the medium term, Canton Grisons aims to define 19 regions as MUs. To fulfil the regional stocking plan, brown trout spawning material from a particular MU should only be used within that MU. The same applies to the offspring of any parent stock. The separation into 19 MUs poses major logistical challenges for the 7 fish hatcheries in the canton of Grisons. For example, in a given hatchery, the fish used for stocking and also the mother strains of up to six MUs must be kept strictly separate. The Canton is aware that there is a wide range of rivers within the 19 MUs in terms of elevation, but further refinement of the MUs into elevation bins is not currently feasible. However, if elevation, rather than geographic unit, is the main driver of local adaptation, then it is worth considering dividing the MUs into cross-regional elevation bins rather than regions (sub-catchments).

Finally, and most importantly, the threshold for stocking requirements must be further refined. Specifically, fish stocking should only be applied where it can be proven that natural spawning cannot make a sufficient contribution to a usable trout stock. The Canton has a legal mandate that includes ensuring sustainable use. Correctly executed fish stocking and river-specific catch regulations continue to be an important component of modern fisheries management.