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Effects of physical habitat features on the density of juvenile brown trout (*Salmo trutta* L.) in a small stream in Bergen, Norway

Master's thesis

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Photo: Lukas Ittner

Juvenile brown trout hiding in the substrate of the river bed.

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Abstract

This study deals with the effects of spawning ground area, spawning ground density, shelter availability (i.e. holes and interstitial spaces in the substrate), substrate composition, riparian vegetation, woody debris, algae cover and moss cover on the density of juvenile brown trout in an anadromous and non-anadromous reach of a small stream in Bergen, Norway. First, habitats were defined based on uniform substrate composition and mapped regarding the aforementioned habitat features, except for spawning grounds, which were mapped during the previous spawning season. Then, electrofishing was performed in each habitat to estimate densities of age classes 0+, 1+ and >1+. Finally, statistical analyses were used to assess the influence of the habitat features on the densities per age class. Spawning ground area and spawning ground density had significant, positive influence on the densities of 0+ and 1+ brown trout (in both reaches), most likely because these variables determine crucially egg density. Spawning ground area was a better predictor than spawning ground density for the density of age class 0+. In contrast, spawning ground density was the better predictor for the density of 1+ brown trout in the non-anadromous reach. This is difficult to explain, but might imply that 1+ fish remained close to their native sites and used other shelter forms provided by the riverbank. Furthermore, shelter availability had significant, positive influence on the density of 0+ and 1+ brown trout in the anadromous reach. This is primarily associated with the heterogeneity of the river bed, which is linked to shelter availability, and thus determines the number of potential territories. Shelter availability was a better predictor for the density of age class 1+ than 0+. Juvenile brown trout in the anadromous and non-anadromous reach seemed to differ in shelter use, perhaps due to distinct intercohort competition. In this context, further research is needed. The densities of >1+ brown trout remained unaffected by spawning ground area, spawning ground density and shelter availability, indicating different habitat preferences. In addition, almost none of the other habitat features influenced fish densities, most likely as a result of the scale used for this study or reduced preferences to these habitat features. Only gravel and stone had significant, positive influence on the density of 0+ and 1+ brown trout in the non-anadromous reach and on the density of 1+ brown trout in the anadromous reach, respectively. This is due to the influence of gravel on spawning ground area and spawning ground density, as well as the influence of stone on shelter availability. The present study shows that densities of juvenile brown trout may be regulated by spawning grounds and shelter availability, corroborating restoration measures aiming to enhance these physical habitat features in degraded rivers.

1 Introduction

The majority of salmonid species (ca. 41 %) occurring in European freshwater ecosystems are considered to be endangered (Freyhof and Brooks 2011). Among the species that face the most dramatic decline in numbers are the brown trout (*Salmo trutta* L.) (Burkhardt-Holm et al. 2005, Freyhof and Brooks 2011, Thorstad and Forseth 2015a) and the Atlantic salmon (*Salmo salar* L.) (Parrish et al. 1998, Aas et al. 2011, Thorstad and Forseth 2015b).

Anthropogenic disturbances in the form of altered, degraded and fragmented stream habitats are probably the most important factors for this negative trend (Aarts et al. 2004, Gosset et al. 2006, Freyhof and Brooks 2011). These disturbances are the result of agricultural activities, deforestation, hydropower development (Baras and Lucas 2001), urbanization (Nelson et al. 2009), aquaculture (Thorstad and Forseth 2015a, 2015b) and other human impacts. Particularly the loss of suitable spawning and juvenile habitats, but also parasites, such as the salmon louse (*Lepeophtheirus salmonis*), appear to be among the primary contributing factors to the trend. The loss of habitats is commonly linked to decreased habitat heterogeneity. In the context of the river bed, reduced heterogeneity can result in the degradation of spawning grounds and a reduction of shelter availability in the substrate. This may be caused by embeddedness through high loads of fine sediments (Suttle et al. 2004, Bolliet et al. 2005), canalization (Millidine et al. 2012) or deficits of suitable substrate sizes (Finstad et al. 2007).
However, salmonids, which exhibit a highly complex habitat use, are dependent on these physical habitat features to fulfill their ontogeny. Thus, both spawning grounds and shelter availability may play a key role in determining the population density (= number of individuals of a species per unit area or spatial unit, Wehner and Gehring 2007) of salmonids (Forseth and Harby 2014). Brown trout and Atlantic salmon often occur in ecosystems with a high degree of impaired physical habitat features and therefore are particularly threatened species.

Population density usually varies over time and space, and is affected by distinct factors, which interact in complex ways. In the context of salmonids, population density is regulated by mortality, im- and emigration, as well as recruitment. Its long long-term maximum is set by the carrying capacity of a habitat (Jonsson and Jonsson 2011). These regulators, in turn, are directly or indirectly affected by density-dependent factors, acting negatively (e.g.

predation) or positively (e.g. predator protection), and density-independent factors (e.g. water flow).

For instance, if the population density is high in relation to the habitat's resources (e.g. food availability), then density-dependent regulation mechanisms (e.g. inter-/intraspecific competition) increase mortality rates (Elliott 1994). This therefore leads to a reduction of population density, which finally adapts to the stream's carrying capacity (Elliott 1994). In the same way, also growth rates may be negatively related to population density (Jenkins et al. 1999). On the other hand, if the population density is low in relation to the habitat's resources, then density-independent factors (e.g. reduced water flow following drought) may play an important role for regulating population density, irrespective of density-dependent mechanisms (Jonsson and Jonsson 2011). Figure 1 illustrates an example of factors that influence population density and how these may interact.

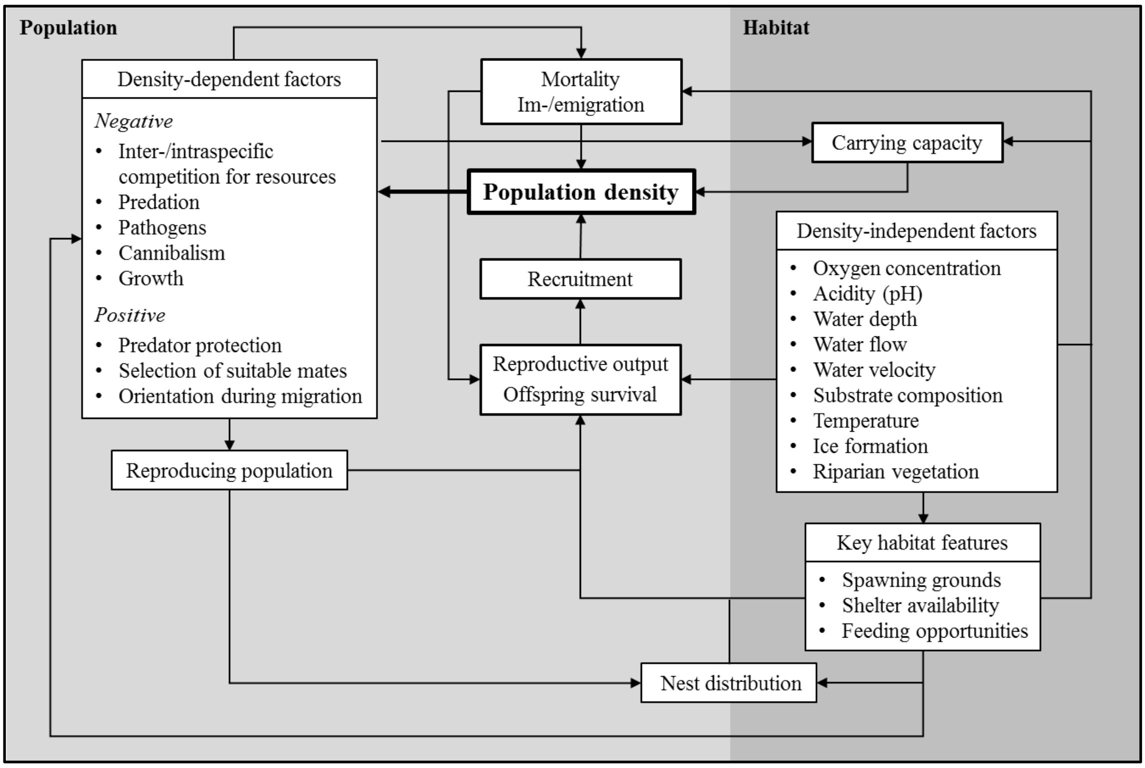

Figure 1: An example of possible factors influencing the population density of salmonids. Arrows indicate potential ways how these might interact.

Extremely high mortality rates, caused by density-dependent mechanisms, typically occur in the early life stages of salmonids, i.e. during the so-called alevin and/or parr stage (Elliott 1994). In these life stages, inter- and intraspecific competition for habitat- and food-related resources represents the most important density-dependent regulation mechanism. This is especially the case in territorial fish species, such as brown trout and Atlantic salmon, which use a very similar ecological niche. Physical habitat features, such as spawning grounds and shelter availability, can be among the limiting resources of habitats and act as bottlenecks in streams (Forseth and Harby 2014) by regulating fish density. Although identified early as key habitat features (Allouche 2002), there is still a limited number of studies dealing with the effects of spawning grounds and shelter availability on the density of salmonids.

The quality and quantity of spawning grounds substantially influences spawning conditions in streams and are therefore of particular importance for the reproductive output, a major determinant for recruitment (Jonsson and Jonsson 2011, Pulg et al. 2013). In this context, it was demonstrated that the spawning ground area is positively correlated with the density of juvenile brown trout and grayling (*Thymallus thymallus* L.) (Pulg 2009). It was also found that nest area (= the pit dug by a female where she spawns eggs, Jonsson and Jonsson 2011) is positively correlated with the density of 0+ Atlantic salmon (Teichert et al. 2011). In addition, the density of redds (= series of nests usually placed in a row by a female, Jonsson and Jonsson 2011) was detected to be positively correlated with the density of 0+ brown trout (Beard and Carline 1991).
Of no less importance is the spatial distribution of spawning grounds and nests therein, affecting significantly the fish production (Forseth and Harby 2014) and density distribution (Einum et al. 2008a), respectively. Despite the awareness that spawning ground area, as well as redd density and distribution essentially affect fish density, it is not clear how spawning ground density influences density.

Besides reproductive output, recruitment is determined by offspring survival, in which shelter availability plays a crucial role. Shelter fulfills two major tasks: Providing protection from predators and reducing energy expenditure. Thus, shelter availability is of particular importance for the survival of alevins and parrs. Depending on the age class, body size, biotic (e.g. food availability) and abiotic habitat factors (e.g. temperature, water flow etc.), as well as other factors (e.g. day time, season, stocked vs. wild fish etc.) shelter use can differ (Jonsson 1989, Vehanen et al. 2000, Griffiths and Armstrong 2002). In addition, there are different forms of shelter used, typically accumulations of woody debris, aquatic and riparian vegetation, larger stones, as well as holes and interstitial spaces in the substrate. The latter is the main subject of this study and meant hereafter when using the term shelter availability. Studies analyzing the relationship between shelter availability and fish density tested it either as a non-measurable variable in the form of substrate heterogeneity or as a measurable variable by quantifying number and size of holes and interstitial spaces in the substrate. In doing so, shelter availability has been shown to be positively correlated with the density of juvenile Atlantic salmon under both semi-natural (Kalleberg 1958, Finstad et al. 2009) and natural conditions (Dolinsek et al. 2007, Venter et al. 2008, Finstad et al. 2009). Additionally, it was found that shelter availability is negatively correlated with the growth performance of juvenile salmonids (Finstad et al. 2007, 2009), because of behavioral changes (Finstad et al. 2007). Also, the spatial arrangement of shelter availability plays an important role as a factor influencing the density and distribution of Atlantic salmon and brown trout, particularly on the local-scale (Finstad et al. 2009, Normann 2011).

Evidently, the density of juvenile brown trout and Atlantic salmon is regulated by spawning grounds and shelter availability, acting as limiting resources in the course of density-dependent mechanisms. Thereby, the number of juvenile fish joining the population (recruits, Jonsson and Jonsson 2011) is determined. Despite the awareness that spawning grounds and shelter availability may play a key role in controlling population densities, their combined effects under natural conditions have hardly been investigated. This, however, would be reasonable, since juvenile fish exhibit low mobility during the early life stages, and therefore require habitats with spawning grounds and shelter availability in close vicinity (Bjornn and Reiser 1991) in order to survive. In the context of shelter availability, specifically surveys about brown trout in small streams are lacking, although these represent their typical spawning habitats. Larger streams, in contrast, are often dominated by Atlantic salmon, representing here a stronger competitor (Jonsson and Jonsson 2011). Furthermore, shelter availability was hitherto exclusively studied for Atlantic salmon and brown trout in anadromous waters, while resident salmonids (e.g. resident brown trout) were neglected. However, these might exhibit differences in shelter use, because of distinct intraspecific competition and predation risk.

Based on the knowledge gaps described above, the present study aims to investigate the effects of spawning ground area, spawning density and shelter availability on the density of anadromous and resident juvenile brown trout in a small stream. The brown trout constitutes an interesting and proper subject for this survey, due to the highly variable habitat use during its ontogeny and different forms (Jonsson 1989, Heggenes et al. 1999, Jonsson and Jonsson 2011). The ontogeny of the brown trout is described in more detail below (chapter 2).

In the framework of this study the following hypotheses are analyzed:

(i) The density of 0+ and 1+ brown trout is positively correlated with spawning ground area and spawning ground density.

(ii) The density of 0+ and 1+ brown trout is positively correlated with shelter availability.

(iii) Spawning ground area and spawning ground density are the best predictors for the density of 0+ brown trout, whereas shelter availability is the best predictor for the density of 1+ brown trout.

(iv) Spawning ground area and spawning ground density have a similar effect on the density of 0+ and 1+ brown trout in both the anadromous and non-anadromous reach, while shelter availability is a better predictor for the density of 0+ and 1+ brown trout in the anadromous reach.

To test these hypotheses, a small stream in Bergen, Norway, with an anadromous and non-anadromous reach was chosen and divided into distinct habitats based on substrate composition. The habitats were mapped regarding spawning grounds, shelter availability, substrate composition, riparian vegetation, woody debris, algae cover and moss cover, and finally fished. By means of statistical analyses it was investigated how the aforementioned habitat features affected the densities of 0+, 1+ and >1+ brown trout in the anadromous and non-anadromous reach.

This study aims to contribute to a better understanding of the relationships between physical habitat features and the density of juvenile brown trout. New insights in this complex issue may have implications for restoration and conservation measures, which are essential to promote and preserve threatened fish species (Einum et al. 2008a and references therein).

2 Ontogeny of the brown trout

Brown trout are among the most studied salmonid species (Klemetsen et al. 2003, Northcote and Lobón-Cerviá 2008) and reveal high variations in habitat use during their ontogeny (Elliott 1994, Jonsson and Jonsson 2011).

They commonly spawn over stone and gravel bottoms in running waters. Lake spawning has been observed (e.g. Brabrand 2002), but can be considered as an exception (Pulg 2009). Reproduction takes place during autumn and winter, dependent on water temperature, and therefore varies with latitude and altitude (Klemetsen et al. 2003, Riedl and Peter 2013). Brown trout females dig nests in the substrate of the river bed at locations, where physical habitat factors (i.e. water velocity, water depth, substrate size, percentage of fine sediments) (Kondolf and Wolman 1993, Armstrong et al. 2003, Louhi et al. 2008) ensure for sufficient oxygen supply of the eggs. In the course of the spawning process, females spawn their eggs over the nests, while males fertilize these simultaneously by releasing milt. After sinking of the fertilized eggs into the interstitial of the substrate within the excavated nests, females finally cover these with gravel and stones (Klemetsen et al. 2003, Pulg 2009). The incubation period of the eggs, i.e. the time during which the embryo in an egg develops before hatching, ranges between one to several months (408 degree-days according to Elliott 1994), depending majorly on water temperature (Klemetsen et al. 2003, Jonsson and Jonsson 2011).

The larvae of the brown trout, also called alevins, commonly hatch during the following spring (Klemetsen et al. 2003). In the first weeks after hatching the alevins stay within the interstitial of the substrate, feeding exclusively on yolk from a yolk sac beneath their belly (Klemetsen et al. 2003). After another ca. 300 day degrees, when most of the yolk sac is consumed (Klemetsen et al. 2003), the alevins enter the fry-stage. During this life-stage the fish emerge from the interstitial of the substrate and start to live in the river. After emergence the fry stay either in or close to the area of the spawning ground or move up- or downstream (Klemetsen et al. 2003 and references therein), starting external feeding (Jonsson and Jonsson 2011) and setting up territories. In this early life stage natural mortality rates are extremely high due to competition for food and space (Jonsson and Jonsson 2011).

The transition to the parr-stage takes place in the first summer after hatching. During this stage mortality rates decrease again. Juvenile brown trout feed majorly on epibenthic and drifting arthropods (e.g. insect larvae), but also on surface arthropods (e.g. flying insects), as well as small crustaceans and molluscs (Jonsson 1989, Klemetsen et al. 2003, Jonsson and Jonsson 2011). With increasing body size and mobility, the juvenile brown trout disperse further, as habitat requirements for food and space shift (Klemetsen et al. 2003). Optimal territories for parr are those with a high food availability in close vicinity (energy uptake), minimized costs for food intake and swimming activities (energy expenditure) and low predation risk (Jenkins 1969, Bachmann 1984, Fausch 1984).

Shallow water areas (< 30 cm) with gravel substrate, moderate water velocities (0.2-0.5 m/s) and numerous shelter opportunities, such as woody debris, aquatic and riparian vegetation, large stones, undercut banks and interstitial spaces and holes in the substrate, are preferred (Heggenes et al. 1999, Armstrong et al. 2003, Klemetsen et al. 2003). Brown trout have variable life histories, which exhibit essential differences in migration behavior, habitat use and appearance during the sub-adult and adult stage (Pulg 2009). Anadromous brown trout undergo smoltification usually at a length of 10-15 cm (Jonsson and Jonsson 2011) and migrate to the ocean to feed, mostly staying in the estuaries or coastal areas (Klemetsen et al. 2003). Besides this form, there are freshwater resident brown trout, which can be distinguished in two further forms: Stream-dwelling brown trout and lacustrine brown trout. According to their name, stream-dwelling brown trout fulfill their ontogeny exclusively in running waters, often because there is no access to a lake or the ocean. If accessible, migrations to richer feeding habitats, for instance to a larger river or river sections downstream, can be performed (Klemetsen et al. 2003). Lacustrine brown trout, finally, migrate to lakes for feeding. All three forms of brown trout may occur in the same population and reproduce in their natal streams. Additionally, anadromous and lacustrine brown trout may return to their natal streams for wintering. Also, intermediate forms have been described.

Anadromous and lacustrine brown trout often exhibit a silverfish coloring with black dots and reach large body sizes; stream dwelling brown trout, in contrast, commonly show a yellow to brown coloring with black and red dots and reach smaller sizes. While stream-dwelling brown trout often mature with a length between 15 and 25 cm, anadromous and lacustrine brown trout reach maturation with a length of 40-60 cm (Pulg 2009).

3 Material and methods

This chapter starts with a brief description of the study design to get a gross overview about the different working steps of the present thesis, and how these were linked to each other. Then, the study area is presented with emphasis on its abiotic and biotic characteristics. Subsequently, the study sites are shown and described in more detail. Also, the most important anthropogenic impacts present in the study area, as well as the conducted restoration measures are demonstrated. Finally, each working step is explained comprehensively, following the chronological performance of this study.

3.1 Study design

This study is divided into habitat mapping (chapter 3.3) and fish sampling (chapter 3.4) in the field, and data analysis (chapter 3.5). In the course of habitat mapping, study reaches were subdivided into habitats based on substrate composition (chapter 3.3.1). In doing so, areas exhibiting similar substrate sizes were defined as one habitat, independent of their size or any other environmental factors. Subsequently, specific habitat features were mapped in each previously defined habitat, focusing primarily on shelter availability (chapter 3.3.3), substrate composition, riparian vegetation, woody debris, algae cover and moss cover (chapter 3.3.4). Spawning grounds were mapped briefly after the previous spawning season (chapter 3.3.2). Following on from habitat mapping, electrofishing was carried out in each habitat (chapter 3.4.1). Based on the absolute frequency of fish caught per habitat and age class, densities for 0+, 1+ and >1+ brown trout were calculated. In the end, data sets obtained from habitat mapping and electrofishing were connected and statistically analyzed in order to investigate how habitat features affect the densities of juvenile brown trout.

3.2 Study area

The present study was carried out in the Apeltun drainage basin, situated in the Bergen Municipality, Hordaland County, Norway. It is located in the valley Nordåsdalen and discharges in the southeast into the fjord Nordåsvannet. It has an area of ca. 6.6 km^2 and a mean discharge of ca. 400 l/s (Pulg et al. 2011). The Apeltun drainage basin includes three lakes, the Apeltun- (0.1 km^2, 32 m.a.s.l.), Igla- (0.017 km^2, 49 m.a.s.l.), and Trannevannet (0.047 km^2, 54 m.a.s.l.) (Pulg et al. 2011). These lakes are drained and connected to each other by several streams, differing regarding discharge. The location of the study area in Norway is shown in Figure 2.

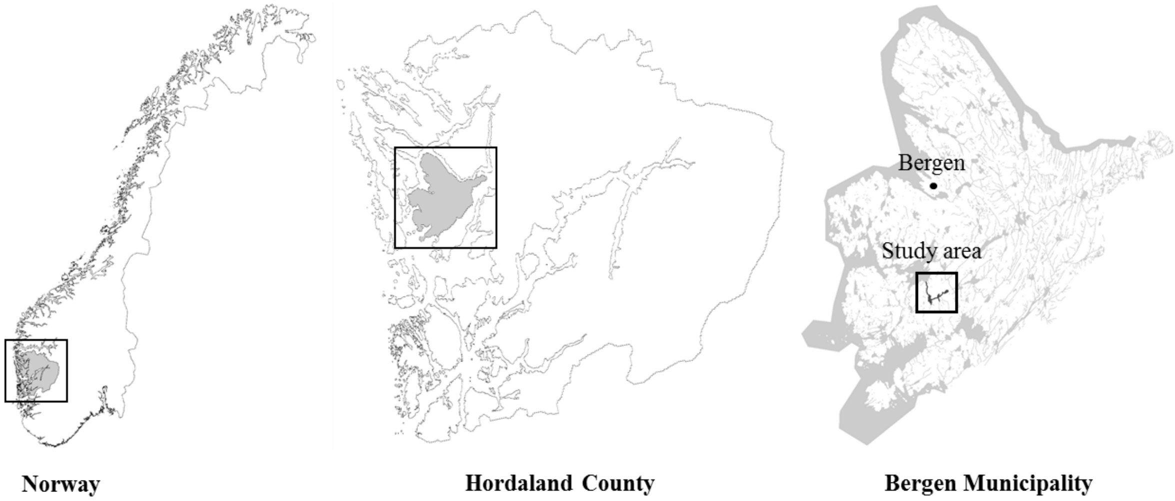

Figure 2: Location of the study area in Norway.

3.2.1 Habitat

Given several morphological alterations, which will be discussed more detailed in chapter 3.2.5, the environmental status of the anadromous reach was considered as bad according to the Water Framework Directive (Pulg et al. 2011). This was majorly associated with artificial migration barriers, channelization and partially water pollution.

Originally, the anadromous reach is estimated to have covered a length of ca. 2420 m (ca. 10808 m^2). In 2010 only 56 % of the original anadromous reach were accessible, since a culvert, called Osbanenkulverten, prevented fish migration. Because of this situation, the study area offered the possibility to compare brown trout in an anadromous reach (downstream of Osbanenkulverten) and non-anadromous reach (upstream of Osbanenkulverten). In 2010 only 18 % of the original anadromous reach were without human induced morphological alterations, meaning that ca. four fifth of the area has been modified morphologically since 1951.

According to Pulg et al. (2011) the stream area was divided into four main habitat types (spawning area, riffle, run, culvert). In the anadromous reach riffles were the dominating habitat type (44.4 %), followed by runs (22.1 %) and culverts (19.1 %). Spawning areas (Figure 3) were available to a lesser extent (14.4 %) and were chiefly concentrated in four locations situated in the upper stream sections of the anadromous reach. Moreover, there were some smaller spawning areas patchily distributed over the entire anadromous reach. Table 1 shows the original anadromous reach (1951) based on aerial photos and the anadromous reach of 2010, as well as areas of different habitat types related to the anadromous reach of 2010 (Pulg et al. 2011).

Table 1: Original (1951) and anadromous reach of 2010, absolute and relative area proportions of different habitat types (spawning area, riffle, run, culvert) based on the anadromous reach of 2010, as well as original and anadromous reach of 2010 without morphological alterations (Pulg et al. 2011).

Anadromous reach	Original (1951)	2010		Reduction
	(m^2)	(m^2)	%	%
Total	10808	6025	55.7	44.3
Spawning area	-	868	14.4	-
Riffle	-	2677	44.4	-
Run	-	1329	22.1	-
Culvert	-	1151	19.1	-
Without morphological alterations	10808	1994	18.4	81.6

The non-anadromous reach covered ca. 40 % of the original anadromous reach in 2010 and contained in general the same habitat types and similar morphological alterations as the anadromous reach. Spawning areas were concentrated in four locations, revealing good habitat quality (Figure 5). The gradient and discharge was on average lower in the non-anadromous reach (personal observation). In the context of the river bed, this resulted in reduced substrate sizes and increased proportions of fine sediments (Figure 6). In contrast, the anadromous reach, with higher gradients, often exhibited larger substrate sizes (Figure 4). In general, there were more alternative shelter opportunities, for instance in the form of undercut banks (Figure 7) and woody debris (Figure 8), in the non-anadromous reach.

Figure 3: Spawning area with good habitat quality in the anadromous reach.

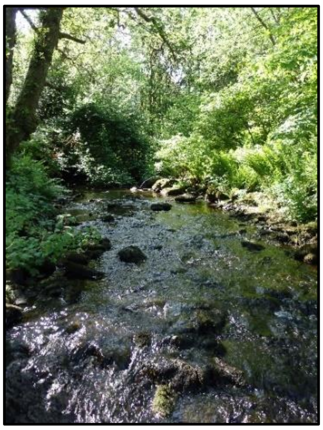

Figure 4: Gradients are higher and substrate sizes larger in the anadromous reach.

Figure 5: Spawning area with good habitat quality in the non-anadromous reach.

Figure 6: Gradients are lower and substrate sizes smaller in the non-anadromous reach.

Figure 7: Undercut banks occurred in higher frequencies in the non-anadromous reach.

Figure 8: Accumulations of woody debris occurred in higher frequencies in the non-anadromous reach.

3.2.2 Water quality

The Apeltun drainage basin can be characterized as nutrient-rich and moderate calcareous (Pulg et al. 2011). It is partially subject to water pollution, which is described in more detail below. Physical and chemical water parameters were surveyed in May 2010 at the inlet into the fjord Nordåsvannet. The results of the water quality analysis are presented in Table 2.

Table 2: Values of conductivity, water temperature, pH, total phosphor (TP), total nitrogen (TN), total organic carbon (TC), ammonium (NH_4), nitrate (NO_3), alkalinity (Alk), aluminum (Al) and calcium (Ca) of the water quality analysis from May 2010.

Water quality parameter	Value
Conductivity (µS/cm)	270
Water temperature (°C)	11.7
pH	8.1
TP (µg/l)	21
TN (µg/l)	1265
TC (mg/l)	3.5
NH_4 (µg/l)	>5
NO_3 (µg/l)	703
Alk (mmol/l)	0.401
Al (µg/l)	17
Ca (mg/l)	15.3

The Apeltunvannet has developed a stable salt water layer caused by intensive salting of roads and parking lots in the drainage basin, and therefore represents a meromictic lake. The layer ranges from the bottom at maximum 28 m depth up to ca. 5 m depth and exhibits only very low oxygen concentration (< 10 % at a depth exceeding 9 m).

3.2.3 Fish population

Given the low number of spawning areas due to a high degree of human impacts, there was still a relatively high fish production in parts of the Apeltun drainage basin. This is primarily linked to the high amount of nutrients alongside with other suitable habitat conditions there (e.g. substrate, oxygen concentration, shelter availability etc.). Brown trout was the dominating fish species. There were an anadromous (downstream of Osbanenkulverten) and a freshwater resident brown trout population (upstream of Osbanenkulverten) in the study area. Juvenile brown trout cannot be strictly referred to as anadromous or resident. The life histories (i.e. anadromous or freshwater resident) of both the parental fish and the juvenile fish are unclear. As a consequence, in the present study it is distinguished between juvenile brown trout in the anadromous and non-anadromous reach. Atlantic salmon occurred in the lower stream sections close to the fjord, but in substantially lower numbers. Also, European eel and flounder could be occasionally found here.

In 2010 densities of juvenile brown trout (i.e. age classes 0+, 1+, 2+) amounted to maximum 402/100 m^2 and 246/100 m^2 in spawning areas with good habitat quality (Pulg et al. 2011). Stream reaches with lower habitat quality, for instance those with a high degree of morphological alterations showed densities of juvenile fish lower than 6/100 m^2 (Pulg et al.

2011). According to Pulg et al. (2011) the total number of juvenile brown trout was estimated to 4700 in the anadromous reach of 2010 and 12900 in the original area. Thus, fish production in the anadromous reach of 2010 amounted to ca. one third compared to the original production.

3.2.4 Study sites

Field work took place in five different study reaches, hereinafter referred to as study reaches 1, 2, 3, 4 and 5 (Table 3, Figure 9). The main part of this study was performed in study reaches 1, 3 and 5, situated in the small stream Apeltunelva (mean width < 5 m), representing a typical spawning stream for anadromous brown trout.

Study reach 1 was situated between the Apeltun- and Nordåsvannet, whereas study reaches 3 and 5 were located between the Apeltun- and Iglavannet and the Igla- and Trannevannet, respectively, connecting these water bodies. Study reaches 2 and 4 were also located in small-sized streams, draining into the Apeltun- and Iglavannet, respectively.

Study reaches 1, 2 and 3 were accessible for anadromous fish up to the Osbanenkulverten in study reach 3, acting as permanent migration barrier. In contrast, the upper part of study reach 3, as well as study reaches 4 and 5 were not accessible for anadromous fish and exhibited resident fish populations. Study reach 1 was the longest and largest one, followed by study reach 3; the remaining study reaches were relatively small regarding length and area. In the following, location, length, area and number of the defined habitats according to each study reach are presented in Table 3. Additionally, Figure 9 gives an overview about the study area and sites.

Table 3: Location (latitude and longitude at the inlet), length, area and absolute number of habitats (N_H) defined per study reach.

Study reach	Location	Length (m)	Area (m^2)	N_H
1	60°18’39.5752’’ N, 5°19’35.5863’’ E	1284.3	5033.8	16
2	60°17’39.4352’’ N, 5°20’7.9538’’ E	137.7	207.3	2
3	60°17’49.4580’’ N, 5°20’10.9880’’ E	375.4	1306.3	8
4	60°17’57.8867’’ N, 5°20’48.9564’’ E	180.2	306.0	3
5	60°17’58.9726’’ N, 5°20’50.4960’’ E	264.6	763.9	2
Sum		2242.2	7617.3	31

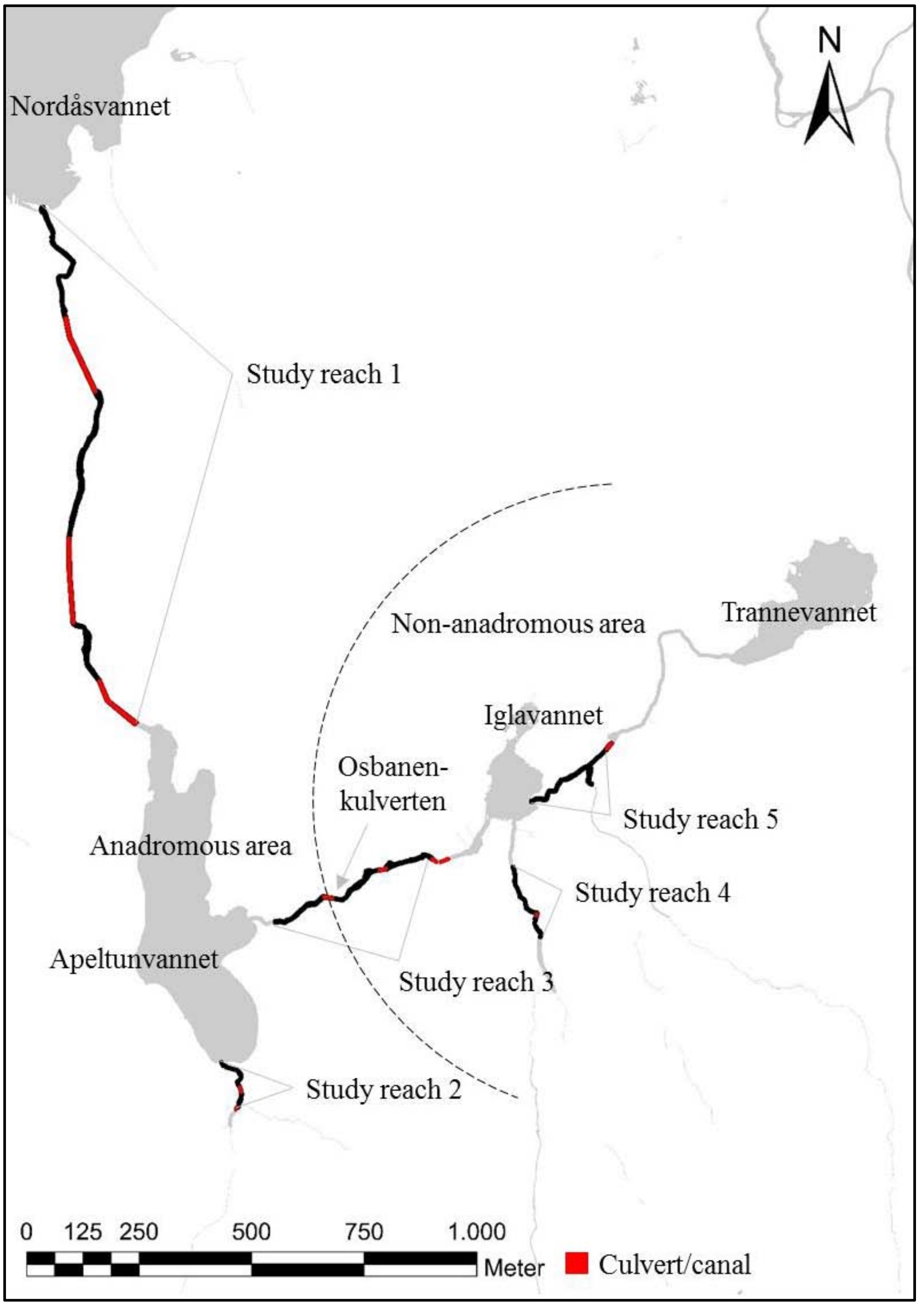

Figure 9: Location of the study sites in the study area. The Osbanenkulverten acted as artificial migration barrier and separated the anadromous from the non-anadromous area.

3.2.5 Anthropogenic impacts

Typical urban impacts can be found in the entire study area. Culverts (Figure 10), canals (Figure 11), bank stabilizations in the form of concrete walls (Figure 12) and water pollution (Figure 13) represent the dominating anthropogenic impacts. Further, a whole stream reach with an area of ca. 500 m^2, which drains into the Apeltunvannet, flows within a subterraneous canal, and there are partially sections of the stream with removed riparian vegetation.

The culverts and the concrete canal amount to almost one third of the anadromous reach of 2010, and thus impair fish production to a large degree. In this context, fish production was particularly reduced because of impaired migration possibilities and lacking spawning areas. The latter is especially caused through absent or reduced natural addition of suitable substrate due to erosion protection. This influences the overall substrate transport and thus also affects stretches without direct anthropogenic impacts (Pulg et al. 2011).

Apart from that, water pollution also plays an important role for fish production. The pollution is caused by waste water, road salt and further unknown sources. Particularly TN- and TP-values (Table 2) indicated nutrient pollution. Moreover, high salinity values, up to ca. 3 PSU, were detected and may represent a potential hazard for the reproduction success of salmonids. In some places, water pollution may be exacerbated through reduced infiltration potential because of constructed and sealed areas.

Figure 10: Culverts are the central human impact in the study area.

Figure 11: The concrete canal in study reach 1 essentially reduces habitat quality.

Figure 12: Bank stabilization in the form of a stone wall.

Figure 13: Water pollution is a major problem in the study area.

3.2.6 Restoration measures

Several restoration measures already took place in the study area since 2009, aiming to increase the environmental status of the study area. Among these measures were chiefly the addition of suitable gravel (Figure 14) to improve and create spawning areas, ripping of the river bed's substrate to improve juvenile habitats by increasing shelter availability, installation of metal bars and large stones in the concrete canal (Figure 15) to improve fish migration, placing of substrate in the culverts (Figure 16) to improve the river bed's conditions and construction of two fish ways (Figure 17) to reestablish connectivity to the non-anadromous reach. The lower fish way was built in 2009 and is located relatively close to the inlet in the Nordåsvannet. The upper fish way was built during summer 2015 at the Osbanenkulverten in order to extend the anadromous reach. Thereby, the anadromous reach was almost doubled. Additionally, migration conditions were/are improved by regular cleanings of the rusts occurring at some culverts.

Water quality, finally, is planned to be enhanced by reducing the sources of pollution (e.g. wastewater, road salt, rubbish). For instance, waste water should be directly piped into the wastewater system and to a wastewater treatment plant. In this context, regular analyses were/are conducted to control specific water quality parameters. Also, it has been started to remove the permanent salt layer from the Apeltunvannet. In doing so, the salinity was/is reduced by pumping out water from the layer, which finally will lead to a mixing of the surface and the deep waters.

Apart from the measures carried out, further ones are planned for the future. For instance, it is planned to remove the concrete canal and restore the river course in order to enhance habitat quality and reduce flood risk in this area. Further, bank stabilizations, such as concrete walls, shall be removed and restored. Finally, the stream reach flowing in the subterraneous canal is projected to be opened and restored. Both measures would extend the stream area and essentially augment the environmental status.

By realizing all projected restoration measures, the original fish production might be reached in the Apeltun drainage basin (Pulg et al. 2011).

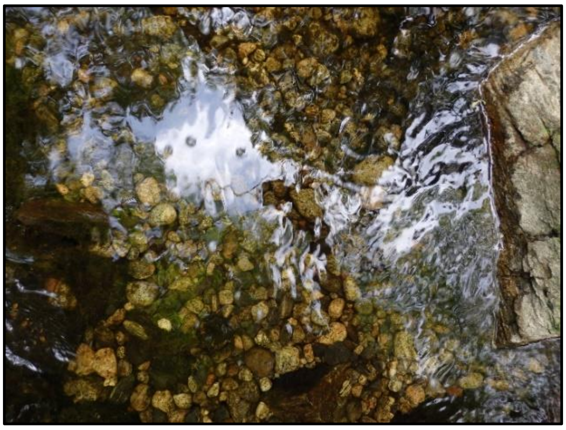

Figure 14: Addition of suitable gravel to improve spawning conditions.

Figure 15: Metal bars and large stones to improve fish migration.

Figure 16: Substrate was placed in some culverts to improve the river bed's conditions.

Figure 17: A fish ladder was installed to reestablish connectivity to the non-anadromous reach.

3.3 Habitat mapping

Habitat mapping took place on the 15th, 18th, 19th and 20th of Mai, as well as on the 12th, 15th, 16th and 18th of June 2015. Mapping always was carried out upstream, starting from the lower end of each study reach. In the following each working step is described, focusing in particular on the different habitat features mapped.

3.3.1 Definition of habitats

Initially, specific habitats were defined based on uniform substrate compositions to obtain homogenous areas with similar substrate sizes. This is reasonable, as spawning grounds and shelter availability are closely linked to the river bed's substrate and their influence on fish densities should be compared between the habitats. Whereas the functioning of spawning grounds is dependent on specific substrate sizes (Armstrong et al. 2003), shelter availability is positively correlated with substrate size (Jocham 2010, Forseth and Harby 2014).

Visual surveys were carried out applying dominating and sub-dominating substrate classes (silt: < 0.06 mm, sand and fine gravel: 0.06-20 mm, gravel: 2-6 cm, stone: 6-20 cm, boulder: 20-40 cm, bedrock: > 40 cm; Wentworth 1922, Forseth and Harby 2014) to divide the study reaches into habitats. A total number of 31 habitats were defined throughout the study reaches, partially differing strongly in area (range = 24.5-802.5 m^2, mean = 245.7 m^2 ± 222.2 SD) and length (range = 10.8-219.8 m, mean = 72.3 m ± 55.2 SD) (Table 4). Finally, study reach 1 comprised 16 habitats, study reach 2 two habitats, study reach 3 eight habitats, study reach 4 three habitats and study reach 5 two habitats (Table 3).
In study reach 1 two habitats were culverts and one was a concrete canal (Table 4). In addition, there were several culverts in the other study reaches (Figure 9). Habitats 1 and 2 were not included in statistical analyses, because of their proximity to the fjord and salinity concentrations. Thereby, biased values through too high salinity and permanent water level fluctuations should be prevented.

3.3.2 Spawning grounds

Spawning grounds were detected by means of visual surveys during December 2014, wading and snorkeling (Forseth and Harby 2014, Pulg et al. 2016). Only those spawning grounds were considered, exhibiting clear indications of spawning activities in the form of redds. After locating spawning grounds, these were drawn in aerial photos, since GPS technology did not work in the study area because of reception problems (riparian vegetation). To record the spawning grounds as precise as possible, specific map elements, such as buildings, contour lines etc., served as landmarks.

Then, the information of the maps was transferred and digitalized in ArcGIS 10.2 (ESRI, Redlands, CA, USA), in order to compute values for spawning ground area and spawning ground density for each habitat. Subsequently, absolute values of spawning ground area and spawning ground density were standardized to m^2/100 m^2 and n/100 m^2 per habitat, respectively. Finally, spawning ground area and spawning ground density were divided each into three classes. The classes were developed according to equal percentiles based on the total number of relevant cases. Accordingly, the following classes were built for spawning ground area: low (< 1.1 m^2/100 m^2), moderate (1.1-6.0 m^2/100 m^2) and high (> 6.0 m^2/100 m^2). Analogously, classes for spawning ground density were defined as follows: low (0/100 m^2), moderate (1-2/100 m^2) and high (> 2/100 m^2).

3.3.3 Shelter availability

Shelter availability was measured according to Finstad et al. (2007). In doing so, shelter availability was quantified by measuring how many times (= number of shelters) and how far down (= size of shelters) a plastic hose (diameter = 13 mm) could be inserted into interstitial spaces in the substrate within a defined area (0.25 m^2) of a steel frame (0.50 x 0.50 m) (Figures 18 and 19).

Figure 18: Plastic hoses to measure number and size of shelters.

Figure 19: Steel frame (0.50 x 0.50 m) to measure the shelter availability in a defined area (0.25 m^2).

There are three size categories (S1: 2-5 cm, S2: 5-10 cm, S3: > 10 cm), represented by markings (adhesive tape) on the hose at 2, 5 and 10 cm (from the lower end), in order to measure shelter size (Figure 18). Accordingly, size category S1 is recorded if the hose can be inserted as far down that the marking at 2 cm is exceeded, while the marking at 5 cm remains visible. Size category S2 is recorded if the marking at 5 cm is exceeded, while the marking at 10 cm remains visible. Size category S3, finally, is recorded if the marking at 10 cm is exceeded and there are no markings visible any more. The number of shelters measured for each size category can be summed up and weighed to obtain the final shelter availability value by means of the following formula (Forseth and Harby 2014):

Shelter availability = S1 + S2 x 2 + S3 x 3

According to Forseth and Harby (2014), there are three shelter availability classes, reflecting shelter availability in terms of number and size: low (< 5), moderate (5-10) and high (> 10). Since several measurements were conducted per habitat, a mean shelter availability value was calculated by dividing the sum of all shelter availability values by the number of measurements.

To guarantee for randomly distributed measurements, the steel frame was thrown into the stream. In doing so, the measurements should be representatively distributed according to the habitat. This means that sampling should cover different areas of the river bed, for instance one sample in the middle of the river and two closer to the left and right riverbank. One throw, i.e. the quantification of shelter availability within the area of one steel frame, constituted one measurement. In frame of this study three to four measurements were carried out in each habitat, depending on the habitat's area. Three measurements were taken in habitats with areas < 400 m^2, whereas four measurements were conducted in habitats exhibiting areas ≥ 400 m^2. In total, 99 measurements were performed in all 31 habitats; three measurements were carried out in 25 of the 31 habitats and four measurements in the remaining six habitats.

Diving equipment (diving mask, snorkel, diving suit) was used to ensure a precise detection of each interstitial space. In five habitats specific structures of measurably size, for example undercut stone or concrete walls, were included in the shelter measurements, to guarantee for representativeness. This means, for instance, that two measurements were carried out within the river and one closer or within a stone wall located along the riverbank. Shelter availability is a dimensionless value, and therefore had not to be standardized to 100 m^2.

3.3.4 Further habitat features

In addition to spawning grounds and shelter availability, the following habitat features were recorded in each habitat: substrate composition (silt: < 0.06 mm, sand and fine gravel: 0.06-20 mm, gravel: 2-6 cm, stone: 6-20 cm, boulder: 20-40 cm, bedrock: > 40 cm), riparian vegetation, woody debris, algae cover and moss cover. These habitat features were recorded by visual estimates and as percentages (accuracy 5 %) related to the habitat's area.
Documenting these habitat features was important, since they are partially linked to spawning grounds and shelter availability (i.e. substrate composition), and may also affect

fish densities. The values of all further habitat features can be found in the appendix (chapter 9.3, Table 15).

3.4 Fish sampling

Fish sampling was performed by the LFI (Laboratory for freshwater Ecology and Inland fisheries) on the 28th, 29th, 30th of September and 1th of October 2015 (Pulg et al. 2016). Electrofishing always was performed upstream, starting from the lower end of each study reach. This chapter explains the electrofishing method used in this study, and describes how age classes were developed and how fish densities were estimated.

3.4.1 Electrofishing

Electrofishing was based on the transect method according to Forseth and Forsgren (2008). In doing so, single-pass electrofishing of longitudinal transects with variable length and constant width (1 m) was carried out upstream. Transect length was dependent on the habitat's size and accessibility. By multiplying length and width of a transect, the area fished per habitat was calculated. In total, 31 transects (one per habitat) were fished with a mean area of 53 m^2 ± 38 SD (range = 18-185 m^2).
Single-pass electrofishing is a cost- and time-effective method to estimate spatial variation in fish abundance in a similar way to multi-pass approaches, which however are more accurate (Teichert et al. 2011, Foldvik et al. 2016).
Each fish caught was identified to species-level and measured for length (total length, ± 0.5 cm), and subsequently released. Only caught fish were included in further statistical analyses, as the fish's length was essential for a clear classification into age classes; observed and escaped ones were counted and noted, but not further considered in the present study. The fished areas of each habitat are listed in Table 4.

3.4.2 Definition of age classes and estimation of fish densities

Age classes, i.e. 0+, 1+ and >1+, for brown trout were built based on age structure of length-frequency plots (Figures 22-25). This is a fast and conservative method where fish do not have to be killed as it is, for instance, the case when determining age classes based on otoliths.

Age classes 0+ and 1+ of brown trout were clearly detectable in all length-frequency plots. Since brown trout of an anadromous and a non-anadromous reach should be compared in this study, and they occurred close to each other in the same stream system under similar biotic (e.g. food availability etc.) and abiotic (e.g. temperature etc.) conditions, similar growth performance could be assumed for both populations. Consequently, the length-frequency distribution plot showing brown trout of the anadromous and non-anadromous reach in combination (Figure 22) was used as basis for defining age classes.

Two approaches were applied, hereinafter referred to as approach 1 and 2, to define age classes, since specific length classes do not allow a clear assignation to an age class. For instance, length classes 80, 90 and 100 mm may contain simultaneously fish from age classes 0+ and 1+.

In approach 1, age classes were separated by means of clear length ranges as follows: < 90 mm = 0+, 90-150 mm = 1+, > 150 mm = >1+. Thus, length classes, not facilitating a clear assignation to an age class, were considered in the definition of age classes. Advantage of this approach is that all caught fish could be included in the analyses. However, statistical consistency might be affected adversely due to possibly biased numbers of fish per age class following overlapping length ranges.

Contrarily, in approach 2 those length classes were excluded, which did not allow a clear assignation to an age class. Thus, length classes 80, 90 and 100 mm, herein called age class 0+/1+, as well as 160 and 170 mm, herein called age class 1+/>1+, were not considered in the definition of age classes. Age classes were defined according to the following length classes: < 80 mm = 0+, 110-150 mm = 1+, >170 mm = >1+. By using this approach, not all fish could be included in the analyses. Advantage of this approach might be a stronger and more secured statistical consistency and validity, since overlapping is minimized.

Finally, the density per 100 m^2 (n/100 m^2) was extrapolated for each age class and habitat, in order to obtain standardized values required for further statistical analyses. In doing so, the absolute number of fish caught per age class and habitat was divided by the fished area of the habitat and then multiplied by 100. Fish densities were calculated based on absolute values obtained from both approach 1 and 2.

3.5 Statistical analyses

Statistical analyses of the present study were carried out by using IBM SPSS Statistics (version 21.0) and MS Excel 2016.

The study design of this investigation specifically aimed to analyze the relationship between the density of brown trout, as dependent variable, and spawning ground area, spawning ground density and shelter availability, as independent variables. Since several further habitat features were recorded, a principal component analysis (PCA) was used as pre-analysis to reduce the number of independent variables to the most important ones.
In doing so, each of the dependent variables (densities of 0+, 1+ and >1+ brown trout in the anadromous/non-anadromous reach) was analyzed with all independent variables (spawning ground area, spawning ground density, shelter availability, silt, sand and fine gravel, gravel, stone, boulder, riparian vegetation, woody debris, algae and moss). The aim was to find components with a minimum of variables explaining as much variance of the total variance as possible (Lamprecht 1992). To maximize the correlation of each variable with one of the components (Lamprecht 1992), component-rotation (method: Varimax with Kaiser Normalization) was applied.
The PCA was applied for the fish densities obtained from approach 1 and 2. In total, twelve PCA were computed, i.e. one PCA per age class in the anadromous and non-anadromous reach for both approach 1 and 2. From each rotated component matrix of the PCA only the component that contained the dependent variable with the highest correlation coefficient was chosen for further statistical analyses. First, only variables with correlation coefficients higher and lower than 0.45 and -0.45, respectively, were considered (Lamprecht 1992). Further, since age classes and reaches (anadromous versus non-anadromous reach) should be compared, only those independent variables were selected for further statistical analyses, whose correlation coefficients occurred most frequently and simultaneously throughout the relevant components. Components, not showing similarities to other components regarding the correlation coefficients of the independent variables, were treated as particular cases and analyzed individually.

Regression analyses were carried out to model the relationships between fish densities of specific age classes and the independent variables obtained from the PCA. First, simple linear regression was applied with the aim to analyze individually how each of the independent variables affected fish densities. In order to find the independent variables, which acted as best predictors for fish density per age class in the anadromous and non-anadromous reach, multiple linear regression using backward elimination of variables was applied. For the density of >1+ brown trout in the anadromous reach multiple linear regression could not be applied, since there was only one relevant independent variable found by the PCA.

Durbon-Watson statistics and the variance inflation factor (VIF) were used in the multiple linear regression models to assess autocorrelation and multicollinearity, respectively. Durbon-Watson values can range between 0 and 4. The closer to 2 the value is, the weaker is autocorrelation. While values lower than 2 indicate a positive autocorrelation, values higher than 2 imply negative autocorrelation. Values between 1.5 and 2.5 are within an acceptable range for the model. Values of VIF should be lower than 10 to ensure that multicollinearity is within an acceptable range.

In addition to regression analysis, differences between medians of fish densities were tested based on the classes developed for spawning ground area (chapter 3.3.2), spawning ground density (chapter 3.3.2) and shelter availability (chapter 3.3.3). This was accomplished by means of the median test, a non-parametric significance test that tests whether two or more independent samples are drawn from populations with identical medians (null hypothesis).

Finally, to test for possible effects in fish densities through competitive effects of larger fish or other fish species (i.e. Atlantic salmon), the relationships between densities of younger and older age classes, as well as between densities of brown trout and Atlantic salmon were analyzed by means of simple linear regression. Competitive effects could be assumed as present if there were negative relationships between fish densities of age classes or species.

The levels of significance for all statistical analyses were 5 % ($p < 0.05$) and 1 % ($p < 0.01$). Thus, p-values between 0.05 and 0.01 were referred to as significant (*) and p-values < 0.01 as highly significant (**).

4 Results

Chapter 4 initially presents the results obtained by habitat mapping and fish sampling. Then, the outcomes of the PCA are shown, which served to select relevant variables for further statistical analyses. In the following chapters, the main findings of this study are presented. These deal primarily with the effects of spawning ground area, spawning ground density and shelter availability on the densities of 0+ and 1+ brown trout in the anadromous and non-anadromous reach. Finally, the results of the analysis for potential competitive effects are presented.

4.1 Habitat mapping

In total, the spawning ground area of the study area (7617.3 m^2) was 310.5 m^2, i.e. 4.1. % of the study reaches were spawning grounds. In the anadromous reach (5670.0 m^2), spawning ground area amounted to 191.0 m^2 (3.4 %). In the non-anadromous reach (1947.3 m^2) spawning ground area was 119.5 m^2 (6.1 %).

The absolute, mean spawning ground area was 10.0 m^2 ± 10.6 SD, ranging between 0.0-40.6 m^2. The absolute, mean spawning ground density amounted to 2/habitat ± 1.9 SD with a range of 0-9. All absolute values are shown in the appendix (chapter 9.3, Table 14).

The extrapolated spawning ground area per habitat was on average 8.9 m^2/100 m^2 ± 16.8 SD and ranged between 0.0 and 90.6 m^2/100 m^2, whereas the mean spawning ground density per habitat amounted to 1/100 m^2 ± 1.8 SD, ranging between 0 and 8/100 m^2. Mean shelter availability measured per habitat was 7 ± 4.4 SD (range = 0-20).

All relative values of spawning ground area, spawning ground density and shelter availability can be found in Table 4. Figures 20 and 21 give an overview about spawning ground area and shelter availability, respectively, in the study area. Absolute values for spawning ground area, spawning ground density and shelter availability, as well as all further habitat features are listed in the appendix (chapter 9.3, Tables 14 and 15).

Table 4: Length, area, fished area, spawning ground area (SGA), spawning ground density (SGD) and shelter availability (SA) per habitat of the anadromous and non-anadromous reach. [a] = excluded from further statistical analyses, [b] = culvert, [c] = canal.

	Habitat	Length (m)	Area (m^2)	Fished area (m^2)	SGA (m^2/100 m^2)	SGD (n/100 m^2)	SA
Anadromous reach	1[a]	24.6	136.5	26	0.0	0	13
	2[a]	24.8	86.9	25	15.3	2	3
	3	26.1	80.7	30	5.9	4	7
	4	54.7	157.5	50	5.7	3	10
	5	34.9	92.8	31	6.7	3	5
	6	47.8	106.5	75	10.2	2	9
	7	81.3	235.1	50	0.8	0	9
	8[b]	176.1	701.7	30	0.0	0	2
	9	173.7	802.5	120	2.2	0	7
	10	138.2	724.6	130	0.8	0	5
	11	31.6	83.5	31	27.2	2	11
	12[c]	187.3	577.9	185	0.0	0	1
	13	61.9	248.6	55	16.3	4	20
	14	62.0	349.3	46	2.2	1	8
	15	31.7	111.5	31	1.3	1	7
	16[b]	127.6	538.2	129	0.0	0	3
	17	87.0	121.9	49	2.9	2	4
	18	50.7	85.4	48	24.7	5	6
	19	87.6	266.3	64	9.2	2	4
	20	40.9	162.6	40	0.0	0	7
	Sum	1550.5	5670.0	1245	-	-	-
	Mean	77.5	283.5	62	6.6	1	7
Non-anadromous reach	21	49.1	115.9	40	4.2	1	3
	22	35.7	195.8	36	9.7	1	2
	23	50.3	192.4	40	9.0	1	8
	24	54.7	195.1	55	16.6	2	11
	25	34.5	109.6	34	0.0	0	9
	26	22.6	68.6	58	0.0	0	9
	27	117.6	184.9	25	0.0	0	0
	28	10.8	24.5	18	90.6	8	12
	29	51.8	96.6	20	5.5	1	9
	30	219.8	611.9	40	1.2	0	0
	31	44.8	152.0	30	0.0	0	11
	Sum	691.7	1947.3	396	-	-	-
	Mean	62.9	177.0	36	13.1	1	7
	Total sum	2242.2	7617.3	1641.0	-	-	-
	Total mean	72.3	245.7	53	8.9	1	7

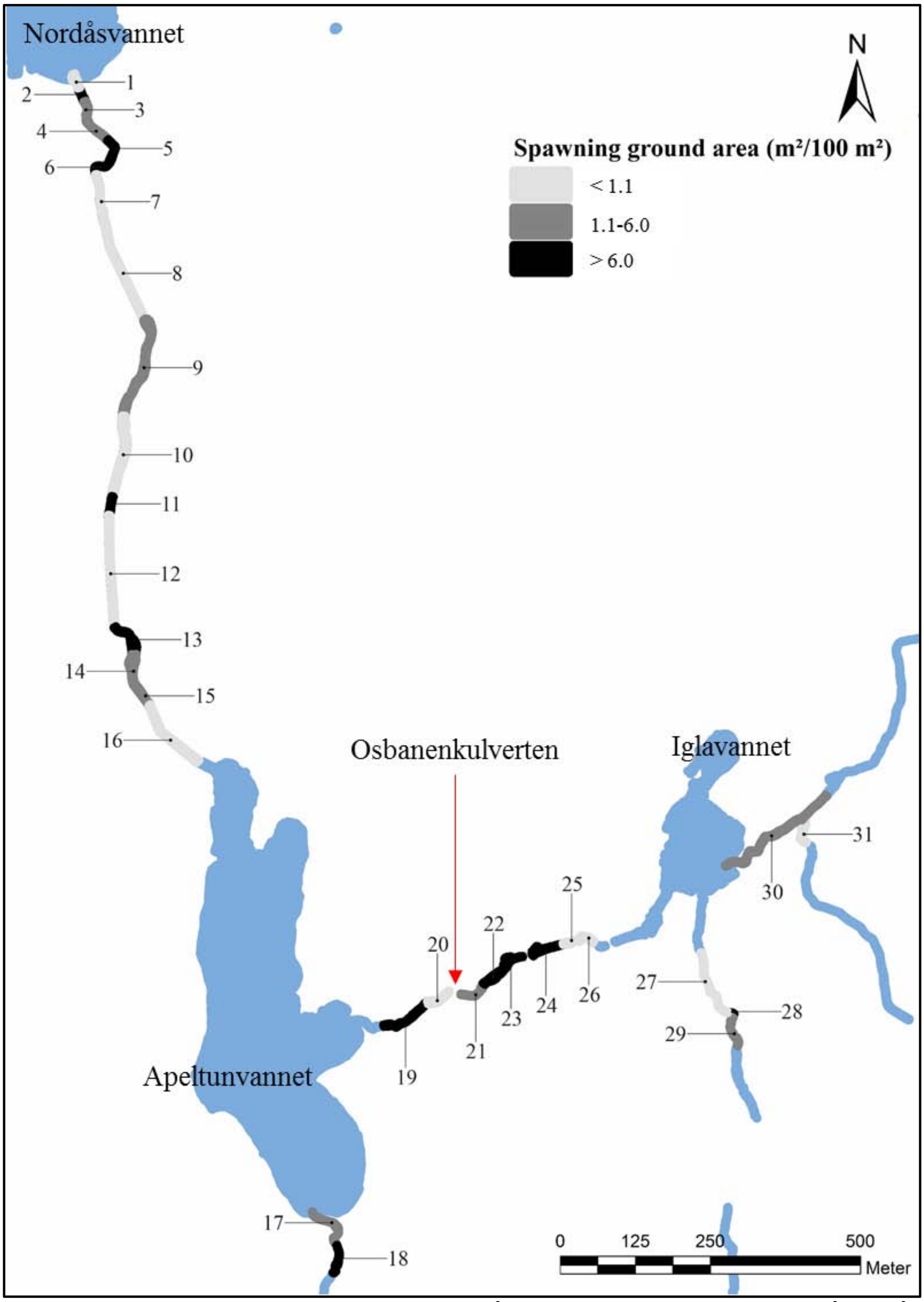

Figure 20: Spawning ground area standardized to 100 m^2 according to the classes low (< 1.1 m^2/100 m^2), moderate (1.1-6.0 m^2/100 m^2) and high (> 6.0 m^2/100 m^2). The arrows show habitat number and always point to the middle of each habitat.

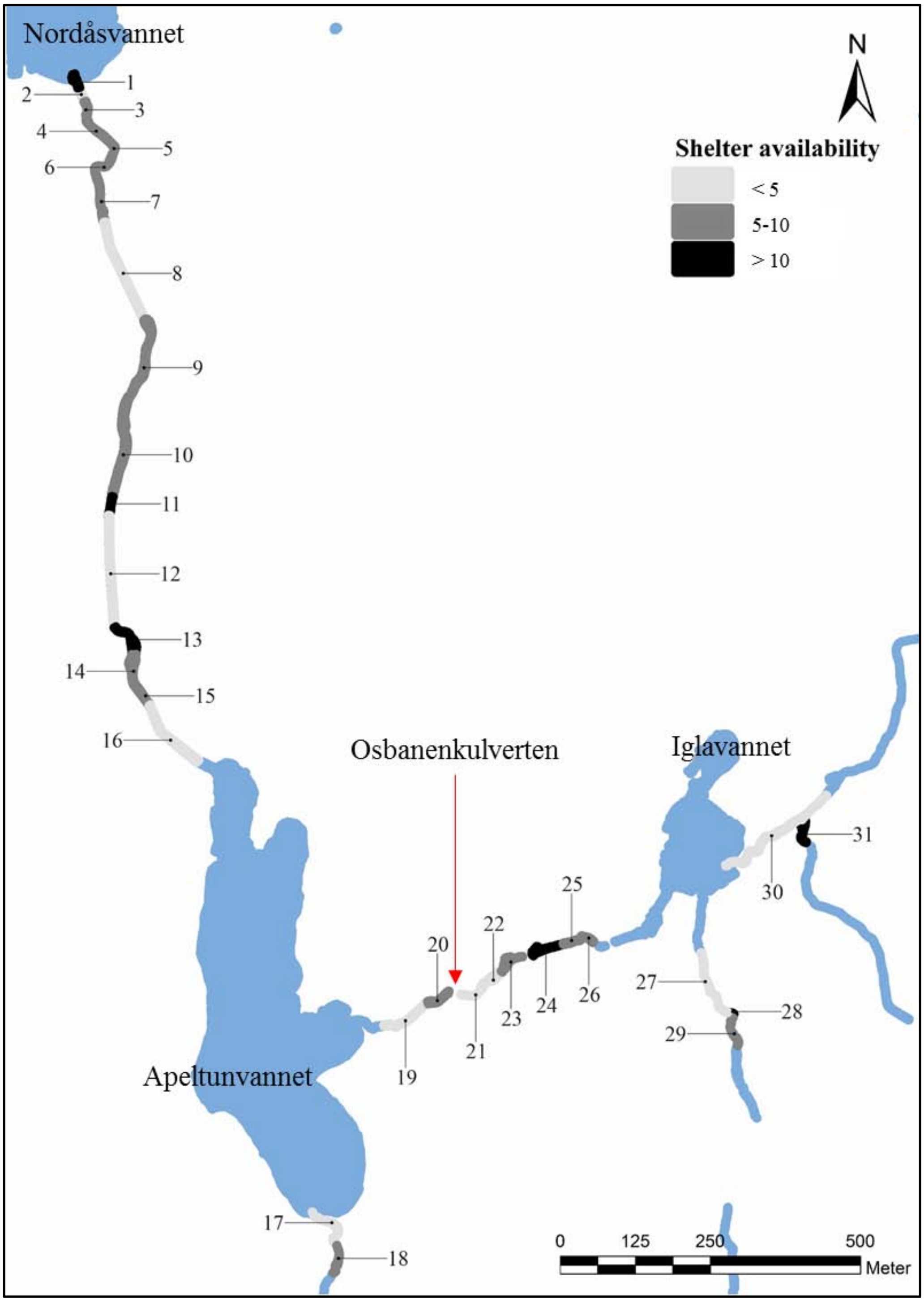

Figure 21: Shelter availability according to the classes low (< 5), moderate (5-10) and high (> 10). The arrows show habitat number and always point to the middle of each habitat.

Spawning ground area (simple linear regression, $R^2 = 0.094$, $p = 0.215$) and spawning ground density (simple linear regression, $R^2 = 0.038$, $p = 0.438$) were not significantly affected by substrate class gravel in the anadromous reach. In the non-anadromous reach spawning ground area was not significantly correlated with gravel (simple linear regression, $R^2 = 0.337$, $p = 0.061$). However, a significant, positive relationship was found between spawning ground density and gravel (simple linear regression, $R^2 = 0.374$, $p = 0.045$*). Additionally, a highly significant, positive relationship was detected between spawning ground area and spawning ground density in both the anadromous (simple linear regression, $R^2 = 0.566$, $p < 0.001$**) and non-anadromous reach (simple linear regression, $R^2 = 0.936$, $p < 0.001$**).
Substrate class stone had significant and highly significant, positive influence on shelter availability in the anadromous (simple linear regression, $R^2 = 0.243$, $p = 0.038$*) and non-anadromous reach (simple linear regression, $R^2 = 0.556$, $p = 0.008$**), respectively. Furthermore, shelter availability was not significantly affected by spawning ground area (simple linear regression, $R^2 = 0.199$, $p = 0.169$) and spawning ground density (simple linear regression, $R^2 = 0.251$, $p = 0.117$) in the non-anadromous reach. In contrast, spawning ground area had significant, positive influence on shelter availability (simple linear regression, $R^2 = 0.234$, $p = 0.042$*). Spawning ground density was not significantly related to shelter availability (simple linear regression, $R^2 = 0.21$, $p = 0.056$).

4.2 Fish data analysis

A total of 1458 fish were caught. Brown trout represented the dominating proportion with ca. 91 %, while Atlantic salmon amounted to ca. 9 % (Table 5, Figure 22). The catch of brown trout in the anadromous reach (67.1 %) was almost three times higher than the catch of brown trout in the non-anadromous reach (23.5 %).

According to approach 1 brown trout of age class 1+ (40.7 %) represented the highest proportion followed by age class 0+ (27.8 %) and >1+ (22.2 %). In this context, brown trout of the anadromous reach revealed a similar trend, whereas 0+ was the dominating age class of brown trout in the non-anadromous reach followed by >1+ and 1+. Table 5 shows absolute and relative numbers of brown trout and Atlantic salmon caught in specific age classes and in total according to approach 1.

Table 5: Absolute (N) and relative number (%) of Atlantic salmon (AS) and brown trout (BT) according to specific age classes (0+, 1+, >1+) and in total based on approach 1.

Species	0+		1+		>1+		Total	
	N	%	N	%	N	%	N	%
AS	23	1.6	114	7.8	0	0.0	137	9.4
BT anadromous reach	280	19.2	495	34.0	203	13.9	978	67.1
BT non-anadromous reach	125	8.6	97	6.7	121	8.3	343	23.5
Sum	428	29.4	706	48.5	324	22.2	1458	100.0

Analogous to approach 1, the overall trend remained similar by applying approach 2: Brown trout of age class 1+ (32.8 %) constituted the largest share followed by age class 0+ (23.0 %) and >1+ (17.1 %). By using approach 2 the numbers of brown trout per age class in the anadromous and non-anadromous reach showed a similar trend to that of approach 1.
Overall, the absolute and relative numbers of brown trout in each age class decreased by using approach 2, resulting from the exclusion of the overlapping age classes 0+/1+ (12.6 %) and 1+/>1+ (5.1 %). Table 6 demonstrates absolute and relative numbers of brown trout and Atlantic salmon in specific age classes and in total according to approach 2.

Table 6: Absolute (N) and relative number (%) of Atlantic salmon (AS) and brown trout (BT) according to specific age classes (0+, 1+, >1+) and in total based on approach 2. Age classes 0+/1+ and 1+/>1+ ([a]) were excluded from further statistical analyses.

Species	0+		0+/1+[a]		1+		1+/>1+[a]		>1+		Total	
	N	%	N	%	N	%	N	%	N	%	N	%
AS	18	1.2	34	2.3	85	5.8	0	0.0	0	0.0	137	9.4
BT anadromous reach	226	15.5	141	9.7	408	28.0	53	3.6	150	10.3	978	67.1
BT non-anadromous reach	109	7.5	43	2.9	70	4.8	22	1.5	99	6.8	343	23.5
Sum	353	24.2	218	14.9	563	38.6	75	5.1	249	17.1	1458	100.0

In the following the length-frequency distribution plots (Figures 22-25) used for the definition of age classes are shown.

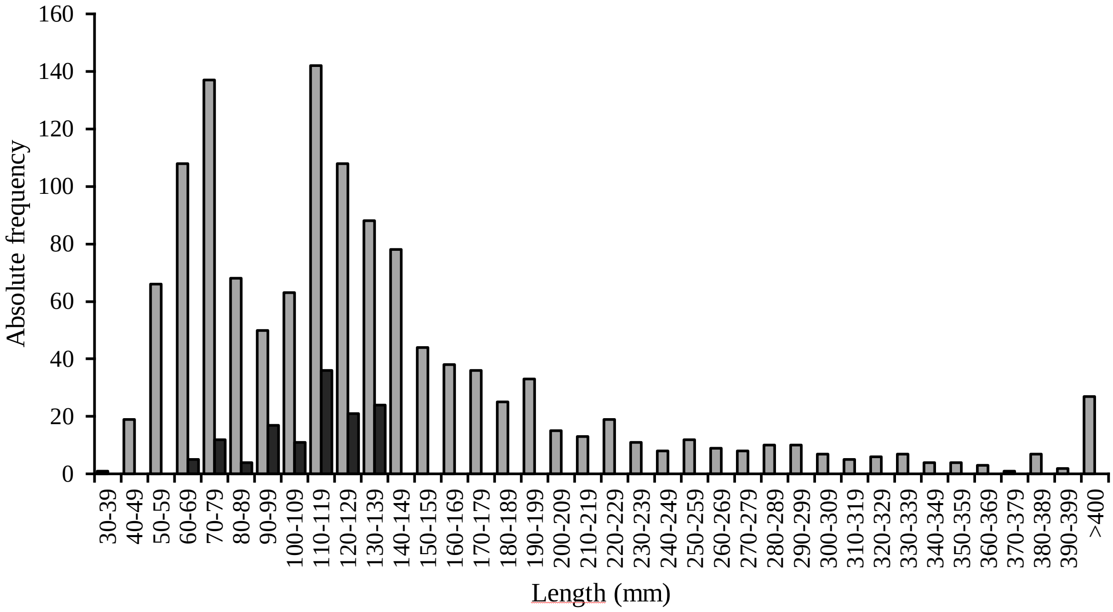

Figure 22: Absolute length-frequency distribution of Atlantic salmon (dark bars) and brown trout (light bars) in the anadromous and non-anadromous reach. Fish > 400 mm were summarized in one length class (>400 mm).

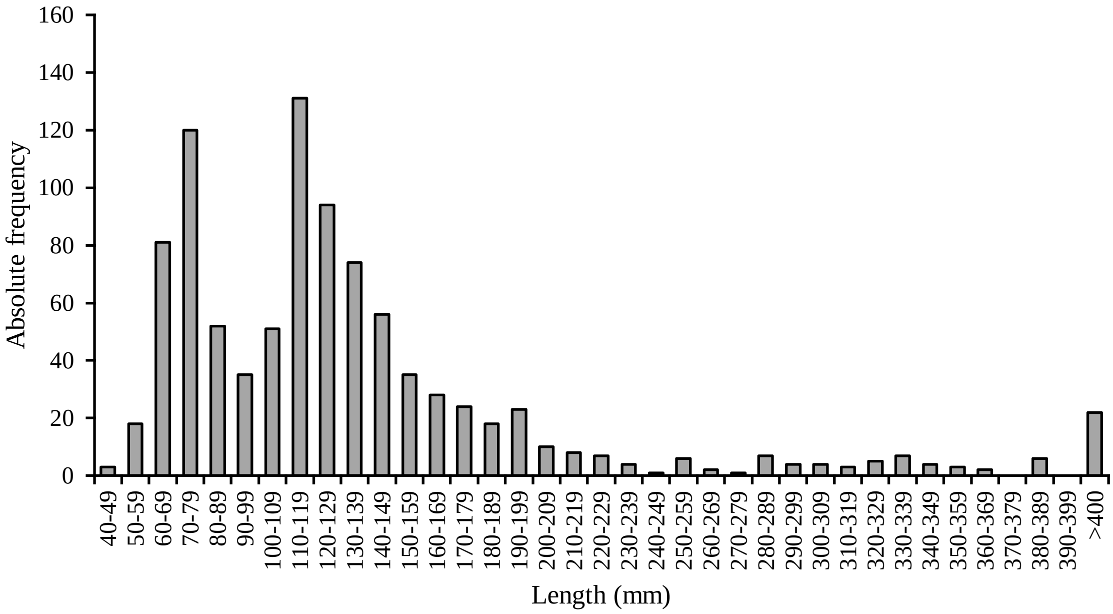

Figure 23: Absolute length-frequency distribution of brown trout in the anadromous reach. Fish > 400 mm were summarized in one length class (>400 mm).

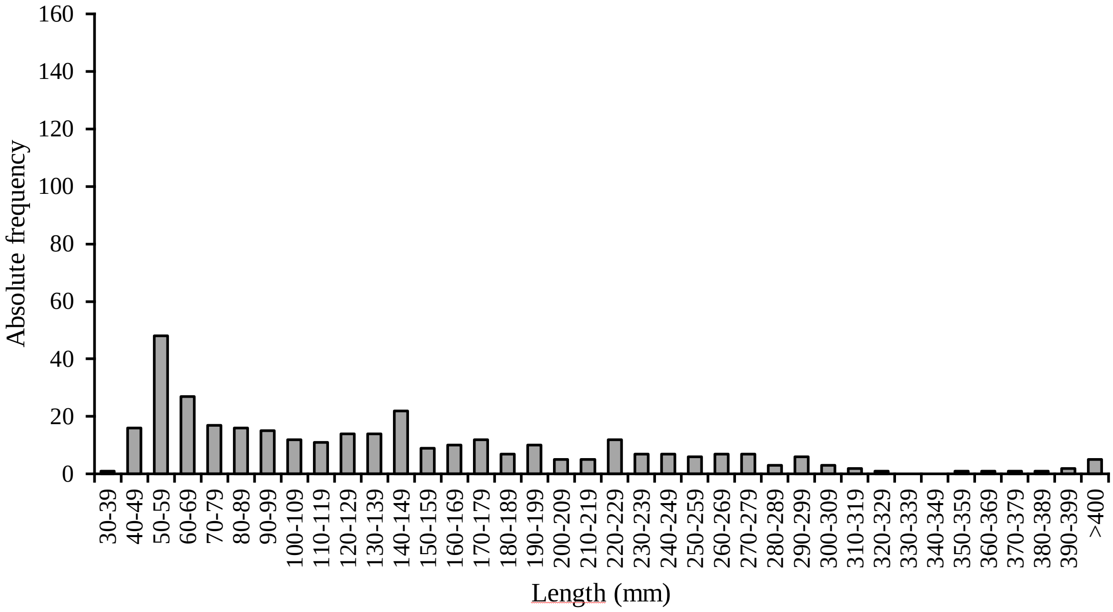

Figure 24: Absolute length-frequency distribution of brown trout in the non-anadromous reach. Fish > 400 mm were summarized in one length class (>400 mm).

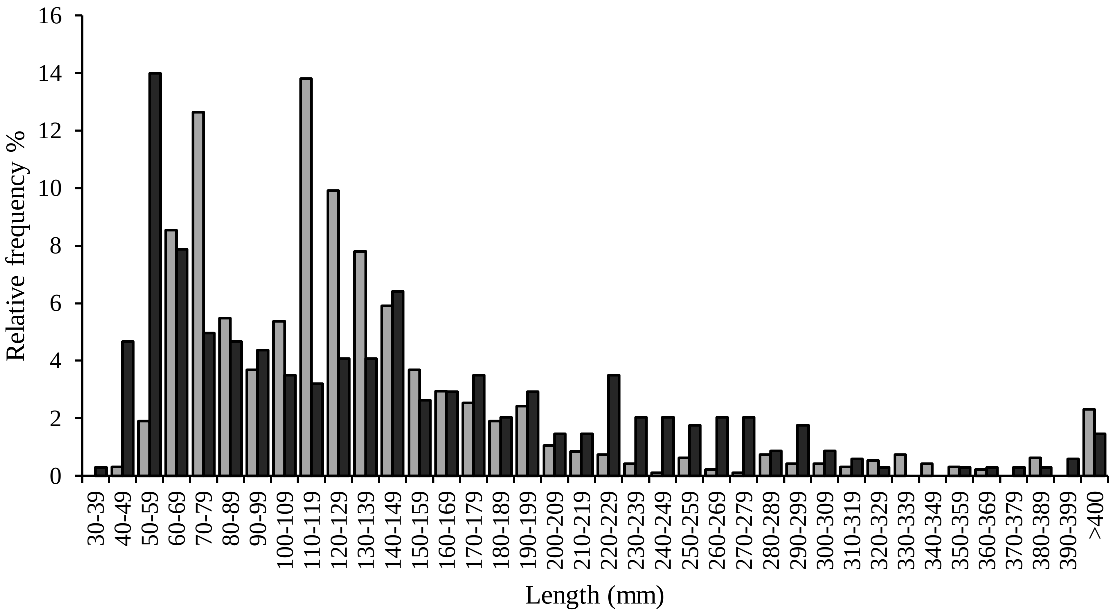

Figure 25: Relative length-frequency distribution of brown trout in the anadromous (light bars) and the non-anadromous reach (dark bars). Fish > 400 mm were summarized in one length class (>400 mm).

In addition to the length-frequency plots used for defining age classes, a length-frequency distribution plot was produced with weighted frequencies according to the total fished areas in the anadromous (1245 m^2) and the non-anadromous reach (396 m^2) (Figure 26, Table 4). The density of brown trout was lower in the anadromous reach (76/100 m^2) than in the non-anadromous reach (87/100 m^2).

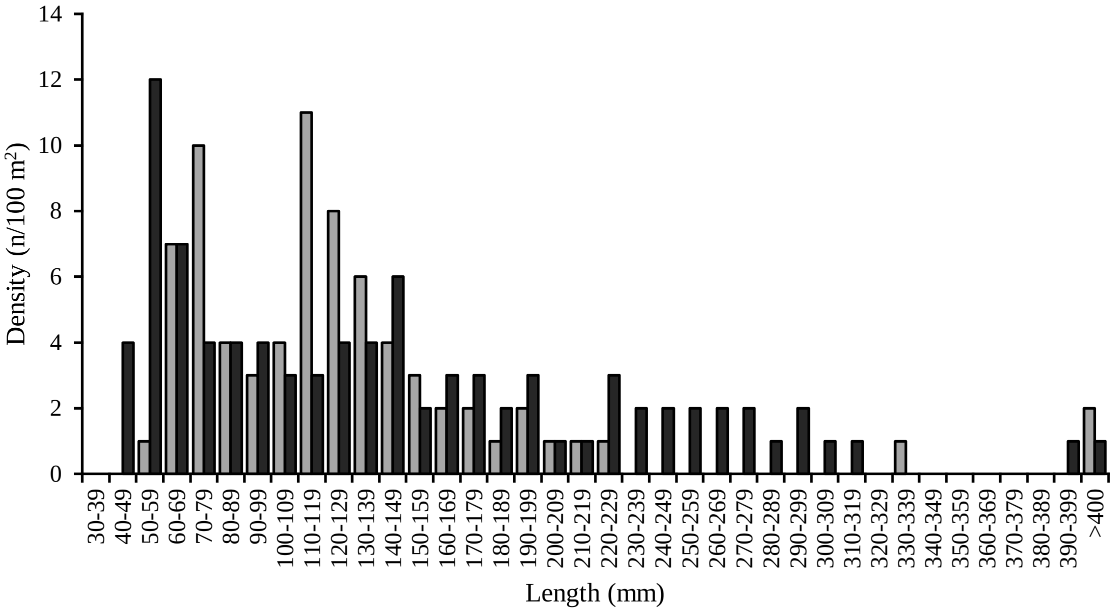

Figure 26: Length-frequency distribution for the density of brown trout per 100 m^2 in the anadromous (light bars) and the non-anadromous reach (dark bars). Fish > 400 mm were summarized in one length class (>400 mm).

On average 43 brown trout (± 34.5 SD) were caught per habitat with a range between 1 and 166.

According to approach 1 the mean number of 0+, 1+ and >1+ brown trout per habitat was 16 ± 14.7 SD (range = 0-47), 19 ± 18.9 SD (range = 1-91) and 11 ± 9.8 SD (range = 0-45), respectively.

By applying approach 2 the mean number of 0+, 1+ and >1+ brown trout per habitat was 14 ± 14.0 SD (range = 0-47), 15 ± 14.6 SD (range = 1-70), and 9 ± 8.7 SD (range = 0-40), respectively.

In total, a mean of 93 brown trout per 100 m^2 (± 72.1 SD) was estimated per habitat, ranging between 3 and 306. The extrapolated mean density (n/100 m^2) per habitat based on approach 1 for 0+, 1+ and >1+ brown trout was 34/100 m^2 ± 52.2 SD (range = 0-228), 38/100 m^2 ± 26.2 SD (range = 3-118) and 22/100 m^2 ± 18.2 SD (range = 0-69), respectively.

According to approach 2 the extrapolated mean density of 0+, 1+ and >1+ brown trout amounted to 29/100 m^2 ± 51.5 SD (range = 0-222), 31/100 m^2 ± 20.1 SD (range = 3-89) and 17/100 m^2 ± 14.8 SD (range = 0-56), respectively.

All extrapolated fish densities per age class and habitat according to both approaches are listed in Table 7; the corresponding absolute values can be found in the appendix (chapter 9.4, Tables 16 and 17). Figures 27, 28 and 29 visualize the densities of 0+, 1+ and >1+ brown trout (approach 2), respectively. Figures 30 and 31 show total population density and densities of 0+, 1+ and >1+ of brown trout (approach 2) in comparison, respectively.

Table 7: Densities of 0+, 1+ and >1+ brown trout based on approach 1 and 2, as well as the total density of brown trout according to each habitat of the anadromous and non-anadromous reach. [a] = excluded from further statistical analyses, [b] = culvert, [c] = canal.

	Habitat	Approach 1			Approach 2			Total
		0+	1+	>1+	0+	1+	>1+	
		(n/100 m^2)						
Anadromous reach	1[a]	0	42	4	0	42	0	46
	2[a]	24	32	12	16	28	12	68
	3	0	67	33	0	50	20	100
	4	38	82	12	36	48	12	132
	5	3	39	10	3	32	10	52
	6	33	51	17	31	47	13	101
	7	10	42	2	8	38	0	54
	8[b]	0	3	0	0	3	0	3
	9	25	76	38	19	58	33	138
	10	8	24	6	7	20	4	38
	11	48	68	10	45	65	6	126
	12[c]	4	9	7	2	9	6	19
	13	84	118	16	64	89	7	218
	14	46	63	17	37	52	7	126
	15	29	55	68	26	48	45	152
	16[b]	4	22	10	2	20	8	36
	17	67	31	6	57	24	4	104
	18	77	29	50	71	27	42	156
	19	9	17	19	2	17	8	45
	20	13	13	18	3	10	15	43
	Mean	26	44	18	21	36	13	88
Non-anadromous reach	21	0	10	23	0	8	18	33
	22	3	28	69	0	25	56	100
	23	3	15	33	0	15	23	50
	24	24	31	56	11	18	51	111
	25	0	3	9	0	3	6	12
	26	5	28	17	2	12	16	50
	27	188	60	28	188	36	20	276
	28	228	50	28	222	44	28	306
	29	25	30	10	15	30	10	65
	30	8	15	25	3	13	18	48
	31	37	23	20	37	20	17	80
	Mean	47	27	29	43	20	24	103
	Total mean	34	38	22	29	31	17	93

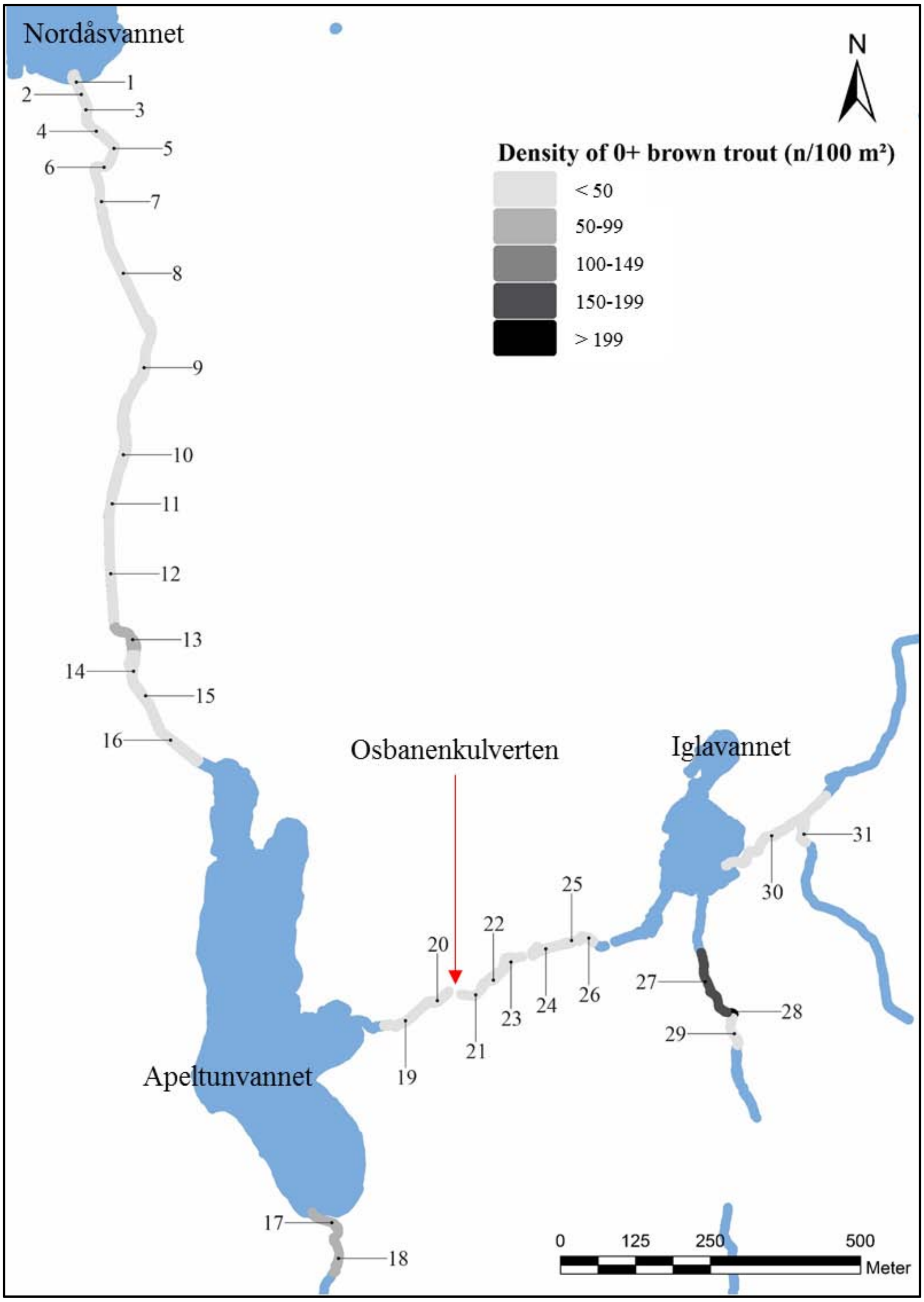

Figure 27: Density of 0+ brown trout per habitat in the study area according to approach 2. The arrows show habitat number and always point to the middle of each habitat.

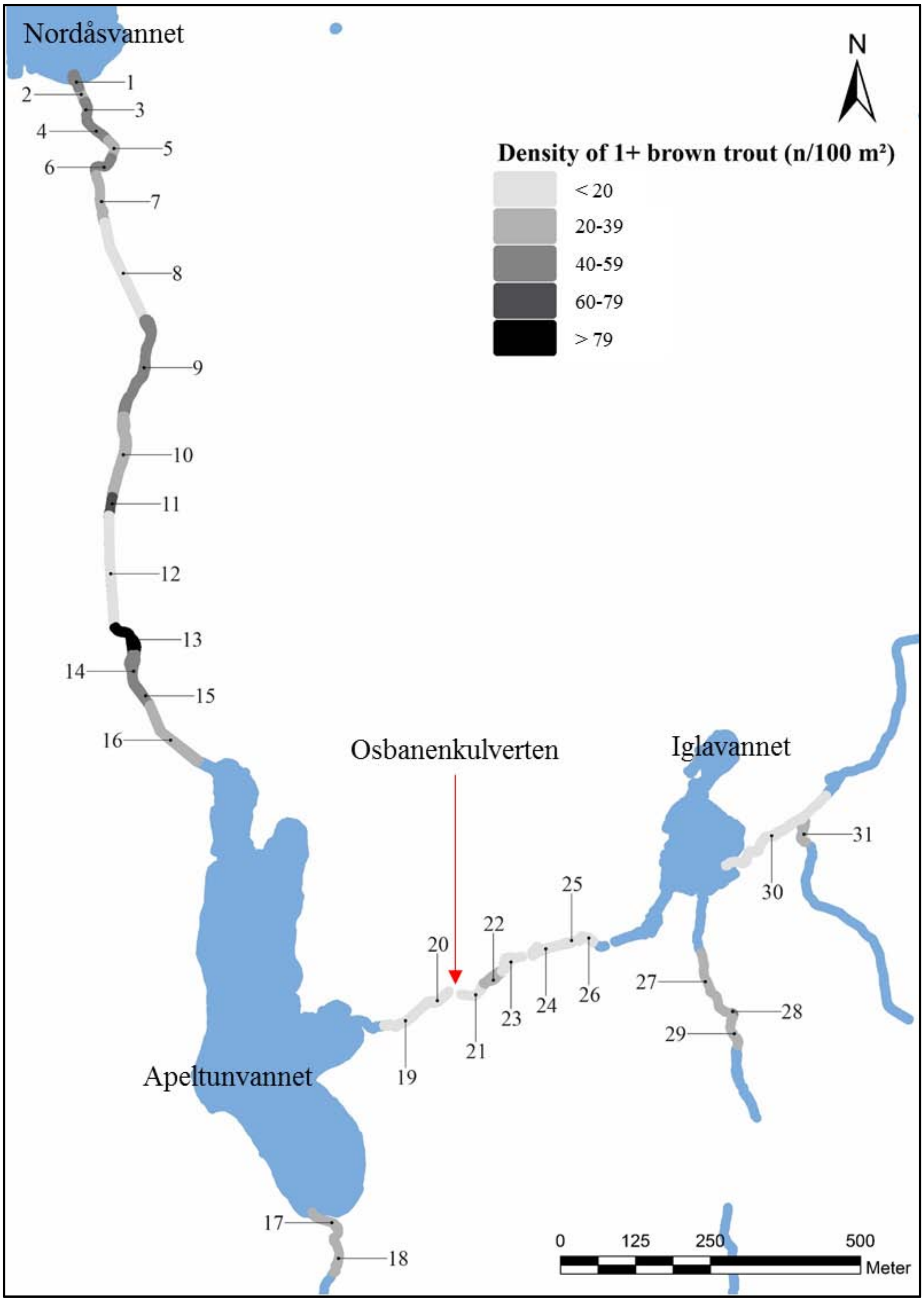

Figure 28: Density of 1+ brown trout per habitat in the study area according to approach 2. The arrows show habitat number and always point to the middle of each habitat.

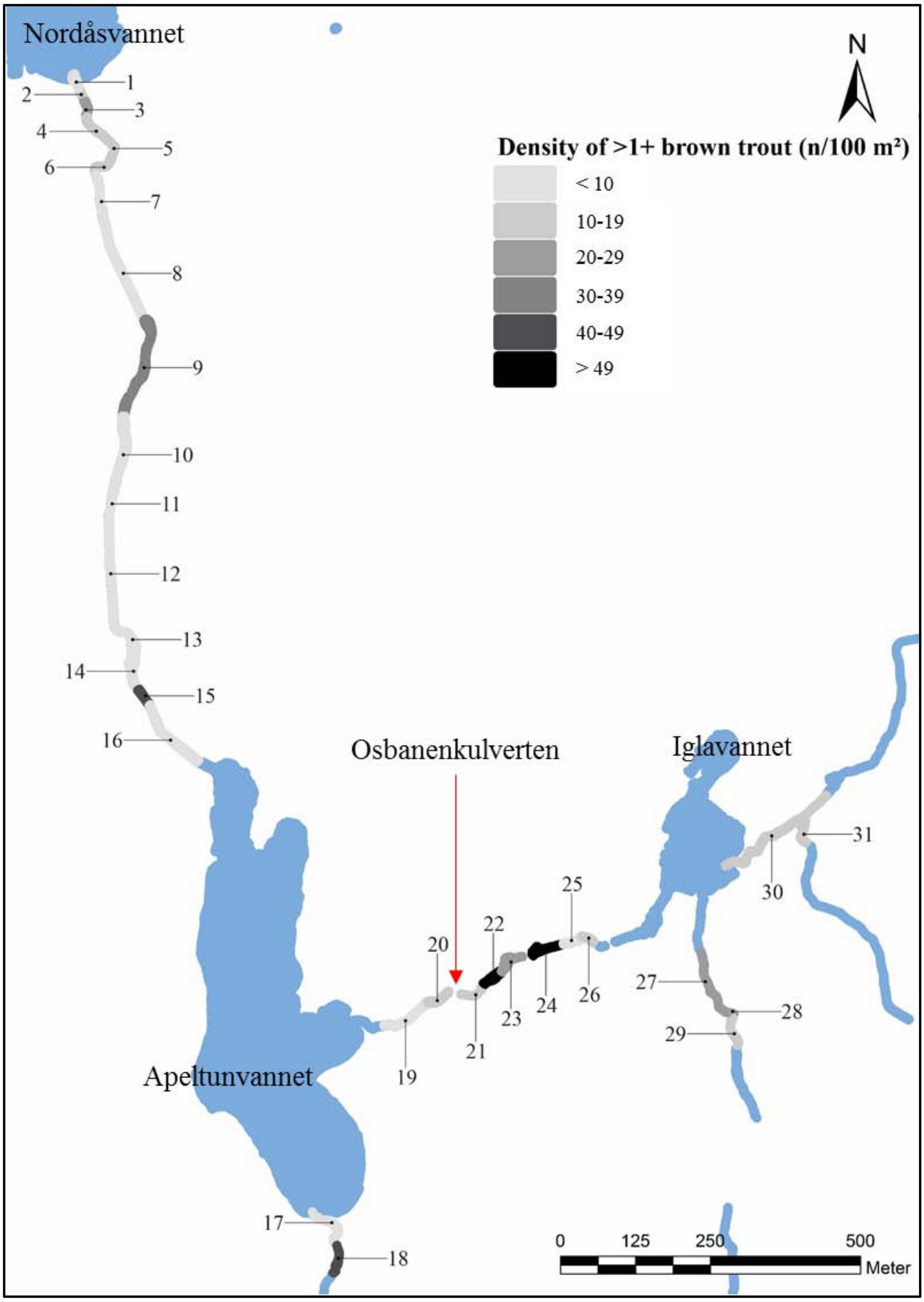

Figure 29: Density of >1+ brown trout per habitat in the study area according to approach 2. The arrows show habitat number and always point to the middle of each habitat.

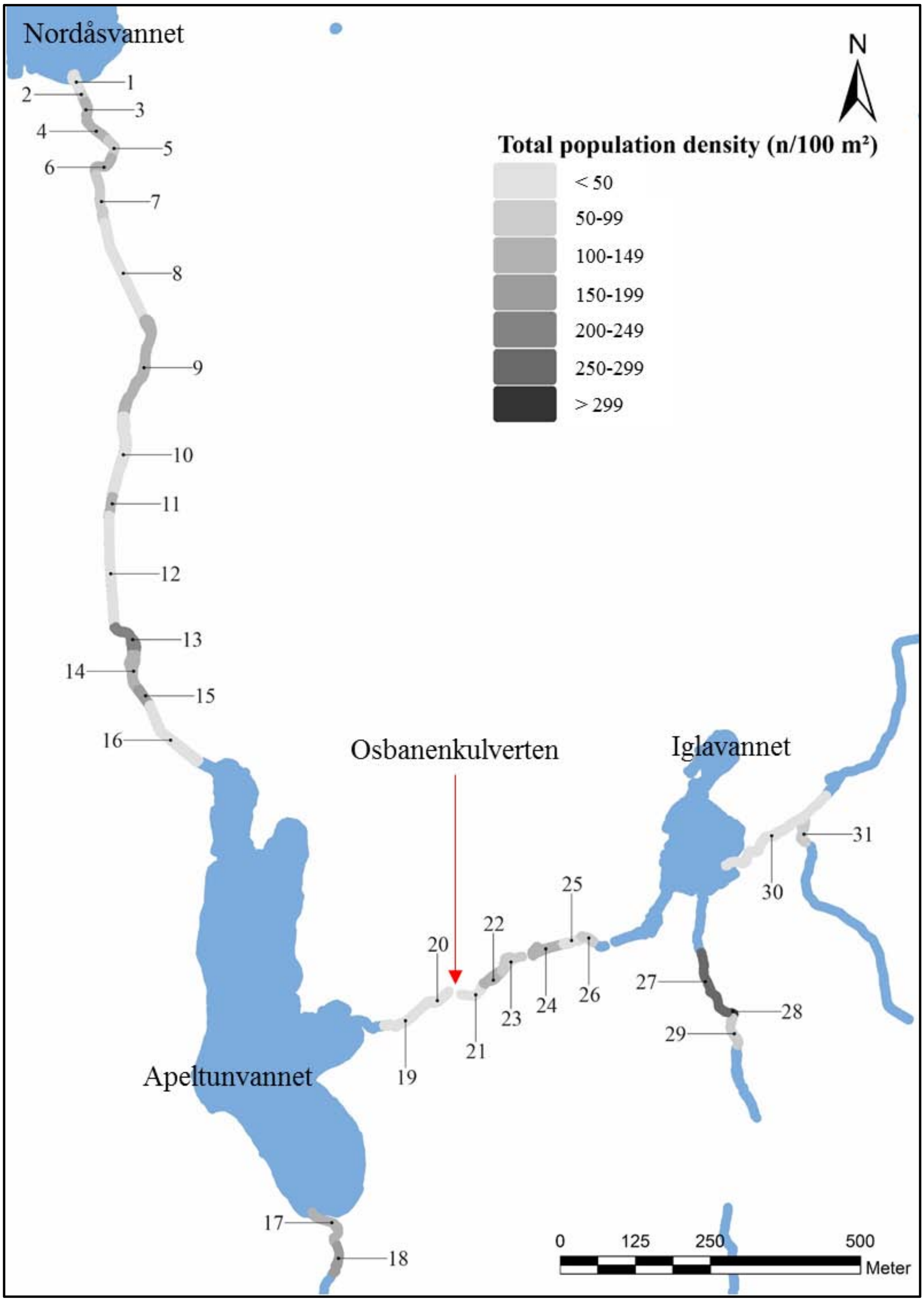

Figure 30: Total population density of brown trout per habitat in the study area. The arrows show habitat number and always point to the middle of each habitat.

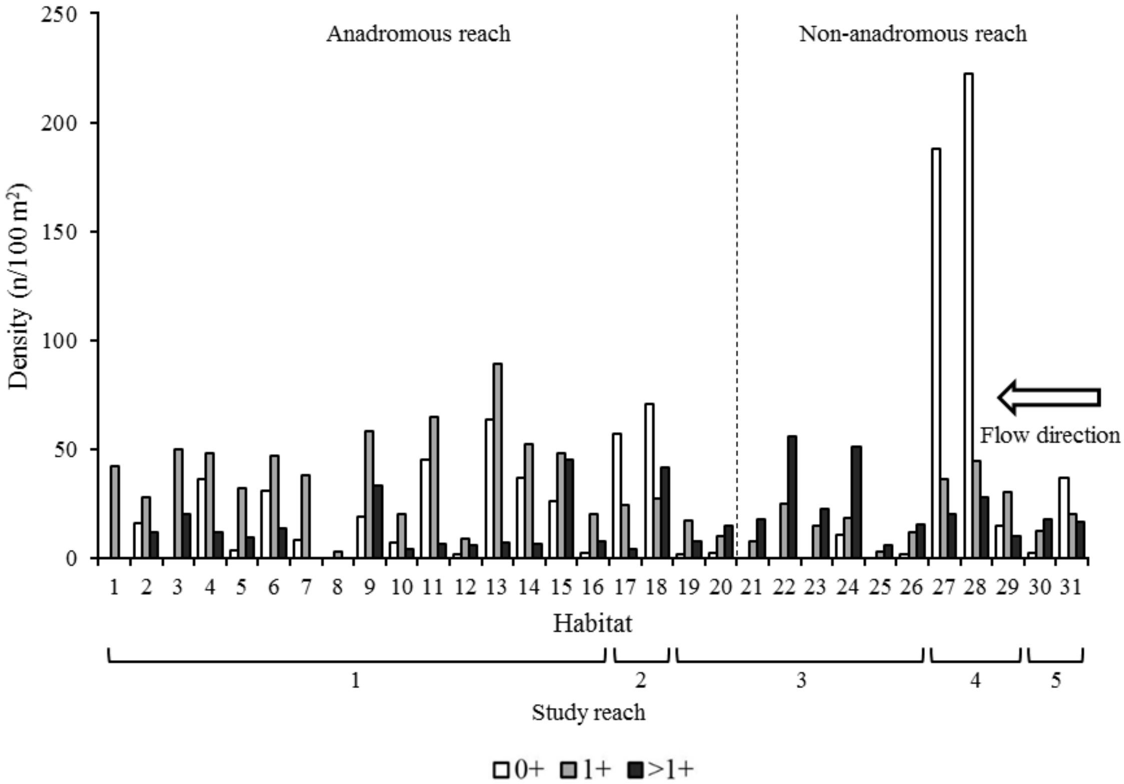

Figure 31: Densities of 0+ (light bars), 1+ (grew bars) and >1+ brown trout (dark bars) estimated for each habitat according to approach 2.

4.3 Selection of relevant variables

In the PCA using fish densities of approach 1 the correlation coefficients of spawning ground area, spawning ground density and shelter availability occurred most frequently and simultaneously in the components 1 (0+ brown trout, anadromous reach), 2 (0+ brown trout, non-anadromous reach), 3 (1+ brown trout, anadromous reach) and 5 (>1+ brown trout, anadromous reach). According to the aforementioned order each of the relevant components explained ca. 22, 32, 22 and 17 % of the total variance. The components 4 (1+ brown trout, non-anadromous reach) and 6 (>1+ brown trout, non-anadromous reach) explained each ca. 24 and 15 % of the total variance, respectively.

All relevant components obtained from the PCA of approach 1 are revealed in Table 8. All individual results of the PCA for approach 1 are demonstrated in the appendix (chapter 9.5, Tables 18-23).

Table 8: Summary of the six principal component analyses (PCA) computed for the densities of 0+, 1+ and >1+ brown trout (approach 1) in the anadromous and non-anadromous reach (dependent variables) and all mapped habitat features (independent variables). Only those components (1-6) of the rotated component matrices are shown that contained the dependent variable with the highest correlation coefficient. Correlation coefficients of potential independent variables chosen for further analyses are in bold.

	Variable	Component					
		1	2	3	4	5	6
Dependent	0+ anadromous reach (n/100 m^2)	0.839					
	0+ non-anadromous reach (n/100 m^2)		0.886				
	1+ anadromous reach (n/100 m^2)			0.712			
	1+ non-anadromous reach (n/100 m^2)				0.918		
	>1+ anadromous reach (n/100 m^2)					0.527	
	>1+ non-anadromous reach (n/100 m^2)						0.742
Independent	Spawning ground area (m^2/100 m^2)	**0.878**	**0.892**	**0.838**	-	**0.869**	-
	Spawning ground density (n/100 m^2)	**0.800**	**0.892**	**0.858**	-	**0.824**	-
	Shelter availability	**0.723**	**0.455**	**0.782**	-	**0.586**	-
	Silt %	-	-0.320	-	-	-	-
	Sand and fine gravel %	-	-	-	**0.623**	-	**-0.532**
	Gravel %	-	0.806	-	**0.766**	-	-
	Stone %	-	-	-	**-0.452**	-	-
	Boulder %	-	-0.374	-	**-0.764**	-	-
	Riparian vegetation %	0.310	-0.636	-	-	-	**-0.496**
	Woody debris %	-	-0.304	-	-	-	-
	Algae %	-	-	0.417	-	-	**0.810**
	Moss %	-	-0.381	-	**-0.637**	-	-
Variance explained %		22.370	31.927	22.225	24.435	17.111	14.965

The PCA using fish densities of approach 2 was slightly different: The correlation coefficients of spawning ground area, spawning ground density and shelter availability occurred most frequently and simultaneously in the components 1 (0+ brown trout, anadromous reach), 2 (0+ brown trout, non-anadromous reach), 3 (1+ brown trout, anadromous reach) and 4 (1+ brown trout, non-anadromous reach). According to this order, each of the components explained ca. 22, 32, 23, 33 % of the total variance. The components 5 (>1+ brown trout, anadromous reach) and 6 (>1+ brown trout, non-anadromous reach) explained each ca. 11 and 16 % of the total variance, respectively.

The results of the PCA using the fish densities of approach 2 was selected as basis for further statistical analyses because of two reasons. First, correlation coefficients of spawning ground area, spawning ground density and shelter availability occurred most frequently and simultaneously in components 1, 2, 3 and 4, which contained also the age classes of interest for this study, i.e. 0+ and 1+. Secondly, statistical consistency is higher, as an overlapping of age classes in minimized.

Thus, based on the findings of the PCA (Table 9) densities of 0+ and 1+ brown trout in the anadromous and non-anadromous reach were analyzed with spawning ground area, spawning ground density and shelter availability.

The components 5 (>1+ brown trout, anadromous reach) and 6 (>1+ brown trout, non-anadromous reach) were treated as individual cases, as their independent variables did not overlap with the ones of components 1, 2, 3 and 4. Accordingly, the density of >1+ brown trout in the anadromous reach was analyzed with woody debris and the density of >1+ brown trout in the non-anadromous reach with sand and fine gravel, riparian vegetation and algae. Table 9 demonstrates all relevant components obtained from the PCA of approach 2. All individual results of the PCA for approach 2 can be found in the appendix (chapter 9.5, Tables 24-29).

Table 9: Summary of the six principal component analyses (PCA) computed for the densities of 0+, 1+ and >1+ brown trout (approach 2) in the anadromous and non-anadromous reach (dependent variables) and all mapped habitat features (independent variables). Only those components (1-6) of the rotated component matrices are shown that contained the dependent variable with the highest correlation coefficient. Correlation coefficients of potential independent variables chosen for further analyses are in bold.

	Variable	Component					
		1	2	3	4	5	6
Dependent	0+ anadromous reach (n/100 m^2)	0.842					
	0+ non-anadromous reach (n/100 m^2)		0.876				
	1+ anadromous reach (n/100 m^2)			0.758			
	1+ non-anadromous reach (n/100 m^2)				0.867		
	>1+ anadromous reach (n/100 m^2)					-0.584	
	>1+ non-anadromous reach (n/100 m^2)						0.756
Independent	Spawning ground area (m^2/100 m^2)	**0.892**	**0.891**	**0.843**	**0.883**	-0.310	-
	Spawning ground density (n/100 m^2)	**0.809**	**0.893**	**0.838**	**0.888**	-	-
	Shelter availability	**0.696**	**0.453**	**0.797**	**0.468**	-	-
	Silt %	-	-0.325	-	-	-	-
	Sand and fine gravel %	-	-0.369	-	-	-	**-0.539**
	Gravel %	-	0.807	-	0.824	-	-
	Stone %	-	-	-	-	-	-
	Boulder %	-	-	-	-0.436	0.336	-
	Riparian vegetation %	-	-0.636	-	-0.673	-	**-0.522**
	Woody debris %	-	-	-	-0.347	**0.795**	-
	Algae %	-	-	0.398	-	-	**0.795**
	Moss %	-	-0.379	-	-0.397	-	-
Variance explained %		22.478	31.720	22.726	32.720	11.035	15.550

4.4 Effects of spawning grounds and shelter availability on juvenile density

The results of the simple linear regression analysis showed that the effects of spawning ground area, spawning ground density and shelter availability on the densities of 0+ and 1+ brown trout varied within and among age classes and reaches (anadromous versus non-anadromous reach).

Within age class 0+ significant relations were found between the density of brown trout in the anadromous reach and spawning ground area, spawning ground density and shelter availability, as well as between the density of brown trout in the non-anadromous reach and spawning ground area and spawning ground density. The density of 0+ brown trout in the anadromous reach was positively correlated with spawning ground area, spawning ground density and shelter availability. Spawning ground area had the most significant influence on 0+ brown trout in the anadromous reach ($p = 0.003$**). The density of 0+ brown trout in the non-anadromous reach was positively correlated with spawning ground area and spawning ground density. Analogous to brown trout in the anadromous reach, spawning ground area had the most significant influence ($p = 0.022$*).

Further, within age class 1+ significant relationships were found between the density of brown trout in the anadromous reach and spawning ground density and shelter availability, as well as between the density of brown trout in the non-anadromous reach and spawning ground area and spawning ground density. The density of 1+ brown trout in the anadromous reach was positively correlated with spawning ground density and shelter availability. The relation between density and shelter availability was highly significant ($p < 0.001$**). The density of 1+ brown trout in the non-anadromous reach was positively correlated with spawning ground area and spawning ground density. Both had a similar significant influence on fish density (spawning ground area: $p = 0.033$*, spawning ground density: $p = 0.034$*).

According to the substrate classes that are most important for spawning grounds (i.e. gravel) and shelter availability (i.e. stone), it was found significant, positive influence of gravel on the density of 0+ ($R^2 = 0.433$, $p = 0.028$*,) (Table 31) and 1+ brown trout in the non-anadromous reach ($R^2 = 0.518$, $p = 0.012$*) (Table 33), as well as stone on the density of 1+ brown trout in the anadromous reach ($R^2 = 0.228$, $p = 0.045$*) (Table 32). Finally, there were no significant relationships found between the densities of >1+ brown trout and the relevant independent variables selected for this age class by PCA. Also, the remaining independent variables did not have an influence on the density of >1+ brown trout.

Overall, the effects of spawning ground area and spawning ground density on fish densities were more significant in age class 0+. Shelter availability revealed significant effects only on densities of 0+ and 1+ brown trout in the anadromous reach. The influence of shelter availability increased from age class 0+ to 1+ in terms of both significance and strength. In contrast, densities of 0+ and 1+ brown trout in the non-anadromous reach were only significantly affected by spawning ground area and spawning ground density, whose significance and strength decreased from age class 0+ to 1+. The results of the simple linear regression analysis on the effects of relevant habitat features on fish densities are listed in Table 10. Additionally, the results obtained from simple linear regression of all remaining habitat features can be found in the appendix (chapter 9.6, Tables 30-35).

Table 10: Simple linear regression analysis for the variables selected by the PCA. Densities of 0+, 1+ and >1+ brown trout in the anadromous and non-anadromous reach were used as dependent variables. Spawning ground area (SGA), spawning ground density (SGD), shelter availability (SA), woody debris, sand and fine gravel, riparian vegetation and algae represented the independent variables. Coefficient of determination (R^2), p-value (p), constant (b_0) and non-standardized regression coefficient (b_1) are given for each simple linear regression model.

Dependent Variable	Independent variable	R^2	p	b_0	b_1
0+ anadromous reach (n/100 m^2)	SGA (m^2/100 m^2)	0.438	0.003**	10.73	1.89
	SGD (n/100 m^2)	0.325	0.013*	9.16	9.02
	SA	0.315	0.015*	1.00	3.16
0+ non-anadromous reach (n/100 m^2)	SGA (m^2/100 m^2)	0.459	0.022*	16.05	2.09
	SGD (n/100 m^2)	0.428	0.029*	11.20	22.31
	SA	0.001	0.919	39.27	0.62
1+ anadromous reach (n/100 m^2)	SGA (m^2/100 m^2)	0.216	0.052	28.43	1.25
	SGD (n/100 m^2)	0.226	0.046*	25.70	7.07
	SA	0.760	< 0.001**	4.45	4.62
1+ non-anadromous reach (n/100 m^2)	SGA (m^2/100 m^2)	0.415	0.033*	16.39	0.30
	SGD (n/100 m^2)	0.411	0.034*	15.53	3.34
	SA	0.005	0.844	0.18	0.18
>1+ anadromous reach (n/100 m^2)	Woody debris %	0.012	0.663	14.47	-0.12
>1+ non-anadromous reach (n/100 m^2)	Sand and fine gravel %	0.014	0.729	24.92	-0.17
	Riparian vegetation %	0.142	0.254	34.35	-0.20
	Algae %	0.167	0.212	16.06	0.91

In total, five multiple linear regression models were calculated. In four of these, optimal models could be found. In the first (0+ brown trout, anadromous reach) and second model (0+ brown trout, non-anadromous reach), spawning ground density and shelter availability were excluded from the initial model. Consequently, only spawning ground area was included in the optimal model. From the third model (1+ brown trout, anadromous reach) spawning ground area and spawning ground density were excluded, resulting in the inclusion of shelter availability into the optimal model. In the fourth model (1+ brown trout, non-anadromous reach) spawning ground area and shelter availability were excluded from the initial model and spawning ground density was included in the optimal model. In the fifth multiple linear regression model (>1+ brown trout, non-anadromous reach) all independent variables were excluded and no optimal model could be calculated. Table 11 shows the variables of the initial model and the optimal model.

Table 11: Number of each multiple linear regression model computed (Nr), dependent and relevant independent variables of the initial model, as well as dependent and independent variables included in the optimal model (y ~ x). Independent variables selected from the initial model for the optimal model are in bold. [a] = no optimal model was found.

Nr	Initial model		Optimal model (y ~ x)
	Dependent variable	Independent variables	
1	0+ anadromous reach	**Spawning ground area**	0+ anadromous ~ spawning ground area
		Spawning ground density	
		Shelter availability	
2	0+ non-anadromous reach	**Spawning ground area**	0+ resident ~ spawning ground area
		Spawning ground density	
		Shelter availability	
3	1+ anadromous reach	Spawning ground area	1+ anadromous ~ shelter availability
		Spawning ground density	
		Shelter availability	
4	1+ non-anadromous reach	Spawning ground area	1+ resident ~ spawning ground density
		Spawning ground density	
		Shelter availability	
5[a]	>1+ non-anadromous reach	Sand and fine gravel	-
		Riparian vegetation	
		Algae	

Since all four optimal models comprised finally only one independent variable, coefficient of determination (R^2), p-value (p), constant (b_0) and non-standardized regression coefficient (b_1) revealed identical values as in the simple linear regression analysis (Table 10).

According to the optimal models obtained from the multiple linear regression analysis, spawning ground area was the best predictor for the density of 0+ brown trout in the anadromous reach (R^2 = 0.438) and the non-anadromous reach (R^2 = 0.459), revealing similar strong effects on fish densities in both reaches (β = 0.662 and 0.678, respectively) and positive correlations (Figures 32 and 34).

In contrast, shelter availability was the best predictor for the density of 1+ brown trout in the anadromous reach ($R^2 = 0.760$), showing a positive effect with a strength of $\beta = 0.872$ (Figure 36). Finally, spawning ground density was the best predictor for the density of 1+ brown trout in the non-anadromous reach ($R^2 = 0.411$), exhibiting positive influence with an effect strength of $\beta = 0.641$ (Figure 38).

Although correlations were detected between several independent variables (chapter 4.1), for instance between spawning ground area and spawning ground density, autocorrelation and multicollinearity could be excluded from the optimal models. This was due to the inclusion of only one independent variable in each optimal model. Therefore, Durbin-Watson and VIF values had not to be considered in the optimal models.
An overview about the results of the optimal models computed by multiple linear regression is given in Table 12.

Table 12: Dependent and independent variables (y ~ x), coefficient of determination (R^2), p-value (p), standardized regression coefficient (β), constant (b_0), non-standardized regression coefficient (b_1) of the optimal linear regression models. Values of R^2, p, b_0 and b_1 are identical to the ones obtained from simple linear regression.

Optimal model (y ~ x)	R^2	p	β	b_0	b_1
0+ anadromous reach ~ spawning ground area	0.438	0.003**	0.662	10.729	1.894
0+ non-anadromous reach ~ spawning ground area	0.459	0.022*	0.678	16.053	2.093
1+ anadromous reach ~ shelter availability	0.760	< 0.001**	0.872	4.452	4.615
1+ non-anadromous reach ~ spawning ground density	0.411	0.034*	0.641	15.534	3.341

The medians of the density of 0+ brown trout in the anadromous reach showed highly significant differences between spawning ground area classes low (< 1.1 m^2/100 m^2), moderate (1.1-6.0 m^2/100 m^2) and high (> 6.0 m^2/100 m^2) (median test, p = 0.009**; Figure 33). Contrarily, no significant differences were found between spawning ground area classes for the medians of the density of 0+ brown trout in the non-anadromous reach (median test, p = 0.676; Figure 35).

Between shelter availability classes low (< 5), moderate (5-10) and high (> 10) significant differences were detected for the medians of the density of 1+ brown trout in the anadromous reach (median test, p = 0.020*; Figure 37). The medians of the density of 1+ brown trout in the non-anadromous reach did not reveal significant differences between spawning ground density classes low (0/100 m^2), moderate (1-2/100 m^2) and high (> 2/100 m^2) (median test, p = 0.209; Figure 39).

In the following, all optimal models obtained from multiple linear regression analysis, as well as corresponding median analyses are graphically illustrated (Figures 32-39).

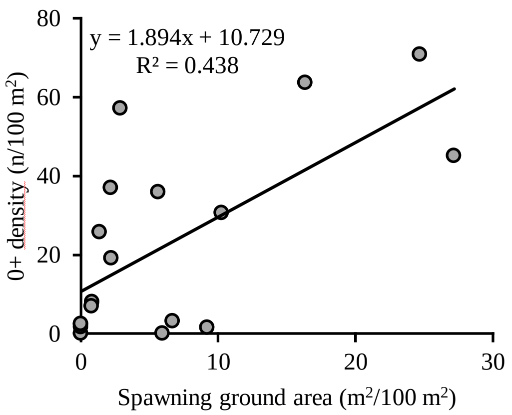

Figure 32: Relationship between the density of 0+ brown trout in the anadromous reach and spawning ground area (N = 18, p = 0.003**).

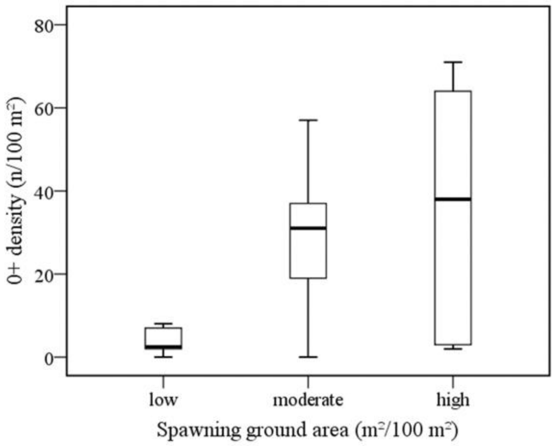

Figure 33: The density of 0+ brown trout in the anadromous reach in spawning ground area classes low (< 1.1 m^2/100 m^2), moderate (1.1-6.0 m^2/100 m^2) and high (> 6.0 m^2/100 m^2). (Box-and-whisker plot; whisker: 0.05 and 0.95 percentile; box: lower quartile, median and upper quartile; outliers and extreme outliers are marked by circles and stars, respectively).

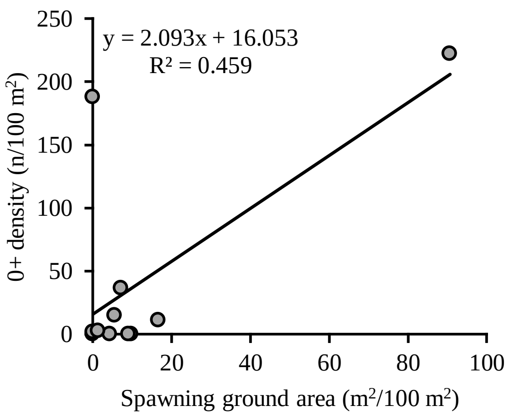

Figure 34: Relationship between the density of 0+ brown trout in the non-anadromous reach and spawning ground area (N = 11, p = 0.022*).

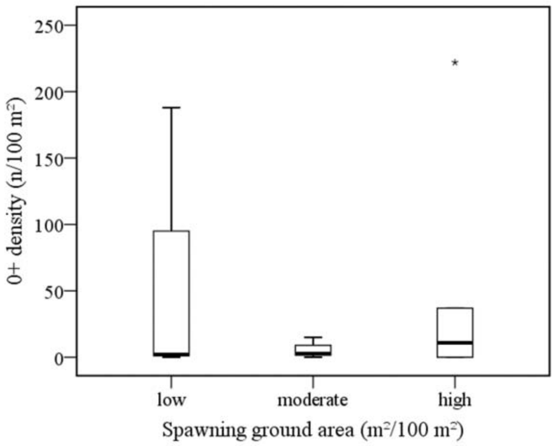

Figure 35: The density of 0+ brown trout in the non-anadromous reach in spawning ground area classes low (< 1.1 m^2/100 m^2), moderate (1.1-6.0 m^2/100 m^2) and high (> 6.0 m^2/100 m^2). (Box-and-whisker plot; whisker: 0.05 and 0.95 percentile; box: lower quartile, median and upper quartile; outliers and extreme outliers are marked by circles and stars, respectively).

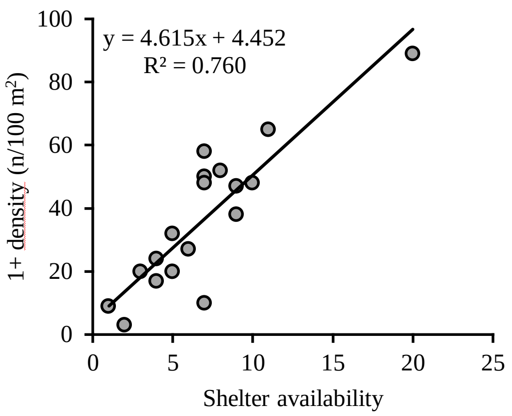

Figure 36: Relationship between the density of 1+ brown trout in the anadromous reach and shelter availability (N = 18, $p < 0.001$**).

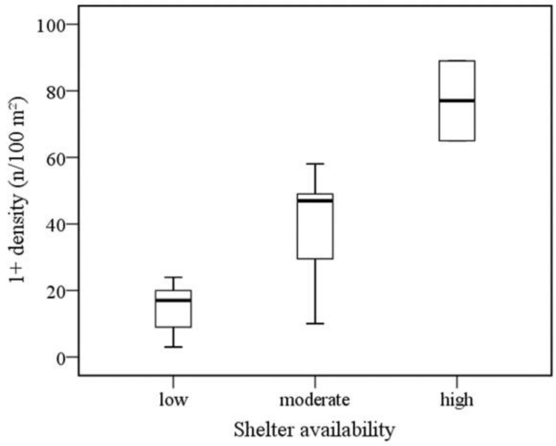

Figure 37: The density of 1+ brown trout in the anadromous reach in shelter availability classes low (< 5), moderate (5-10) and high (> 10). (Box-and-whisker plot; whisker: 0.05 and 0.95 percentile; box: lower quartile, median and upper quartile; outliers and extreme outliers are marked by circles and stars, respectively).

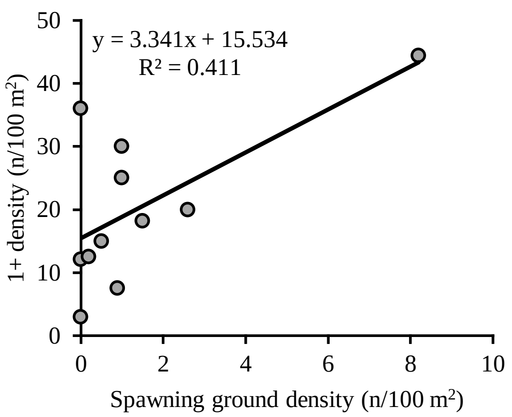

Figure 38: Relationship between the density of 1+ brown trout in the non-anadromous reach and spawning ground density (N = 11, $p = 0.034$*).

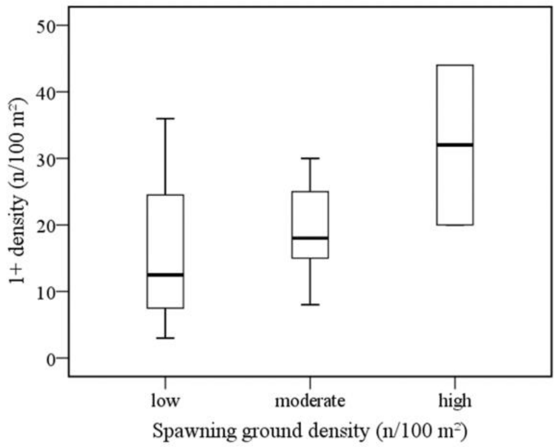

Figure 39: The density of 1+ brown trout in the non-anadromous reach in spawning ground density classes low (0/100 m^2), moderate (1-2/100 m^2) and high (> 2/100 m^2). (Box-and-whisker plot; whisker: 0.05 and 0.95 percentile; box: lower quartile, median and upper quartile; outliers and extreme outliers are marked by circles and stars, respectively).

The combined influence of spawning ground area and shelter availability on densities of 0+ and 1+ brown trout in the anadromous reach was analyzed descriptively. Spawning ground area and not spawning ground density was used in this analysis, because it was found to be the best predictor for the density of 0+ brown trout. Based on the classes developed for spawning ground area (chapter 3.3.2) and shelter availability (chapter 3.3.3), the mean density of 0+ and 1+ brown trout was calculated for those habitats exhibiting simultaneously low spawning ground area and shelter availability, moderate spawning ground area and shelter availability or high spawning ground area and shelter availability.

In doing so, it was found that habitats with low classes of spawning ground area and shelter availability exhibited the least density of 0+ and 1+ fish (mean = 12/100 m^2 ± 9.7 SD). In habitats comprising moderate classes of spawning ground area and shelter availability a substantially higher density of 0+ and 1+ fish was found (mean = 80/100 m^2 ± 8.0 SD). Finally, habitats with high spawning ground area and shelter availability classes showed the highest density of 0+ and 1+ fish (mean = 131/100 m^2 ± 30.0 SD). The mean density of 0+ and 1+ brown trout in habitats containing simultaneously low, moderate or high classes of spawning ground area and shelter availability is illustrated in Figure 40.

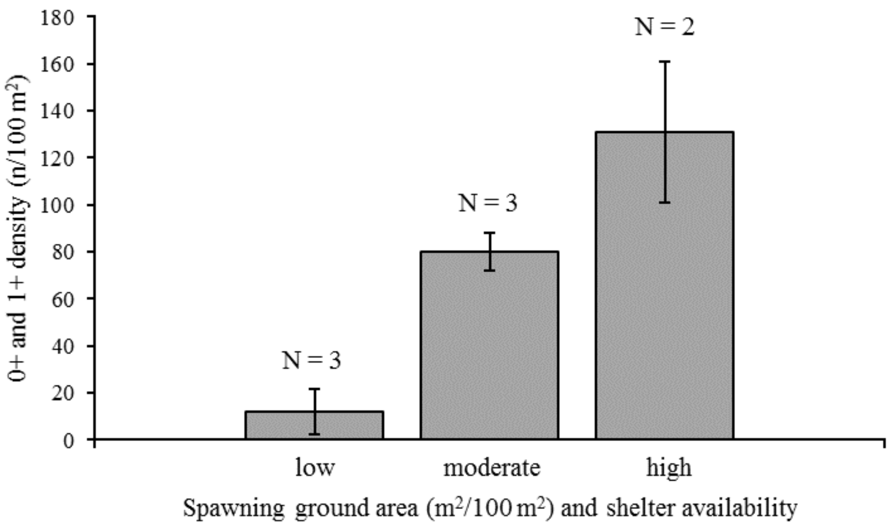

Figure 40: Mean density of 0+ and 1+ brown trout with standard deviation in habitats exhibiting classes of low spawning ground area and shelter availability, moderate spawning ground area and shelter availability, as well as high spawning ground area and shelter availability.

4.5 Competitive effects

Simple linear regression models were computed for each age class and species constellation in which potential competitive effects could have been expected. Significant relationships were detected between densities of 0+ and 1+ brown trout in the anadromous (R^2 = 0.293, p = 0.020*) and non-anadromous reach (R^2 = 0.679, p = 0.002**). These were positively correlated (b_1 = 0.576 and 5.392, respectively). The remaining constellations did not show significant relationships. Table 13 summarizes the results obtained from simple linear regression for all age classes and species constellations.

Table 13: Dependent and independent variables, coefficient of determination (R^2), p-value (p), constant (b_0), non-standardized regression coefficient (b_1) of the simple linear regression models. BT = brown trout, AS = Atlantic salmon.

Dependent Variable	Independent variable	R^2	p	b_0	b_1
0+ BT anadromous reach	0+ AS	0.190	0.463	3.788	1.596
	1+ AS	0.115	0.577	3.505	0.336
	1+ BT anadromous reach	0.293	0.020*	1.931	0.576
	>1+ BT anadromous reach	0.072	0.282	16.556	0.479
1+ BT anadromous reach	1+ AS	0.051	0.715	39.286	0.103
	>1+ BT anadromous reach	0.039	0.434	32.088	0.331
0+ BT non-anadromous reach	1+ BT non-anadromous reach	0.679	0.002**	-66.353	5.392
	>1+ BT non-anadromous reach	0.000	0.995	43.709	-0.011
1+ BT non-anadromous reach	>1+ BT non-anadromous reach	0.062	0.459	15.686	0.196

5 Discussion

Chapter 5 starts with the discussion about the effects of spawning ground area and spawning ground density on fish density (hypotheses (i), (iii) and (iv)), as well as shelter availability on fish density (hypotheses (ii), (iii) and (iv)). Subsequently, the effects of shelter availability and spawning ground area in combination are discussed, and the influence of further habitat features on density is highlighted. Finally, methodological problems, competitive effects and recommendations for river restoration are discussed.

5.1 Effects of spawning grounds on juvenile density

The findings of the present study provide evidence that spawning ground area and spawning ground density had significant, positive influence on the density of 0+ and 1+ brown trout in both the anadromous and non-anadromous reach. Based on the multiple linear regression analysis spawning ground area was the best predictor for 0+ densities of brown trout.

These findings confirm hypothesis (i) and the first part of hypothesis (iii) and (iv) of the present study (page 5). Furthermore, the results are in line with previous studies, which showed that spawning ground area (Pulg 2009, Normann 2011) and nest area (Teichert et al. 2011) are positively related to the density of juvenile brown trout and Atlantic salmon, respectively.

The positive relationship between the density of 0+ brown trout and spawning ground area was most probably associated with egg density (Elliot and Hurley 1998, Syrjänen et al. 2014) that is indirectly determined by the amount of spawning ground area.
In practice this does not imply that densities of juvenile brown trout increase infinitely and directly proportionate with egg densities. On the contrary, if the spawning stock and thus egg densities exceed a certain limit, survival rates decrease and densities of juvenile fish reach a balance according to the habitat's carrying capacity or even decrease further (Milner et al. 2003). This is due to density-dependent regulation processes, often in the form of inter- and intraspecific competition for limited resources (food and space), which increase when fish densities approach carrying capacity (Elliott 1994, Milner et al. 2003, Jonsson and Jonsson 2011, Forseth and Harby 2014). In these processes, key habitat features (e.g. spawning grounds, shelter availability and food availability) may act as limiting resources

and create bottlenecks, typically occurring during the early life stages (Elliott 1993, Jonsson et al. 1998), but also during the adult stages (Elliot and Hurley 1998).

Such processes were not visible in the data analysis of the present study, since linear regression models were used to describe the relationships between fish densities and habitat features (chapter 4.4). The use of linear models had two major reasons: First, this model type fit best to the data and, secondly, linear models describe relations in the easiest way. However, because linear relationships are uncommon in nature and strongly abstract reality, the results of the linear regression analysis do not imply that there were no density-dependent processes in the study area and population density can be increased to infinity.

Given density-dependent mechanisms, logistic functions might have reflected a more realistic relation between juvenile density and habitat features. Nevertheless, it is likely that spawning ground area is the limiting factor of the study area, i.e. the bottleneck constraining fish production (Pulg et al. 2011). Migration barriers corroborate this situation by partially impeding the accessibility to spawning grounds.

Food availability appears not to be among the limiting resources constraining fish production in the Apeltunelva. This is, for instance, obvious from the length-frequency distribution plot of the non-anadromous reach (Figure 24), which shows several specimens larger than 40 cm. This implies that there is sufficient food for positive growth over all occurring length classes. On the other hand, if negative growth would have taken place, then larger length classes would not have been detected, since negative growth persisting over longer time periods may cause emigration or mortality (Unfer 2012). Furthermore, the high amount of nutrients and favorable water temperatures (Table 2) make it unlikely that food availability was a constraining factor for fish production.

In juxtaposition to the second part of hypothesis (iii) of the present study (page 5), it was found that spawning ground density was the best predictor for 1+ brown trout in the non-anadromous reach. Since spawning grounds consist predominantly of gravel, it was also detected that gravel had significant, positive influence on the density of 1+ fish in the non-anadromous reach (appendix, chapter 9.6, Table 33).

This result is difficult to explain and to interpret, but suggests that the 1+ fish remained close to their native sites. This observation supports the findings of a previous study conducted by Teichert et al. (2011). A possible explanation might be that the 1+ brown trout preferred other shelter possibilities closely located to the spawning grounds where they emerged. In this context, it is likely that fish used typical shelter forms of the riverbank, such as riparian vegetation or undercut banks (Figure 7). The riverbank may play an important role in providing shelter for juvenile fish, particularly in small-sized streams as the Apeltunelva. However, the relationship between the 1+ fish and riverbank shelter remains an assumption, because the scale used in the present study did not include microhabitat features. A preference to gravel because of increased food availability on this substrate type (Wood and Armitage 1997, Merz and Chan 2005, Barnes et al. 2013, Graf et al. 2016) is unlikely.

The effects of spawning ground area and spawning ground density on densities of 0+ and 1+ brown trout were positive and relatively similar in respect to significance values (Table 10). The highly significant, positive relationship found between spawning ground area and spawning ground density confirms that there was multicollinearity between these variables (chapter 4.1). The high degree of multicollinearity was favored by the small size of the study reaches. Spawning ground area and spawning ground density cannot be clearly distinguished in the present study. Misinterpretations, however, are unlikely, since both independent variables were analyzed individually by simple linear regression (Table 10; appendix, chapter 9.6, Tables 30-35), and there always remained only one of both independent variables in the optimal models of the multiple linear regression analysis.

The results of the multiple linear regression analysis showed that spawning ground area was the best predictor for the density of 0+ brown trout in the Apeltunelva. Therefore, spawning ground area can be recommended as proper variable for studies that aim to analyze relations between 0+ brown trout and spawning grounds, particularly in small-sized streams.

Likely of more importance than spawning ground density, is the distribution of redds in determining fish density, as shown by several studies (Einum et al. 2008a, Foldvik et al. 2010, Teichert et al. 2011). As this study put the focus on potential spawning areas, i.e. not specifically on redds, and because the experimental set up aimed to investigate different relationships, the distribution of spawning grounds was not investigated.

Research might benefit from the analysis of the influence of spawning ground distribution on fish density. This is because most studies to date have only concentrated on the distribution of redds on spawning grounds. However, the spatial arrangement of spawning grounds restricts the distribution of redds (Armstrong et al. 2003).

Comparatively large spawning areas were concentrated to relatively few habitats in the study area, whereas other habitats exhibited only small or no spawning grounds (chapter 3.2.1, Figure 20). Even though sizes of sampled habitats were relatively large, some habitats may have influenced adjacent, closely located habitats in respect to densities of 0+ fish. Such effects could be assumed if an up- or downstream located habitat exhibited high densities of 0+ fish and simultaneously no or only small spawning ground areas.

The densities of 0+ brown trout in habitats 9 and 10 (study reach 1), exhibiting only very small spawning ground areas, were probably increased by habitat 11, which showed both a relatively large spawning ground area (27.2 m^2/100 m^2) and a high density of 0+ fish (45/100 m^2). Further, the density of 0+ brown trout in habitat 17 (study reach 2) was likely affected by habitat 18, revealing a large spawning ground area (24.7 m^2/100 m^2) and a high density of 0+ fish (71/100 m^2). Finally, the density of 0+ brown trout in habitat 27 (study reach 4) with a spawning ground area of 0.0 m^2/100 m^2 was probably strongly increased by habitat 28 (spawning ground area = 90.6 m^2/100 m^2, density of 0+ fish = 222/100 m^2).

The most probable explanation for the strong increase in densities of 0+ brown trout in the aforementioned habitats are downstream movements of 0+ fish from habitats with increased fish production because of a higher amount of spawning grounds. Downstream movements of alevins and/or parr from their spawning and nursery habitats (Armstrong et al. 2003) have been observed by several authors (e.g. Bujold et al. 2004, Einum et al. 2008) and occur typically in larger rivers.

An interesting and particular case was found in habitats 14, 15 and 16 (Figure 41, dashed circle). These exhibited 0+ fish, although there were only very small (habitats 14 and 15) or no (habitat 16) spawning ground areas, and no defined habitats upstream, which could have influenced densities of 0+ fish through downstream movements. In the case of habitat 14, the density of 0+ brown trout was most probably increased by upstream migrated 0+ fish from habitat 13, which comprised a relatively large spawning ground area (16.3 m^2/100 m^2) and a high density of 0+ fish (64/100 m^2). Upstream movements of 0+ brown trout play a role in small streams (Ulrich Pulg, personal communication) and are facilitated through the small scale in such waters. This means that suitable habitats are closer than in larger rivers and therefore easier to reach and access. A further upstream migration to habitats 15 and 16 however, appears unlikely, as water velocities were too high between habitats 14 and 15 (personal observation). A more logical explanation for the occurrence of 0+ brown trout in habitats 15 and 16 might be a relatively large spawning ground upstream of habitat 16 in the outlet area of the Apeltunvannet. Figure 41 gives an overview about potential effects of spawning grounds on the density of 0+ brown trout in adjacent habitats throughout all study reaches in the anadromous and non-anadromous reach.

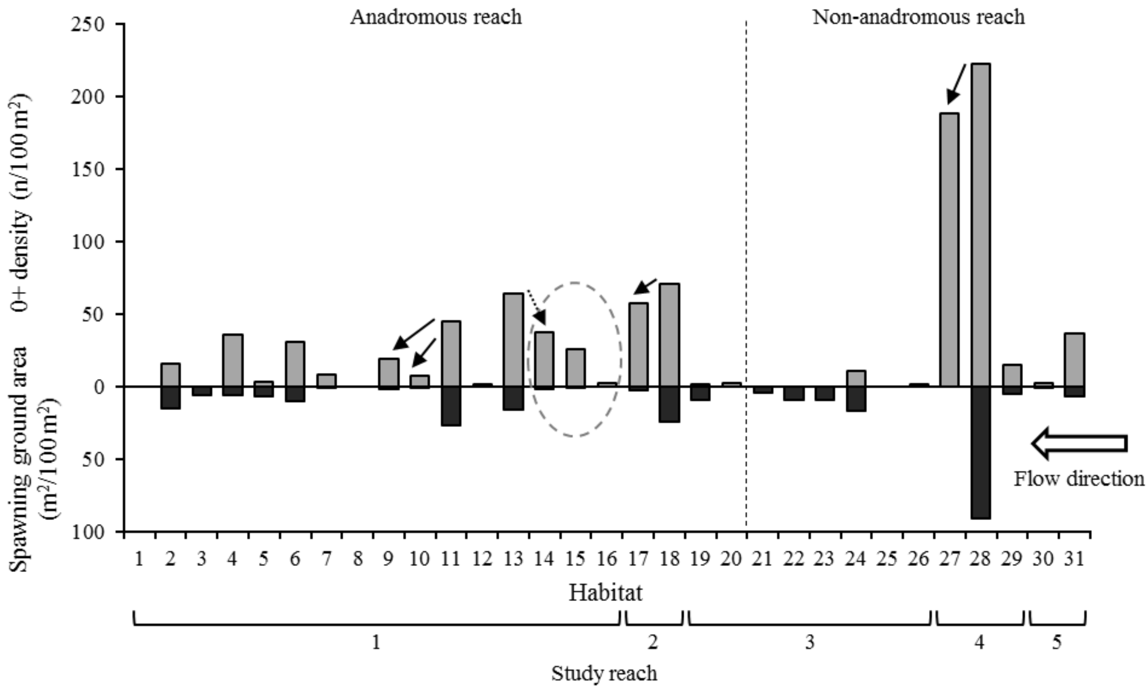

Figure 41: Potential effects of spawning ground area on the density of 0+ brown trout in adjacent habitats throughout all study reaches in the anadromous and non-anadromous reach. Arrows indicate possible effects of habitats with a large spawning ground area and high 0+ densities on 0+ densities in adjacent habitats, exhibiting no spawning grounds or only a very small spawning ground area. The dashed circle shows a particular case.

In the present study some outliers were presumably caused by downstream moving 0+ fish. In this context, habitats 17 and 27 were strongly concerned. Despite this clear bias, these outliers were included in statistical analyses, on the one hand because sample size was in general low and, on the other hand, to guarantee for statistical consistency.

Furthermore, there were only very low densities of 0+ brown trout in study reach 3 (habitats 19-26), despite a moderate amount of spawning grounds in this reach (Figure 41). This finding is difficult to interpret and might have different reasons. Downstream of the Osbanenkulverten (located between habitat 20 and 21; dashed line, Figure 41) 0+ fish could have been emigrated from habitat 19 and/or 20 into the Apeltunvannet. Additionally, densities 0+ fish could have been reduced through predation due to the high frequencies of larger brown trout (30-40 cm) in study reach 3 (Table 7, Figures 29 and 31). Finally, the reduced overall catch efficiency could have contributed to the low numbers of 0+ fish detected in study reach 3.

5.2 Effects of shelter availability on juvenile density

Shelter availability (i.e. holes and interstitial spaces in the substrate) had significant and highly significant, positive influence on the densities of 0+ and 1+ brown trout, respectively, in the anadromous reach. This outcome confirms partially hypothesis (ii) of the present study (page 5) and suggests a strong preference of brown trout in the anadromous reach for habitats with high shelter availability. Based on the multiple linear regression analysis shelter availability constituted the best predictor for the density of 1+ brown trout in the anadromous reach, and thus confirms partially hypothesis (iii) of this study (page 5).

The positive correlation between juvenile brown trout and shelter availability is primarily associated with habitat heterogeneity, whose degree determines territory size and thus the number of territories that can be established (Kalleberg 1958, Imre et al. 2002). Habitat heterogeneity is linked, amongst others, to substrate composition of the river bed that, in turn, determines shelter availability (Jocham 2010, Forseth and Harby 2014). This means that shelter availability increases with increasing substrate sizes. For instance, a river bed dominated by stones (6-20 cm) and gravel (2-6 cm) is more heterogeneous than a river bed consisting predominantly of sand and fine gravel (0.06-20 mm) and silt (< 0.06 mm), and thus exhibits higher shelter availability and ultimately a higher amount of territories. Hence, shelter availability may directly regulate the density (Finstad et al. 2007) of territorial fish, such as brown trout and Atlantic salmon, particularly on the local scale (Finstad et al. 2009).

In the course of density-dependent regulation mechanisms, shelter availability represents, besides spawning grounds, a limiting resource, and thus may create bottlenecks by defining carrying capacity (Forseth and Harby 2014). This is particularly the case during age classes 0+ and 1+ when fish occupy favorable territories providing access to shelter and food. Here shelter availability can influence density regulation via affecting survival rates and/or im- and emigration (Finstad et al. 2009) by fulfilling the following essential tasks: Protection from predators, refugium during winter and floods, as well as reducing energy expenditure (Heggenes et al. 1993, Valdimarsson and Metcalfe 1998, Millidine et al. 2006). The latter has been subject to several studies (e.g. Millidine et al. 2006, Finstad et al. 2007, 2009, Hoogenboom et al. 2013) and is most likely caused by reduced metabolic costs associated with distinct factors, such as anti-predator behavior (decreased foraging efficiency and increased predator alertness), competition, light conditions and water velocity (Finstad et al. 2004, 2007, Millidine et al. 2006). Also, food availability (Finstad et al. 2007) and prior residency advantages (Kvingedal and Einum 2011a) can be influenced by shelter availability and may therefore indirectly affect population density.

The findings of the present study support, in general terms, the results of several other studies (Kalleberg 1958, Dolinsek et al. 2007, Venter et al. 2008, Finstad et al. 2009, Höjesjö et al. 2014), underlining the importance of shelter in regulating density and, ultimately, population demographics of salmonids. Despite the awareness that heterogeneity of the river bed affects positively the population density of salmonids, the influence of shelter availability on the density of brown trout has never been tested before. In a recently published study, only the biomass of juvenile brown trout in an anadromous water has been shown to be positively correlated with shelter availability (Foldvik et al. 2016)

In line with Finstad et al. (2009), this study provides strong evidence that brown trout in the anadromous reach of the Apeltunelva used shelter of the substrate equal to Atlantic salmon (Finstad et al. 2007). Coinciding with literature (e.g. Heggenes et al. 1999, Klemetsen et al. 2003, Jonsson and Jonsson 2011), this result confirms that Atlantic salmon and anadromous brown trout exhibit a very similar habitat use during their ontogeny. Also consistent with Finstad et al. (2009), the density of 1+ fish could be better predicted by shelter availability compared to 0+ fish, although there is a specific size category (S1 = 2-5 cm, chapter 3.3.3) included in the method (Finstad et al. 2007) for considering age class 0+. The influence of shelter availability using size category S1 on the density of 0+ brown trout was tested by means of simple linear regression and did not reveal significant effects in the anadromous ($R^2 = 0.001$, $p = 0.920$) and non-anadromous reach ($R^2 = 0.004$, $p = 0.862$). The reason why shelter availability was a better predictor for the density of 1+ fish might therefore be linked to the hose diameter used for measuring shelter availability and intercohort competition. Since only holes and interstitial spaces with a diameter of at least 13 mm (hose diameter = 13 mm, chapter 3.3.3) were considered, 1+ fish could have outcompeted 0+ fish for shelters that were large enough to be accessed. Thus, it appears likely that 0+ fish partially used other shelter forms, either because they were expelled from shelters by larger fish or shelters were already occupied by larger fish, defending their territory more successful due to the larger body size (Cutts et al. 1999) and prior residency advantage (Kvingedal and Einum 2011a). Although 13 mm hoses became established to measure shelter availability and were shown to predict best fish densities (Finstad et al. 2007, Forseth and Harby 2014), it has not been analyzed in the field if densities of 0+ fish may be better explained by using smaller hose diameters.

Not in line with hypotheses (ii) and (iii) of the present study (page 5) densities of 0+ and 1+ brown trout in the non-anadromous reach did not correlate with shelter availability. Perhaps, this might indicate differences in shelter use between brown trout of the anadromous and non-anadromous reach.

This outcome is most probably linked to the distinct physical habitat conditions in the non-anadromous reach. In total, there were lower gradients and more fine sediments compared to the anadromous reach (Figure 6). This led partially to a relatively heterogeneous distribution of the substrate shelter throughout the habitats, often in some distance to spawning grounds. The spatial arrangement of substrate shelter (Finstad et al. 2009) in addition to a high amount of alternative shelter forms, particularly undercut banks (Figure 7) and woody debris (Figure 8), perhaps resulted in a shift in shelter use.

The differences in shelter use could also be associated with intercohort competition for space in the brown trout population of the non-anadromous reach. As cohorts of older age classes permanently coexist with those of younger ones in the non-anadromous reach (N slund et al. 1998), it appears likely that larger fish (>1+) outcompete smaller ones from the substrate shelter (Cutts et al. 1999, Johnsson et al. 1999, Vehanen and Mäki-Petäys 1999), resulting in a more complex sheltering behavior. In this context, also predation may be of importance in the non-anadromous reach, since many brown were found here large enough (30-40 cm) to feed on 0+ and 1+ fish (Figures 24 and 26).

This means that larger fish could have occupied more favorable habitats, whereas smaller ones were eaten or expelled to habitats dominated by other shelter forms. A study conducted by Riedl and Unfer (2010) in several small streams in the Austrian Alpine foothills showed that juvenile brown trout preferred particularly pocket-pools, substrate and dead wood as habitats. However, if densities of adult fish were low, then juvenile brown trout occupied also adult habitats (locations with water depths ≥ 25 cm, water velocities ≥ 25 cm/s and shelter possibilities for larger fish), underlining the potential effects of intercohort competition on shelter use.

Since Riedl and Unfer (2010) examined also resident brown trout, presumably with a similar population structure as in the non-anadromous reach of the Apeltunelva, the assumption of shifts in shelter use through intercohort competition appears likely. Given the large share of freshwater resident brown trout populations, intercohort competition might play an important role for shelter use in many inland waters. Intercohort competition in respect to shelter use has only been studied scarcely in freshwater resident brown trout populations and represents a research gap.

In brown trout populations of anadromous waters, intercohort competition for space through older age classes is relaxed most time of the year, except during spawning season. Intra- and interspecific competition in the younger age classes, however, tends to be higher in these populations due to increased egg density (Bohlin et al. 2001) of anadromous brown trout and co-occurring Atlantic salmon (Heggenes and Saltveit 1990, Mäki-Petäys et al. 1997, Jonsson and Jonsson 2011). Predation through larger fish, on the other hand, is reduced in anadromous waters.

This study analyzed how substrate shelter affects the densities of juvenile brown trout in an anadromous and non-anadromous reach of a small stream in Norway. It was found that juvenile brown trout in the anadromous reach of the Apeltunelva had a high preference to substrate shelter. In line with previous field surveys (Finstad et al. 2009, Foldvik et al. 2016), the present study suggests that shelter provided by the substrate of the river bed may play a central role for juvenile anadromous brown trout and Atlantic salmon in Norwegian rivers. However, the use of substrate shelter by juvenile anadromous brown trout does not apply to every running water, neither in Norway, nor on a global-scale.

In general, shelter use of brown trout is strongly dependent on different shelter forms (e.g. woody debris, undercut banks, substrate etc.) occurring in a river.

Holes and interstitial spaces in the substrate often represent the dominating shelter form in Norwegian rivers. This is primarily associated with relatively large substrate sizes, which, in turn, depend on the geological conditions of the catchment, catchment area, gradient etc. (Jocham 2010, Forseth and Harby 2014, Foldvik et al. 2016).

As every river and its catchment is different and thus represents a unique system, shelter use of brown trout can vary significantly between running waters. But also within rivers, as suggested by the present study and other surveys (Riedl and Unfer 2010, Normann 2011).

For instance, many Alpine rivers are dominated by smaller substrate sizes (gravel) compared to Norwegian rivers. In such waters substrate shelter has probably reduced influence on the density of juvenile brown trout, particularly on 1+ fish.

The preferences of juvenile brown trout to different shelter forms have been intensively studied during the last decades (Northcote and Lobón-Cerviá 2008). In this context, several authors showed that brown trout are attracted by structures, such as undercut banks, aquatic and riparian vegetation, as well as woody debris (Hermansen and Krog 1984, Wesche et al. 1987, Davis 1989, Haury et al. 1995, Zika and Peter 2002, Degerman et al. 2004, Johansen et al. 2005, Riedl and Unfer 2010). Thus, the shelter forms used by juvenile brown trout depend, ultimately, on the biotic and abiotic conditions of a river and, as discussed above, on intercohort competition. Therefore, and because of several other factors, shelter use of brown trout is a highly complex issue and differs within and among rivers.

5.3 Effects of spawning ground area and shelter availability on juvenile density

The density of 0+ and 1+ brown trout in the anadromous reach was lowest in those habitats comprising simultaneously low amounts of spawning ground area and shelter availability. In contrast, habitats exhibiting simultaneously moderate or high amounts of spawning ground area and shelter availability showed substantially higher densities of 0+ and 1+ fish.

According to chapters 5.1 and 5.2 this finding may be explained by different habitat needs of the different life stages. In the anadromous reach high densities of 0+ brown trout were primarily found in habitats with large spawning ground areas (e.g. habitat 18), whereas high densities of 1+ brown trout were detected more often in habitats with high shelter availability (e.g. habitats 3 and 4, Tables 4 and 7), as also shown by the simple linear regression models in chapter 4.3 (Table 10). Because of the habitat preferences of 0+ fish to spawning grounds and 1+ fish to substrate shelter, the density of juvenile brown trout was highest in habitats containing large spawning ground areas in combination with a high degree of shelter availability (Figure 40). Those habitats exhibit optimal prerequisites for high birth (egg density) and survival rates (favorable territories). Especially due to the limited mobility of juvenile fish shelter opportunities should be located closely to natal sites (Bjornn and Reiser 1991). Therefore, restoration measures should aim to enhance both spawning grounds and shelter availability, ideally in close distance to each other and well distributed.

A significant, positive relationship was found between shelter availability and spawning ground area in the anadromous reach. This multicollinearity had probably two major reasons: First, the substrate of spawning grounds offers shelter, and, secondly, there were several habitats in the anadromous reach with moderate or large spawning ground areas and simultaneously moderate or high shelter availabilities. Misinterpretations are unlikely, since spawning ground area and shelter availability were analyzed individually by simple linear regression (Table 10; appendix, chapter 9.6, Tables 30-35), and there always remained only one of both independent variables in the optimal models of the multiple linear regression analysis. Furthermore, spawning ground area and shelter availability affected densities of 0+ and 1+ brown trout in the anadromous reach with different strength and significance values and in accordance with hypothesis (iii) of the present study (page 5). Therefore, the influence of spawning ground area and shelter availability can be distinguished from each other.

5.4 Effects of further habitat features on juvenile density

Despite a relatively high number of further habitat features measured, there were no significant relationships found between these and fish densities, except for gravel and stone (appendix, chapter 9.6, Tables 30-35). This is not in line with other studies, which have shown that numerous habitat features, for instance woody debris or riparian vegetation, affect salmonid populations (Hermansen and Krog 1984, Wesche et al. 1987, Davis 1989, Haury et al. 1995, Zika and Peter 2002, Degerman et al. 2004, Johansen et al. 2005, Riedl and Unfer 2010).

Significant positive relationships were found between densities of 0+ and 1+ brown trout in the non-anadromous reach and gravel, as well as between the density of 1+ brown trout in the anadromous reach and stone. These findings are most likely associated with the influence of gravel (Kondolf and Wolman 1993) and stones (Jocham 2010, Forseth and Harby 2014) on spawning grounds and shelter availability, respectively.

5.5 Methodological problems

In the present study the catch efficiency of 0+ brown trout was reduced compared to older fish (Pulg et al. 2011, 2016). This is also obvious from the length-frequency distribution plots (Figures 22-26), revealing more fish in age class 1+ than 0+. The effects of spawning ground area and spawning ground density on 0+ brown trout might therefore be biased by the underestimated number of 0+ fish.

The investigations of the present study were carried out based on the reach scale (Frissell et al. 1986), which has been approved for surveys of spawning grounds (Einum et al. 2008a, Teichert et al. 2011) and shelter availability (Finstad et al. 2009, Foldvik et al. 2016), using correlative approaches. Applying this scale might have contributed to detect significant relationships between the density of 0+ brown trout and spawning grounds. Fish, which were located further away from their redds of emergence, could be sampled and thus related to their original spawning grounds. Despite limited mobility, 0+ fish disperse after emergence, and are not necessarily found in or in close vicinity to their spawning grounds. In this context, up- or downstream movements may be of importance.

However, there were some drawbacks owing to the scale used in the present work, which should be taken into account for future research in this field. The relatively large scale, in which most habitats were defined, reduced the number of samples, especially in the non-anadromous reach (N = 11), due to the in general limited size of the study area. As a consequence, the effects of spawning ground area and spawning ground density on the density of 0+ and 1+ brown trout in the non-anadromous reach cannot be considered as statistically proven and need to be verified again. As obvious from the outcomes of the anadromous reach, a higher number of samples could have contributed to clearer results. An ideal sample size for such kinds of investigations should range between 20 and 30.

By using microhabitat scale, sample size could have been extremely increased. Thus, the selection of an appropriate scale should not only be based on the variables that are planned to be sampled and the research questions, but also fit to the dimensions of the study area. Also, the influence of further habitat features (i.e. substrate composition, riparian vegetation, woody debris, algae cover and moss cover) on fish densities might have been analyzed more properly by conducting measurements on smaller scales, as shown, for instance, by Riedl and Unfer (2010). In this context, electrofishing according to the point abundance sampling method (e.g. Riedl and Unfer 2010) might have provided clearer results. Especially for the density of >1+ brown trout, showing different habitat preferences compared to 0+ and 1+ fish (Heggenes et al. 1999), applying this approach would have been more advantageous.

However, using such approaches makes it occasionally difficult to produce correlations, since some microhabitat types (e.g. woody debris) are difficult to measure and hence caught fish cannot be properly related to a unit area or spatial unit. Selecting an appropriate scale and proper methods for a study is essential to obtain high-quality data, but one should also consider that each scale and method have advantages and disadvantages.

5.6 Competitive effects

There were no intercohort competitive effects (negative correlations) found, neither for brown trout, nor between brown trout and Atlantic salmon. Analogously, no interspecific competition was detected between brown trout and Atlantic salmon. Although antagonistic effects are expected between age classes and species, for example in the form of interference or exploitative competition, (Kaspersson and Höjesjö 2009, Kvingedal and Einum 2011b), the density of 0+ brown trout was positively correlated with the density of 1+ brown trout in both the anadromous and non-anadromous reach.

Similar observations have been made in previous studies conducted by Teichert et al. (2011) and Kvingedal and Einum (2011). The most probable explanation for the positive relation between 0+ and 1+ brown trout are the relatively large habitats, which often contained spawning grounds and substrate shelter in combination, and thus offered suitable habitat requirements for both age classes. Finally, it might also be possible that 1+ brown trout remained in close vicinity to their spawning grounds where they emerged, as shown by the positive relationship between 1+ fish and spawning grounds in the non-anadromous reach.

Evidently, population density of brown trout can be regulated by the habitat's limiting resources, as these influence the population carrying capacity in streams (Finstad et al. 2009, Forseth and Harby 2014). If fish densities are high in relation to the limiting resources, then density-dependent processes, mostly in the form of competition for food and space, reduce population sizes according to the population carrying capacity. In such cases, limiting resources, such as spawning grounds and shelter availability, act as habitat bottlenecks, and thus mediate the strength of density-dependent mechanisms (Finstad et al. 2009, Forseth and Harby 2014).

Regulation of growth and population size through density-dependent processes is among the central topics in salmonid ecology and has been comprehensively studied. There is clear evidence in literature that density-dependent mechanisms affect survival and growth of Atlantic salmon and brown trout (e.g. Elliott 1994, Milner et al. 2003, Jonsson and Jonsson 2011).

However, density-dependent processes do not apply to every brown trout or Atlantic salmon population, but are strongly dependent on the environmental conditions in a river. This means that population density of brown trout and Atlantic salmon may also be regulated by density independent factors, such as water temperature, discharge, drought etc. (Figure 1).

There are studies, which found clear indications that population structure and specifically the density of juvenile life stages are primarily regulated by density-independent factors, particularly by discharge (Jensen and Johnsen 1999, Lobón-Cerviá and Rincón 2004, Lobón-Cerviá and Mortensen 2005, Lobón-Cerviá 2009, Unfer et al. 2011). The influence of density-independent factors on population structure and density increases with increasing harshness and consequently distinct hydro-morphological chances (Haldane 1953, Unfer et al. 2011). For instance, density-independent may play a more important role for salmonid populations in Alpine rivers with annually high discharge dynamics (snow melt) than in lowland rivers with a relatively constant discharge regime and less natural dynamics. The question to what extent density-dependent and/or density-independent factors influence the structure and density of brown trout populations is difficult to answer and will remain unclear. However, there is clear evidence that both types of factors play an essential role in shaping population dynamics, and may differ dramatically between and within rivers.

5.7 Recommendations for river restoration

The findings of the present study showed that the density of juvenile brown trout increases with increasing spawning ground area, spawning ground density and shelter availability in the Apeltunelva. In the context of river restoration, this implies that the population density of brown trout might be further increased in the study area by measures that aim to enhance spawning grounds and/or shelter availability, for instance by adding suitable spawning gravel and ripping of the river bed’s substrate. Since spawning habitats are unevenly distributed to a few locations (Figure 20) and amounted only to 4.1 % of the study area in 2015, fish production could be increased by increasing number and area of spawning grounds. Also, shelter availability is partially heavily reduced in the study area, as obvious from Figure 21. In these river sections, fish densities might be promoted by increasing shelter availability.

Ideally, spawning grounds and shelter availability should be restored in close vicinity to each other in order to increase carrying capacity for both 0+ and 1+ brown trout. In addition, spawning grounds and shelter should be well distributed in the river with the aim to minimize density-dependent processes, typically acting on the local scale. However, spawning areas should not be too numerous, since brown trout older than 0+, for instance, have other habitat preferences than fry.

Besides the addition of spawning gravel and ripping of the river bed’s substrate to increase shelter availability, the removal of canals and culverts might play a crucial role in increasing fish production, as these represent a large share of the entire study area and reduce natural fluvial processes.

In general, one should first try to reestablish natural dynamics, as these often represent the main cause of habitat degradation in rivers. If this is not possible, then mitigation measures, such as adding spawning gravel or ripping of the river bed’s substrate, should be applied (Pulg 2009, Pulg et al. 2013). Although those measures often have been shown to be successful (Barlaup et al. 2008, Pulg 2009, Pulg et al. 2013, Forseth and Harby 2014), they do not solve the problem in a sustainable way. Furthermore, each river is unique and restoration measures must be planned thoroughly and adapted to the prevailing problems.

6 Summary

The outcomes of the present study show how spawning grounds and shelter availability may regulate the density of juvenile brown trout in a small stream in Norway. In line with previous surveys (e.g. Beard and Carline 1991, Finstad et al. 2007, 2009, Teichert et al. 2011), this study suggests that spawning grounds and shelter availability may play a key role as limiting resources by determining the population carrying capacity in streams.

In juxtaposition to most investigations focusing more on the influence of redd area and density on juvenile salmonids, this study analyzed the effects of spawning ground area and spawning ground density on the density of juvenile brown trout. As hypothesized both variables influenced significantly 0+ densities. However, spawning ground area was the better predictor for 0+ brown trout. As a consequence, it can be recommended for future research to use spawning ground area as relevant predictor variable when analyzing relations between 0+ brown trout and spawning grounds in small streams.

Furthermore, this study showed clearly that the juvenile brown trout in the anadromous reach rely in a similar way on shelter in the substrate as the related Atlantic salmon (Finstad et al. 2007, 2009), using shelter as hiding possibility from predators and to reduce energy expenditure. Therefore, the present study suggests coinciding sheltering behavior of juvenile brown trout in anadromous waters and juvenle Atlantic salmon.
The density of juvenile brown trout in the non-anadromous reach was not affected by shelter availability. This might indicate differences in shelter use compared to brown trout in anadromous waters, and was perhaps associated with increased intercohort competition and/or the physical habitat conditions of the non-anadromous reach. Because of the low sample size in the non-anadromous reach and the highly variable shelter use of brown trout (Hermansen and Krog 1984, Wesche et al. 1987, Davis 1989, Haury et al. 1995, Zika and Peter 2002, Degerman et al. 2004, Johansen et al. 2005, Riedl and Unfer 2010), further studies are strongly recommended that investigate the use of substrate shelter by juvenile brown trout in non-anadromous waters. Most interesting would be a comparative study that investigates the effects of shelter availability on juvenile brown trout in geological different drainage basins, since this affects shelter availability and thus may influence productivity and population structure.

This study highlighted how the density of juvenile brown trout in the Apeltunelva is regulated by two essential physical habitat features, which has been shown to be successfully enhanced in frame of restoration measures (Pulg 2009, Whiteway et al. 2010, Pulg et al. 2013). Thus, the restoration of spawning grounds and shelter availability via, for example, gravel addition, ripping of the river bed's substrate etc. can be recommended in the study area to improve fish production. However, the reestablishment of natural fluvial processes, for instance by removing culverts and canals should be preferred in the Apeltunelva, and is in general top priority in river restoration, as this preserves rivers in the most sustainable way.

7 Zusammenfassung

Laichplätze und Unterstandsmöglichkeiten in Form von Hohlräumen und interstitiellen Räumen im Substrat des Bachbettes stellen essentielle Habitateigenschaften für juvenile Bachforellen dar. Diese können unter bestimmten Umständen als limitierende Faktoren wirken und so die Kapazität eines Ökosystems für eine Population eines Fließgewässers bestimmen. Besonders während der juvenilen Entwicklungsstadien, die von hoher inter- und intraspezifischer Konkurrenz gekennzeichnet sind, können Laichplätze und Unterstandsmöglichkeiten als dichte-regulierende Faktoren wirken. Die vorliegende Arbeit untersucht den Einfluss von Laichplatzfläche, Laichplatzdichte, Unterstandsmöglichkeiten, Substratzusammensetzung, Ufervegetation, Totholz, Algenbewuchs und Moosbewuchs auf die Dichte von juvenilen Bachforellen in einer anadromen und nicht anadromen Strecke eines kleinen Fließgewässers in Bergen, Norwegen. Dabei wurden die folgenden Hypothesen untersucht: (i) Die Dichten von 0+ und 1+ Bachforellen korrelieren positiv mit Laichplatzfläche und Laichplatzdichte. (ii) Die Dichten von 0+ und 1+ Bachforellen korrelieren positiv mit Unterstandsmöglichkeiten. (iii) Laichplatzfläche und Laichplatzdichte haben den größten Einfluss auf die Dichte von 0+ Bachforellen, während Unterstandsmöglichkeiten den größten Einfluss auf die Dichte von 1+ Bachforellen haben. (iv) Laichplatzfläche und Laichplatzdichte haben einen ähnlich großen Einfluss auf die Dichten von 0+ und 1+ Bachforellen in der anadromen und nicht anadromen Strecke, während Unterstandsmöglichkeiten einen größeren Einfluss auf die Dichte von 0+ und 1+ Bachforellen in der anadromen Strecke haben. Im ersten Arbeitsschritt dieser Studie wurden Habitate aufgrund von gleichförmiger Substratzusammensetzung definiert und hinsichtlich Unterstandsmöglichkeiten, Substratzusammensetzung, Ufervegetation, Totholz Algenbewuchs und Moosbewuchs kartiert. Laichplätze wurden vorher, kurz nach der vorangegangenen Laichsaison, kartiert. Anschließend wurden die Habitate befischt, um die Dichten pro Altersklasse abzuschätzen. Auf Grundlage der erhobenen Daten, wurde schließlich die statistische Auswertung durchgeführt. Hypothese (i) konnte bestätigt werden, Hypothesen (ii), (iii) und (iv) nur teilweise. Eine signifikante und positive Korrelation wurde zwischen der Dichte von 0+ Bachforellen (in beiden Strecken) und Laichplatzfläche sowie Laichplatzdichte nachgewiesen. Wahrscheinlich, weil diese Variablen die Rogendichte maßgeblich mitbestimmen. Die Dichte von 0+ Bachforellen wurde besser durch Laichplatzfläche als Laichplatzdichte erklärt. Laichplatzdichte erklärte hingegen am besten die Dichte von 1+ Bachforellen in der nicht anadromen Strecke, was bedeuten könnte, dass diese nahe ihrer Geburtsstätten blieben und dort andere Arten von Unterstandsmöglichkeiten nutzten, beispielsweise in Form von Uferstrukturen (Ufervegetation, unterspülte Ufer etc.). Die Dichten von 0+ und 1+ Bachforellen in der anadromen Strecke korrelierten signifikant und positiv mit Unterstandsmöglichkeiten. Dies ist mit hoher Wahrscheinlichkeit auf die Heterogenität des Bachbettes zurückzuführen, dessen Grad die Quantität an Unterstandsmöglichkeiten bestimmt und somit auch die Zahl der zu besetzenden Territorien. Die Dichte von 1+ Bachforellen wurde besser durch die Variable Unterstandsmöglichkeiten erklärt als die der Altersklasse 0+. Zwischen den Dichten von 0+ und 1+ Bachforellen in der nicht anadromen Strecke und Unterstandsmöglichkeiten wurde kein Zusammenhang festgestellt, was darauf hindeuten könnte, dass die Bachforellen in der nicht anadromen Strecke allgemein andere Unterstandsmöglichkeiten nutzen als die in der anadromen Strecke. Dies könnte vielleicht an der erhöhten Konkurrenz zwischen Altersklassen bei Bachforellen in nicht anadromen Fließgewässern liegen. Da die Datengrundlage in der nicht anadromen Strecke jedoch unzureichend war, um diesen Zusammenhang zu belegen, sind weitere Studien nötig. Des Weiteren wurden keine Effekte von Laichplatzfläche und Laichplatzdichte sowie Unterstandsmöglichkeiten auf die Dichte von >1+ Bachforellen festgestellt. Dies deutet wahrscheinlich auf andere Habitatpräferenzen dieser Altersklasse hin. Analog dazu konnten nahezu keine Zusammenhänge zwischen den Dichten aller Altersklassen und den anderen Habitateigenschaften detektiert werden. Dies lag höchstwahrscheinlich am gewählten Untersuchungsmaßstab für diese Studie oder an geringeren Präferenzen für die Habitateigenschaften. Es konnte lediglich ein signifikanter und positiver Zusammenhang zwischen den Dichten von 0+ und 1+ Bachforellen der nicht anadromen Strecke und kiesigem Substrat sowie zwischen der Dichte von 1+ Bachforellen der anadromen Strecke und steinigem Substrat nachgewiesen werden. Dieses Ergebnis ist darauf zurückzuführen, dass Kies maßgeblich die Qualität und Quantität von Laichplätzen bestimmt und Steine einen entscheidenden Einfluss auf die Anzahl von Unterstandsmöglichkeiten im Substrat haben. Die vorliegende Arbeit unterstreicht die Bedeutung von Laichplätzen und Unterstandsmöglichkeiten als dichte-regulierende Faktoren für juvenile Bachforellen und deutet somit auf die Wichtigkeit von Renaturierungsmaßnahmen hin, die auf die Verbesserung von degradierten Laich- und Jungfischhabitaten abzielen.

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9 Appendix

9.1 List of figures

9.2 List of tables

9.3 Habitat mapping

Table 14: Absolute values of spawning ground area (SGA), spawning ground density (SGD) and each individual measurement of shelter availability (SA1-4), as well as mean shelter availability (SA) according to each habitat. [a] = excluded from further statistical analyses, [b] = culvert, [c] = canal.

	Habitat	SGA (m^2)	SGD (n/habitat)	SA1	SA2	SA3	SA4	Mean SA
Anadromous reach	1[a]	0.0	0	8	2	28	-	13
	2[a]	13.3	2	3	5	2	-	3
	3	4.8	3	1	3	16	-	7
	4	8.9	4	17	5	7	-	10
	5	6.2	3	5	7	4	-	5
	6	10.9	2	8	14	4	-	9
	7	1.9	1	7	12	7	-	9
	8[b]	0.0	0	3	1	1	2	2
	9	17.7	3	4	9	8	6	7
	10	5.8	1	5	14	0	0	5
	11	22.7	2	9	4	21	-	11
	12[c]	0.0	0	0	0	0	4	1
	13	40.6	9	17	23	21	-	20
	14	7.6	2	6	5	13	-	8
	15	1.5	1	4	2	14	-	7
	16[b]	0.0	0	5	2	1	2	3
	17	3.5	2	5	7	0	-	4
	18	21.1	4	0	8	11	-	6
	19	24.5	4	2	9	0	-	4
	20	0.0	0	5	9	6	-	7
Non-anadromous reach	21	4.9	1	3	4	3	-	3
	22	19.0	2	6	0	0	-	2
	23	17.3	1	10	9	5	-	8
	24	32.3	3	13	7	12	-	11
	25	0.0	0	7	19	0	-	9
	26	0.0	0	13	9	5	-	9
	27	0.0	0	0	0	0	-	0
	28	22.2	2	13	4	20	-	12
	29	5.3	1	10	10	7	0	9
	30	7.6	1	0	0	0	-	0
	31	10.9	4	3	17	13	-	11

Table 15: Values of further habitat features recorded (silt, sand and fine gravel, gravel, stone, boulder, sealed, riparian vegetation, woody debris, algae, moss) according to each habitat. [a] = excluded from further statistical analyses, [b] = culvert, [c] = canal.

	Habitat	Silt	Sand and fine gravel	Gravel	Stone	Boulder	Sealed	Riparian vegetation	Woody debris	Algae	Moss
		%	%	%	%	%	%	%	%	%	%
Anadromous reach	1[a]	0	5	50	30	15	0	80	0	85	0
	2[a]	0	15	80	5	0	0	95	10	75	0
	3	0	5	60	15	20	0	15	15	80	15
	4	0	0	25	65	10	0	5	5	70	15
	5	0	0	10	50	40	0	25	0	60	40
	6	0	5	45	40	10	0	45	10	60	30
	7	0	20	50	30	0	0	90	5	40	60
	8[b]	0	5	45	45	5	0	0	0	10	0
	9	0	15	40	45	0	0	75	15	20	90
	10	40	30	15	10	5	0	70	20	15	0
	11	0	0	20	55	25	0	75	0	5	85
	12[c]	0	0	0	5	5	90	60	0	5	95
	13	0	5	35	45	15	0	80	20	50	30
	14	0	0	10	45	45	0	90	50	10	85
	15	0	0	50	30	10	10	50	0	15	35
	16[b]	0	0	65	30	5	0	0	0	5	0
	17	0	45	40	10	5	0	95	10	0	0
	18	25	45	10	10	10	0	65	5	0	0
	19	5	40	40	10	5	0	95	10	5	5
	20	0	5	50	40	5	0	50	5	5	5
Non-anadromous reach	21	0	0	0	35	65	0	85	20	5	95
	22	50	5	30	15	0	0	40	10	15	0
	23	0	0	35	35	30	0	65	10	15	75
	24	0	0	35	45	20	0	40	0	10	60
	25	0	0	10	40	50	0	85	0	0	85
	26	0	0	55	40	5	0	35	0	20	30
	27	15	35	50	0	0	0	85	20	0	0
	28	0	0	75	20	5	0	0	0	10	5
	29	0	10	35	35	20	0	70	0	0	75
	30	75	15	5	5	0	0	75	15	5	0
	31	0	0	55	35	10	0	10	15	15	50

9.4 Electrofishing

Table 16: Absolute values of brown trout and Atlantic salmon caught per age class (approach 1) according to each habitat. [a] = excluded from further statistical analyses, [b] = culvert, [c] = canal.

	Habitat	Catch brown trout				Catch Atlantic salmon		
		0+	1+	>1+	Total	0+	1+	Total
Anadromous reach	1[a]	0	11	1	12	1	3	4
	2[a]	6	8	3	17	1	2	3
	3	0	20	10	30	2	16	18
	4	19	41	6	66	9	46	55
	5	1	12	3	16	3	17	20
	6	25	38	13	76	7	20	27
	7	5	21	1	27	0	10	10
	8[b]	0	1	0	1	-	-	-
	9	30	91	45	166	-	-	-
	10	10	31	8	49	-	-	-
	11	15	21	3	39	-	-	-
	12[c]	7	16	13	36	-	-	-
	13	46	65	9	120	-	-	-
	14	21	29	8	58	-	-	-
	15	9	17	21	47	-	-	-
	16[b]	5	28	13	46	-	-	-
	17	33	15	3	51	-	-	-
	18	37	14	24	75	-	-	-
	19	6	11	12	29	-	-	-
	20	5	5	7	17	-	-	-
Non-anadromous reach	21	0	4	9	13	-	-	-
	22	1	10	25	36	-	-	-
	23	1	6	13	20	-	-	-
	24	13	17	31	61	-	-	-
	25	0	1	3	4	-	-	-
	26	3	16	10	29	-	-	-
	27	47	15	7	69	-	-	-
	28	41	9	5	55	-	-	-
	29	5	6	2	13	-	-	-
	30	3	6	10	19	-	-	-
	31	11	7	6	24	-	-	-

Table 17: Absolute values of brown trout and Atlantic salmon caught per age class (approach 2) according to each habitat. [a] = excluded from further statistical analyses, [b] = culvert, [c] = canal.

	Habitat	Catch brown trout						Catch Atlantic salmon			
		0+	0+/1+	1+	1+/>1+	>1+	Total	0+	0+/1+	1+	Total
Anadromous reach	1[a]	0	0	11	1	0	12	1	1	2	4
	2[a]	4	3	7	0	3	17	0	1	2	3
	3	0	5	15	4	6	30	2	5	11	18
	4	18	18	24	0	6	66	6	19	30	55
	5	1	2	10	0	3	16	3	4	13	20
	6	23	5	35	3	10	76	6	2	19	27
	7	4	3	19	1	0	27	0	2	8	10
	8[b]	0	0	1	0	0	1	-	-	-	-
	9	23	28	70	5	40	166	-	-	-	-
	10	9	6	26	3	5	49	-	-	-	-
	11	14	2	20	1	2	39	-	-	-	-
	12[c]	3	4	16	2	11	36	-	-	-	-
	13	35	27	49	5	4	120	-	-	-	-
	14	17	9	24	5	3	58	-	-	-	-
	15	8	3	15	7	14	47	-	-	-	-
	16[b]	3	4	26	3	10	46	-	-	-	-
	17	28	8	12	1	2	51	-	-	-	-
	18	34	4	13	4	20	75	-	-	-	-
	19	1	5	11	7	5	29	-	-	-	-
	20	1	5	4	1	6	17	-	-	-	-
Non-anadromous reach	21	0	1	3	2	7	13	-	-	-	-
	22	0	2	9	5	20	36	-	-	-	-
	23	0	1	6	4	9	20	-	-	-	-
	24	6	14	10	3	28	61	-	-	-	-
	25	0	0	1	1	2	4	-	-	-	-
	26	1	11	7	1	9	29	-	-	-	-
	27	47	6	9	2	5	69	-	-	-	-
	28	40	2	8	0	5	55	-	-	-	-
	29	3	2	6	0	2	13	-	-	-	-
	30	1	3	5	3	7	19	-	-	-	-
	31	11	1	6	1	5	24	-	-	-	-

9.5 Principal component analysis

Table 18: Rotated component matrix obtained from principal component analysis containing the density of 0+ brown trout in the anadromous reach (approach 1) and all recorded habitat features.

Variable	Component				
	1	2	3	4	5
0+ anadromous reach	0.839	-	-	-	-
Spawning ground area (m^2/100 m^2)	0.878	-	-	-	-
Spawning ground density (n/100 m^2)	0.800	-	0.446	-	-
Shelter availability	0.723	0.390	-	-	0.398
Silt %	-	-0.813	-	-	-
Sand and fine gravel %	-	-0.824	-0.328	-	-
Gravel %	-	-	-	-0.881	-
Stone %	-	0.769	-		-
Boulder %	-	-	0.311	0.692	0.339
Riparian vegetation %	0.310	-	-0.731		0.472
Woody debris %	-	-	-		0.943
Algae %	-	-	0.780		-
Moss %	-	0.608	-0.459	0.456	-
Variance explained individual %	22.370	20.818	14.943	13.474	12.018
Variance explained cumulative %	22.370	43.188	58.131	71.605	83.622

Table 19: Rotated component matrix obtained from principal component analysis containing the density of 0+ brown trout in the non-anadromous reach (approach 1) and all recorded habitat features.

Variable	Component		
	1	2	3
0+ non-anadromous reach	-309	0.886	-
Spawning ground area (m^2/100 m^2)	-	0.892	-
Spawning ground density (n/100 m^2)	-	0.892	-
Shelter availability	0.767	0.455	-0.350
Silt %	-0.802	-0.320	-
Sand and fine gravel %	-0.753	-	0.521
Gravel %	-	0.806	-0.376
Stone %	0.936	-	-
Boulder %	0.708	-0.374	0.470
Riparian vegetation %	-	-0.636	0.722
Woody debris %	-0.528	-0.304	0.308
Algae %	-	-	-0.918
Moss %	0.859	-0.381	-
Variance explained individual %	33.300	31.927	19.157
Variance explained cumulative %	33.300	65.226	84.383

Table 20: Rotated component matrix obtained from principal component analysis containing the density of 1+ brown trout in the anadromous reach (approach 1) and all recorded habitat features.

Variable	Component				
	1	2	3	4	5
1+ anadromous reach	0.425	0.712	-	-	-
Spawning ground area (m^2/100 m^2)	-	0.838	-	0.302	-0.443
Spawning ground density (n/100 m^2)	-	0.858	-	-	-
Shelter availability	0.317	0.782	-	-	-
Silt %	-0.800	-	-	-	0.327
Sand and fine gravel %	-0.863	-	0.318	-	-
Gravel %	-	-	-	-0.873	-
Stone %	0.757	-	-	-	-
Boulder %	-	-	-	0.726	-
Riparian vegetation %	-	-	0.848	-	-
Woody debris %	-	-	-	-	0.628
Algae %	0.302	0.417	-0.628	-	0.354
Moss %	0.604	-	0.558	0.382	-0.343
Variance explained individual %	22.498	22.225	13.901	13.526	12.567
Variance explained cumulative %	22.498	44.723	58.625	72.151	84.718

Table 21: Rotated component matrix obtained from principal component analysis containing the density of 1+ brown trout in the non-anadromous reach (approach 1) and all recorded habitat features.

Variable	Component			
	1	2	3	4
1+ non-anadromous reach	-	0.918	-	-
Spawning ground area (m^2/100 m^2)	-	-	0.961	-
Spawning ground density (n/100 m^2)	-	-	0.960	-
Shelter availability	0.832	-	0.380	-0.317
Silt %	-0.938	-	-	-
Sand and fine gravel %	-0.478	0.623	-0.301	0.535
Gravel %	0.340	0.766	0.393	-0.329
Stone %	0.838	-0.452	-	-
Boulder %	0.394	-0.764	-	0.425
Riparian vegetation %	-	-	-0.581	0.688
Woody debris %	-0.593	-	-	-
Algae %	-	-	-	-0.933
Moss %	0.659	-0.637	-	-
Variance explained individual %	27.990	24.435	21.562	17.413
Variance explained cumulative %	27.990	52.425	73.987	91.401

Table 22: Rotated component matrix obtained from principal component analysis containing the density of >1+ brown trout in the anadromous reach (approach 1) and all recorded habitat features.

Variable	Component				
	1	2	3	4	5
>1+ anadromous reach	-	0.527	-	-	-
Spawning ground area ($m^2/100\ m^2$)	-	0.869	0.320	-	-
Spawning ground density ($n/100\ m^2$)	-	0.824	-	0.418	-
Shelter availability	0.367	0.586	-	-	0.560
Silt %	-0.807	-	-	-	-
Sand and fine gravel %	-0.862	-	-	-	-
Gravel %		-	-0.899	-	-
Stone %	0.769	-	-	-	-
Boulder %	0.344	-	0.694	-	0.306
Riparian vegetation %	-	-	-	-0.690	0.570
Woody debris %	-	-	-	-	0.895
Algae %	0.347	-	-	0.735	-
Moss %	0.588	-	0.356	-0.582	-
Variance explained individual %	21.642	17.111	13.871	13.864	12.628
Variance explained cumulative %	21.642	38.754	52.624	66.488	79.116

Table 23: Rotated component matrix obtained from principal component analysis containing the density of >1+ brown trout in the non-anadromous reach (approach 1) and all recorded habitat features.

Variable	Component			
	1	2	3	4
>1+ non-anadromous reach	-0.356	-	-	0.742
Spawning ground area ($m^2/100\ m^2$)	-	0.969	-	-
Spawning ground density ($n/100\ m^2$)	-	0.963	-	-
Shelter availability	0.900	0.360	-	-
Silt %	-0.834	-	-	-
Sand and fine gravel %	-0.662	-	-0.405	-0.532
Gravel %	0.347	0.432	-0.789	-
Stone %	0.896	-	0.362	-
Boulder %	0.316	-	0.893	-
Riparian vegetation %	-0.361	-0.562	0.487	-0.496
Woody debris %	-0.649	-	-	-
Algae %	0.314	-	-0.337	0.810
Moss %	0.607	-	0.701	-
Variance explained individual %	31.885	20.938	20.318	14.965
Variance explained cumulative %	31.885	52.823	73.140	88.105

Table 24: Rotated component matrix obtained from principal component analysis containing the density of 0+ brown trout in the anadromous reach (approach 2) and all recorded habitat features.

Variable	Component				
	1	2	3	4	5
0+ anadromous reach	0.846	-	-	-	-
Spawning ground area (m^2/100 m^2)	0.892	-	-	-	-
Spawning ground density (n/100 m^2)	0.809	-	0.440	-	-
Shelter availability	0.696	0.397	-	-	0.425
Silt %	-	-0.810	-	-	-
Sand and fine gravel %	-	-0.824	-0.323	-	-
Gravel %	-	-	-	-0.877	-
Stone %	-	0.773	-	-	-
Boulder %	-	0.300	0.304	0.695	0.337
Riparian vegetation %	-	-	-0.729	-	0.496
Woody debris %	-	-	-	-	0.938
Algae %	-	-	0.774	-	-
Moss %	-	0.607	-0.473	0.438	-
Variance explained individual %	22.478	20.900	14.744	13.256	12.068
Variance explained cumulative %	22.478	43.379	58.122	71.378	83.446

Table 25: Rotated component matrix obtained from principal component analysis containing the density of 0+ brown trout in the non-anadromous reach (approach 2) and all recorded habitat features.

Variable	Component		
	1	2	3
0+ non-anadromous reach	-0.318	0.876	0.302
Spawning ground area (m^2/100 m^2)	-	0.891	-
Spawning ground density (n/100 m^2)	-	0.893	-
Shelter availability	0.766	0.453	-0.354
Silt %	-0.802	-0.325	-
Sand and fine gravel %	-0.751	-	0.522
Gravel %	-	0.807	-0.376
Stone %	0.936	-	-
Boulder %	0.709	-0.369	0.473
Riparian vegetation %	-	-0.636	0.722
Woody debris %	-0.528	-	0.320
Algae %	-	-	-0.913
Moss %	0.860	-0.379	-
Variance explained individual %	33.322	31.720	19.258
Variance explained cumulative %	33.322	65.042	84.300

Table 26: Rotated component matrix obtained from principal component analysis containing the density of 1+ brown trout in the anadromous reach (approach 2) and all recorded habitat features.

Variable	Component				
	1	2	3	4	5
1+ anadromous reach	0.758	0.419	-	-	0.405
Spawning ground area (m^2/100 m^2)	0.843	-	-	-0.307	-
Spawning ground density (n/100 m^2)	0.838	-	-0.323	-	
Shelter availability	0.797	0.302	-	-	0.359
Silt %	-	-0.792	-	-	-
Sand and fine gravel %	-	-0.875	-	-	-
Gravel %	-	-	-	-0.887	-
Stone %	-	0.754	-	-	-
Boulder %	-	0.311	-	0.702	0.367
Riparian vegetation %	-	-	0.826	-	0.355
Woody debris %	-	-	-	-	0.933
Algae %	0.398	0.305	-0.645	-	-
Moss %	-	0.604	0.571	0.370	-
Variance explained individual %	22.726	22.589	13.920	13.358	12.294
Variance explained cumulative %	22.726	45.315	59.235	72.593	84.886

Table 27: Rotated component matrix obtained from principal component analysis containing the density of 1+ brown trout in the non-anadromous reach (approach 2) and all recorded habitat features.

Variable	Component		
	1	2	3
1+ non-anadromous reach	-0.363	0.867	-
Spawning ground area (m^2/100 m^2)	-	0.883	-
Spawning ground density (n/100 m^2)	-	0.888	-
Shelter availability	0.774	0.468	-0.318
Silt %	-0.805	-	-
Sand and fine gravel %	-0.752	-	0.530
Gravel %	-	0.824	-0.338
Stone %	0.931		-
Boulder %	0.705	-0.436	0.420
Riparian vegetation %	-	-0.673	0.688
Woody debris %	-0.534	-0.347	-
Algae %	-	-	-0.939
Moss %	0.850	-0.397	-
Variance explained individual %	33.589	32.720	17.516
Variance explained cumulative %	33.589	66.309	83.826

Table 28: Rotated component matrix obtained from principal component analysis containing the density of >1+ brown trout in the anadromous reach (approach 2) and all recorded habitat features.

Variable	Component				
	1	2	3	4	5
>1+ anadromous reach	-	-	-	-	-0.584
Spawning ground area (m^2/100 m^2)	-	0.783	-	-	-0.310
Spawning ground density (n/100 m^2)	-	0.885	-	-	-
Shelter availability	0.347	0.780	-	-	-
Silt %	-0.805	-	-	-	-
Sand and fine gravel %	-0.866	-	-	-	-
Gravel %	-	-	-	-0.891	-
Stone %	0.768	-	-		-
Boulder %	0.325	-	-	0.691	0.336
Riparian vegetation %	-	-	0.886	-	-
Woody debris %	-	-	-	-	0.795
Algae %	0.340	0.475	-0.548	-	-
Moss %	0.587	-	0.575	0.417	-
Variance explained individual %	21.606	19.486	13.863	13.482	11.035
Variance explained cumulative %	21.606	41.093	54.955	68.437	79.472

Table 29: Rotated component matrix obtained from principal component analysis containing the density of >1+ brown trout in the non-anadromous reach (approach 2) and all recorded habitat features.

Variable	Component			
	1	2	3	4
>1+ non-anadromous reach	-		-	0.756
Spawning ground area (m^2/100 m^2)	-	0.965	-	-
Spawning ground density (n/100 m^2)	-	0.955	-	-
Shelter availability	0.896	0.353	-	-
Silt %	-0.848	-	-	-
Sand and fine gravel %	-0.678	-	-0.379	-0.539
Gravel %	0.320	0.426	-0.813	-
Stone %	0.907	-	0.326	-
Boulder %	0.361	-	0.868	-
Riparian vegetation %	-0.342	-0.534	0.502	-0.522
Woody debris %	-0.630	-	-	-
Algae %	0.303	-	-0.357	0.795
Moss %	0.640	-	0.666	-
Variance explained individual %	31.910	20.653	19.843	15.550
Variance explained cumulative %	31.910	52.563	72.406	87.956

9.6 Simple linear regression

Table 30: Dependent (density of 0+ brown trout, anadromous reach, approach 2) and independent variables, coefficient of determination (R^2), p-value (p), constant (b_0) and non-standardized regression coefficient (b_1) of all simple linear regression models computed. SGA = spawning ground area, SGD = spawning ground density, SA = shelter availability.

Dependent variable	Independent variable	R^2	p	b_0	b_1
0+ anadromous reach (n/100 m^2)	SGA (m^2/100 m^2)	0.438	0.003**	11.78	1.89
	SGD (n/100 m^2)	0.325	0.013*	9.16	9.02
	SA	0.315	0.015*	1.00	3.16
	Silt %	0.011	0.680	22.04	0.23
	Sand and fine gravel %	0.084	0.245	17.81	0.42
	Gravel %	0.083	0.248	35.07	-0.36
	Stone %	0.014	0.642	17.00	0.15
	Boulder %	0.025	0.527	19.28	0.30
	Riparian vegetation %	0.155	0.106	7.37	0.29
	Woody debris %	0.053	0.359	18.70	0.45
	Algae %	0.006	0.761	24.68	-0.07
	Moss %	0.000	0.943	22.54	0.01

Table 31: Dependent (density of 0+ brown trout, non-anadromous reach, approach 2) and independent variables, coefficient of determination (R^2), p-value (p), constant (b_0) and non-standardized regression coefficient (b_1) of all simple linear regression models computed. SGA = spawning ground area, SGD = spawning ground density, SA = shelter availability.

Dependent variable	Independent variable	R^2	p	b_0	b_1
0+ non-anadromous reach (n/100 m^2)	SGA (m^2/100 m^2)	0.459	0.022*	16.05	2.09
	SGD (n/100 m^2)	0.428	0.029*	11.20	22.31
	SA	0.001	0.919	39.27	0.62
	Silt %	0.021	0.668	49.34	-0.46
	Sand and fine gravel %	0.200	0.168	23.85	3.32
	Gravel %	0.433	0.028*	-36.85	2.29
	Stone %	0.270	0.102	120.05	-2.76
	Boulder %	0.153	0.235	70.49	-1.45
	Riparian vegetation %	0.092	0.364	86.71	-0.81
	Woody debris %	0.004	0.848	38.31	0.63
	Algae %	0.043	0.542	63.79	-2.36
	Moss %	0.273	0.099	92.25	-1.13

Table 32: Dependent (density of 1+ anadromous reach, approach 2) and independent variables, coefficient of determination (R^2), p-value (p), constant (b_0) and non-standardized regression coefficient (b_1) of all simple linear regression models computed. SGA = spawning ground area, SGD = spawning ground density, SA = shelter availability.

Dependent variable	Independent variable	R^2	p	b_0	b_1
1+ anadromous reach (n/100 m^2)	SGA (m^2/100 m^2)	0.216	0.052	28.43	1.25
	SGD (n/100 m^2)	0.226	0.046*	25.70	7.07
	SA	0.760	< 0.001**	4.45	4.62
	Silt %	0.058	0.335	38.46	-0.50
	Sand and fine gravel %	0.084	0.242	41.35	-0.40
	Gravel %	0.000	0.970	36.12	0.01
	Stone %	0.228	0.045*	17.60	0.59
	Boulder %	0.131	0.140	28.69	0.64
	Riparian vegetation %	0.052	0.363	28.02	0.16
	Woody debris %	0.130	0.141	30.23	0.66
	Algae %	0.218	0.051	26.62	0.39
	Moss %	0.162	0.097	28.04	0.26

Table 33: Dependent (density of 1+ non-anadromous reach, approach 2) and independent variables, coefficient of determination (R^2), p-value (p), constant (b_0) and non-standardized regression coefficient (b_1) of all simple linear regression models computed. SGA = spawning ground area, SGD = spawning ground density, SA = shelter availability.

Dependent variable	Independent variable	R^2	p	b_0	b_1
1+ non-anadromous reach (n/100 m^2)	SGA (m^2/100 m^2)	0.415	0.033*	16.39	0.30
	SGD (n/100 m^2)	0.411	0.034*	15.53	3.34
	SA	0.005	0.844	0.18	0.18
	Silt %	0.001	0.937	20.53	-0.01
	Sand and fine gravel %	0.170	0.208	17.60	0.47
	Gravel %	0.518	0.012*	6.95	0.38
	Stone %	0.242	0.125	31.44	-0.40
	Boulder %	0.358	0.052	26.69	-0.34
	Riparian vegetation %	0.186	0.185	29.76	-0.18
	Woody debris %	0.003	0.872	21.03	-0.08
	Algae %	0.006	0.817	21.55	-0.14
	Moss %	0.321	0.069	28.45	-0.19

Table 34: Dependent (density of >1+ anadromous reach, approach 2) and independent variables, coefficient of determination (R^2), p-value (p), constant (b_0) and non-standardized regression coefficient (b_1) of all simple linear regression models computed. SGA = spawning ground area, SGD = spawning ground density, SA = shelter availability.

Dependent variable	Independent variable	R^2	p	b_0	b_1
>1+ anadromous reach (n/100 m^2)	SGA (m^2/100 m^2)	0.041	0.418	11.23	0.33
	SGD (n/100 m^2)	0.098	0.206	9.10	2.77
	SA	0.001	0.924	12.81	0.08
	Silt %	0.017	0.610	12.71	0.16
	Sand and fine gravel %	0.009	0.715	12.41	0.08
	Gravel %	0.004	0.796	11.79	0.05
	Stone %	0.009	0.713	15.52	-0.07
	Boulder %	0.006	0.767	14.30	-0.08
	Riparian vegetation %	0.002	0.870	14.25	-0.02
	Woody debris %	0.012	0.663	14.47	-0.12
	Algae %	0.001	0.889	13.78	-0.02
	Moss %	0.000	0.980	13.41	-0.00

Table 35: Dependent (density of >1+ anadromous reach, approach 2) and independent variables, coefficient of determination (R^2), p-value (p), constant (b_0) and non-standardized regression coefficient (b_1) of all simple linear regression models computed. SGA = spawning ground area, SGD = spawning ground density, SA = shelter availability.

Dependent variable	Independent variable	R^2	p	b_0	b_1
>1+ non-anadromous reach (n/100 m^2)	SGA (m^2/100 m^2)	0.054	0.490	22.07	0.14
	SGD (n/100 m^2)	0.032	0.596	22.18	1.20
	SA	0.004	0.848	25.44	-0.23
	Silt %	0.074	0.417	21.77	0.17
	Sand and fine gravel %	0.014	0.729	24.92	-0.17
	Gravel %	0.017	0.701	20.80	0.09
	Stone %	0.011	0.763	26.87	-0.11
	Boulder %	0.108	0.324	28.34	-0.24
	Riparian vegetation %	0.142	0.254	34.35	-0.20
	Woody debris %	0.003	0.866	24.79	-0.11
	Algae %	0.167	0.212	16.06	0.91
	Moss %	0.130	0.276	30.48	-0.15