Brown trout spawning activity and recruitment

The influence of temperature and discharge
in Alpine headwater streams

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Abstract

Rivers and streams experience yearly fluctuations in the recruitment and structure of brown trout (*Salmo trutta*) populations. Rising global temperatures have been shown to directly affect the thermal and hydrological regimes of Alpine rivers. In turn, these environmental changes can influence trout spawning behavior. This thesis investigated the degree to which temperature and discharge influenced the spawning and recruitment of brown trout in small Alpine streams.

Three streams located in the Piesting headwaters of Lower Austria were selected for the study. A combination of redd counts and stock assessments were used to identify the spawning behavior and recruitment success of the brown trout populations within these streams. Redd counts were used to quantify the onset, duration, and intensity of spawning activity. Stock assessments were used to evaluate the recruitment and age structure of the population. Water temperature and discharge data were used for modeling the environmental conditions of the streams. The relationship between mean summer water temperature and spawning activity was explored. A bivariate approach was also used to investigate how spawning activity parameters influenced population recruitment. Additionally, correlations between maximum discharge during different YOY life stages and recruitment were examined.

Water temperature showed an upward trend during the study but did not significantly affect the onset or duration of spawning. However, increased temperature was linked with lower redd density. This may have impacted the population, as redd density was positively correlated with successful recruitment. There was also high probability that discharge during the spawning period was positively correlated with recruitment, whereas high flows during incubation were negatively correlated with recruitment success. The acquired knowledge provided better understanding of brown trout population dynamics and nursery habitat use in small headwater streams.

Keywords: Brown trout, Alpine rivers, spawning, recruitment, temperature, discharge

Zusammenfassung

Reproduktionserfolg und Struktur der Bachforellenpopulationen unterliegen jährlichen Schwankungen in Flüssen und Bächen. Durch den globalen Temperaturanstieg wird das thermische und hydrologische Regime alpiner Flüsse direkt beeinflusst, wodurch wiederum das Laichverhalten der Forellen beeinflusst wird. In dieser Arbeit wurde untersucht, inwieweit Temperatur und Abfluss das Laichen und die Reproduktion von Bachforellen in kleinen Alpenbächen beeinflussen.

Für die Untersuchung wurden drei Bäche im Oberlauf der Piesting ausgewählt. Zur Identifikation von Laichverhalten und Reproduktionserfolg der Bachforellenpopulationen in diesen Bächen wurde eine Kombination aus Laichplatzzählungen und Bestandsbeurteilungen verwendet. Laichplatzzählungen wurden zur Einschätzung von Laichbeginn, -dauer und -intensität der Forellen verwendet. Bestandsabschätzungen wurden zur Bewertung von Reproduktionserfolg und Altersstruktur der Forellenpopulation verwendet. Wassertemperatur- und Abflussdaten wurden zur Modellierung der Umweltbedingungen der Bäche verwendet wurden. Zudem wurde die Beziehung zwischen der mittleren sommerlichen Wassertemperatur und der Laichaktivität untersucht. Zur Untersuchung, wie Laichaktivitätsparameter die den Reproduktionserfolg der Population beeinflussen, wurde ein bivariater Ansatz verwendet. Zusätzlich wurden Korrelationen zwischen dem maximalen Abfluss während verschiedener YOY-Lebensstadien und der Reproduktion untersucht.

Die Wassertemperatur zeigte während der Studie einen Aufwärtstrend, beeinflusste aber weder den Beginn noch die Dauer des Laichzeit signifikant. Die erhöhte Temperatur war jedoch mit einer geringeren Laichplatzdichte verbunden. Dies könnte sich auf die Population ausgewirkt haben, da die Laichplatzdichte positiv mit der Reproduktionserfolg korreliert war. Es bestand auch eine hohe Wahrscheinlichkeit, dass die Abfluss während der Laichzeit positiv mit der Reproduktion korrelierte, während hohe Abflüsse während der Inkubation negativ mit dem Reproduktionserfolg korrelierten. Das erworbene Wissen ermöglichte ein besseres Verständnis der Populationsdynamik der Bachforelle und der Nutzung des Aufzuchthabitats in Gebirgsbächen.

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Abbreviations

a.s.l.	above sea level
0+ fish	fish less than 1 year old according to length
1+ fish	fish between 1 and 2 years old according to length
2+ fish	fish older than 2 years according to length
HQ1	flood event discharge ($m^3\,s^{-1}$) that statistically occurs every year
HQ5	flood event discharge ($m^3\,s^{-1}$) that statistically occurs every five years
HQ10	flood event discharge ($m^3\,s^{-1}$) that statistically occurs every ten years
HQ100	flood event discharge ($m^3\,s^{-1}$) that statistically occurs every one hundred years
LOESS	locally estimated scatterplot smoothing non-parametric regression
MJNQT	mean annual low flow ($m^3\,s^{-1}$) estimated by averaging the lowest flow of each year
MQ	mean annual discharge ($m^3\,s^{-1}$) within the average hydrologic year
YOY	young-of-year; 0+ fish, or those born within the past year

1 Introduction

Rising global and regional temperatures have been predicted throughout the next century with climatic modeling (Perkins-Kirkpatrick & Gibson, 2017; Warren et al., 2011). Increases in river and lake temperatures are anticipated to occur with the shift in climate conditions (Cianfrani et al., 2015; Isaak et al., 2012). Changes in climate are expected to have especially severe effects on the thermal and hydrological regimes of rivers in the Austrian Alps (Ács et al., 2018; Hanzer et al., 2018; Zoboli et al., 2017). Changes in biological phenomena related to climatic events (phenology) have been well documented in many organisms. Climate change has been found to affect the life-history traits of a multitude of species; the timing of bird migrations (Zaifman et al., 2017), early emergence of Ephemeroptera (Harper & Peckarsky, 2006), the synchronization of moth egg hatching with oak bud burst (Visser & Holleman, 2001), and a host of other influences have been directly linked to rising temperatures. Fish are no exception and are also heavily influenced by thermal variances in their habitats.

While some warm water fish species may benefit from increased temperatures, many cold water species have been found to suffer from detrimental consequences (Comte et al., 2013; Santiago et al., 2017). The majority of studies assessing the effects of climate change on fish have been dedicated to cold water fish species, mainly salmonids (Comte et al., 2013). However, much of the research that has been conducted has been fixated on anadromous salmonid species and not populations found in mountainous areas (Bryant, 2009; Dahl et al., 2004; Scheuerell et al., 2009). Very few studies have directly addressed the impact of thermal shift on juvenile populations in high elevation headwater streams.

Brown trout (*Salmo trutta*) are a strictly cold water species, susceptible to rising temperatures, which makes it a very well-known ecological indicator species (Clavero et al., 2017; Tisseuil et al., 2012). The thermal tolerance of trout has been heavily studied in relation to aquaculture production (Pankhurst & King, 2010; Réalis-Doyelle et al., 2016). This research has produced information which can also be applied to wild populations. While the water temperatures of the streams in the study area do not approach critical thresholds, small changes in temperature have been observed to affect the early life stages of trout substantially more than adults. Elevated water temperatures can delay spawning (Pankhurst & Munday, 2011; Riedl & Peter, 2013; Warren et al., 2012), which can lead to later spring emergence and thus decreased survival rates due to competition from other organisms (Skoglund et al., 2012). Delayed spawning causes decreased egg survival (Réalis-Doyelle et al., 2016), depressed parr growth rates (Jonsson & Jonsson, 2009) and increased juvenile mortality (Scheuerell et al., 2009). Slight increases in water temperature have the potential to significantly hinder population recruitment.

Salmonid migration and reproductive behavior are triggered by changes in temperature and other environmental conditions (Crisp, 2000; Lucas et al., 2001). Brown trout typically begin to spawn in autumn as water temperatures decrease. Studies have shown that phenology and temperature

related behaviors can vary between brown trout populations. Jonsson & Jonsson (2009) noted that salmonid populations exhibit specific adaptations regarding spawning time, and the adaptations depend heavily on water temperature. This implies that trout populations have become acclimated to the local conditions in which they live. Specific trout populations may have a smaller thermal niche than the generally accepted thermal range for growth and development (Álvarez et al., 2006). Populations that exhibited adaptations tailored for local conditions were found to be genetically different from populations which did not show the same attributes (Fraser et al., 2011). Further studies carried out by Keller et al. (2012) showed adaptive divergence between populations in different drainages provided added fitness for environmental conditions. Jensen et al. (2008) also found evidence that adaptation in early life traits of brown trout populations increased fitness in localized temperature conditions. This means that phenological characteristics linked to local climatic conditions may be maladaptive if predicted temperature increases come into being. A regional increase in temperature of just a few degrees has the potential to seriously alter the dynamics of the trout population.

Hydrology is also a crucial component of trout ecology. As a lithophilic species, brown trout require flowing water and gravel substrate for spawning (Crisp, 2000). Natural fluctuations in discharge are known to influence trout population dynamics. High flows have been shown to have significant effects on population recruitment if they occur at a vulnerable point in the early stages of brown trout development (Cattanéo et al., 2002; Nicola et al., 2009). The survival rate of juveniles is also negatively affected by high flow conditions (Jensen & Johnsen, 1999) However, natural population dynamics show that trout are adept at dealing with natural variations in hydrological conditions (Unfer et al., 2011). On the other hand, the effects of unnatural (anthropogenic) variations in hydrological conditions on trout populations are not as well understood.

Anthropogenic influence of discharge and the associated effects experienced by fish populations is a growing area of scientific study. Water abstraction, hydroelectric production, channelization and flood protection measures significantly alter the hydrological regime, which in turn can affect the fish populations within. For example, reduced discharge due to water abstraction has been shown to reduce the availability of trout spawning habitat during low flow conditions (Garbe et al., 2016). Furthermore, climate change has been shown to alter the hydrological regime in ways which reduce brown trout habitat by affecting the seasonality of flooding (Santiago et al., 2017; Wenger et al., 2011). More precipitation falls as rain instead of snow in locations where the historical air temperature has been near freezing. Temporal shifts in the flow conditions related to snow melt have the potential to significantly alter the trout population in small streams due to riverbed scour during the incubation period (Goode et al., 2013). Predictions by Muñoz-Mas et al. (2018) suggest that hydrological changes caused by climate change could reduce the available spawning habitat of some populations by up to 48%. The effect of changes in hydrological discharge on population recruitment in small headwater streams has not been thoroughly examined.

A number of studies have observed trout disappearing from their native habitat at an alarming rate (Hari et al., 2005; Lassalle & Rochard, 2009; Zimmerli et al., 2007). Trout populations in Europe (Hari et al., 2005; Muñoz-Mas et al., 2018), as well as North America (Wenger et al., 2011), have been predicted to decline in the coming decades as a result of climate change. Due to their sensitivity to rising temperatures, significant shifts in the distribution of brown trout are anticipated in the future (Isaak et al., 2012; Santiago, 2017). Few studies have focused on evaluating climatic impacts on population recruitment in pre-Alpine tributaries. Headwater streams are often overlooked in fisheries management due to the fact they are typically very low in discharge and unable to support adult fish for extended periods (Louison & Stelzer, 2016). Small headwater streams are an important source of spawning grounds and provide nursery habitat for juvenile fish. The successful recruitment of juveniles to a population is a key indicator of a healthy fish stock (Unfer & Pinter, 2018). If these habitats are lost, or rendered unsuitable due to rising temperatures, brown trout populations will continue their decline. It is of vital importance to better understand the nursery habitat of wild trout as this is where populations are replenished through reproduction and recruitment.

In this study, nine years of data was used to investigate the relationship between environmental conditions and the dynamics of the local trout population. Fish stock assessments and redd counts were documented from three headwater streams in the Austrian Alps. The biotic data was examined in conjunction with water temperature and hydrological flow. The response of spawning behavior to temperature fluctuation was analyzed according methods described by Warren et al. (2012). Links between the spawning activity and population recruitment were also explored. As hydrology has been found to alter population dynamics, the role of discharge in terms of juvenile recruitment was investigated. This research has provided insight into the longitudinal distribution of the trout populations within the Piesting catchment. The results could be used to develop a better understanding of how headwater nursery habitat contributes to wild brown trout populations.

2 Research Questions

The main purpose of this research was to investigate how brown trout spawning activity and recruitment have been influenced by the environmental factors in the headwaters of the Piesting River. Headwater streams are an important source of spawning grounds for adult fishing living in the lower reaches of the river. They also offer nursery habitat and shelter for juvenile fish, which will eventually migrate downstream and supplement the downstream population. This study will provide insight into how headwater streams contribute to brown trout populations in larger river catchments. To facilitate this investigation, the following research questions have been developed. Each research question was addressed with three hypotheses.

2.1 How does temperature influence spawning activity?

Temperature has been identified as a biological trigger for the migration and spawning of brown trout (Belica, 2007; Svendsen et al., 2004). Reproductive activity usually begins when the water temperature drops below a certain threshold, however this point may differ between populations (Jonsson & Jonsson, 2009). Furthermore, growth and reproductive development are regulated by water temperature (Réalis-Doyelle et al., 2016). Increases in summer water temperature have been shown to delay spawning activity and reduce the number of redds constructed by salmonids (Warren et al., 2012). It was assumed that increases in water temperature would negatively impact spawning activity occurring in the study sites by delaying the onset of spawning, reducing the duration of active spawning, or decreasing the number of redds found in the streams.

H_1 Increased summer[1] temperatures delay the onset of spawning.

H_2 Increased summer temperatures result in shorter periods of active spawning.

H_3 Increased summer temperatures result in decreased redd density.

2.2 Is spawning activity correlated with recruitment?

Recruitment can be an effective measure of reproductive success, and brown trout reproduction begins with the onset of spawning activity in the autumn. It was assumed that spawning activity would have a significant impact on recruitment success. The quantity of redds in the river is directly related to the number of eggs and corresponding juvenile trout which could potentially hatch. Spawning behavior in trout usually begins when environmental conditions match inherited biological cues (Jonsson & Jonsson, 2009). If summer temperatures were to delay the onset of spawning, it was speculated that recruitment would be reduced as a result. Moreover, this delayed onset would reduce the duration of the spawning window, making the redds more susceptible to failure as the temporal dispersion would be limited (Sternecker et al., 2014).

H_4 Increased redd density leads to increased juvenile recruitment.

H_5 Earlier onset of spawning activity positively influences recruitment.

H_6 The duration of spawning activity has a positive relationship with recruitment.

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[1] June 1 – August 31

2.3 How does discharge influence recruitment?

High flow events periodically occur in the Gutenstein area. It was thought that these periods of high discharge would have an influence on the successful recruitment of juvenile trout. Previous studies have shown high discharge levels to be correlated with mortality and population recruitment (Jensen & Johnsen, 1999). Further studies have found that high discharge during or just before the spawning period had increased recruitment as it was thought to improve habitat conditions, whereas high discharge during the incubation period had the opposite effect caused by the destruction of redds (Cattanéo et al., 2002; Unfer et al., 2011). It was expected that upon reaching a certain stage of development, juveniles would be able to seek out shelter during elevated discharge to remain relatively unaffected.

H_7 High discharge before and during the spawning period will increase recruitment.

H_8 High discharge during the incubation period will decrease recruitment.

H_9 High discharge during the juvenile stages does not have an impact on recruitment.

3 Study Area

The study area is located in the pre-Alpine limestone region of Lower Austria, near the town of Gutenstein. This area contains the headwaters of the Piesting River (Fig. 1). These small rivers and streams provide plentiful spawning grounds and offer habitat for juvenile and subadult trout. Three small tributaries have been selected for this study (see Table 1 for site descriptions). These tributaries and the trout populations within are the main focus of the research.
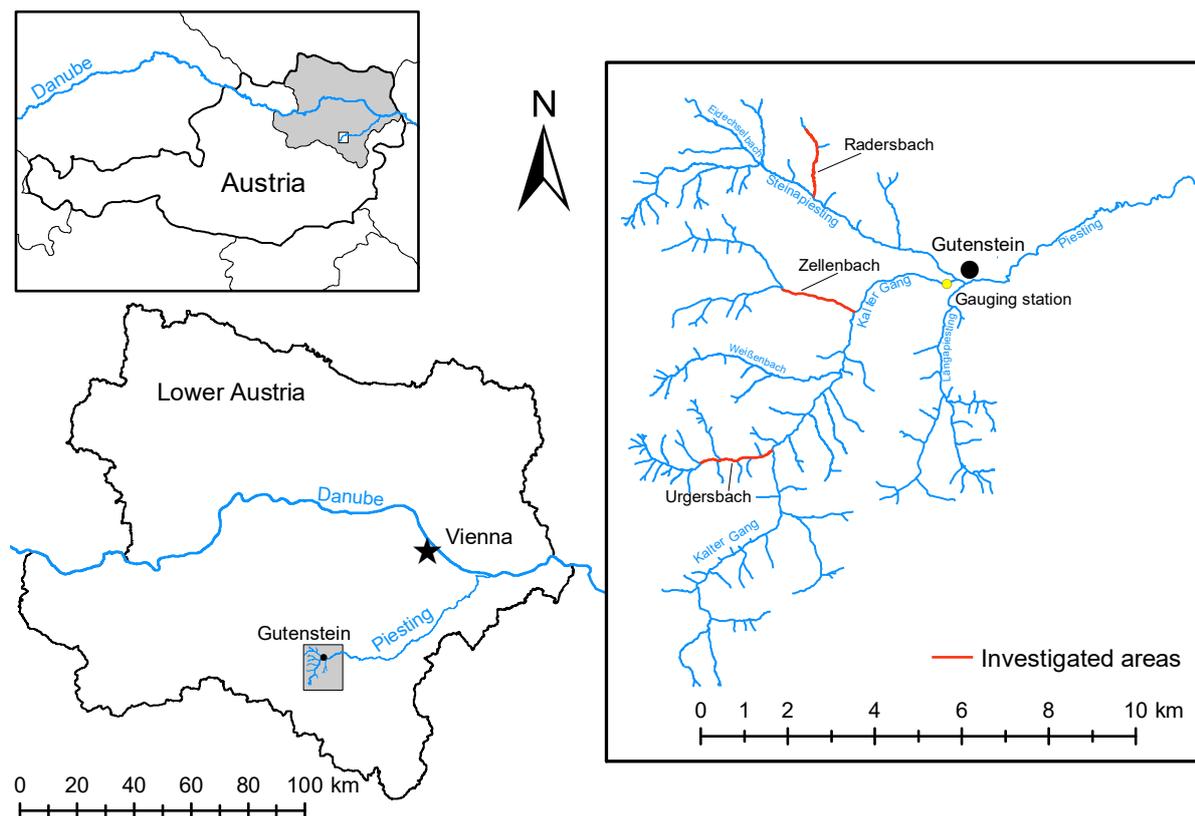
Figure 1. The Piesting headwaters are located near Gutenstein in Lower Austria. The investigated sites have been highlighted in red. The gauging station provided the discharge and water temperature data used for interpolation.

3.1 Piesting tributaries

The Piesting is a river in the south of the state of Lower Austria. Its source is located north of Schneeberg, the highest mountain within Lower Austria (2,076 m elevation). The Kalter Gang, Steinapiesting, and Längapiesting are the tributaries that come together near Gutenstein to form the Piesting. The three sub-catchments account for $91.6\,\mathrm{km^2}$ of the Piesting's total drainage area ($348.4\,\mathrm{km^2}$). These catchments are exclusively in the epirithral fish region and are home to brown trout (*Salmo trutta*), bullhead (*Cottus gobio*) and the occasional non-native rainbow trout (*Oncorhynchus mykiss*). After passing through Gutenstein, the Piesting continues northeast for approximately 77 km before joining the Fischa River in Gramatneusiedl. The Fischa then enters the Danube east of the Austrian capital of Vienna.

As the Piesting's headwaters are located in the epirithral fish region, they are characterized by cold temperature, gravel substrate, and high flow velocity. The steep stream gradient induces bed-load transport. The resulting high rate of sediment turnover flushes away fine sediments, leading to course gravel riverbeds. Alternating pool and riffle sections are common throughout the streams in the study area. These conditions are consistent with brown trout spawning areas and nursery habitat for juvenile fish.

Kalter Gang

The Kalter Gang is the largest stream in the study area with a length of 13.6 km and 50.5 km^2 catchment area. Its source lies north of Schneeberg at approximately 1,180 m above sea level. It flows north toward Gutenstein with several streams feeding into it along the way. Right-side tributaries of notable size are the Klausgraben, Schwarzgraben and Jörglhansbach. The left-side tributaries are considerably larger due to topography. The first large left-side tributary is the Urgersbach followed by the Weißenbach and then Zellenbach. The Zellenbach is the largest and final tributary to feed into the Kalter Gang before it joins with the Steinapiesting. Shortly after its confluence with the Zellenbach, the Kalter Gang changes direction and flows east towards Gutenstein, where it passes a hydraulic gauging station at a mean discharge of 0.95 m^3 s^{-1}. After the gauging station, it joins the Steinapiesting and then Längapiesting at an elevation of 475 m. At the confluence of the three rivers, the watercourse becomes known as the Piesting.

Steinapiesting

The Steinapiesting is the second largest sub-catchment in the study area. The river begins at the confluence of the Winsabach and Eidechselbach, with the Rannersbach entering immediately after. The Eidechselbach is unlike other streams in the study area because, in addition to snow melt and precipitation, it is fed by spring water. With a mean width of 3.7 m, the Steinapiesting flows east toward Gutenstein, joining the Kalter Gang just below the gauging station. The Radersbach and Matzingtalbach further contribute to the Steinapiesting along its 6 km course, bringing the total drainage to 24.0 km^2. Under most discharge conditions, a weir constructed near the river mouth limits upstream fish migration from the Piesting. With increased discharge, the weir becomes a passable obstacle for adult trout moving upstream.

Längapiesting

The Längapiesting, which has the smallest catchment area of 17.1 km^2, enters the Piesting 200 m downstream of the Steinapiesting. From its source, the Längapiesting follows a 6.3 km course northward, picking up the tributaries of Öhlerbach, Wandbach, and Schaftersbach along the way. While the Längapiesting has not been sampled in this study, it has been included here as it shares comparable hydromorphological characteristics with the other sub-catchments. The brown trout habitat availability in the Längapiesting drainage should be similar to the other stream networks of the Piesting catchment in the Gutenstein area. Inferences into brown trout spawning and recruitment in the Längapiesting can be made from the results of this study.

3.2   Investigation sites

There are over 130 km of river length in the study area which offer potential habitat for brown trout. While habitat accessibility and suitability greatly diminish that number, it would not be feasible to attempt to quantify all available habitat. Three small streams have been selected as investigations sites as they represent the types of habitat conditions found within the majority of the Piesting headwaters. The Radersbach, a tributary of the Steinapiesting, was monitored from 2010 through 2018. The Urgersbach and Zellenbach, both tributaries of the Kalter Gang, were monitored from 2011 – 2018. Spawning activity was surveyed from October to January and stock assessments were performed annually by way of electrofishing in early autumn. Detailed descriptions of the sampling processes can be found in section 4.1 (Data sources). A brief summary of the physical attributes of the streams as described by Rottensteiner (2011) can be found in Table 1 below.

Table 1. Physical descriptions of the investigation sites. The Radersbach was the smallest catchment followed by the Urgersbach. The Zellenbach was the largest investigation site and nearly twice the size of Radersbach.

		Radersbach	Urgersbach	Zellenbach
Source	(m a.s.l.)	660	656	680
Mouth	(m a.s.l.)	531	554	504
Length	(km)	2.2	3.3	4.5
Stream order		2	2	3
Catchment	(km^2)	5.52	7.26	10.60
MQ	(L s^{-1})	60	80	90
Gradient	(%)	3.3	2.7	3.3
Mean width	(m)	1.5	1.8	2.5
Mean temp.	(°C)	8.5	7.8	8.5

Note: Data from Rottensteiner (2011).

Radersbach

The Radersbach is the smallest of the investigation sites. The source is situated at 660 m a.s.l. and it follows a slightly torturous path for approximately 2.2 km across a gravel substrate while draining a catchment area of 5.6 km^2. Based on the models described in section 4.2.1, maximum daily temperatures rarely rise above 13 °C and the mean annual temperature is 8.5 °C. The Kalbenschwaigbach is the sole tributary of the Radersbach, feeding in 1.1 km upstream of the river mouth. The Radersbach has a mean width of 1.5 m and an estimated MQ of 60 L s^{-1}. It enters the Steinapiesting approximately 4 km upstream of the confluence with the Kalter Gang.

The Radersbach provides ideal habitat for brown trout spawning, however its limited depth and low discharge renders it unsuitable for supporting large fish. The course gravel substrate provides adequate interstitial space for egg incubation and the shelter of alevins. Abundant riparian vegetation serves as cover for the developing juvenile fish. While the entire length of the Radersbach is passable, the migration barrier at the mouth of the Steinapiesting ensures that the majority of adult fish utilizing the Radersbach for spawning are residents of the Steinapiesting.

Urgersbach

The source of the Urgersbach can be traced to the eastern slope of Winsaberg Mountain to an elevation of 656 m. It flows eastward for 3.3 km where it joins the Kalter Gang at 554 m a.s.l. The Urgersbach drainage area is 7.3 km^2 and is composed of several tributaries, the largest two being the Gummelbach and Ottentalbach. The mean annual temperature of 7.8 °C makes it the coldest study site. With an approximate MQ of 80 L s^{-1} and mean width of 1.8 m it is the second largest investigated stream.

The Urgersbach provides habitat for all age-classes of trout. Low discharge and several barriers make migration to the upper reaches unlikely, therefore only the section below the inflow of the Ottentalbach has been considered. The course gravel substrate is suitable habitat for spawning and several pools in the lower reaches are able to support large adult fish. A paved road has been constructed alongside the length of the Urgersbach, reducing the cover available from riparian vegetation. Though several natural and man-made barriers are present, the majority of obstacles are passable for upstream fish migration.

Zellenbach

The largest among the investigated streams, the Zellenbach is 4.5 km long and has a 10.6 km^2 catchment area. The source of Zellenbach is located east of the Rohrer Sattel mountain pass at 680 m a.s.l. The river is fed from the north by the Reischergrabenbach, which has its mouth in the middle reaches of the Zellenbach. This confluence is the upper limit of the study area. The lower boundary is where the Zellenbach flows into the Kalter Gang, about 2.5 km west of Gutenstein. The mean river width is 2.5 m and MQ is 90 L s^{-1}. The mean annual temperature is the same as the Radersbach at 8.5 °C. The natural course of the Zellenbach has been modified due the construction of a road. A stretch of approximately 1.4 km has been straightened and flood protection measures, in the form of riverbed sills and ramps, have been installed.

Like the other sites, the Zellenbach's course gravel substrate offers suitable spawning grounds for brown trout. The flood protection methods hinder upstream migration, but do not outright prevent it. Natural riparian areas are only found near the river mouth and below the confluence with the Reischergrabenbach due to river straightening. Deep pools near the river mouth and unobstructed connectivity with the Kalter Gang provide potential habitat for large fish.

4 Material and Methods

The basis of this thesis is the joint analysis of data compiled from several sources. Four data types have been collected from the investigation sites. The raw data was processed and combined before being further analyzed. Descriptive statistical analyses were first performed on each data type before correlation and regression analyses were used to investigate the relationships between data sets. All statistical analyses were completed using R 3.5.3 (R Core Team, 2019). A basic overview of the work steps can be seen in Fig. 2.
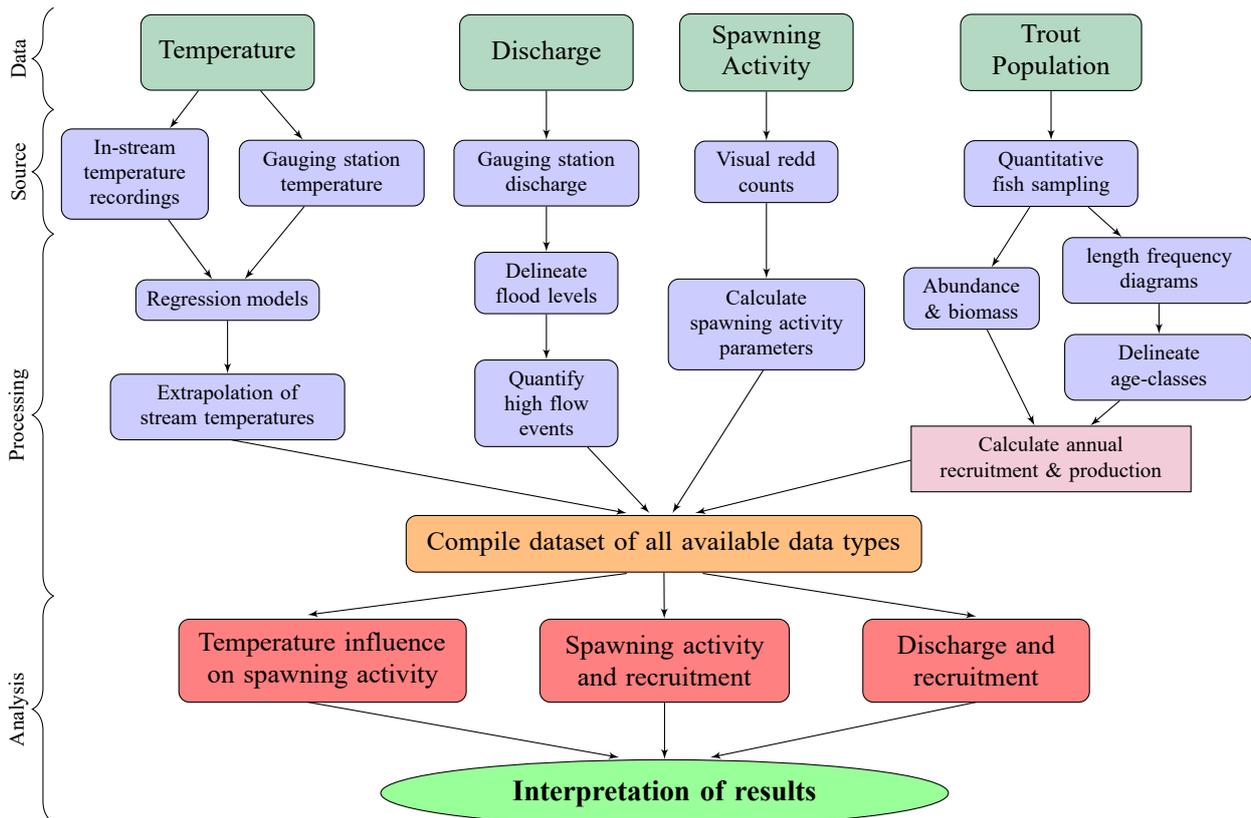
Figure 2. Schematic overview of the workflow performed during this thesis.

4.1 Data sources

4.1.1 Temperature

Water temperature has long been considered an abiotic trigger of brown trout spawning (Crisp, 2000; Svendsen et al., 2004). This study aimed to identify any relationships between water temperature and spawning activity in the headwaters of the Piesting catchment. The mean daily water temperature was selected as the parameter to be used for analysis. A Lascar Electronics EasyLog EL-USB data logger was used to measure water temperature near the mouths of the investigated streams. Water temperature was recorded in one-hour intervals, which was used to calculate the mean daily water temperature. Due to technical limitations, water temperature at the investigation sites was only able to be recorded during spawning season. To mitigate this constraint, temperature data from two additional sites has been included in this study.

The Eidechselbach and Weißenbach (see Fig. 1) are similar in size to the investigated streams. The former being a tributary of the Steinapiesting, while the latter feeds into the Kalter Gang. The water temperature of the Eidechselbach and Weißenbach have previously been recorded year-round during a study carried out by Pinter et al. (2018). This additional data was used to corroborate the regression models developed to estimate water temperature in the investigation sites. The dates during which stream temperatures were recorded are visible in Table 2.

Table 2. Water temperature measurements were taken at the investigation sites during the spawning season. Two other sites were monitored year-round and were used for calibration of the temperature regression models.

River	Start	End
Investigation sites		
Radersbach	17.08.2015	23.04.2016
Urgersbach	20.08.2015	06.01.2015
Zellenbach	13.10.2011	15.03.2012
Calibration sites		
Eidechselbach	09.05.2007	14.09.2008
Weißenbach	09.05.2007	15.09.2008

As recorded stream temperatures only covered a limited portion of the nine-year study period, extrapolation of data was required to supplement the measured values. The mean daily water temperature of the Kalter Gang is recorded by the Gutenstein river gauging station (No. 208272) and is regularly published by the Provincial Government of Lower Austria (N.Ö., 2019). The gauging station monitors the temperature of the Kalter Gang just above its confluence with the Steinapiesting. Using regression models (see section 4.2.1), the daily mean temperatures of the investigated streams have been estimated for the study period, which spanned from January 1st, 2010 through January 31st, 2018. Mean summer water temperature has been designated as the mean June – August water temperature. The study period has been further defined using the life stages of YOY-fish (see Table 3) from each annual cohort following Unfer et al. (2011). The spawning life stage begins in October and is the period in which adult fish deposit their eggs in the substrate. The incubation period follows, during which the eggs continue to develop in the interstitial, eventually hatching into alevins. Emergence from substrate marks the beginning of the early-juvenile stage (fry). The fish continue to develop throughout the summer months. The juvenile stage (parr) is the final period before the fish reach the 1+ age-class. The date of emergence was used to define cohort year.

Table 3. The first year of life has been divided into 4 stages, which began in October. The first stage was Spawning, followed by Incubation in February. The Early-juvenile stage in May coincided with emergence and early development. The juvenile stage lasted from August through September.

Life stage	Period
Spawning	Oct. – Jan.
Incubation	Feb. – Apr.
Early-juvenile	May – Jul.
Juvenile	Aug. – Sep.

4.1.2 Discharge

Discharge has been observed to play a role in population recruitment (Cattanéo et al., 2002). Unfer et al. (2011) found that high flow before and during the spawning period was positively correlated with successful recruitment. Conversely, high flow during incubation and the early-juvenile stage was found to be negatively correlated with recruitment (Unfer et al., 2011). This study explored the relationship between discharge and recruitment in the Piesting headwaters. Discharge of the Kalter Gang was recorded by the Gutenstein gauging station in cubic meters per second ($m^3 s^{-1}$). MQ was calculated as the arithmetic mean of annual discharge. HQ1 – HQ10 are statistical values (expected values) of flood discharge, calculated using the long-term record. The Provincial Government of Lower Austria publishes daily minimum and maximum discharge values, MQ and flood (HQ1, HQ2, HQ5, HQ10) discharge levels (N.Ö., 2019). Furthermore, multiples of MQ have also been included for analysis ($3 \times MQ$ and $5 \times MQ$). These discharge values covered a range of conditions that could impact spawning activity (Cattanéo et al., 2002).

Discharge data was not available for the investigation streams due to their size. Discharge levels at the Kalter Gang gauging station were assumed to be representative of the flow conditions of the Kalter Gang tributaries. Variations in discharge timing between the investigation sites and gauging station have been mitigated by using temporal intervals which contained those variations (Pattison et al., 2014). If the gauging station had experienced high discharge it was presumed that the tributaries had also experienced concurrent high flows. Therefore, discharge values obtained from the gauging station were used to evaluate the flow conditions of the study sites. The discharge measurements of the gauging station were of less importance than the flow conditions (high vs. low flow). Daily minimum and maximum discharge values from the Gutenstein gauging station have been collected for the study period (01.10.2010 – 31.01.2018) and were subdivided by month and cohort life stages as described in Table 3 above.

4.1.3 Spawning activity

Brown trout spawn in gravel substrate during autumn or early winter, with earlier spawning occurring at higher altitudes due to lower temperatures which require longer periods of egg incubation (Klemetsen et al., 2003). When a female trout has located a suitable spawning site, it turns to its side and creates a small excavation by creating a pulse of water with repetitive tail motions (cutting). This pulse of water creates a 'pit' by washing fine sediments and small gravel downstream into the 'tailspill' (Crisp, 2000). The brown trout life cycle begins when the female deposits approximately 300 – 2500 eggs, depending on size and age, in the exposed gravel at the bottom of the pit while the male fertilizes them with sperm (Jonsson & Jonsson, 1999; Avery, 1985). After fertilization, the female uses its tail to cover the eggs with small gravel upstream of the pit (Klemetsen et al., 2003). Brown trout eggs are most often found in the front half of the tailspill at a depth of 9 – 12 cm below the substrate surface in mountain streams (Grost et al., 1991). While female brown trout have been observed to dig one or more redds, Crisp & Carling (1989) suggested one redd per female is most usual.

This study quantified spawning activity using redd counts obtained from the Österreichische Fischereigesellschaft. During visual assessment of the river substrate, redds can be recognized as oval-shaped gravel excavations, which are lighter in color than the undisturbed substrate surrounding it (Crisp & Carling, 1989). Redds can be separated into two distinct components. The 'pit' lies upstream and is an excavation with a course gravel bottom whereas the 'tailspill' is immediately downstream of the pit and is the loose pile of excavated materials (Fig. 3).
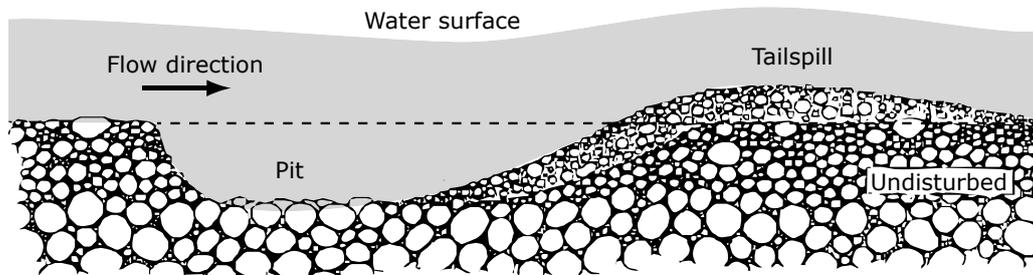
Figure 3. Diagram depicting the cross section of a spawning redd. The pit is excavated by the female trout prior to egg deposition. After fertilization, the eggs are buried with loose sediment forming the tailspill. The pit is oriented upstream of the tailspill. Figure adapted from Gallagher et al. (2007).

The survey area for each stream started at the mouth and extended upstream approximately 1,800 m. This length encompassed the lower reaches of the Urgersbach and Zellenbach, where spawning habitat was more readily accessible. Beyond this length, physical obstructions in the form of rock ledges or weirs block the majority of upstream migration (Rottensteiner, 2011). The survey area comprised almost the entire length of the Radersbach. Visual observations of the river substrates were carried out following guidelines suggested by Gallagher et al. (2007). The streams were surveyed in $7 - 16$ day intervals from the beginning of October until no new redds were found on subsequent visits, typically near the end of January (see Appendix A for annual redd counts). Due to the limited stream width and depth, redds were able to be identified by walking along the riverbank of the survey stretch. Each redd was photographed and the location marked via GPS to distinguish newly excavated redds from existing redds (see Appendix B for redd locations). The number of surveys conducted varied between streams and years, with the Radersbach being the most well documented. Surveys were carried out during spawning season from 2010 through 2018 with the exception of the Zellenbach, which was not surveyed during the 2010 spawning season.

4.1.4 Trout population

Trout populations can experience large fluctuations under natural conditions due to seasonal environmental influences, landscape features, and migration efforts (Bohlin et al., 2001; Jones et al., 2019; Unfer et al., 2011). The headwaters of the Piesting have undergone slight human interventions in the form of flood protection and road construction, however they remain in near natural conditions. This study investigated the influence that thermal variances and discharge levels had on the trout population within the Piesting headwaters. The connection between observed spawning activity and successful population recruitment has also been examined.

Population assessment is an integral part of fisheries management (Crisp, 2000). Electrofishing is used for sampling salmonids due to its relatively inexpensive nature and ability to be carried out in a variety of conditions (Temple & Pearsons, 2007). An electrical current is passed between two electrodes to stun fish entering the electrical field. The fish are then captured by hand net and measured before being returned to the water. Several techniques have been developed to estimate populations through the serial removal of fish. When estimating salmonid populations using electrofishing methods, there are inherent biases which must be taken into consideration (Bohlin et al., 1989; Rodtka et al., 2015). Overestimation of capture efficiency can lead to underestimation of fish abundances (Meyer & High, 2011).

Regular stock assessments were performed to obtain a better understanding of the structure and dynamics of the local trout populations. The results were used to calculate annual abundance and biomass of the populations. Recruitment estimates of each cohort were also derived from the data. Annual quantitative fish stock assessments were carried out in early autumn from $2011 - 2018$ following the Austrian guidelines established by Haunschmid et al. (2010). A record of the stock assessments performed in the study sites and Steinapiesting can be found in Appendix C. Assessments were conducted by the Österreichische Fischereigesellschaft using a direct current (DC) backpack electrofishing ($1.5 - 2.5\,\text{kW}$) unit. A two-pass removal method was employed with all captured fish being measured to the nearest $5\,\text{mm}$. The Radersbach was the most well sampled river in the study. Four sample stretches of approximately $50\,\text{m}$, covered 10% of the Radersbach length. The Urgersbach and Zellenbach were assessed less frequently, therefore data availability was limited. Both rivers had three sample stretches of $50\,\text{m}$, however only two from the Urgersbach and one from the Zellenbach were sampled every year. The Steinapiesting was sampled every other year. Further statistical analyses used to determine age-classes, abundance and biomass are described in section 4.2.4.

4.2 Data processing

4.2.1 Temperature regression models

Extrapolation of temperature data was required to supplement the recorded temperatures of the investigation sites. Several models that used air and water temperature as input variables were considered. The various models were tested for ability to predict the recorded temperatures of the investigated streams. Of the tested models, the best performing were linear regression models using water temperature from the Gutenstein gauging station as the predictor variable. Linear regression has been used to model the relationship between the temperature of a river and its tributaries (Benyahya et al., 2007). As the investigation streams are tributaries of the Kalter Gang, this model was chosen for temperature extrapolation.

Regression models were created for each site (Table 4) and the daily mean water temperature of the streams were extrapolated for the study period. These estimated values were used to calculate the monthly mean water temperature, as well as the mean temperature during the different YOY

life stages. Graphs of the linear regression models are included in Appendix D and tables of the predicted mean monthly temperatures are found in Appendix E.

Table 4. Coefficients of temperature regression models which used Gutenstein gauging station water temperature as the input variable. The regression models estimated the water temperature at the mouth of the investigation streams.

River	β_0	β_1	Adj. R^2
Radersbach	4.2	0.509	0.971
Urgersbach	0.8	0.843	0.988
Zellenbach	4.2	0.518	0.954
Eidechselbach	2.9	0.566	0.937
Weißenbach	0.9	0.842	0.944

4.2.2 Quantifying discharge conditions

Discharge data from the Gutenstein gauging station was used to identify flow conditions within the Piesting tributaries. A time series was composed for each cohort (2011 – 2019) relating to the early life stages of YOY trout. Starting in October, the daily mean discharge was recorded through the end of the following September covering the four YOY life stages. Plotting of the time series (Fig. 4) provided an overview of the discharge regime during the study period. The graph indicates that flood events occurred during the spawning period of the 2013, 2015 and 2019 cohorts. A ten-year flood (HQ10) took place during the early-juvenile period of the 2014 cohort. Literature suggests these events could have a potential influence on trout recruitment (Cattanéo et al., 2002; Unfer et al., 2011). Discharge levels exceeded the multiples of MQ in all life stages, however no flood events occurred during the juvenile stage.
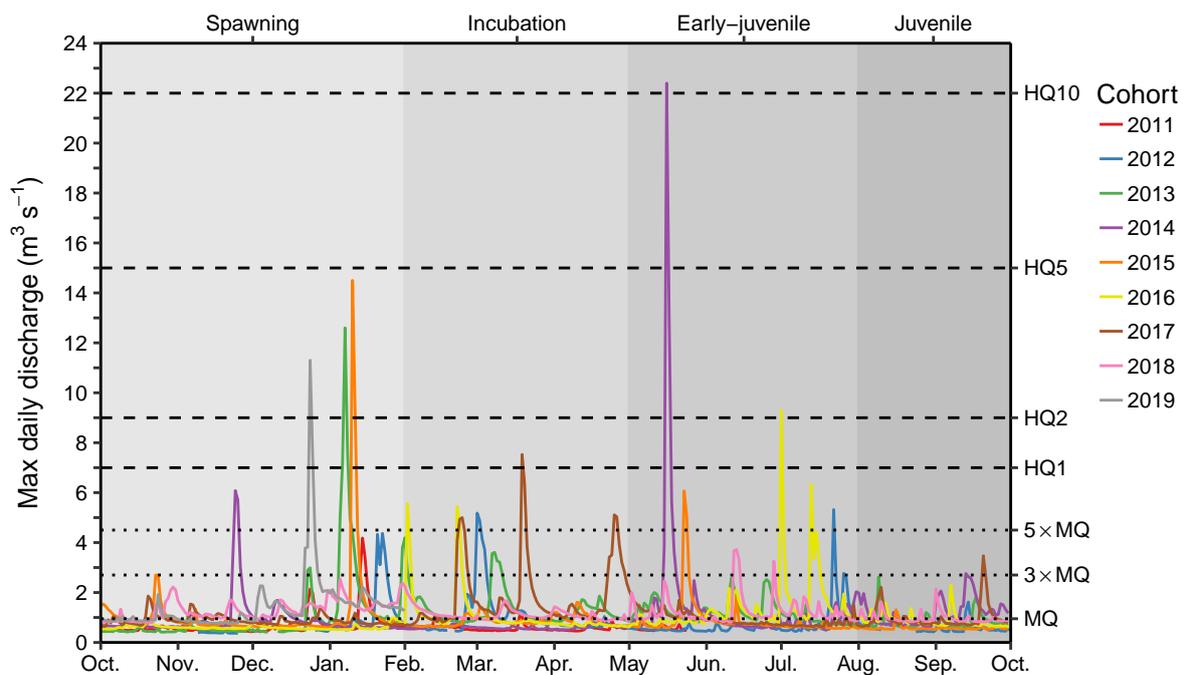
Figure 4. Maximum daily discharge ($m^3 s^{-1}$) at the Gutenstein gauging station. Each cohort was divided into the four YOY life stages as indicated at the top of the figure. High flow event thresholds are found on the right axis.

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To quantify high flow events in a statistically meaningful way, maximum daily discharge was compared to the discharge thresholds in Table 5. High flow events were defined as periods of discharge greater than $3 \times$ MQ. Discharge events above each threshold were quantified and the number of days in which discharge exceeded $3 \times$ MQ were tallied for each event. High flow events were then classified according to peak discharge and separated by cohort and life stage.

Table 5. Discharge levels used to determine high flow conditions. Discharge greater than $3 \times$ MQ was classified as high flow and used for further analysis.

	MJNQT	MQ	$3 \times$ MQ	$5 \times$ MQ	HQ1	HQ2	HQ5	HQ10
Discharge $(m^3\,s^{-1})$	0.47	0.95	2.85	4.75	7.00	9.00	15.00	22.00

4.2.3 Spawning activity parameters

Periodic visual surveys were used to obtain annual redd counts for each stream. These redd counts were used to calculate the spawning activity parameters used in subsequent data analyses. Survey dates and number of redds counted during each observation are found in Appendix A. The parameters derived from these redd counts were spawning onset, midpoint, duration and redd density. The annual spawning parameters of each investigation stream were calculated independently.

To determine the relative timeline of accumulation, redds were counted in $7 - 16$ day intervals and the number of redds on each observation date was compared to the annual redd total found in each stream. Onset of spawning activity (date of first redd construction) was predicted using locally estimated scatterplot smoothing (LOESS) regression of the percentage of accumulated redds on the observation dates. The onset of spawning fell between surveys with no visible redds and the earliest observed redds. This provided an accurate estimate of the first day in which spawning activity occurred. Similarly, the midpoint of spawning activity was determined when the LOESS regression predicted 50% redd construction. This was also in alignment with redd observations. The endpoint was calculated as 100% of redd construction using LOESS and occurred before the last survey in which new redds were detected. Duration of spawning activity was determined by the number of days between the calculated onset and endpoint of spawning activity.

The number of redds constructed in a given area (redd density) is indicative of the intensity of spawning activity taking place in that location. There has been some criticism of using redd surveys to monitor spawning due to female trout digging multiple redds (Dunham et al., 2001; Crisp, 2000). As this study examines spawning activity and not the number of spawning females, multiple redds do not jeopardize the validity of the analysis. Redd density of each spawning season was determined by dividing the total observed redds per 1,800 m sample stretch by the mean river width of the investigation stream. This value was then standardized to the number of redds per hectare to make comparison between the investigation sites possible.

4.2.4 Trout population structure and dynamics

Appraisal of salmonid stocks is a useful tool utilized in fisheries management (Crisp, 2000). Short-term population dynamics can be observed through regular stock assessments. Monitoring fish stocks over time is used to identify the naturally occurring fluctuations of the population. Deviation from the natural population dynamics can indicate external pressures. Stock density is typically described as the sum of the individuals (abundance) or sum of the weight (biomass) of defined size classes (Unfer & Pinter, 2018). Changes in fish stocks can be attributed to both density-dependent factors (mortality and emigration) and density-independent factors, such as seasonal environmental influences (Jenkins et al., 1999; Unfer et al., 2011). Monitoring the annual changes in abundance, biomass and age structure provides insight into the overall health of the population (Pope et al., 2010).

The attributes of the brown trout population were derived from calculations using the annual stock assessments. The abundance, biomass and age structure of the populations in the investigation sites were examined. Age structure of a trout population was inferred through length frequency diagrams, which indicated age distribution. Changes in abundance, biomass and population structure were used to determine the magnitude of the short-term population dynamics.

Age structure

The sampled fish populations were divided by length into 10 cm size classes. Annual cohorts within a population were identified by peaks in the multimodal distribution of the size classes (Pope et al., 2010). Size classes with the fewest individuals between age groups were selected as the thresholds for age-class divisions. Through visual analysis of the length frequency diagrams (see 5.4.1), age-classes were defined as described in Table 6. Sampled individuals were assigned to an age-class based on measured fork length. Additionally, the abundance and biomass of each age-class was calculated, providing further insight into the population structure.

Table 6. Length divisions used to define the age-classes of sampled fish. The age structure of the population was evaluated using designated age-classes.

Age-class	Fish length
$0+$	$< 110\,\text{mm}$
$1+$	$110 - 210\,\text{mm}$
$2+$	$> 210\,\text{mm}$

Abundance

Relative abundance of a sampled area can be projected with catch depletion estimates utilizing multiple passes of electrofishing (Bohlin et al., 1989). Fish assessment guidelines put forth by the Austrian Government (Haunschmid et al., 2010) dictate that estimates of abundance using two-pass serial removal should be done following the method established by Seber & Le Cren (1967). Absolute population of the age-classes within each sample stretch was calculated with Equation 1, whereby '$catch_1$' represented the fish caught in the first run and '$catch_2$' the second run. This formula is only applicable if the second run contains less than 50% of the first run.

Equation 1. Absolute population per sample area estimate according to Seber & Le Cren (1967). The estimation population is N, whereas $catch_1$ represents the catch from the first run and $catch_2$ the second run.

$$N = \frac{catch_1{}^2}{catch_1 - catch_2} \tag{1}$$

Abundance was standardized to individuals per hectare (Ind. ha^{-1}) using Equation 2. Abundance of each age-class was calculated using the estimated populations. Total abundance was obtained by pooling the abundance of each age-class. The abundance within the investigation site was determined by the mean of the sample stretches. Decreases in abundances of the 1+ and 2+ age-classes suggest changes in population due to mortality and emigration.

Equation 2. Abundance was determined by dividing the estimated population within the fished area (m^2), then multiplying to estimate Ind. ha^{-1}.

$$abundance = \frac{population}{fished\ area} \times 10{,}000 \tag{2}$$

Biomass

Successive stock assessments measured annual changes in biomass of the cohorts. Following the determination of stock densities using abundance, fluctuations in biomass were used to calculate stock production. Fish production is defined as the "amount of tissue elaborated per unit time per unit area, regardless of its fate" (Clarke et al. (1946) in Mertz & Myers, 1998). Increases in the population biomass can be attributed to production (Elliott, 1984). As cohorts age, biomass increases with fish growth while abundance decreases due to mortality and emigration.

Analyzing the biomass (kg ha^{-1}) in conjunction with abundance provides an idea of the average size of the individuals within the population. Weighing the sampled fish in the field would be impractical and place undue stress on the fish, therefore a length-weight relationship was used to estimate the individual fish weight. The length-weight regression was developed using long-term data obtained from the Ois River (BOKU, 2019). Fish weight (gram) was calculated with Equation 3 using the fork length (mm) measurement obtained during electrofishing surveys. Total mass of the sampled area was obtained by summing the estimated fish weights.

Equation 3. Length-weight equation derived from BOKU (2019). Individual fish weight (gram) was estimated using the measured total fish length (mm).

$$weight = 1.4 \times 10^{-5} \times length^{2.9381} \tag{3}$$

Biomass was calculated using the guidelines established by Haunschmid et al. (2010). The biomass of each age-class was calculated separately using Equation 4. Total biomass of the sample site was obtained by summing the biomass of the age-classes. Biomass was weighted according to sample sites for each investigation stream. Calculating the biomass of the age-classes allowed for changes in the biomass of the cohorts to be detected.

Equation 4. Biomass in kilograms per hectare was calculated by dividing the sum of individual fish weight (kg) by the total number of fish caught and then multiplying it by the calculated abundance ($\mathsf{Ind.\,ha^{-1}}$).

$$biomass = \frac{total\ weight}{total\ catch} \times abundance \tag{4}$$

Recruitment

The success of reproduction can be assessed through population recruitment. Recruitment is the number of juvenile fish that have joined the population from the spawning activity occurring in the prior autumn. To determine recruitment levels of the investigation sites, stock densities were first analyzed by examining the abundances of different age-classes. The abundance of YOY (0+ fish) was used for evaluation of the juvenile recruitment occurring in each cohort. Each annual electrofishing survey saw an addition of 0+ fish abundance, which was representative of the juveniles that had survived from the prior spawning period. These abundance numbers were established as recruitment values and used for further data analysis.

4.3 Data analysis

4.3.1 Temperature influence on spawning activity

In this study, influence of water temperature on the spawning parameters was assessed through correlation analysis. Mean daily water temperature of each investigation site was extrapolated using the regression models described in section 4.2.1. The long-term mean daily water temperature at the gauging station depicts the thermal regime of the study area (Fig. 5). Following Warren et al. (2012), the mean temperature of June through August was chosen as representation of summer water temperature. The temperature typically rises above $10\,°\mathrm{C}$ in early June, peaks in late July, then falls below $12\,°\mathrm{C}$ by the end of September. The extrapolated stream temperatures were used to calculate the summer water temperature for each investigation site.
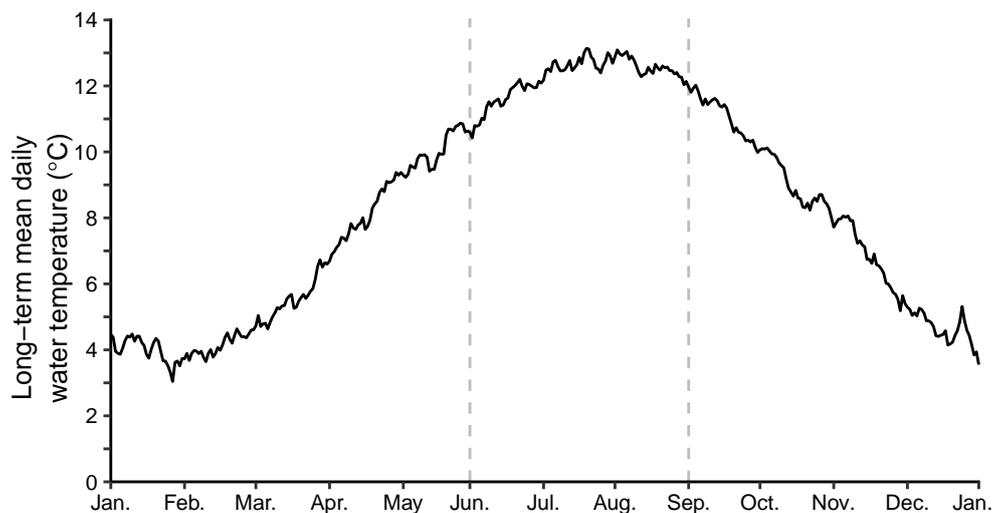
Figure 5. The long-term mean daily water temperature recorded by Gutenstein gauging station from 20.01.2004 through 31.01.2019. The vertical lines indicate the boundaries of the period used to calculate the summer water temperature.

The annual mean summer water temperatures were tested for correlation with total redd count and density using non-parametric methods. Spearman's rank correlation was used for each test. The day of year in which the onset, midpoint, and endpoint occurred were tested for correlation with annual summer temperature. Linear regression was used to model the relationship between temperature and spawning activity. The parameters of the three study sites were then pooled and additional correlation tests were performed. Z-scores were used to normalize the difference of redd densities between study sites. Any detected correlation between summer temperature and spawning parameters were indicative of possible thermal influence on spawning activity.

4.3.2 Spawning activity and recruitment

The influence of spawning activity on recruitment was evaluated through bivariate correlation analyses of spawning activity parameters and the number of new recruits in the associated cohort. Spearman's correlation analysis of redd density and the number of new recruits indicated if the number of redds in the investigation sites affected the recruitment levels. The rivers were analyzed separately, with annual redd densities being correlated with the number of 0+ fish observed in the population assessments conducted the following autumn. A linear regression model was developed for each site and the R^2 was calculated to determine how well the model fit the observations. After examining the investigations sites individually, the data from the different rivers was pooled and joint analyses were performed.

Possible influences that could be attributed to the timing of spawning activity have also been examined. Correlation analyses between population recruitment and the onset, midpoint and duration of spawning activity were performed using non-parametric methods. Each spawning variable was tested for correlation with recruitment individually and the investigation sites were examined separately. A joint analysis of pooled data was not performed. Correlations were identified as potential links between spawning activity and recruitment.

4.3.3 Discharge and recruitment

The relationship between maximum daily discharge and YOY cohort strength was examined during the four separate YOY life stages and the months that comprised them. Relations were tested by Spearman's correlation followed by simple linear regression analysis. Recruitment of the study sites was evaluated using discharge data obtained from the Gutenstein gauging station. Correlation between recruitment and maximum daily discharge was tested for each time period of juvenile cohorts. As shown in Table 3, the four life stages were defined as follows: Spawning (October – January), Incubation (February – April), Early-juvenile (May – July), and Juvenile (August – September). Additionally, the maximum discharge of the individual months was also tested, beginning with the onset of spawning in October. Linear regression was used to model the relationship between variables. The investigation sites were then pooled and the Z-scores of cohort recruitment were analyzed. Recruitment Z-scores were used to normalize the different recruitment levels found in the study sites. Correlation and regression analyses were then performed on the joint data as described above.

5 Results

5.1 Temperature regression

The temperature regression models used in this study relied on the linear relationship between the water temperature of Kalter Gang and its tributaries. The regression model parameters are available in section 4.2.1.

Radersbach

The Radersbach exhibited the coldest long-term mean summer temperature of the investigation sites. The linear regression model was developed using 251 water temperature observations. Recorded temperatures ranged from $4.0 - 11.5\,°C$. The projected temperatures fit the recorded stream temperatures with an adjusted R^2 value of 0.971 (Fig. 6a). The mean summer water temperature of the Radersbach (see Fig. 6b) ranged from a low of $10.2\,°C$ in 2012 to a high of $11.0\,°C$ in 2015. The daily mean temperature in the summer months had the largest range in 2015. The coldest mean summer temperature of just above $8.5\,°C$ occurred in 2013.

(a) Radersbach regression model predictions.　　　　**(b)** Mean summer temperature.
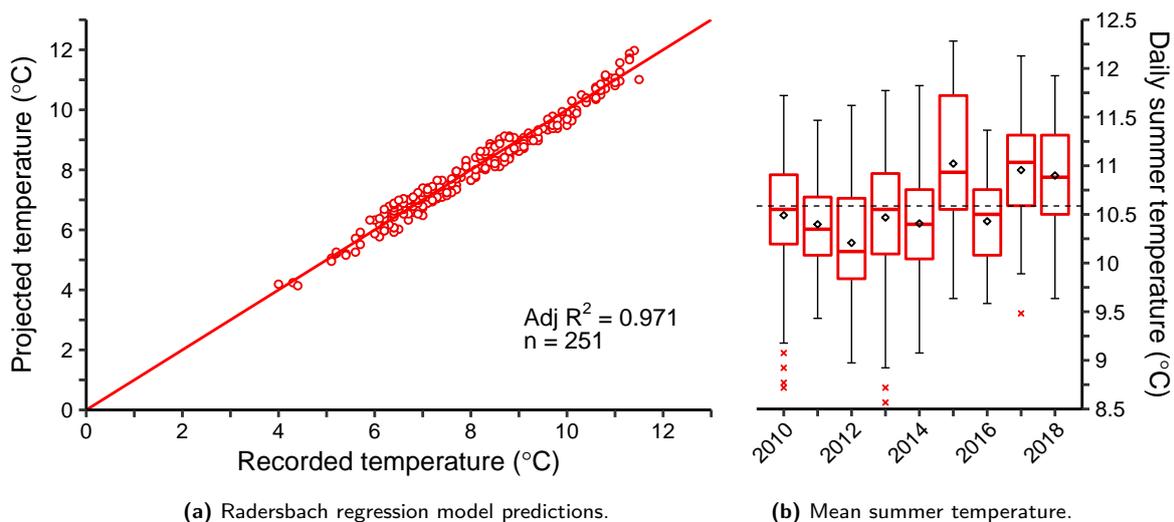
Figure 6. The Radersbach temperature regression model used 251 data points to predict water temperature. The model was used to extrapolate the daily mean temperatures of the study period. The mean summer temperature was calculated from these projections.

Urgersbach

The Urgersbach had the largest thermal variance. The lowest $(2.1\,°C)$ and highest $(12.8\,°C)$ recorded temperatures of the investigation sites were both measured in the Urgersbach. The linear regression model was created with 140 temperature measurements (Fig. 7a). Due to the limited number of observations, the model displayed a high adjusted R^2 value of 0.988. However, this high coefficient combined with the wide range of recorded temperatures indicated that water temperature of the Urgersbach could be estimated accurately using the gauging station temperatures. The mean summer temperature ranged from $10.7 - 12.0\,°C$ (Fig. 7b).

(a) Urgersbach regression model predictions.   **(b)** Mean summer temperature.
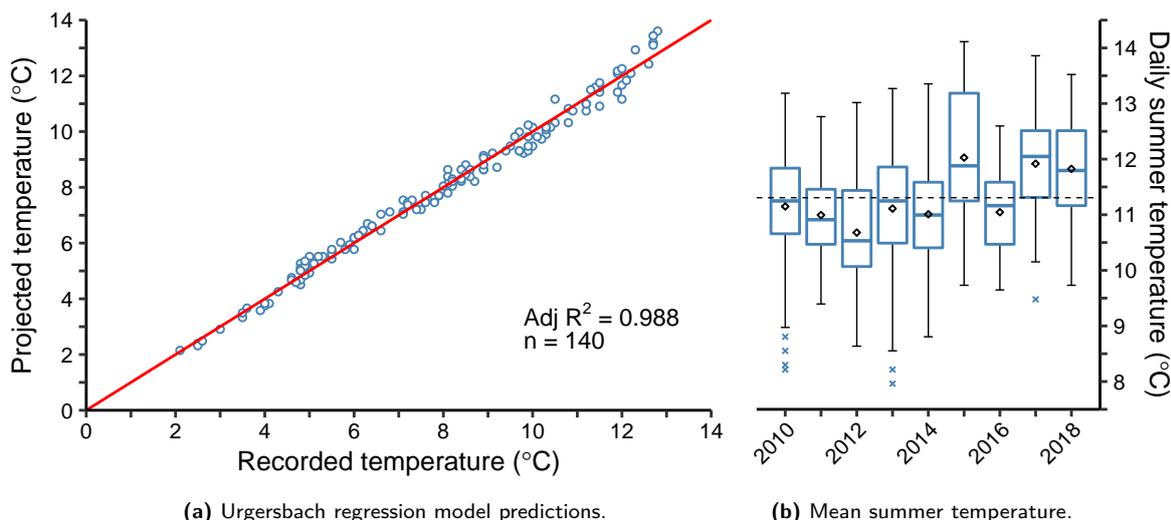
Figure 7. The Urgersbach temperature regression model used 140 data points to predict water temperature. The largest range of observed temperatures were found in the Urgersbach.

Zellenbach

The Zellenbach had the lowest thermal variance of the investigation sites. Recorded daily mean temperatures ranged from $4.0 - 9.0\,°C$. There was only $5\,°C$ of fluctuation in the 155 recorded temperatures (Fig. 8a). This regression model had the lowest adjusted R^2 value of 0.954, which could be explained by the narrow range of recorded temperatures. The coefficients used were very similar to the Radersbach model, which resulted in projected mean summer temperatures close in proximity to those of the Radersbach (Fig. 8b). Long-term mean summer temperature of the Zellenbach was $10.48\,°C$, while the Radersbach and Urgersbach were $10.43\,°C$ and $11.05\,°C$ respectively.

(a) Zellenbach regression model predictions.   **(b)** Mean summer temperature.
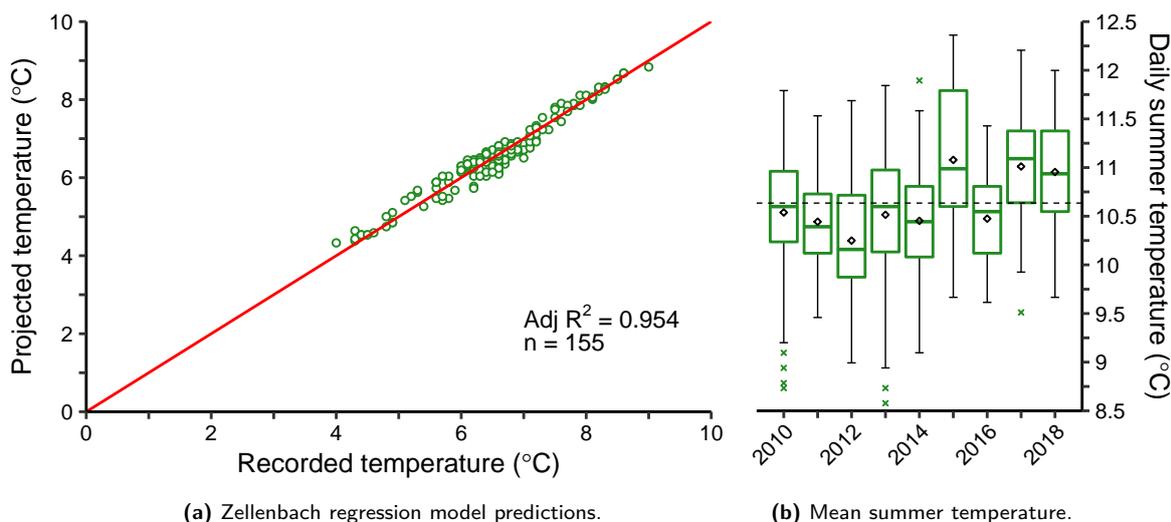
Figure 8. The Zellenbach temperature regression model used 155 data points to predict water temperature. The lowest R^2 value was found in this model due to the narrow range of variance. The model was able to accurately estimate mean daily water temperature.

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5.2 Discharge conditions

Maximum daily discharge at the Gutenstein gauging station was used to identify the severity and duration of high flow events. Table 7 displays the maximum discharge values recorded during the different months and YOY life stages of each respective cohort. The highest recorded discharge during the study period was $22.40\,\mathrm{m^3\,s^{-1}}$, which took place in May 2014. October 2011 (of the 2012 cohort) was the month with the lowest maximum discharge at $0.45\,\mathrm{m^3\,s^{-1}}$, which is less than MJNQT ($0.47\,\mathrm{m^3\,s^{-1}}$). The 2018 cohort experienced the lowest maximum discharge of any cohort, with a peak value of $3.72\,\mathrm{m^3\,s^{-1}}$ in the early-juvenile stage.

Table 7. Gutenstein gauging station maximum daily discharge during the months and YOY life stages of each respective cohort.

		2011	2012	2013	2014	2015	2016	2017	2018	2019
					Maximum daily discharge ($\mathrm{m^3 s^{-1}}$)					
Life stage	Q_{max}Spawning	4.18	4.37	12.60	6.08	14.50	0.98	1.86	2.55	11.30
	Q_{max}Incubation	1.07	5.18	3.61	0.80	1.61	5.56	7.53	1.97	-
	Q_{max}Early-juvenile	0.72	5.32	2.58	22.40	6.07	9.29	2.07	3.72	-
	Q_{max}Juvenile	*	1.62	2.62	2.76	1.31	2.29	3.47	2.15	-
Month	Q_{max}October	0.66	0.45	0.66	0.95	2.70	0.87	1.86	2.22	1.92
	Q_{max}November	0.54	0.47	1.09	6.08	1.33	0.67	1.54	1.71	1.17
	Q_{max}December	2.14	0.50	2.99	1.69	0.76	0.94	1.41	2.08	11.30
	Q_{max}January	4.18	4.37	12.60	0.70	14.50	0.98	1.18	2.55	2.21
	Q_{max}February	1.07	1.98	2.88	0.75	1.18	5.56	5.00	1.97	-
	Q_{max}March	1.05	5.18	3.61	0.76	1.40	1.13	7.53	1.67	-
	Q_{max}April	0.88	1.04	1.86	0.80	1.61	0.83	5.11	1.43	-
	Q_{max}May	0.72	0.75	2.00	22.40	6.07	1.12	2.07	2.46	-
	Q_{max}June	*	0.78	2.58	1.19	1.82	2.17	1.05	3.72	-
	Q_{max}July	*	5.32	1.54	2.03	0.88	9.29	1.51	1.83	-
	Q_{max}August	*	0.79	2.62	1.99	1.31	1.58	2.21	1.63	-
	Q_{max}September	*	1.62	1.79	2.76	0.68	2.29	3.47	2.15	-

* Data not available

Discharge levels during the different life stages varied from cohort to cohort. The juvenile stage had the lowest discharge overall, with a maximum of $3.47\,\mathrm{m^3\,s^{-1}}$ occurring in the 2017 cohort. The early-juvenile stage had the widest range, with $0.72\,\mathrm{m^3\,s^{-1}}$ and $22.40\,\mathrm{m^3\,s^{-1}}$ in the 2011 and 2014 cohorts respectively. The spawning and incubation stages, which were of interest in this study, also fluctuated greatly between cohorts.

A database of high flow events was created to facilitate the investigation of the relationship between flooding and population recruitment. A summary of the database is found in Table 8 and displays the number of high flow events occurring in the life stages of each cohort. The numbers in parentheses are the combined duration of the events in each life stage. The 2017 cohort spent a total of 15 days in high flow conditions during the incubation period. There was only one recorded HQ1 event, which occurred in the juvenile period of the 2017 cohort, and three recorded HQ2 events in other cohorts. The 2014 early-juvenile discharge of $22.40\,\mathrm{m^3\,s^{-1}}$ in Table 7 above coincides with the HQ10 event with a duration of 5 days in Table 8.

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Table 8. The number of high flow events occurring in the study area by severity. The total duration in days of high flow conditions is indicated in parentheses.

Cohort	Life stage	3×MQ	5×MQ	HQ1	HQ2	HQ10
2011	Spawning	1 (2)	-	-	-	-
	Incubation	-	-	-	-	-
	Early-juvenile	-	-	-	-	-
	Juvenile	*	*	*	*	*
2012	Spawning	1 (4)	-	-	-	-
	Incubation	-	1 (4)	-	-	-
	Early-juvenile	-	1 (1)	-	-	-
	Juvenile	-	-	-	-	-
2013	Spawning	1 (2)	-	-	1 (7)	-
	Incubation	2 (7)	-	-	-	-
	Early-juvenile	-	-	-	-	-
	Juvenile	-	-	-	-	-
2014	Spawning	-	1 (4)	-	-	-
	Incubation	-	-	-	-	-
	Early-juvenile	-	-	-	-	1 (5)
	Juvenile	-	-	-	-	-
2015	Spawning	-	-	-	1 (3)	-
	Incubation	-	-	-	-	-
	Early-juvenile	-	1 (2)	-	-	-
	Juvenile	-	-	-	-	-
2016	Spawning	-	-	-	-	-
	Incubation	-	2 (4)	-	-	-
	Early-juvenile	-	1 (4)	-	1 (2)	-
	Juvenile	-	-	-	-	-
2017	Spawning	-	-	-	-	-
	Incubation	-	2 (12)	1 (3)	-	-
	Early-juvenile	-	-	-	-	-
	Juvenile	1 (1)	-	-	-	-
2018	Spawning	-	-	-	-	-
	Incubation	-	-	-	-	-
	Early-juvenile	2 (4)	-	-	-	-
	Juvenile	-	-	-	-	-

* Data not available

5.3 Spawning activity

Spawning activity in terms of redd density varied between annual cohorts and investigation sites. The cohort redd densities in Fig. 9 are from the spawning season (Oct. – Jan.) prior to emergence. The Radersbach had the highest mean redd density with 246 redds per hectare, while Zellenbach had a mean density of 149 redds per hectare. The Urgersbach had the lowest mean density of only 87 redds per hectare. Data from the 2011 cohort was not available for the Zellenbach.
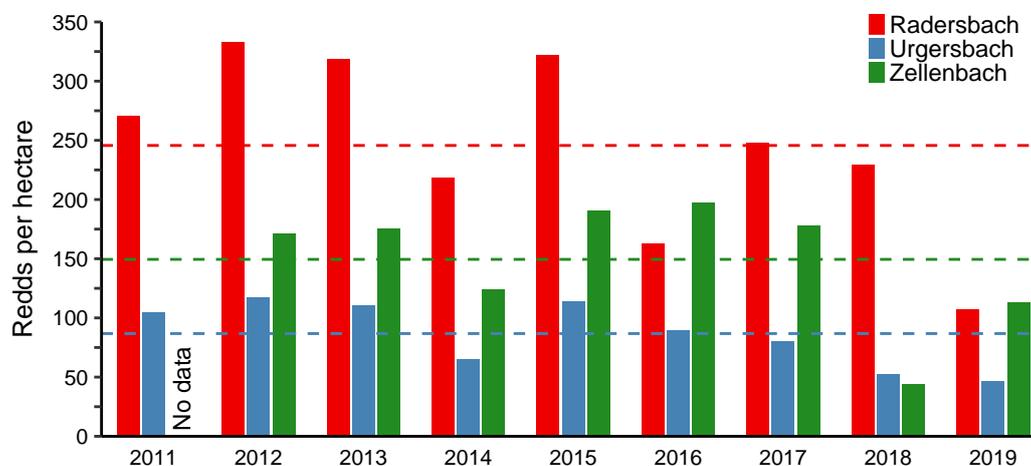
Figure 9. Annual redd densities observed in the investigation sites. Dashed lines represent the mean annual density of the respective sites.

5.3.1 Radersbach

The spawning activity parameters calculated from the Radersbach redd counts are compiled in Table 9. Onset of spawning activity in the Radersbach regularly occurred in the latter half of October. Earliest onset occurred on day 293 in cohorts 2016 and 2019, which also had the lowest redd densities. The endpoint of spawning activity was more varied. Average duration was 69 days, with the shortest lasting 55 days and 84 the longest. The highest redd density was found in the 2012 cohort, followed closely by the 2015 and 2013 cohorts.

Table 9. Radersbach annual spawning activity parameters. Onset is the day of year in which the first redd was constructed, along with midpoint (50%) and endpoint (100%) of redd construction. Duration is the number of days between onset and endpoint. Total redds is the sum of annual redd counts

Cohort	Onset	Midpoint	Endpoint	Spawning duration	Total redds	Redd density (Redds ha^{-1})
2011	295	348	379	84	73	270
2012	296	338	364	68	90	333
2013	297	331	362	65	86	319
2014	302	323	366	64	59	219
2015	294	325	362	68	87	322
2016	293	328	364	71	44	163
2017	301	329	356	55	67	248
2018	297	326	366	69	62	230
2019	293	327	369	76	29	107

The graph in Fig. 10 depicts the Radersbach redd density accumulation, or the rate at which redds were constructed. As discussed above, the onset of spawning activity regularly occurred in the second half of October. The slope of the line indicates the rate in which redds were constructed. The 2014 and 2018 cohorts displayed very similar rates of redd accumulation. The total redd density was comparable between the 2012, 2013 and 2015 cohorts. The 2011 and 2019 accumulation rates converged in late November, before resulting in different densities.
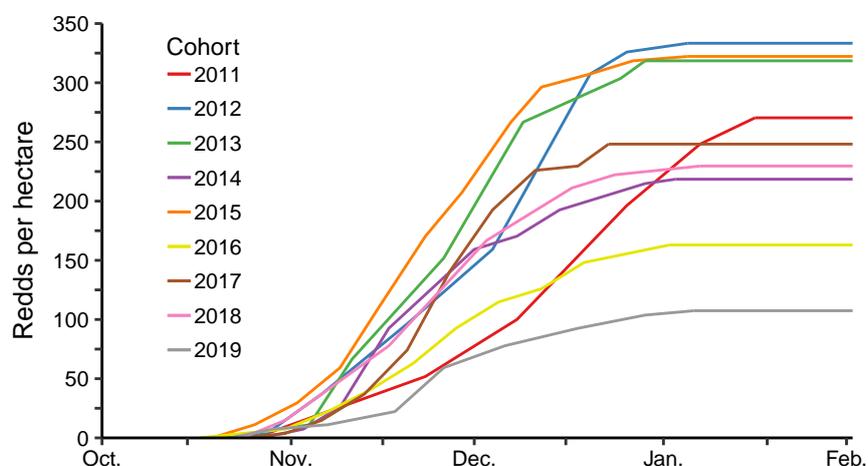
Figure 10. Redd density accumulation of the Radersbach. The slope indicates spawning intensity, with the 2015 cohort having the highest rate of accumulation and 2019 the lowest.

5.3.2 Urgersbach

Spawning parameters of the Urgersbach (Table 10) were much more varied than the Radersbach. Onset of spawning began in the last days of October and early November with the exception of the 2012 cohort, which began in mid-November. This same cohort was also of interest because of its short duration of 39 days, which was 20 days shorter than the average duration of 59. Despite its late onset and short duration, the 2012 cohort had the highest redd density. Redd densities ranged from 46 – 117 redds per hectare. Like the Radersbach, the lowest redd density was associated with the 2019 cohort.

Table 10. Urgersbach annual spawning activity parameters. Onset is the day of year in which the first redd was constructed, along with midpoint (50%) and endpoint (100%) of redd construction. Duration is the number of days between onset and endpoint. Total redds is the sum of annual redd counts

Cohort	Onset	Midpoint	Endpoint	Spawning duration	Total redds	Redd density (Redds ha^{-1})
2011	308	314	373	65	34	105
2012	319	331	351	32	38	117
2013	294	338	365	71	36	111
2014	301	318	369	68	21	65
2015	297	324	365	68	37	114
2016	298	319	346	48	29	90
2017	294	328	348	54	26	80
2018	307	324	360	53	17	52
2019	293	325	354	61	15	46

The redd density accumulation graph depicted the extent of the 2012 cohort's deviation from the others (Fig. 11). The sharp incline indicates a high number of redds constructed in a short time period. The gradual slope of the 2018 cohort illustrates a long period in which few redds were created. In correspondence with the Radersbach, the three highest densities were found in the 2012, 2013 and 2015 cohorts. Similarly, the 2011 cohort also had the fourth highest density. The three lowest densities (2014, 2018, and 2019) had comparable redd accumulation rates.
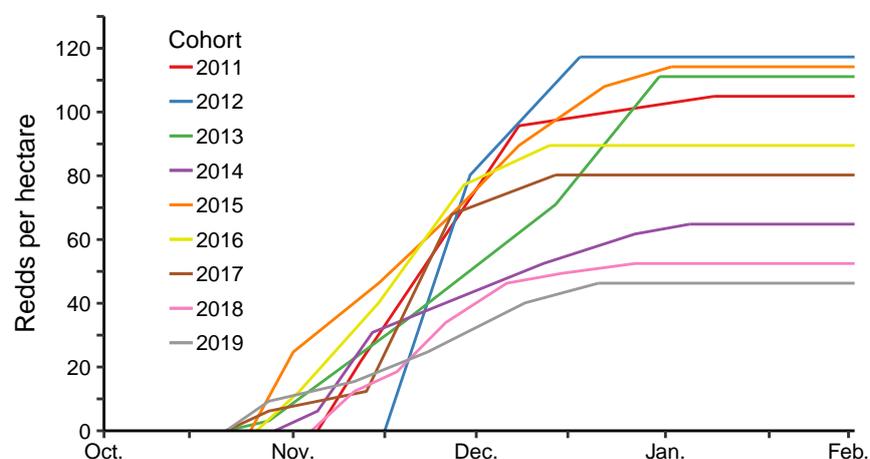
Figure 11. Redd density accumulation of the Urgersbach. The 2012 cohort had the highest redd density, latest onset and shortest duration of spawning activity.

5.3.3 Zellenbach

The spawning parameters in Table 11, calculated from the Zellenbach redd counts, show that the values of the Zellenbach were in line with the other investigation sites. Unlike the other streams, the lowest redd density of the Zellenbach belonged to the 2018 cohort. With just 44 redds per hectare, the 2018 cohort had less than 30% of the annual mean density. Similar to the other streams, the second highest density was the 2015 cohort. However, the highest density was found with the 2016 cohort. The Zellenbach had the highest variance of onset, but lowest variance in spawning duration when compared with the other sites.

Table 11. Zellenbach annual spawning activity parameters. Onset is the day of year in which the first redd was constructed, along with midpoint (50%) and endpoint (100%) of redd construction. Duration is the number of days between onset and endpoint. Total redds is the sum of annual redd counts

Cohort	Onset	Midpoint	Endpoint	Spawning duration	Total redds	Redd density (Redds ha^{-1})
2012	309	334	373	64	77	171
2013	294	325	363	69	79	176
2014	303	315	371	68	56	124
2015	311	331	366	55	86	191
2016	292	335	364	72	89	198
2017	292	326	357	65	80	178
2018	297	326	358	61	20	44
2019	298	330	365	67	51	113

The redd accumulation rates of the Zellenbach (Fig. 12) could easily be divided into three groups. The 2018 cohort was distinct in that it had a moderate slope and low density. The 2014 and 2019 cohorts could be distinguished by their similar accumulation rates and final redd densities. The remaining cohorts made up the final division and were comprised of the five highest densities. The accumulation rates and redd densities of the last group were comparable, although the onset of spawning activity for the 2012 and 2016 cohorts occurred later in the year.
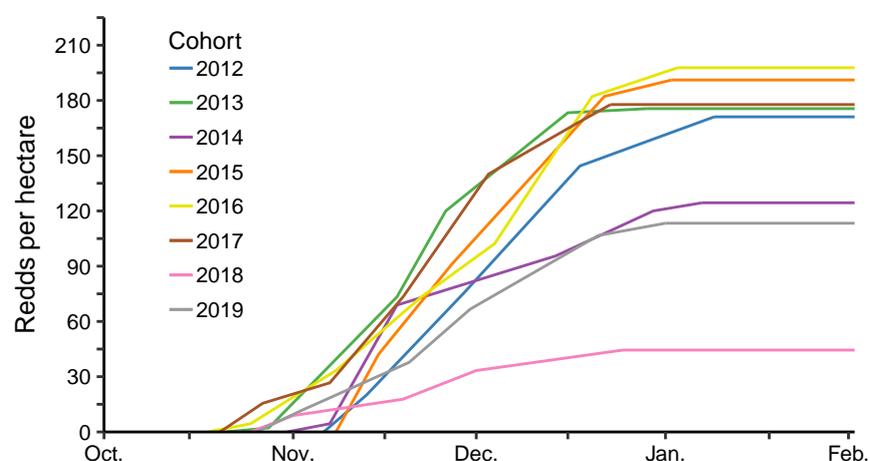
Figure 12. Redd density accumulation of the Zellenbach. The 2014 and 2019 cohorts had similar accumulation rates and low redd densities while the 2018 cohort had a significantly lower redd density.

5.4 Population structure

The age structure of the population could be inferred by examining length frequency diagrams. Analysis of the abundance and biomass of the different age-classes provided further insight into the population structure.

5.4.1 Length frequency diagrams

The length frequency diagrams showed the catch percentages of the different size classes. Fish with a length of less than 110 mm have been designated as age-class 0+, while fish greater than 110 mm were age-class 1+ and all fish larger than 210 mm were specified as age-class 2+. These classes are estimates of age based on the overall population structure.

Radersbach

The population of the Radersbach was predominantly composed of juvenile fish. The relative length frequency diagram of the combined 2011 – 2018 catch (Fig. 13) indicated that 94.5% of the sampled population was less than 110 mm in length, placing them in the 0+ class (YOY). The remaining 5.5% of the population were of the 1+ class. There were no 2+ class fish sampled.
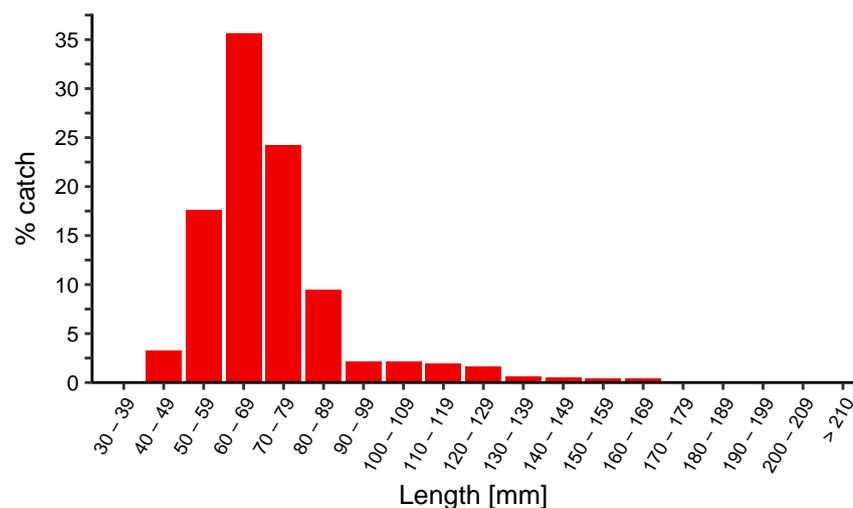
Figure 13. Length frequency diagram of combined 2011–2018 Radersbach stock assessments. Shares of each 10 mm size class have been weighted by sample sites.

The Radersbach age structure was not very dynamic during the study period. The annual length frequency diagrams in Fig. 14 showed that population samples were almost entirely YOY fish. Few adult fish were sampled during the study period, with the largest fish of 200 mm in length being found in 2013. The highest proportion of 0+ fish (98.4%) was sampled in 2015, while 2013 had the highest share of 1+ (8.5%). The median size class of all years was 60 – 69 mm, accounting for 35.6% of the total catch. The surveys conducted in 2014, 2016 and 2018 found high portions of 0+ fish above the median size class, indicating a YOY cohort made of larger individuals. Conversely, 2011 and 2012 surveys showed high shares of 0+ fish which were below the median size class, indicating a cohort of smaller individuals. Size differences within a single age-class influenced the biomass of that age-class.
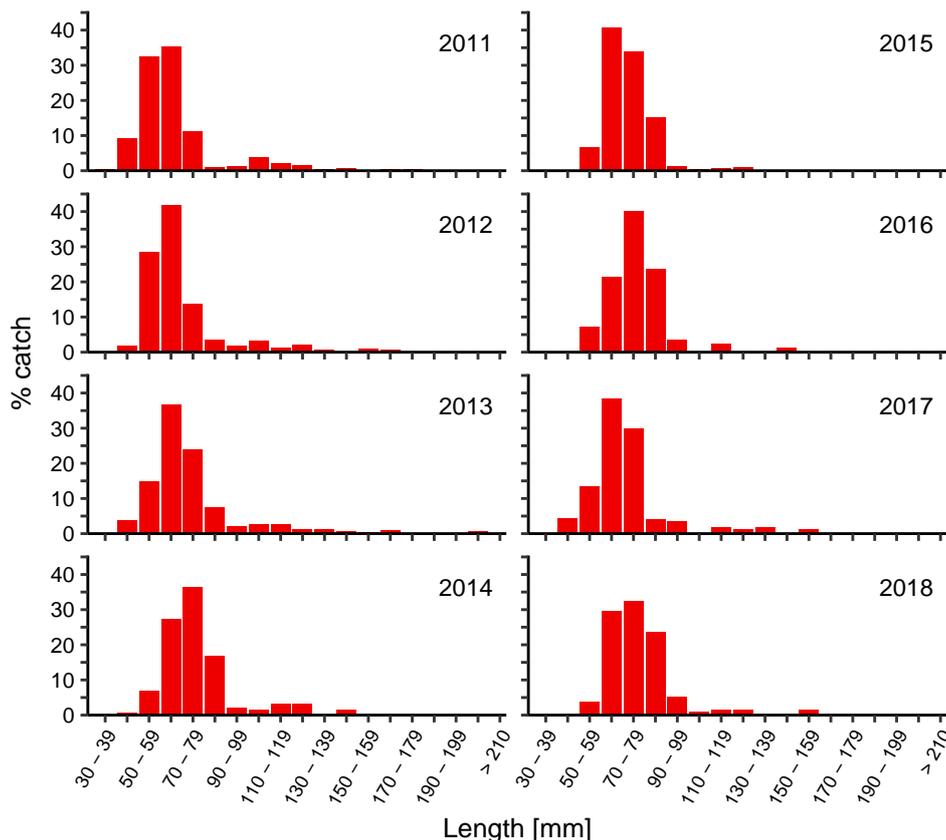
Figure 14. Length frequency diagrams of the 2011–2018 cohorts. Shares of each 10 mm size class have been weighted by sample sites.

Urgersbach

The age structure of the Urgersbach (Fig. 15) was more heterogeneous than the Radersbach population. Fish that belonged to the 0+ age-class comprised 65.3% of the total catch, while the 1+ age-class accounted for 30.7%. The few 2+ fish that were sampled represented only 4.0% of the total population. As only three sample stretches were included in the stock assessments, the resulting population data may not have been representative of the entire investigation site.
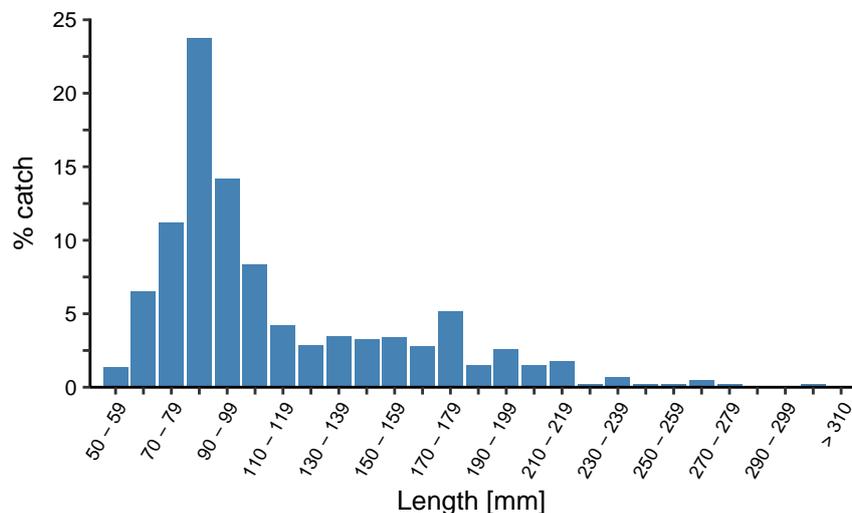
Figure 15. Length frequency diagram of combined (2011–2018[a]) Urgersbach catch. Shares of each 10 mm size class have been weighted by sample sites.

[a]2012 data not available

The annual population structure of the Urgersbach (Fig. 16) was much more dynamic than that of the Radersbach. The 2011 survey exhibited a healthy fish population with visible age-class divisions. The high share (61.5%) of YOY fish in the sample indicated a successful spawning period the prior year. No assessments were performed in 2012, rendering population data from 2012 unavailable. Within the 2013 survey, the 0+ age-class accounted for 13.4% of population, while 1+ and 2+ fish made up 66.7% and 20.0% respectively. The low share of YOY fish in 2013 was indicative of poor spawning results. The 2015 (42%) and 2018 (48%) surveys also had low percentages of juveniles, suggesting less successful reproduction. Conversely, the 2014 assessment had a high proportion (86.6%) of juveniles, which indicated successful spawning. The 2016 (78.9%) and 2017 (80.6%) fish surveys also had high shares of YOY fish. The number of fish sampled in 2018 was substantially lower than in other years, which affected the population distribution. Fish of the 2+ age-class were found in every assessment aside from 2017 and 2018.
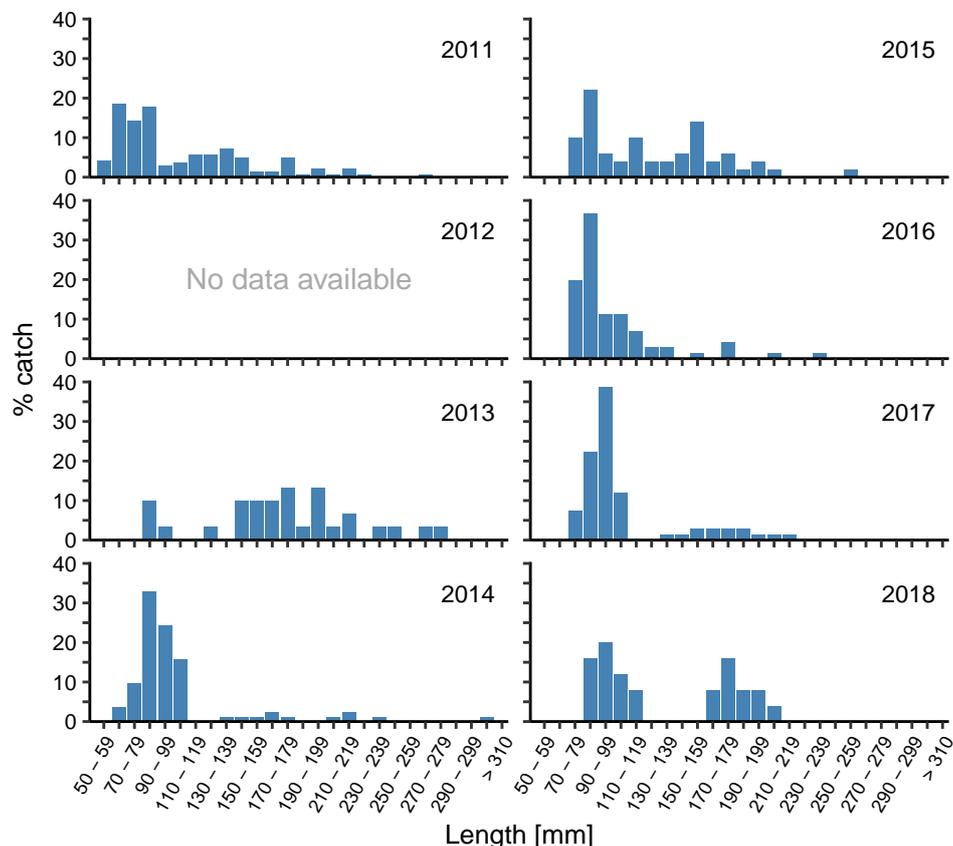

Figure 16. Length frequency diagrams of the 2011–2018 cohorts. Shares of each 10 mm size class have been weighted by sample sites. The population was quite dynamic between the annual surveys.

Zellenbach

The Zellenbach age structure (see Fig. 17) was similar to that of the Urgersbach. YOY fish comprised 69.5% of the total catch, while the 1+ age-class accounted for 28.2%. The remaining 2.3% of the population were 2+ fish. Only one sample stretch of 50 m was analyzed, yielding results which may have been non-representative of the entire Zellenbach. Furthermore, stock assessments of the Zellenbach were not conducted in 2012 or 2018.
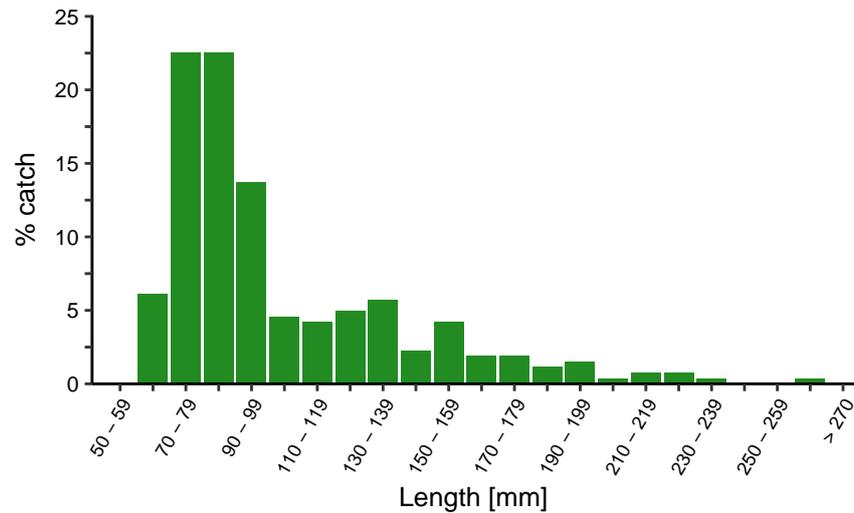
Figure 17. Length frequency diagram of combined (2011–2018[b]) Zellenbach catch. Shares of each size class have been determined from a single sample site.

Annual fish stock assessments showed that the Zellenbach population structure was also quite dynamic (Fig. 18). High percentages of the 0+ age-class were present in the 2011 (78.6%), 2014 (65.4%), 2016 (94.7%) and 2017 (70.8%) surveys. The high shares of YOY fish indicated successful reproduction. Unsuccessful spawning was suggested by the low levels of juveniles in the 2013 (37.8%) and 2015 (34.5%) surveys. Fish belonging to the 2+ age-class were sampled in all but the 2014 and 2017 stock assessments.
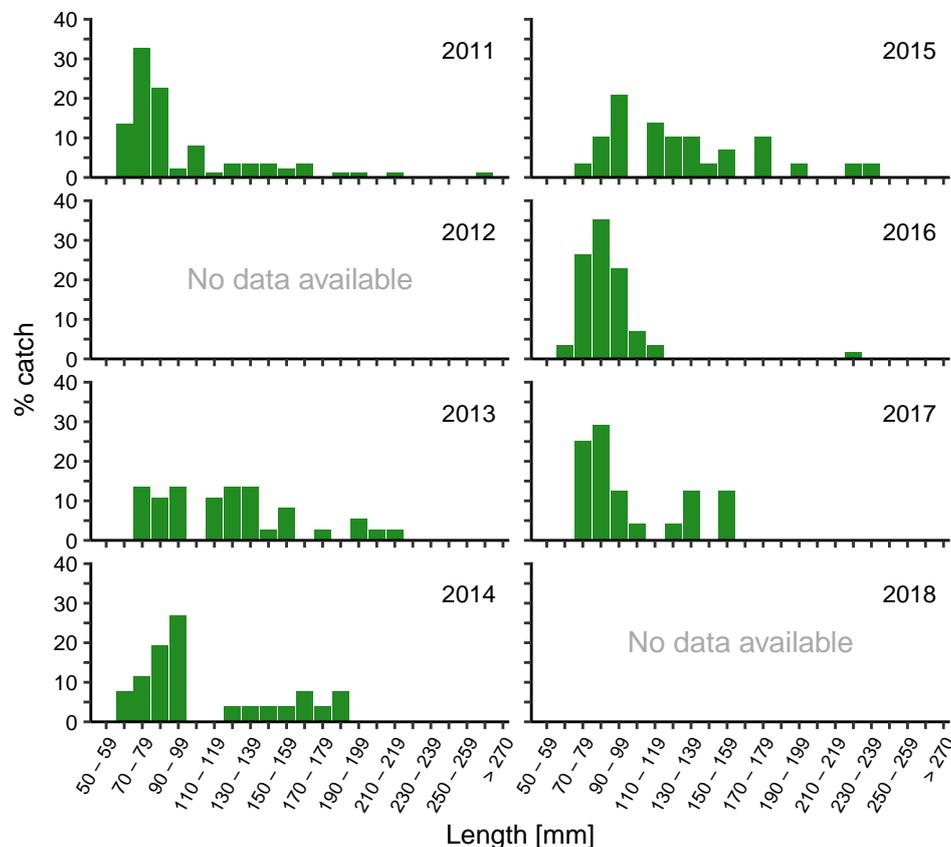

Figure 18. Length frequency diagrams of the 2011–2018 cohorts. Shares of each 10 mm size class have been determined from a single sample site.

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[b]2012 and 2018 data not available   31

5.4.2 Abundance and biomass

Examining the abundance and biomass of the different age-classes within a population allows for further assessment of the population structure. The number of fish producing a given biomass conveyed an idea of the average fish size within that population.

Radersbach

There was an overall decline in abundance of the Radersbach during the study period (Fig. 19a). The 2011 abundance of 8333 individuals per hectare was the highest recorded observation. The surveys conducted in 2012 and 2013 showed an approximate abundance of 5500 Ind. ha^{-1} before dropping to 4100 Ind. ha^{-1} in 2014. The abundance then rose back to 5500 Ind. ha^{-1} in 2015. There was a sharp decrease in the number of individuals in 2016, when it fell to just 1650 per hectare. The abundance increased by 660 individuals in 2017 and again by 670 in 2018.

The Radersbach biomass (Fig. 19b) exhibited similar characteristics to the abundance. As the population was mostly composed of juveniles, biomass was directly proportional to abundance. The highest biomass of 34.6 kg ha^{-1} was found in the 2011 sample, while 2016 had the lowest biomass of just 8.3 kg ha^{-1}. These coincided the highest and lowest abundance values. A slight deviation in the 2013 biomass can be explained by the 200 mm fish that was present in the sample (see Fig. 14). Likewise, the abundance-biomass ratio of 2014 can be attributed to a higher proportion of 1+ fish than other years.

(a) Radersbach abundance.   (b) Radersbach biomass.
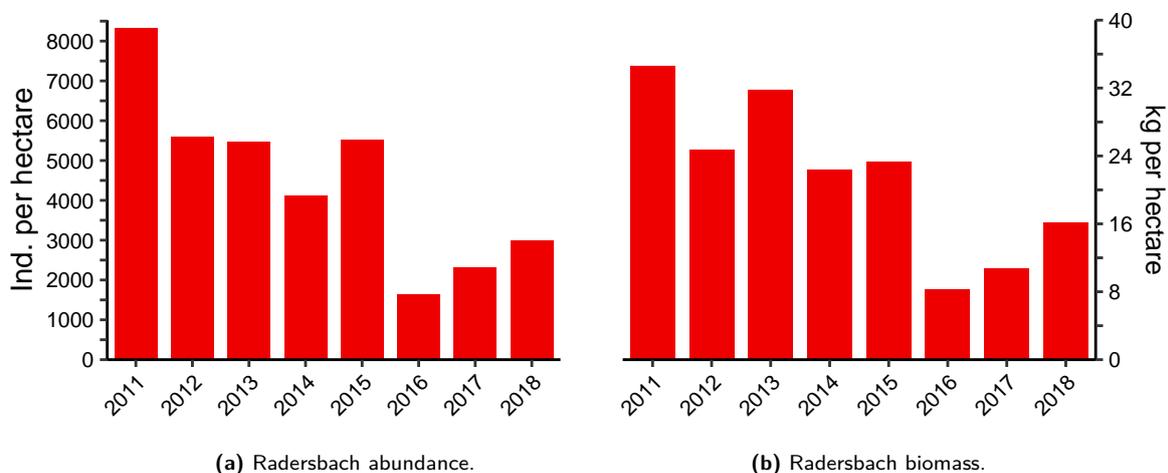
Figure 19. The abundance and biomass of the Radersbach exhibited similar changes between cohorts. The high abundance and low biomass were indicative of a population that was predominantly juveniles.

Urgersbach

The Urgersbach also exhibited overall declines in both abundance and biomass during the study period (Fig. 20). Abundance of the 2011 survey was just under 7000 Ind. ha^{-1}, with a biomass of 133.2 kg ha^{-1}. As the 2011 population was well distributed across age-classes, the high number of 1+ and 2+ individuals made considerable contributions to the biomass. The 2013 survey reported the second lowest abundance (1531 Ind. ha^{-1}) but the second highest biomass (97.4 kg ha^{-1}), indicating a smaller population of substantially larger fish. The 2014 survey had a high abundance

of juveniles, however the presence of a small number of 2+ fish increased the biomass of the population. Age structure of the 2015 and 2018 populations showed a low share of juveniles, which corresponded with a much lower abundance and slightly lower biomass. The years with large decreases in abundance, but small decreases in biomass are indicative of a lack of YOY fish due to poor reproductive success. The changes in the population structure of the Urgersbach indicated that the presence of juveniles considerably affected abundance, but did not substantially influence biomass.

(a) Urgersbach abundance. (b) Urgersbach biomass.
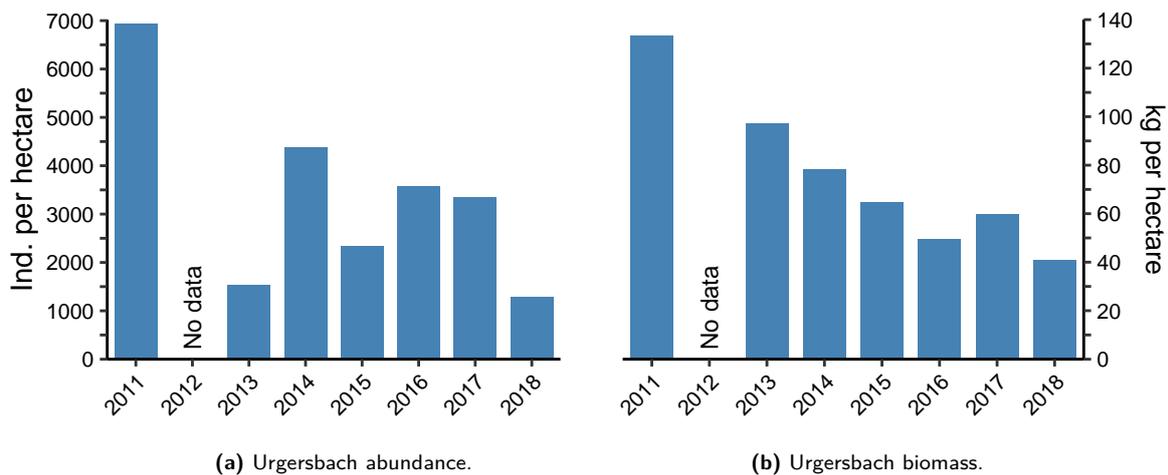
Figure 20. The abundance and biomass of the Urgersbach have been steadily decreasing since 2011. The high abundance suggested a population of juveniles, while the biomass indicated there were also adult fish within the population.

Zellenbach

Like the other sites, the Zellenbach had a high abundance and biomass in 2011. There were no recognizable links between the two values upon examination of the other survey results (Fig. 21). This suggested a dynamic population structure that experienced regular annual fluctuations. High abundance levels indicated that many YOY fish were present in the samples, suggesting successful reproduction. Likewise, biomass was consistently above $25 \, \text{kg} \, \text{ha}^{-1}$, which implied the presence of larger adults within the Zellenbach.

(a) Zellenbach abundance. (b) Zellenbach biomass.
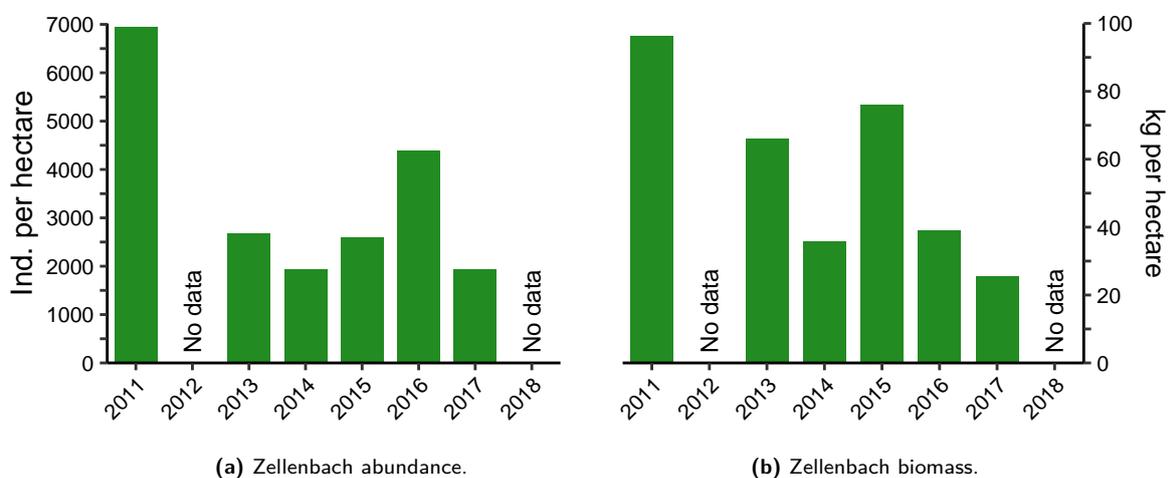
Figure 21. The observed abundance and biomass of the Zellenbach represented a fluctuating population that included both juvenile and adult fish.

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Comparative analysis

The Radersbach had the highest long-term average abundance of the investigation sites. Mean annual abundance of the Radersbach was 4500 Ind. ha^{-1}, while the Urgersbach and Zellenbach were both just under 3500 Ind. ha^{-1} (Fig. 22). The abundance levels of the sites fluctuated throughout the study period, and no single site had the consistently highest abundance. High abundance levels were associated with YOY fish within the investigation sites, which indicated spawning and recruitment were occurring within the streams. Abundance in all three sites had decreased over the duration of the study period.
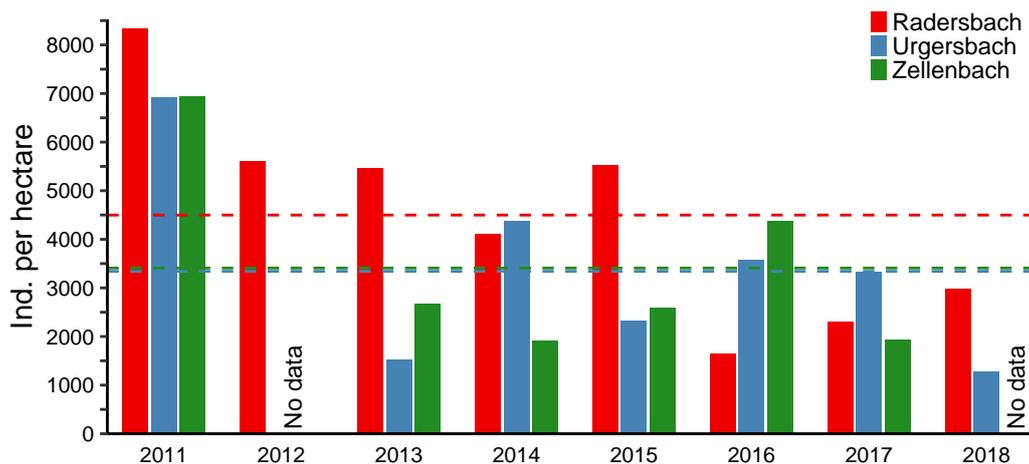
Figure 22. Abundance decreased in all three sites during the study period. The Radersbach had the highest average abundance, while the abundance of the Urgersbach and Zellenbach were similar.

Although the Radersbach routinely had the highest abundance, the biomass was considerably lower than the other sites (Fig. 23). The mean annual biomass of the Radersbach was 21.4 kg ha^{-1}, which was in contrast with the Zellenbach (56.3 kg ha^{-1}) and Urgersbach (74.8 kg ha^{-1}). The higher biomass values suggested the presence of adult fish. Similar to abundance, the biomass of all three sites showed an overall decrease during the study.
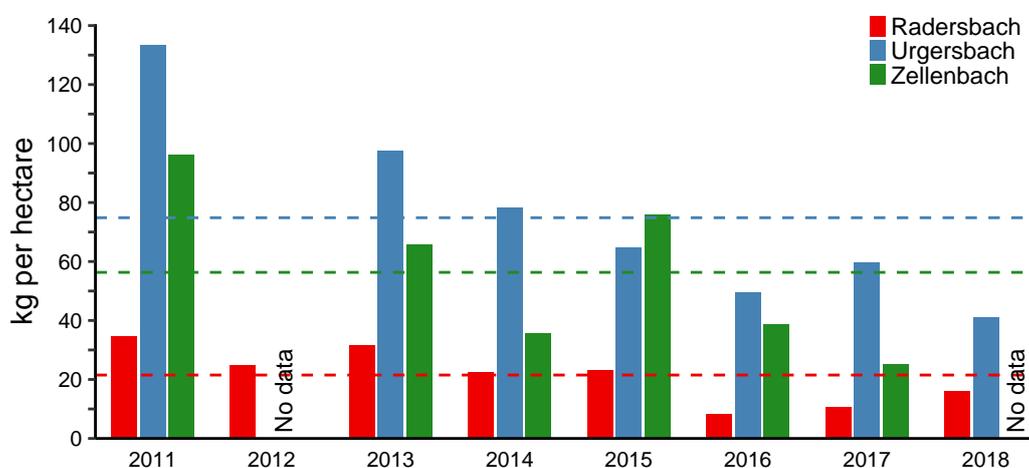
Figure 23. The biomass of the investigations sites varied greatly. Mean annual biomass is indicated by the dashed lines. The biomass of the Radersbach was considerably less than the other sites.

When comparing the abundance and biomass of the investigation sites, it was readily apparent that the Radersbach contained a substantially younger population. The Radersbach had a high abundance with low biomass, which indicated a population comprised mostly of juvenile fish. The Urgersbach had the lowest mean abundance, but the highest mean biomass. This implied the Urgersbach was host to a juvenile population that included many 1+ and 2+ fish, which was reinforced by length frequency diagrams (see Fig. 16). The Zellenbach also supported a population of both adults and juveniles, evident from the high abundance and biomass values. However, the samples taken in the Zellenbach were not representative of the entire length.

5.5   Population dynamics

Age-class specific analysis identified the demographic shifts within the cohorts. Dividing the annual stock assessments into age-classes allowed for the recruitment and production of the cohorts to be calculated. The following tables illustrate the recruitment and production values of the different age-classes sampled during the assessments. The rows are associated with the age-classes, while the columns pertain to the annual electrofishing surveys that were conducted in autumn. Reading the row values from left to right show the changes in each age-class from one survey to the next. The columns encompass the population data captured during each stock assessment, displaying the population age structure of a given year. The bottom row of the table shows the total abundance or biomass, with the superscript value being the net change from the previous year.

The tables are also able to track the annual changes experienced by the individual cohorts. The population dynamics of a given cohort can be followed by reading the table diagonally from the upper left to lower right. Reading the tables in this way shows the fluctuations in abundance and biomass of a specific cohort. The cohorts are delineated by the alternating shaded bands. Each cell within a table contains a large number, which is the data obtained from the annual stock assessment indicated by the column heading. The superscript value is the change that had occurred since the prior assessment. A negative value indicates a loss of abundance or biomass caused by mortality or emigration. Analysis of the shaded cohort bands provided insight into the demographic differences between cohorts.

Radersbach

The annual abundance and recruitment of the Radersbach is recorded in Table 12. Starting with the 2011 assessment, there were 7877 new recruits per hectare of the 2011 cohort. There were also 456 fish of the 1+ age-class per hectare present. By the 2012 survey, 7557 Ind. ha^{-1} of the 2011 cohort had either died or emigrated, as only 320 Ind. ha^{-1} of 1+ fish were found. This represented a decrease of 95.9% of the juvenile population. Of the 456 individuals of 1+ fish sampled in 2011, all had vacated the Radersbach by the 2012 survey as no 2+ fish were sampled. The last row of the table shows that there was a decrease in total abundance of 2725 Ind. ha^{-1} between the 2011 and 2012 population surveys.

The 2012 cohort started with an abundance of 5288 Ind. ha^{-1}, which fell to 462 Ind. ha^{-1} by the 2013 survey. This indicated a 91.3% decrease in cohort population between assessments. The 2012 cohort had entirely vanished from the investigation site by the 2014 survey. This pattern of all fish disappearing before reaching the 2+ age-class could be observed throughout all of the cohorts. The 2015 cohort exhibited the largest decrease of juveniles (98.9%) falling from 5444 to 60 Ind. ha^{-1} between consecutive surveys. The number of new recruits sampled which survived until the following survey ranged from 1.1% to 8.9%. Based on these observations it was evident that as fish aged and grew larger, they left the Radersbach through death or emigration. The Radersbach differed from the other investigation sites in that no 2+ age-class fish were sampled during any of the stock assessments.

Table 12. Radersbach abundance and recruitment (Ind. ha^{-1}) of brown trout. Changes in cohort abundance (superscript figures) between assessments indicate losses due to death or emigration. Recruitment was calculated as abundance of the 0+ age-class.

Size class	Age-class	2011	2012	2013	2014	2015	2016	2017	2018
< 110 mm	0+	$7{,}877^{+7877}$	$5{,}288^{+5288}$	$5{,}000^{+5000}$	$3{,}806^{+3806}$	$5{,}444^{+5444}$	$1{,}590^{+1590}$	$2{,}171^{+2171}$	$2{,}852^{+2852}$
110 - 210 mm	1+	456	320^{-7557}	462^{-4826}	303^{-4697}	90^{-3716}	60^{-5384}	141^{-1449}	131^{-2040}
> 210 mm	2+	0	0^{-456}	0^{-320}	0^{-462}	0^{-303}	0^{-90}	0^{-60}	0^{-141}
Total$^{\text{Total net recruitment}}$		8,333	$5{,}608^{-2725}$	$5{,}462^{-146}$	$4{,}109^{-1353}$	$5{,}534^{+1425}$	$1{,}650^{-3884}$	$2{,}312^{+662}$	$2{,}983^{+671}$

The biomass observed in the Radersbach did not exceed 35 kg ha^{-1} during any of the annual population assessments (Table 13). The mean fish weight of the cohort age-classes could be obtained by dividing the biomass by abundance. The 0+ age-class had a mean fish weight of 3.66 g for the entire study period. The 2011 cohort had the lowest mean weight of 3.03 g per individual in the 0+ age-class. The 2018 cohort had the highest mean YOY fish weight of 4.59 g. Biomass of juvenile fish increases as they grow and mature. The biomass of the 1+ age-class ranged from 1.2 – 13.5 kg ha^{-1}, which coincided with the 1+ abundance levels. The lowest mean weight of 1+ fish (17.4 g) was found in the 2014 cohort, while the highest (29.2 g) was found in the 2012 cohort. The 1+ age-class had a mean fish weight of 24.1 g for the entire study period.

The biomass of the age-classes and cohorts fluctuated throughout the study. The last row of the table displays total annual biomass and net production levels of each annual survey. The mean net production was −2.6 kg ha^{-1} which corresponded with the overall decrease in biomass that was observed.

Table 13. Radersbach biomass and production (kg ha^{-1}) of brown trout. Cohort production (superscript figures) between annual assessments was calculated as the increment of biomass for the respective cohort and age-classes.

Size class	Age-class	2011	2012	2013	2014	2015	2016	2017	2018
< 110 mm	0+	$23.9^{+23.9}$	$16.8^{+16.8}$	$18.2^{+18.2}$	$16.3^{+16.3}$	$21.8^{+21.8}$	$7.0^{+7.0}$	$7.5^{+7.5}$	$13.1^{+13.1}$
110 - 210 mm	1+	10.7	$8.0^{-15.9}$	$13.5^{-3.3}$	$6.1^{-12.1}$	$1.6^{-14.7}$	$1.2^{-20.6}$	$3.3^{-3.7}$	$3.0^{-4.5}$
> 210 mm	2+	0.0	$0.0^{-10.7}$	$0.0^{-8.0}$	$0.0^{-13.5}$	$0.0^{-6.1}$	$0.0^{-1.6}$	$0.0^{-1.2}$	$0.0^{-3.3}$
Total$^{\text{Total net production}}$		34.6	$24.8^{-9.8}$	$31.7^{+6.9}$	$22.4^{-9.3}$	$23.4^{+1.0}$	$8.2^{-15.2}$	$10.8^{+2.6}$	$16.1^{+5.3}$

Urgersbach

The Urgersbach supported populations with individuals in the 2+ age-class. This made it possible to track changes the cohorts had experienced over the course of three stock assessments (Table 14). Only the $2013-2016$ cohorts had complete profiles as a stock assessment was not performed in 2012 and the study ended before the 2017 and 2018 cohorts reached the 2+ age-class. The highest recruitment was found in the 2011 cohort (4267 Ind. ha^{-1}). Recruitment of the 2013 and 2018 cohorts were significantly lower than the others (214 and 616 Ind. ha^{-1} respectively). The number of 1+ fish ranged from a high of 2415 per hectare in the 2011 assessment to a low of 377 in 2014. The number of individuals within the cohorts decreased overtime, however the 2013 cohort was unique in that the number of fish increased from 2013 to 2014 by 163 individuals per hectare. Fish belonging to the 2016 cohort left the system before reaching the 2+ age-class as indicated by the 0 Ind. ha^{-1} abundance 2+ fish in the 2018 assessment.

Table 14. Urgersbach abundance and recruitment (Ind. ha^{-1}) of brown trout. The superscript figures represent changes in cohort abundance between annual population assessments. Recruitment was calculated as abundance of 0+ fish.

Size class	Age-class	2011	2012	2013	2014	2015	2016	2017	2018
< 110 mm	0+	$4{,}267^{+4267}$	-	214^{+214}	$3{,}789^{+3789}$	979^{+979}	$2{,}828^{+2828}$	$2{,}655^{+2655}$	616^{+616}
110 - 210 mm	1+	$2{,}415$	-	$1{,}018$	377^{+163}	$1{,}305^{-2484}$	705^{-274}	634^{-2194}	672^{-1983}
> 210 mm	2+	247	-	300	215^{-803}	47^{-330}	50^{-1255}	55^{-650}	0^{-634}
Total $^{\text{Total net recruitment}}$		$6{,}929$	-	$1{,}532$	$4{,}381^{+3149}$	$2{,}331^{-1835}$	$3{,}583^{+1299}$	$3{,}344^{-189}$	$1{,}288^{-2001}$

The majority of biomass in the Urgersbach was associated with 1+ fish (Table 15). The largest increase of biomass attributed to new recruits was the 2014 cohort, which introduced 29 kg into the system. The 2014 cohort also exhibited the highest gain of biomass between assessments, gaining 21 kg between the 2014 and 2015 surveys. The largest recorded loss of biomass (-43.2 kg) occurred as the 2014 cohort shifted from the 1+ to 2+ age-class. Other cohorts experienced a similar pattern in biomass fluctuations, which consisted of a gain as the fish increased in size from juveniles to adults, and then a large decline as the fish left the system through death or emigration. The large losses of biomass were likely due to the largest fish migrating out of the Urgersbach in search of habitat more suitable for larger individuals. Of the five surveys in which net production was able to be calculated, only three (2014, 2015 and 2017) showed positive net production.

Table 15. Urgersbach biomass and production (kg ha^{-1}) of brown trout. The superscript figures represent annual production of cohorts and was calculated as the yearly increment of biomass for the respective age-classes.

Size class	Age-class	2011	2012	2013	2014	2015	2016	2017	2018
< 110 mm	0+	$21.3^{+21.3}$	-	$1.4^{+1.4}$	$29.0^{+29.0}$	$6.6^{+6.6}$	$20.0^{+20.0}$	$21.8^{+21.8}$	$5.4^{+5.4}$
110 - 210 mm	1+	82.8	-	53.0	$17.2^{+15.8}$	$50.0^{+21.0}$	$22.9^{+16.3}$	$32.3^{+12.3}$	$35.6^{+13.8}$
> 210 mm	2+	29.2	-	43.1	$32.1^{-20.9}$	$8.0^{-9.2}$	$6.8^{-43.2}$	$5.6^{-17.3}$	$0.0^{-32.3}$
Total $^{\text{Total net production}}$		133.3	-	97.5	$78.3^{+23.9}$	$64.6^{+18.4}$	$49.7^{-6.9}$	$59.7^{+16.8}$	$41.0^{-13.1}$

Zellenbach

Similar to the other sites, the 2011 cohort had the highest recorded recruitment. As seen in Table 16, the 2014 cohort had an increase of 267 Ind. ha^{-1} from the 2014 to 2015 survey, while every other cohort decreased in abundance as they transitioned from 0+ to 1+. There were no 2+ fish found from the 2012 or 2015 cohorts. The missing stock assessments of the Zellenbach made calculating population dynamics problematic as only the 2013, 2014 and 2015 cohorts could have their population dynamics tracked through adulthood. The limited assessments and single sample stretch of the Zellenbach produced recruitment levels unlikely to be representative of the entire river length.

Table 16. Zellenbach abundance and recruitment (Ind. ha^{-1}) of brown trout. The superscript figures represent changes in cohort abundance between annual population assessments. Recruitment was calculated as abundance of 0+ fish.

Size class	Age-class	2011	2012	2013	2014	2015	2016	2017	2018
< 110 mm	0+	$5{,}459^{+5459}$	-	$1{,}015^{+1015}$	$1{,}256^{+1256}$	896^{+896}	$4{,}152^{+4152}$	$1{,}366^{+1366}$	-
110 - 210 mm	1+	$1{,}326$	-	$1{,}595$	665^{-350}	$1{,}523^{+267}$	154^{-742}	562^{-3590}	-
> 210 mm	2+	156	-	72	0^{-1595}	179^{-486}	77^{-1446}	0^{-154}	-
Total $^{\text{Total net recruitment}}$		$6{,}941$	-	$2{,}682$	$1{,}921^{-689}$	$2{,}598^{+677}$	$4{,}383^{+1964}$	$1{,}928^{-2378}$	-

The Zellenbach displayed a large range of biomass between the cohorts and age-classes (Table 17). The largest recorded biomass of a single age-class was 52 kg ha^{-1}, belonging to the 1+ fish of the 2012 cohort, which was recorded during the 2013 assessment. That entire cohort was absent from the 2014 assessment the following year. The largest increase of cohort biomass was the transition from 0+ to 1+ of the 2014 cohort, which increased by 40.6 kg ha^{-1}. This increase coincided with an uncharacteristic increase of abundance. The 2012 and 2015 cohorts were lacking observations of individuals that reached the 2+ age-class. Similar to the abundance levels, the reported biomass is unlikely to be representative of the entire Zellenbach. The large variance in biomass could be attributed to the calculations being based on a single sample site.

Table 17. Zellenbach biomass and production (kg ha^{-1}) of brown trout. The superscript figures represent annual production of cohorts and was calculated as the yearly increment of biomass for the respective age-classes.

Size class	Age-class	2011	2012	2013	2014	2015	2016	2017	2018
< 110 mm	0+	$30.3^{+30.3}$	-	$6.4^{+6.4}$	$7.7^{+7.7}$	$6.6^{+6.6}$	$27.3^{+27.3}$	$8.8^{+8.8}$	-
110 - 210 mm	1+	45.0	-	52.0	$27.9^{+21.5}$	$48.3^{+40.6}$	$2.5^{-4.1}$	$16.5^{-10.8}$	-
> 210 mm	2+	21.0	-	7.5	$0.0^{-52.0}$	$21.0^{-6.9}$	$9.0^{-39.3}$	$0.0^{-2.5}$	-
Total $^{\text{Total net production}}$		96.3	-	65.9	$35.6^{-22.8}$	$75.9^{+40.3}$	$38.8^{-16.1}$	$25.3^{-4.5}$	-

To evaluate recruitment variability, uniform distribution was tested in each study site. Z-scores were calculated by subtracting mean recruitment from cohort recruitment and then dividing by the standard deviation of recruitment observations (Table 18). The p-values were calculated from the Z-scores to identify any cohorts which were significantly different from the expected recruitment. No significant differences were found in the cohorts from any of the sample sites. The low number of samples reduced the ability of the test to identify cohorts which deviated from the expected recruitment.

Table 18. Test for uniform distribution of annual recruitment in the study sites from 2011–2018. Cohorts were not significantly different from the observed annual variability in recruitment.

	Radersbach		Urgersbach		Zellenbach	
Year	Z	p	Z	p	Z	p
2011	1.757	0.079	1.297	0.195	1.592	0.111
2012	0.501	0.616	-	-	-	-
2013	0.362	0.717	-1.238	0.216	-0.689	0.491
2014	-0.217	0.828	0.998	0.318	-0.565	0.572
2015	0.577	0.564	-0.759	0.448	-0.750	0.453
2016	-1.291	0.197	0.398	0.691	0.922	0.357
2017	-1.010	0.312	0.289	0.773	-0.509	0.611
2018	-0.679	0.497	-0.986	0.324	-	-

Test statistic: $Z = (\text{observed} - \text{expected})/\sqrt{\text{variance}}$

The YOY biomass of each cohort was also tested for uniform distribution (Table 19). Biomass of the 0+ fish in each cohort was compared to the expected YOY biomass. No statistically different cohorts were found within the data set. Like recruitment, the low sample number reduced the power of the test statistics.

Table 19. Test for uniform distribution of YOY biomass in the study sites from 2011–2018. Recruit biomass was not significantly different from the observed annual variability.

	Radersbach		Urgersbach		Zellenbach	
Year	Z	p	Z	p	Z	p
2011	1.362	0.173	0.600	0.549	1.417	0.156
2012	0.203	0.839	-	-	-	-
2013	0.435	0.664	-1.309	0.191	-0.734	0.463
2014	0.112	0.911	1.333	0.183	-0.610	0.542
2015	1.016	0.310	-0.811	0.417	-0.708	0.479
2016	-1.397	0.162	0.469	0.639	1.148	0.251
2017	-1.324	0.186	0.644	0.520	-0.513	0.608
2018	-0.407	0.684	-0.926	0.354	-	-

Test statistic: $Z = (\text{observed} - \text{expected})/\sqrt{\text{variance}}$

The results of the uniform distribution tests indicated that, although both abundance and biomass of the 0+ age-class varied over the study period, this variance was not statistically significant. The differences between YOY recruitment were within the expected variance. A larger data set containing more annual recruitment observations of the rivers would most likely reduce the variance and provide a better understanding of the natural YOY fluctuations.

The Z-scores of recruitment and YOY biomass from the $2016-2018$ cohorts in the Radersbach were negative, which was in line with the Radersbach total abundance and biomass results found in Fig. 19. The overall decline of the Radersbach population could possibly be explained by this reduction in recruitment. These findings further supported the observations which were discussed in the previous section.

5.6   Temperature influence on spawning activity

5.6.1   Redd density

The Radersbach showed a strong negative correlation between mean summer temperature and redd density with a Spearman's correlation coefficient of -0.80 (Fig. 24). The p-value of 0.014 indicated significance, though the small sample size reduced the power of the test. The 2014 and 2019 cohorts were outside the significance band of the regression analysis with lower than expected values, while the 2012 had slightly higher than expected.
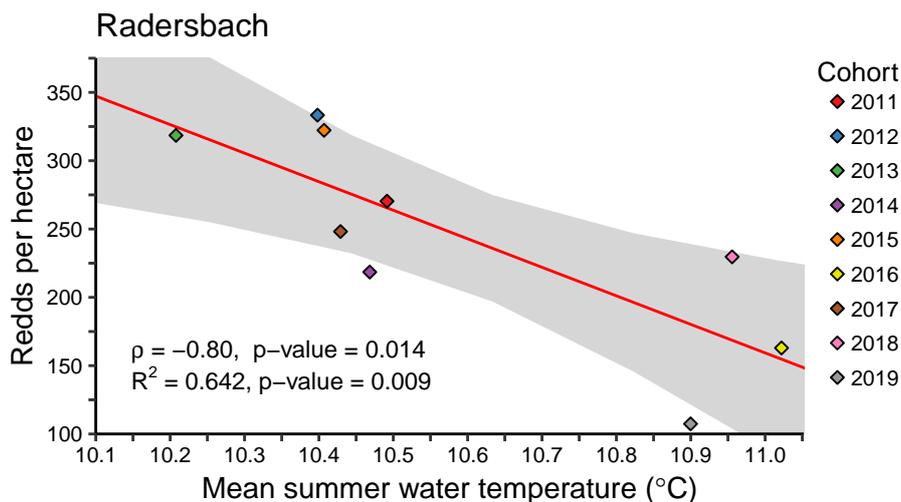
Figure 24. Correlation between the mean summer temperature and redd density in the Radersbach. A significant negative correlation was identified.

Like the Radersbach, there was also a strong negative correlation ($\rho = -0.68$) between mean summer temperature and redd density in the Urgersbach (Fig. 25). With only 9 samples available for testing, the correlation was determined to be non-significant with a p-value of 0.0503. The 2014 cohort had a redd density outside the confidence interval of the linear regression.
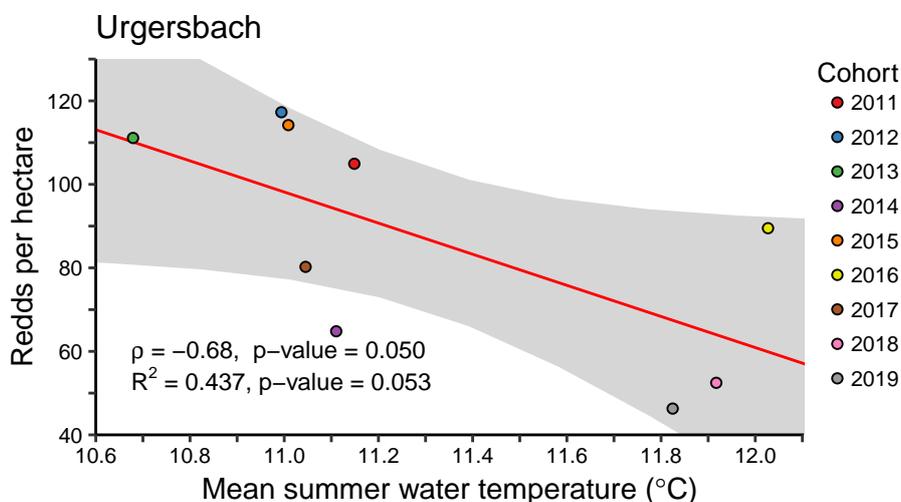
**Figure 25.** Correlation between the mean summer temperature and redd density in the Urgersbach. The negative correlation had a p-value of 0.0503.

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The Zellenbach had very weak negative correlation between mean summer temperature and redd density, which was not significant (Fig. 26). The limited number of samples reduced the testing power of the Spearman's correlation. The 2016 cohort contained both the highest temperature and highest redd density, which had a large impact on the results. Furthermore, the redd density of the 2018 cohort was substantially lower than the other cohorts.
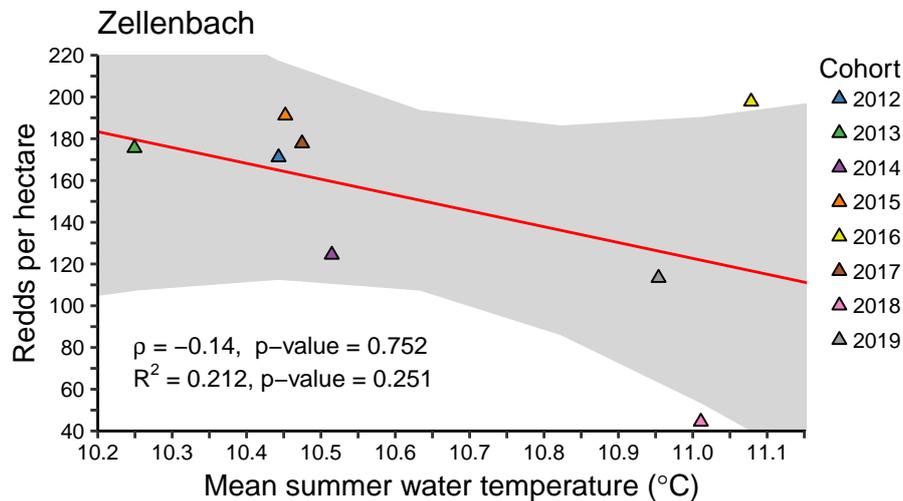
Figure 26. Correlation of the mean summer temperature and redd density in the Zellenbach. There was statistically insignificant negative correlation.

A correlation analysis was also performed on the joint data of the investigation sites. The redd density Z-scores and mean summer temperatures of the investigations sites were pooled and tested with Spearman's correlation. The joint analysis showed negative correlation between redd density and summer temperature (Fig. 27). The correlation ($\rho = -0.43$) was significant with a p-value of 0.029. It should be noted that many of the observations fell outside of the confidence band of the linear regression.
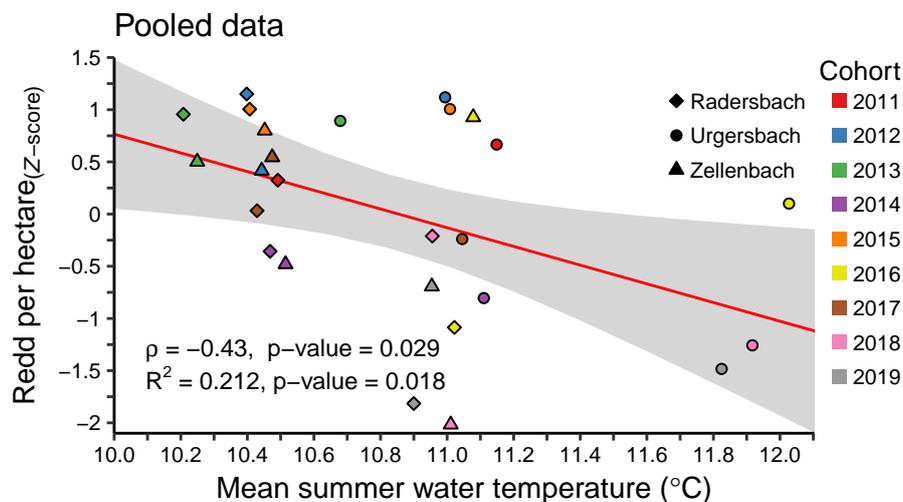
**Figure 27.** Correlation of the mean summer temperatures and the pooled redd densities of the investigation sites. The negative correlation between redd density and summer temperature was statistically significant.

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Linear regression models were developed using redd density as the dependent variable with mean summer water temperature as the independent variable. As with the correlation analyses, the regression models also showed that redd density decreased as temperature increased. The Radersbach regression was the best fitting model with the highest R^2 of 0.642. The Urgersbach model fit the observations with R^2 of 0.437. The other two regression models did not fit the data nearly as well. Models of both the Zellenbach and pooled-data were ill-fitting with R^2 values of only 0.212.

5.6.2 Timing of spawning activity

Temperature did not appear to have any influence on the timing of spawning activity in the trout population. There were no significant relationships between mean summer temperature and the timing parameters. The onset, midpoint and endpoint of spawning activity was fairly consistent between cohorts and among the investigation sites. There were some slight variations in duration of spawning activity, however these differences were not statistically significant.

The timing of spawning activity in the Radersbach did not appear to be heavily influenced by mean summer water temperature (Fig. 28). The onset of spawning in the Radersbach occurred within a 10-day window regardless of temperature. There was slightly more variation in the mid and endpoints of spawning activity, but they were not correlated with temperature. Duration of spawning activity was also found to be uncorrelated with summer temperature and remained consistent across the study period.
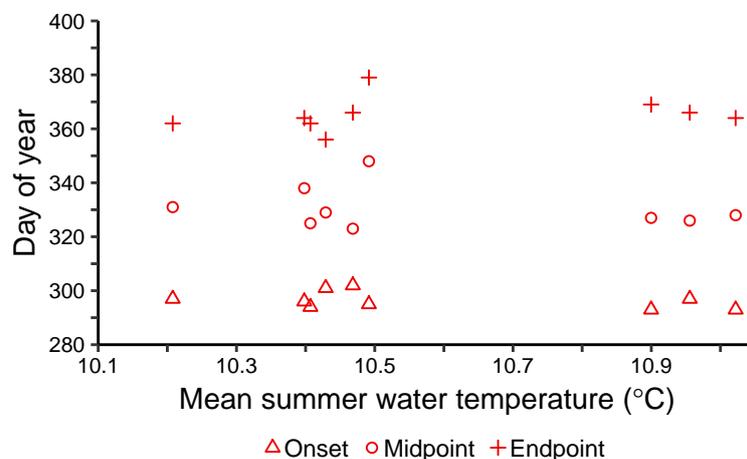
Figure 28. Radersbach temperature and timing of spawning activity. There were no significant correlations between temperature and time of spawning activity.

The timing parameters of spawning activity in the Urgersbach were more varied than those of the Radersbach (Fig. 29). There was negative correlation between mean summer water temperature and the duration of spawning activity which occurred at a non-significant level. The onset, midpoint and endpoint of spawning activity were not correlated with summer temperatures. Spawning activity in years with higher temperatures did not significantly deviate from the other years. Water temperature did not have an influential role in the timing of spawning activity in the Urgersbach.

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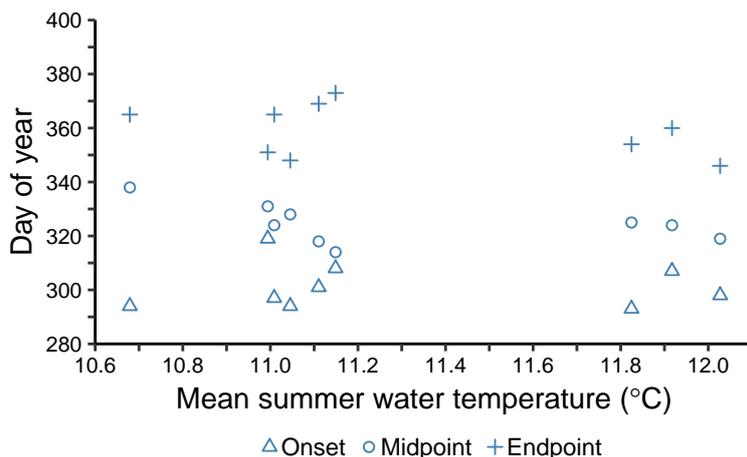
Figure 29. Urgersbach temperature and timing of spawning activity. Duration of spawning was negatively correlated with temperature at a non-significant level.

Mean summer temperature did not significantly influence the timing of spawning activity in the Zellenbach. No significant correlations were found between temperature and the onset, midpoint, endpoint or duration of spawning. Furthermore, the timing parameters of spawning activity remained consistent across the years despite variances in temperature (Fig. 30).
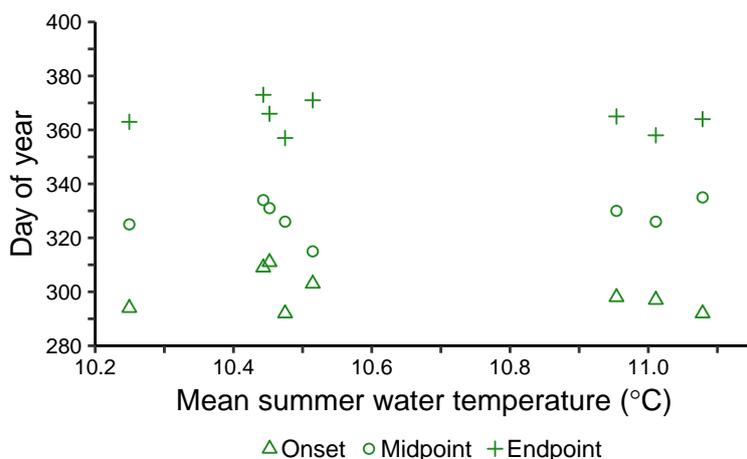
Figure 30. Zellenbach temperature and spawning activity timing. No correlations were found between temperature and time of spawning in the Zellenbach.

A plot of the pooled spawning parameters of the investigation sites is found in Fig. 31. It is evident that the Urgersbach experienced temperatures higher than the other sites. The onset of spawning activity began within a 20-day period in all three sites. The earliest midpoint occurred in the Urgersbach (314) and the latest in the Radersbach (348), providing a range of 34 days. The Urgersbach also had the earliest endpoint at 346 and the Radersbach the latest at 379, producing a range of 33 days. The Zellenbach had the longest duration of spawning activity, lasting 89 days. The Urgersbach had the shortest duration of just 39 days. Although the timing of spawning activity fluctuated between years and investigation sites, it did not appear to be directly related to the summer water temperature.
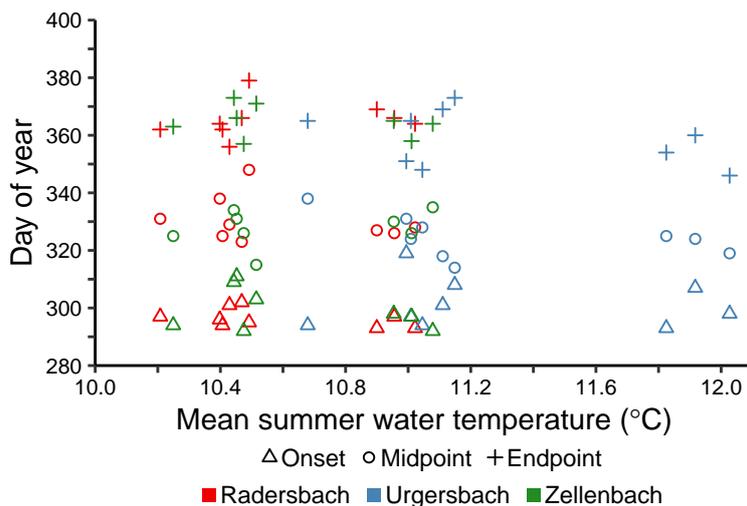
Figure 31. Pooled temperatures and timing of spawning activity. The data showed no discernible relationships between temperature and spawning times.

5.7 Spawning activity and recruitment

5.7.1 Redd density

The influence that redd density had on successful recruitment of juvenile trout was examined through correlation analysis. The highest redd densities and juvenile recruitment found in the study sites were observed in the Radersbach. Correlation between redd density and recruitment was identified in the Radersbach (Fig. 32). The Spearman's rank correlation coefficient of 0.74 and p-value of 0.046 indicated a strong positive correlation which was statistically significant.
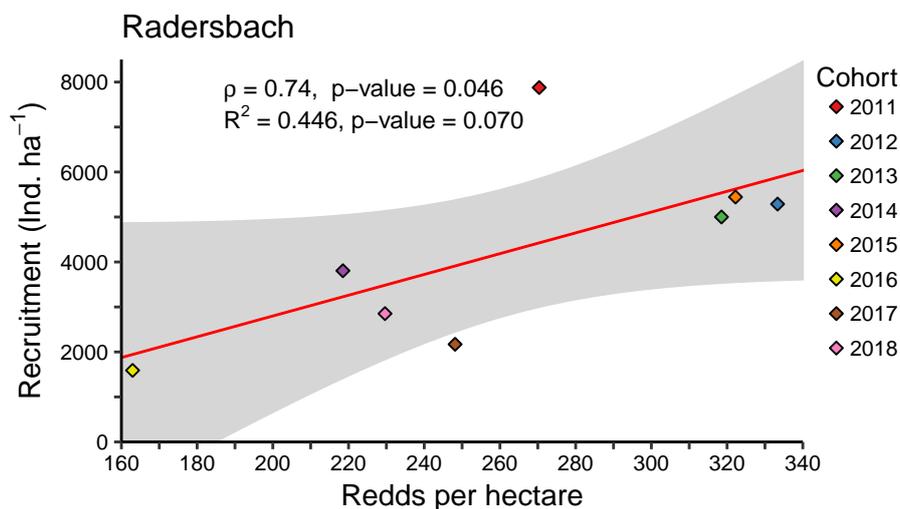
Figure 32. Redd density was positively correlated with population recruitment at a statistically significant level in the Radersbach.

The Urgersbach displayed weak correlation between redd density and population recruitment. The sporadic relationship between redd density and recruitment can be seen in Fig. 33. No clear pattern could be observed within the data set. The negative correlation was statistically insignificant with a p-value of 0.783.

44
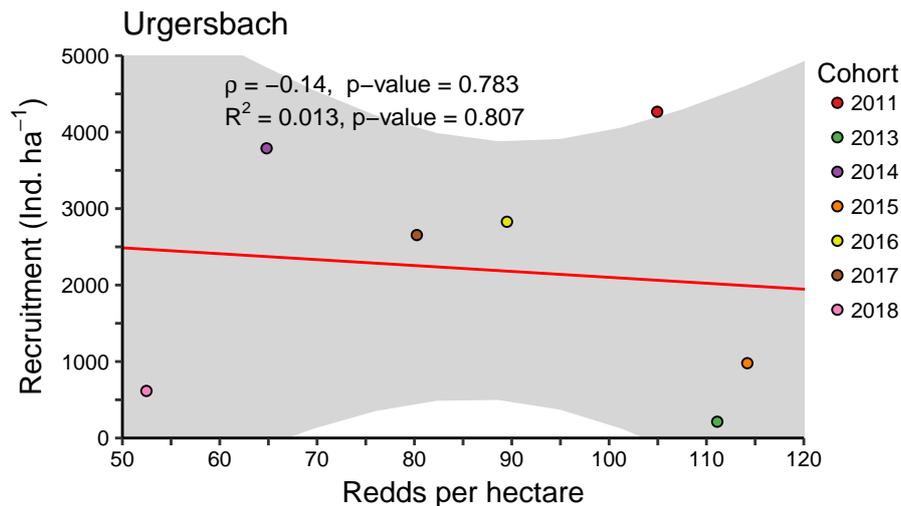
Figure 33. Redd density was not significantly correlated with recruitment in the Urgersbach.

Only five recruitment values were recorded for the Zellenbach (Fig. 34), greatly reducing the statistical power of the Spearman's correlation analysis. Like the Radersbach, a positive correlation was found between redd density and recruitment. However, this correlation was determined to be statistically insignificant (p-value = 0.683). The small sample size of the Zellenbach did not allow for critical analysis of the data.
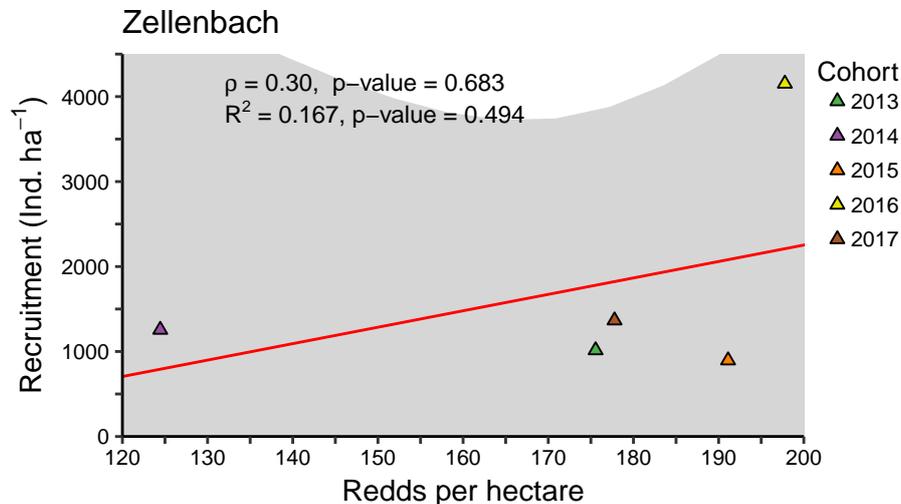
Figure 34. Redd density and recruitment showed a non-significant positive correlation in the Zellenbach.

Analysis of the pooled data from the three study sites revealed a positive correlation between redd density and recruitment (Fig. 35). From the graph, it can be seen that the highest redd densities and recruitment levels were found in the Radersbach. Conversely, the Urgersbach contained both the lowest redd densities and lowest recruitment numbers. The Zellenbach data points fell somewhere in between the observations recorded in the other study sites. The positive correlation ($\rho = 0.57$) was statistically significant, indicating a link between redd density and recruitment. Higher densities of spawning redds resulted in increased levels of recruitment.

45
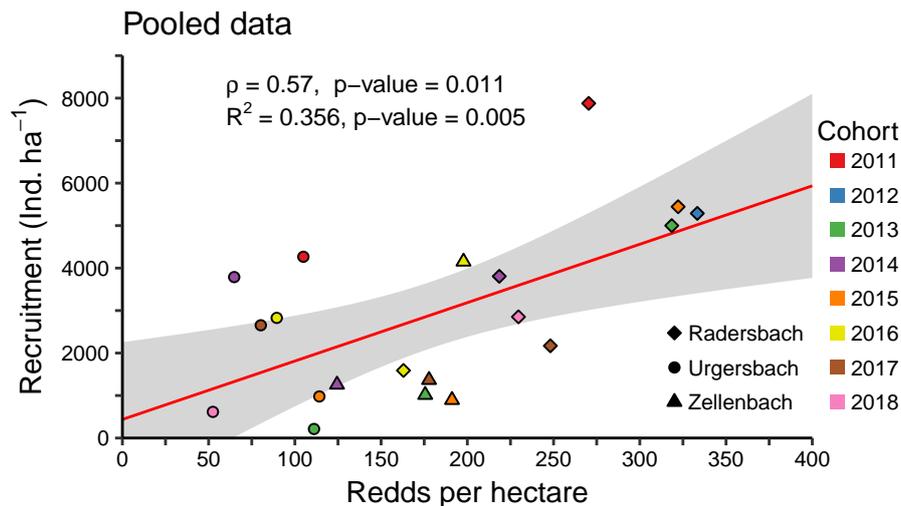
Figure 35. Statistically significant positive correlation was identified between redd density and recruitment in the pooled study site data.

Linear regression models, which used recruitment as the dependent variable and redd density as the regressor, were fit to the investigation site observations. The Radersbach was the best fitting model ($R^2 = 0.446$), however it was found to be statistically insignificant (p-value = 0.070). This was most likely due to the 2011 cohort, which was an outlier with higher than predicted recruitment. The Urgersbach model produced a very ill-fitting model with an R^2 of just 0.013. Similarly, the Zellenbach model was also a poor model, with a low R^2 value. The regression model of the pooled data fit the data nearly as well as the Radersbach with an R^2 of 0.356. The pooled data regression, unlike the Radersbach, was significant with a p-value of 0.005. The missing recruitment observations of the Urgersbach and Zellenbach greatly reduced the ability to determine if redd density had an impact on population recruitment in those rivers.

5.7.2 Timing of spawning activity

The spawning activity timing parameters established in section 4.2.3 were tested for possible influence on juvenile recruitment within the study sites. No significant statistical links were found between the onset of spawning and recruitment numbers. Furthermore, recruitment did not appear to be influenced by the other timing parameters. Although the study sites had similar spawning times, the recruitment levels between sites were quite different. This was possible due to different levels of sampling effort between the sites. Because of these discrepancies, joint data analyses of the study sites were not performed.

A diagram showing recruitment in relation to spawning activity allowed the annual cohorts in the Radersbach to be compared. (Fig. 36). The longest duration of spawning was found in the 2011 cohort. This cohort also had the highest recruitment of juveniles. The 2016 cohort had the earliest onset of spawning and the produced lowest recruitment numbers. Although no statistical links were identified through correlation analysis, some possible trends could be interpreted from the diagram of the Radersbach data. More observations may have made these trends more readily apparent.
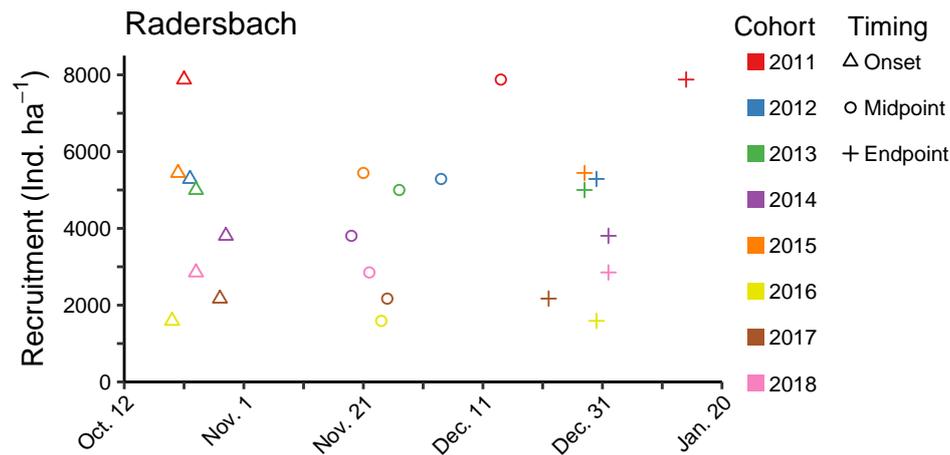
Figure 36. Spawning activity timing did not significantly affect recruitment in the Radersbach. The 2011 cohort had the highest recruitment and longest duration, however other cohorts did not follow a similar pattern.

A plot showing the spawning activity timing parameters and recruitment in the Urgersbach did not contain any visible indications of correlation. The data points were irregularly scattered throughout the graph (Fig. 37). No difference in recruitment was noticed in the 2016 and 2017 cohorts, which had earlier endpoints than other years. Statistical analysis of the data also failed to reveal any connections between the timing parameters of spawning activity and population recruitment.
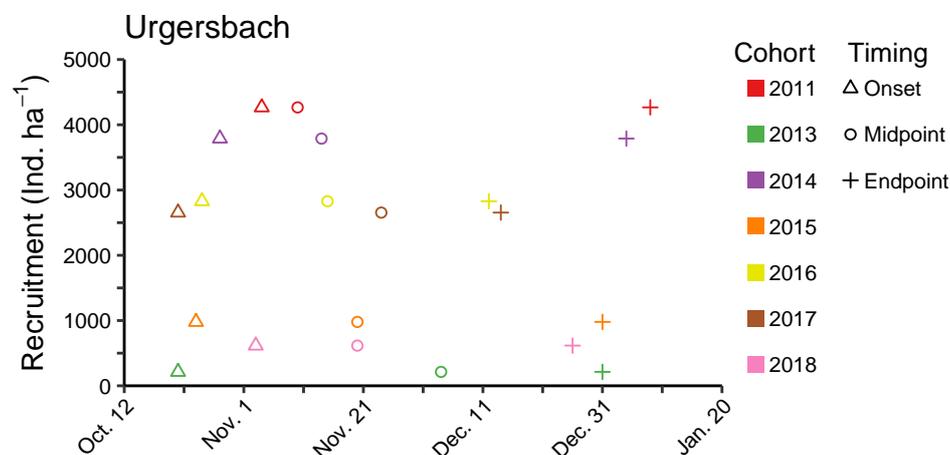
Figure 37. No clear patterns existed in the plot of Urgersbach recruitment and spawning activity. Correlation analysis also failed to find any links between the variables.

The recruitment levels of the Zellenbach were very similar despite differences in timing of spawning activity (Fig. 38). The 2016 cohort was an exception, as it exhibited much higher recruitment than other cohorts. This increased recruitment could not be linked to any of the timing variables, which were in line with the observations of other cohorts. As only 5 cohorts had both their spawning activity and recruitment observed, the omitted cohorts severely limited statistical analysis of the Zellenbach.
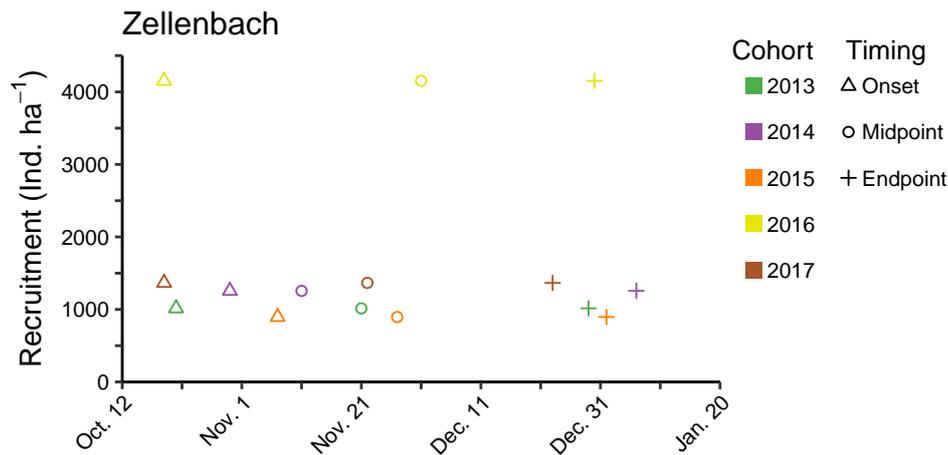
Figure 38. The 2016 cohort had substantially higher recruitment than the others. However, the limited observations reduced the likelihood of identifying any connections between spawning activity and recruitment.

5.8   Discharge and recruitment

Radersbach

Analysis of the relationship between discharge levels and Radersbach recruitment revealed few significant correlations (Table 20). However, spawning period discharge had highly positive correlation ($\rho = 0.69$) at a nearly significant level, suggesting that the discharge influenced recruitment. Recruitment was negatively correlated with maximum flows in September at a significant level ($\rho = -0.82$, p-value = 0.034). January discharge displayed a positive relationship which was very similar to spawning period discharge. February discharge, which occurs during the incubation period, had the opposite effect on recruitment.

Table 20. Correlation (Spearman's ρ) and simple linear regression between maximum discharge and recruitment in the Radersbach.

		Correlation		Linear regression			
		ρ	p	R^2	p	β_0	β_1
Life stage	Spawning	0.69	0.069	0.215	0.247	3,130	190.7
	Incubation	−0.60	0.132	0.310	0.152	5,847	−466.5
	Early-juvenile	−0.29	0.501	0.073	0.519	4,775	−79.9
	Juvenile	−0.61	0.167	0.342	0.168	6,672	−1,267.2
Month	October	−0.25	0.548	0.068	0.534	5,079	−636.6
	November	−0.40	0.327	0.039	0.637	4,628	−222.9
	December	0.07	0.882	0.037	0.650	3,511	474.9
	January	0.69	0.069	0.230	0.229	3,314	183.1
	February	−0.64	0.096	0.515*	0.045	6,329	−814.1
	March	−0.19	0.665	0.049	0.597	4,776	−187.2
	April	0.00	1.000	0.136	0.368	5,153	−530.6
	May	−0.24	0.582	0.007	0.848	4,361	−22.9
	June	−0.21	0.662	0.039	0.669	4,313	−303.3
	July	−0.39	0.396	0.177	0.348	4,428	−216.1
	August	−0.36	0.444	0.059	0.601	4,826	−629.3
	September	−0.82*	0.034	0.539	0.060	6,482	−1,302.3

The strong positive correlation between spawning period discharge and recruitment indicated that high discharge levels during the spawning season corresponded with increased recruitment levels. As shown in Fig. 39, the 2011 cohort was an outlier with higher than expected recruitment based on spawning period discharge. The correlation was not statistically significant, but cannot be discounted as the probability was still quite high (p-value = 0.069). January discharge (which occurs in the spawning period) exhibited a similar relationship.
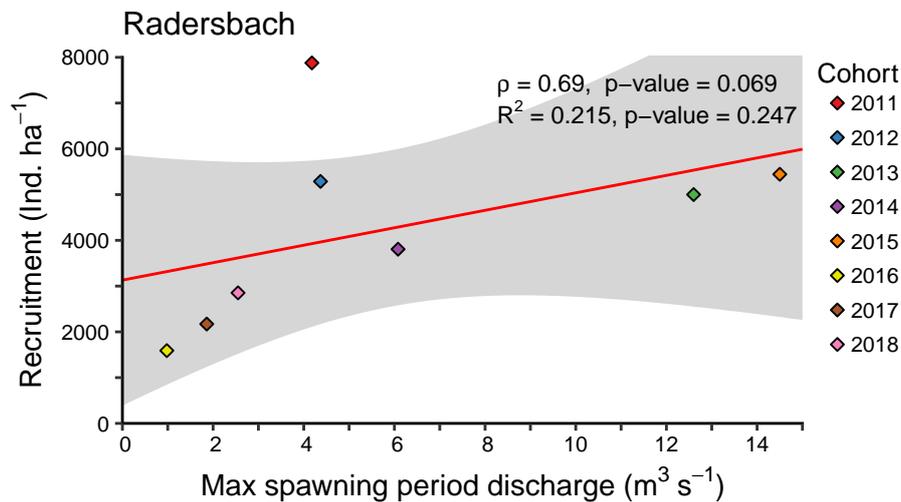
Figure 39. Correlation between maximum spawning period discharge and recruitment in the Radersbach. The positive correlation suggests that spawning period discharge has a beneficial effect on recruitment.

The correlation between maximum observed discharge during the incubation period and successful recruitment was negative. This was a fairly strong correlation (ρ = -0.60), but statistically insignificant. A linear regression model (Fig. 40) was able to explain one third of the variance in recruitment (R^2 of 0.310). This hinted that elevated discharge levels during the incubation period were detrimental to recruitment.
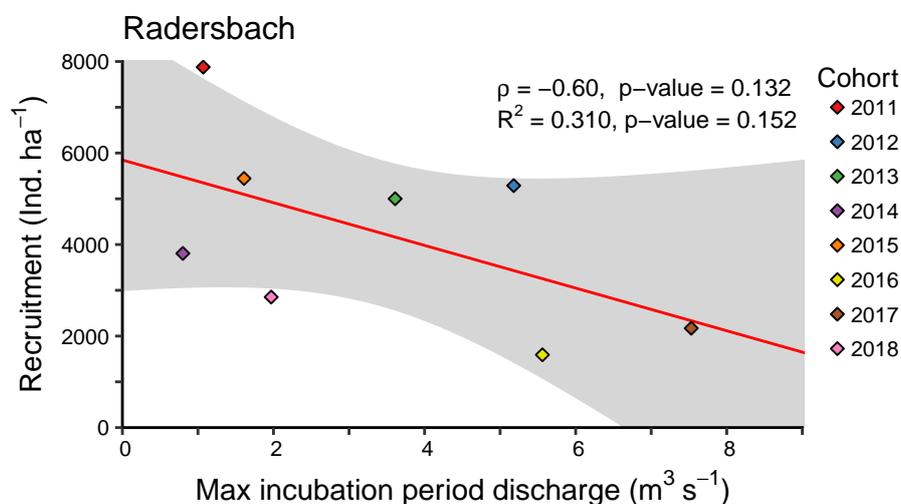
Figure 40. Correlation between maximum incubation period discharge and recruitment in the Radersbach. The negative correlation was indicative that high discharge in the incubation period reduced recruitment.

The relation between September discharge and Radersbach recruitment can be seen in Fig. 41. The strong negative correlation was significant, indicating that high flows in September reduced juvenile recruitment. The linear regression model fit the data with an R^2 of 0.539, but was insignificant with a p-value of 0.060. This suggested a negative linear relationship between September discharge and recruitment, however the discharge values were quite low.
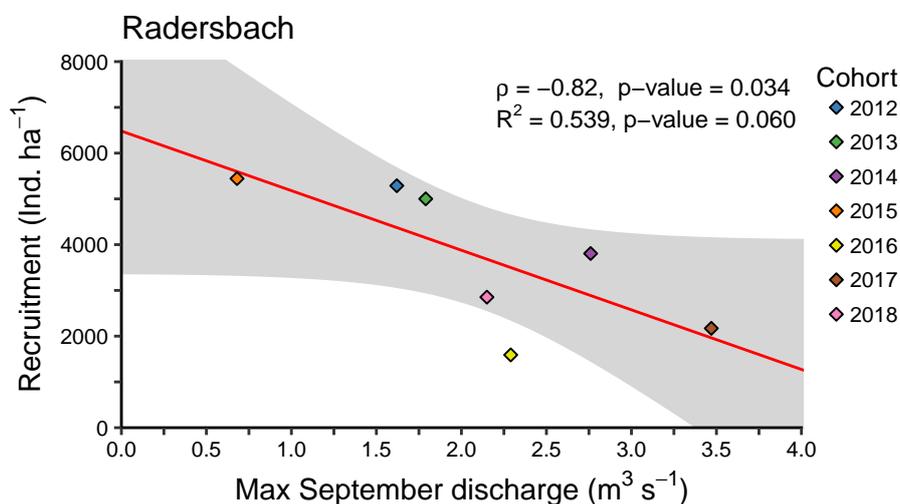
Figure 41. Correlation between maximum September discharge and recruitment in the Radersbach. The negative correlation was statistically significant, although the linear regression was insignificant.

February discharge was also found to be negatively correlated with Radersbach recruitment. The 2016 and 2017 cohorts had the lowest recruitment and experienced February discharge at more than 5 times the mean annual discharge of $0.95\,\mathrm{m^3\,s^{-1}}$ (Fig. 42). The negative correlation ($\rho = -0.64$) was statistically insignificant, but with a p-value of 0.096 it cannot be discounted entirely. This relationship indicated that increased February discharge is likely tied to decreases in successful trout recruitment.
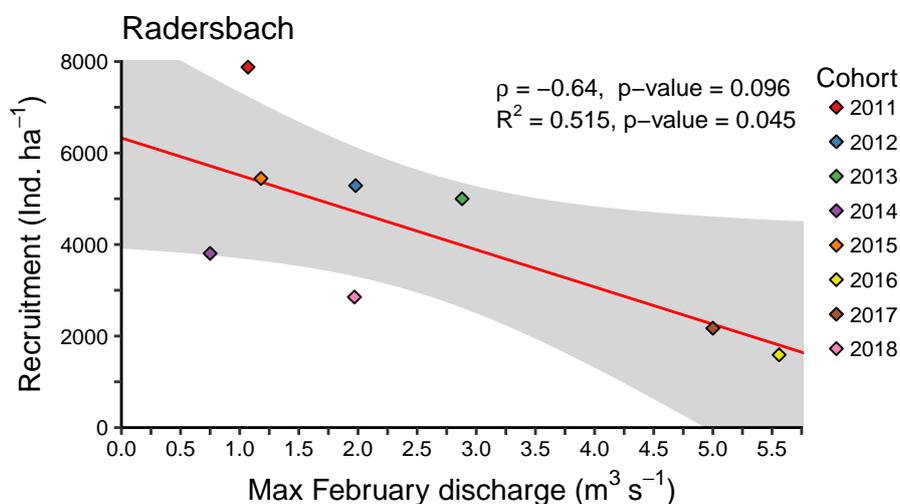

Figure 42. Relation between maximum February discharge and recruitment in the Radersbach. The negative correlation was statistically insignificant, while the linear regression was significant.

Urgersbach

No significant relationships between maximum discharge and recruitment were found in the Urgersbach (Table 21). The majority of the correlation coefficients showed that discharge was negatively correlated with recruitment. Exceptions were the July and September discharge as well as the discharge occurring in the early-juvenile and juvenile life stages. March discharge was negatively correlated ($\rho = -0.75$) with a p-value of 0.066, which was the strongest correlation found. Linear regression of March discharge revealed an R^2 of 0.028 (p-value = 0.721). This indicated that March discharge could not accurately predict recruitment. The other regression models were also statistically insignificant. Limited recruitment observations limited the sample size of the Urgersbach to only seven cohorts. The small sample of recruitment values may have contributed to the lack of findings.

Table 21. Correlation (Spearman's ρ) and linear regression between Urgersbach recruitment and maximum discharge of the life stages and months. No significant relationships were found.

| | | Correlation | | Linear regression | | | |
		ρ	p	R^2	p	β_0	β_1
Life stage	Spawning	−0.29	0.556	0.268	0.234	3,133	−154.0
	Incubation	−0.43	0.354	0.005	0.883	2,330	−43.6
	Early-juvenile	0.04	0.963	0.129	0.429	1,680	76.6
	Juvenile	0.37	0.497	0.207	0.364	−370	911.2
Month	October	−0.29	0.531	0.225	0.282	3,484	−911.5
	November	−0.21	0.662	0.090	0.514	1,729	250.3
	December	−0.14	0.783	0.055	0.612	3,030	−488.3
	January	−0.50	0.267	0.406	0.124	3,109	−174.9
	February	−0.39	0.396	0.003	0.912	2,305	−42.8
	March	−0.75	0.066	0.028	0.721	2,461	−109.7
	April	−0.64	0.139	0.017	0.782	2,436	−136.3
	May	−0.21	0.662	0.102	0.486	1,846	65.7
	June	−0.66	0.175	0.514	0.109	4,027	−1,043.9
	July	0.49	0.356	0.147	0.454	1,354	173.0
	August	−0.26	0.658	0.004	0.904	2,211	−192.5
	September	0.66	0.175	0.397	0.180	−262	963.1

Zellenbach

The Zellenbach had a sample size of six cohort recruitment values. No significant relationships between discharge and recruitment were identified through correlation analysis. The results of the correlation and regression tests can be found in Table 22. The correlation results were insignificant with the exception of spawning period discharge. There was very strong negative correlation ($\rho = -0.83$) between maximum discharge during the spawning period and recruitment which was nearly statistically significant (p-value = 0.058). This was in opposition to the relationship found in the Radersbach. The Zellenbach had the smallest sample size of the study sites. The statistical power of the correlation analyses was significantly reduced as a result.

Table 22. Correlation and simple linear regression with Zellenbach recruitment as the dependent variable and maximum discharge. Regression of July discharge was identified as significant.

		Correlation		Linear regression			
		ρ	p	R^2	p	β_0	β_1
Life stage	Spawning	−0.83	0.058	0.339	0.226	3,706	−201.4
	Incubation	0.09	0.919	0.007	0.874	2,560	−60.4
	Early-juvenile	−0.37	0.497	0.066	0.624	2,801	−61.7
	Juvenile	0.40	0.517	0.000	0.977	1,815	−31.3
Month	October	−0.49	0.321	0.262	0.299	3,911	−1,210.4
	November	−0.54	0.297	0.184	0.396	3,105	−398.9
	December	0.20	0.714	0.000	0.989	2,386	−17.4
	January	−0.49	0.356	0.173	0.412	3,096	−129.8
	February	0.14	0.803	0.009	0.860	2,120	86.6
	March	−0.31	0.564	0.149	0.450	3,094	−285.4
	April	−0.26	0.658	0.166	0.423	3,240	−477.6
	May	−0.71	0.136	0.174	0.411	2,912	−96.8
	June	−0.20	0.783	0.063	0.684	805	529.2
	July	0.70	0.233	0.990*	0.000	559	386.1
	August	0.10	0.950	0.115	0.576	3,479	−897.1
	September	0.70	0.233	0.034	0.768	1,213	238.3

The regression between cohort recruitment of the Zellenbach and maximum July discharge had p-value of 0.000 and a very high R^2 of 0.990. Depicted in Fig. 43, these results were most likely due to the low number of observations available. The 2016 recruitment observation heavily skewed the results of the regression analysis. A larger sample size would have allowed for a more accurate depiction of the underlying relationship.
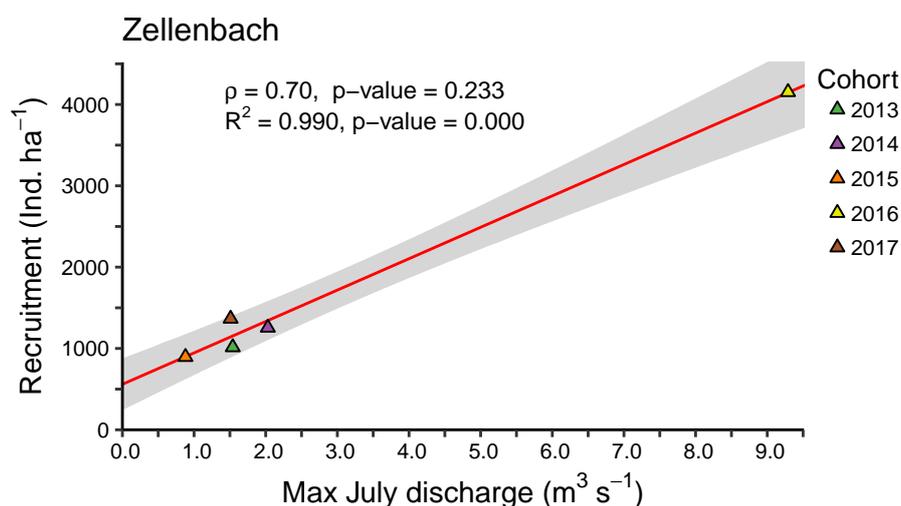
Figure 43. The linear regression between July discharge and Zellenbach was statistically significant even though the correlation was not. The 2016 cohort was an outlier that skewed the results of the regression analysis.

Combined analysis

Differences between recruitment in the study sites were normalized using the cohort recruitment Z-scores. Correlation analysis of discharge and recruitment Z-scores showed that recruitment

decreased as discharge increased during most months and life stages (Table 23). There was weak positive correlation between recruitment and maximum discharge in the juvenile period as well as with December, July and September flows. None of the correlations were significant, although March maximum discharge was negatively correlated ($\rho = -0.75$) with recruitment with a p-value of 0.052. Similarly, none of the regressions were of significance either. The least insignificant regression was October, with a p-value of 0.073 and R^2 of 0.159. The December regression was unable to explain any of the variation in recruitment. No discernible relationships could be observed when looking at the joint study site data.

Table 23. Correlation (Spearman's ρ) and simple linear regression between the Z-score of recruitment as dependent variable and maximum discharge.

		Correlation		Linear regression			
		ρ	p	R^2	p	β_0	β_1
Life stage	Spawning	−0.05	0.839	0.031	0.447	0.204	−0.033
	Incubation	−0.35	0.119	0.065	0.264	0.330	−0.099
	Early-juvenile	−0.17	0.454	0.003	0.814	0.049	−0.007
	Juvenile	0.02	0.931	0.004	0.815	−0.106	−0.063
Month	October	−0.38	0.089	0.159	0.073	0.636	−0.477
	November	−0.38	0.093	0.011	0.656	0.096	−0.053
	December	0.08	0.726	0.000	1.000	0.000	0.000
	January	−0.08	0.735	0.027	0.477	0.151	−0.028
	February	−0.35	0.116	0.062	0.275	0.337	−0.128
	March	−0.43	0.052	0.063	0.271	0.263	−0.101
	April	−0.37	0.096	0.090	0.186	0.347	−0.196
	May	−0.36	0.105	0.002	0.834	0.032	−0.006
	June	−0.29	0.241	0.102	0.197	0.263	−0.271
	July	0.25	0.318	0.059	0.331	−0.440	0.060
	August	−0.19	0.443	0.040	0.425	0.277	−0.290
	September	0.07	0.789	0.000	0.937	−0.295	0.017

6   Discussion

The research questions and underlying objectives are discussed first. Following this, the abiotic conditions of the study sites are described. The last section covers the trout population results.

6.1   Research objectives

This thesis investigated three research questions pertaining to the brown trout population found in the headwaters of the Piesting River. The effects of fluctuations in temperature and discharge on the spawning activity and population recruitment were evaluated with several hypotheses. The outcomes of the research objectives and tested hypotheses are discussed in detail below.

6.1.1   Temperature and spawning

It was thought that water temperature may have influenced the observed spawning activity in the study area. The temperature differences between cohort years did not differ from one another by a considerable measure over the duration of the study. Similarly, the onset and duration of spawning activity was also quite consistent. Redd densities, on the other hand, showed variance between cohort years. The study sites differed in redd density levels but showed similar changes in terms of cohort years. The 2014 cohort, for example, showed a decrease in redd density across all three streams.

Many biological aspects of brown trout are influenced by temperature. Respiration, growth rates, metabolism, sexual development, and feeding behavior are just some of the biological traits directly related to water temperature (Jonsson & Jonsson, 2009; Santiago, 2017). The water temperatures recorded in the study area ranged between $0-16\,°C$. The upper end of this range was well below the upper level of thermal tolerance ($20\,°C$) as described by Jonsson & Jonsson (2009). However, the lower end of the observed temperatures was low enough to limit growth and affect other biological processes (Jonsson & Jonsson, 2009).

While the thermal tolerance of trout has been described in detail, Álvarez et al. (2006) suggested that populations can develop their own thermal niche within these tolerance levels. Genetic studies have also shown populations develop specialized adaptions to local conditions based on drainages and altitude levels (Keller et al., 2012). This suggests that a small increase in water temperature may influence the biological activities of one population but have minimal effect on a different population. The following hypotheses tried to identify evidence of thermal influence on the spawning activity observed in the study sites.

H_1 - Increased summer temperatures delay the onset of spawning
Mean summer temperature was used as the metric to measure the influence of water temperature on spawning activity. The period in which spawning activity began was quite consistent throughout the study sites and cohorts. The Radersbach was the most well documented site, and onset of spawning occurred within a 10-day window during each year. The Urgersbach and Zellenbach

onset windows ran concurrent with the Radersbach although lasting slightly longer. Mean summer temperatures were also quite similar, with the Urgersbach being slightly warmer than the other sites. Visual examination of plotted data revealed no clear patterns between mean summer water temperature and the day spawning activity began. Moreover, statistical analysis found no correlation between the onset of spawning activity and mean summer water temperatures.

Spawning activity in brown trout is triggered by decreases in water temperature during the autumn season (Jonsson & Jonsson, 2009). Changes in discharge, solar cycles and other unknown environmental variables have also been speculated to play a role in the timing of spawning activity (L'Abée-Lund et al., 1989; Taranger et al., 1998). Warren et al. (2012) found that summer temperatures were correlated with the onset of spawning in a population of resident lake trout. Riedl & Peter (2013) found that a combination of temperature and altitude could be used to predict the timing of spawning activity in Alpine streams more accurately than temperature alone.

The study sites shared similar temperature and altitude attributes, as they are small tributaries of the same river system and located within the same geographical area. Because of these similarities, spawning activity in the study sites began within a few days of each other. Spawning onset also occurred at relatively the same time (late October and early November) across the different years. The onset of spawning was rather consistent despite slight variances in water temperature between cohort years.

One possible explanation for this is that the spawning behavior of the local trout population is related to inherited life history traits. Fraser et al. (2011) found genetic evidence that trout species develop local adaptations that increases fitness in their local environments. Research has shown that local adaptation is prominent in salmonid species, occurring approximately $50-70\%$ of the time, and is proportional to geographic scale (Fraser et al., 2011). It is likely that the trout within the study area share common genes that are adapted to the conditions found in the streams near Gutenstein. It is unlikely that the populations of the individual study sites are genetically different. Small differences in temperature between cohort years did not significantly influence when spawning activity began, which indicated that some other biological trigger must be working in conjunction with the water temperatures.

If temperature alone was the trigger for spawning activity, the temperature differences between cohort years should have caused some variance among the onset of redd construction. As it were, the onset of spawning activity was consistent across cohorts and study sites. These findings could be evidence that the population of the upper Piesting catchment has become locally adapted to the environmental conditions. Further evidence of locally adapted behavior was reported by Pinter et al. (2018), who found that wild resident trout outperformed both wild introduced trout and domesticated introduced trout under controlled stocking conditions. Inherited behaviors, which have been passed down through generations, may have a more important role in spawning onset than water temperature. Mean summer water temperature had little effect on when the trout began spawning, therefore the hypothesis (H_1) was rejected.

H_2 - Increased summer temperatures result in shorter periods of active spawning

It was thought that mean summer water temperature may have had an impact on the duration of spawning activity. Increased summer temperatures have been linked to reduced redd construction and decreased periods of spawning activity (Warren et al., 2012). As with the onset of spawning, no clear link between temperature and duration could be identified. The duration of spawning activity ranged from a low of 39 days (Urgersbach 2012) to a high of 84 days (Radersbach 2011). The distribution of spawning duration between cohorts was also uncorrelated, with the study sites experiencing different lengths of duration in the same cohort year.

It was likely that the duration of spawning activity was determined by the number of fish spawning in the individual streams. If one fish had begun spawning in early September and another in late January, the spawning activity would have been at the upper extent of observed duration. It was previously speculated that inherited behavior may have influenced the onset of spawning. If this was the underlying driver, then it was possible that there were a number of fish with different genetic traits that had been introduced into the system. Research in the study area performed by Pinter et al. (2018), found that introduced trout performed poorly in comparison with resident populations. It is possible that introduced trout started spawning at a slightly different period in time, extending the duration of spawning activity.

Future research should control for the number of fish spawning in the area, and also perhaps compare the genetics of early spawners with late spawners. As no correlation could be found between mean summer water temperature and the duration of active spawning, the hypothesis (H_2) was rejected.

H_3 - Increased summer temperatures result in decreased redd density

There was speculation that increased summer water temperature had a negative impact on the redd density of the study sites. Preliminary evidence to suggest this link was found in the analyses conducted in this thesis. As shown in section 5.6.1, there was negative correlation between water temperature and redd density in all three study sites. These correlations were strongly negative and statistically significant in the Radersbach and Urgersbach. This suggested that warmer summers resulted in fewer redds being constructed during the spawning season.

Water temperature directly affects the growth rate of salmonids, with increased temperatures resulting in decreased gonad development (Jonsson & Jonsson, 2009). As temperatures rise, fish metabolism also increases, which can divert energy from gonad development into metabolic activity (Pankhurst & King, 2010). The daily summer temperatures found in the study sites ranged from $8.1 - 14.1\,°C$. This was below the optimal growth range for adult trout feeding on invertebrates ($13.1 - 14.1\,°C$) and piscivorous diets ($16.6 - 17.4\,°C$) as identified by Elliott & Elliott (2010). The mean summer water temperatures observed in the study sites did not exceed the threshold at which gonad development would be diminished (Klemetsen et al., 2003). However, Álvarez et al. (2006) found evidence of variation in metabolic rate and energy storage of brown trout populations related to the thermal regime of their natal streams.

Another possible explanation for the observed relationship between water temperature and redd density is that it was simply a spurious correlation between the variables. Water temperatures did not rise above the generally accepted levels in which sexual development would be affected. There was presumably an untested variable or other underlying reason for the decline in redd density. As spawning activity is density-dependent on the number of spawning adults in the area, the reduced redd density could have possibly been explained by evaluation of the adult population. Based solely on the statistical analysis performed in section 5.6.1, hypothesis (H_3) was accepted. However, further analysis into the density-dependent factors influencing spawning activity is required to confirm these findings.

6.1.2 Spawning and recruitment

Population recruitment is dependent upon successful reproduction. Spawning activity was used to gauge the reproductive effort of trout residing in the headwaters of the Piesting River. The following hypotheses evaluated the extent of the relationship between spawning activity and recruitment. As previously mentioned, the spawning activity parameters were derived from redd counts and recruitment was described as the abundance of 0+ fish calculated from autumn stock assessments. Any fish that belonged to the 0+ age-class were the result of the spawning activity which had occurred several months prior.

The Radersbach was unique from the other streams in that, due to habitat limitations, no 2+ age-class fish were observed. The high density of redds indicated that spawning habitat was being utilized by adult fish, yet very few adults were sampled during stock assessments. Fish will usually reach sexual maturity sometime within the 2+ age-class, however, a small number of fish in the 1+ age-class may become sexually mature (Klemetsen et al., 2003). As these age-classes were determined by fish length, sexual maturity could only be presumed. The high redd densities found in the Radersbach suggested that adults from the Steinapiesting were using it for spawning. The results of stock assessments carried out within the Steinapiesting are shown in Table 24. The number of redds found in the Radersbach increased with the population of 2+ fish in the Steinapiesting (see Fig. H.1 in Appendix H). It was thought that the population density of 2+ fish in the Steinapiesting was directly related to redd constriction in the Radersbach, however the extent of this relationship was unclear with the available data (Fig. H.2). This could potentially be explained by the differing dates of the Steinapiesting stock assessments. Further research into this density-dependent relationship should be considered.

Spawning activity and successful recruitment were observed in all three investigation sites, with high abundances of 0+ age-class fish being documented. The recruitment levels of the Urgersbach and Zellenbach showed very high variance between cohort years. Due to limited sample size, there were some concerns that the stock assessments were not entirely representative of these study sites. This may have explained the high variance found in the population structure of these two streams. The Radersbach, on the other hand, was well documented throughout the duration of the study and provided very reliable measurements of biologic activity.

Table 24. Estimated brown trout abundance (Ind.ha^{-1}) and biomass (kg ha^{-1}) of the Steinapiesting based on autumn stock assessments.

Size class	Age-class	Abundance				Biomass			
		2012	2014	2016	2018	2012	2014	2016	2018
< 110 mm	0+	499	623	579	1,085	4.7	4.4	3.0	4.8
110 - 210 mm	1+	870	1,548	622	403	27.2	64.1	22.5	17.1
> 210 mm	2+	101	263	50	54	14.5	37.2	7.7	6.8
Total		1,470	2,434	1,251	1,542	46.5	105.7	33.1	28.7

Assessing the links between spawning activity and recruitment gave insight into the success of reproductive efforts. Correlating redd density with recruitment levels was fairly straightforward. However, addressing the influence that the onset of spawning had on recruitment proved more difficult as there was not a significant difference in the time that spawning began. Redd density was found to be positively correlated with recruitment, while no definitive link was found between recruitment and the onset of spawning. Spawning duration did not have a direct effect on recruitment, but likely interacted with other variables to influence recruitment success. As there were some uncertainties with the reliability of the recruitment values obtained from the Urgersbach and Zellenbach, the following hypotheses were addressed using the more robust Radersbach data.

H_4 - Increased redd density leads to increased juvenile recruitment

Redd density is indicative of the reproductive effort exerted by the population. The density of spawning redds represented potential reproduction that could result in viable offspring. Redd densities were the highest in the Radersbach, which also produced the highest levels of recruitment. Furthermore, there was a strong correlation found between redd density and recruitment in the Radersbach. This suggested that more reproductive effort resulted in increased recruitment.

Redd density was used to measure spawning activity because of its simplicity and unobtrusive nature in terms of evaluating redds. The number of redds in and of itself was not an accurate measure for the number of eggs deposited in the river substrate. The size and age of the female determines how many eggs are found in each redd (Avery, 1985). Without physically abstracting the eggs from the substrate and counting them, there was no way to know the number of eggs within each redd. Therefore, the redds were assumed to be uniform in size and egg density. Moreover, brown trout have been known to dig 'false redds' in which no eggs are deposited, or even spread their eggs over multiple redds (Crisp & Carling, 1989). The number of spawning adults present also influenced redd density, with more adults resulting in more redds. Using redd counts allowed for the foregoing variables to be disregarded and provided an overall approach to evaluating the reproductive effort. Redd counts were used to measure spawning activity, and both real and false redds expressed active spawning. The number of redds simply represented the amount of spawning activity occurring in the river. It was thought that more spawning activity would result in higher reproductive success. More redds found in the river would provide a higher chance of offspring surviving incubation and emergence.

The substrate and hydrological conditions found in the Radersbach presented ideal brown trout spawning habitat. If spawning habitat had been limited to specific areas, the redds would be concentrated only in areas with available habitat. As redds were distributed throughout the entirety of the Radersbach, it indicated that spawning habitat was plentiful. The map in Fig. B.1 of Appendix B shows the locations of all observed redds in the Radersbach. It should be noted that similar distribution of redds was found in the other study sites as well. High flow events would be more likely to destroy redds if they were all concentrated in specific areas. A higher number of redds dispersed throughout the river meant that the risk of redd destruction was also dispersed across the entire river. It was hypothesized that increased redd densities would lead to increased levels of population recruitment. The hypothesis (H_4) was accepted as it was supported by positive correlation between redd density and population recruitment in the Radersbach. Increases in redd density led to increased recruitment by raising the probability that an egg would hatch and go on to survive through the first season.

H_5 - Earlier onset of spawning activity positively influences recruitment

The onset of spawning across all three study sites was very consistent. Within the Radersbach, the earliest onset of spawning was 21 October and the latest 30 October. Each of the observed cohorts began digging redds within this 10-day window. As a result, there was not much variance in the onset of spawning between cohorts. Due to this limited variance, there was no detectable correlation between onset and population recruitment. The other study sites produced similar findings.

The timing of brown trout migration and spawning behavior is largely determined by elevation, latitude, discharge and water temperature (Jensen et al., 2008; Svendsen et al., 2004). The length of egg incubation is directly related to water temperature, with lower temperatures requiring longer incubation times (Réalis-Doyelle et al., 2016). The development of eggs and subsequent alevin development is temperature sensitive (Pankhurst & King, 2010). Earlier onset of spawning activity provides longer incubation times during more stable winter temperatures, ensuring complete development before exiting the redds (Réalis-Doyelle et al., 2016). It was assumed that delayed onset would lead to shorter incubation times and higher mortality rates. This study found that recruitment levels were significantly different between cohorts, while the onset of spawning activity was constant over the study period. There was no identifiable relationship between spawning onset and recruitment, therefore the hypothesis (H_5) was rejected. It is likely that the onset of spawning is a behavior adapted to local conditions and recruitment was influenced by other environmental factors.

H_6 - The duration of spawning activity has a positive relationship with recruitment

The duration of spawning activity showed more variance between cohorts than the onset of spawning. The longest duration of spawning in the Radersbach was 84 days, while the shortest duration was 55 days. The 2011 cohort had the longest duration as well as the highest recruitment. The other cohorts did not display this same correlation. Duration alone could not predict the

recruitment level and it was speculated that it had an interaction effect with other factors involved in successful recruitment. The duration of spawning activity gave no indication into how much reproductive effort was actually exerted by the population.

The relationship between the duration of brown trout incubation and water temperature has been extensively studied (Jonsson & Jonsson, 2009; Santiago, 2017). Embryonic development is known to be strongly affected by water temperature, with colder temperatures producing longer incubation times (Ojanguren & Braña, 2003; Réalis-Doyelle et al., 2016). From fertilization to hatching approximately 444 degree-days are required, and an additional 220 degree-days needed until redd emergence (Santiago, 2017). With the mean water temperature during the incubation period ranging from $5.0 - 7.5\,°C$, the rates of development varied between cohorts. This was compounded by the length of time in which redds were constructed.

Spatial dispersion of the redds within the study site was thought to decrease the likelihood of an environmental event destroying all the redds. It was also assumed that temporal distribution of the redds would lower the risk of disturbance to the entire stock of incubating eggs. Furthermore, eggs deposited in the substrate earlier in the spawning period are likely to emerge before eggs deposited later. This may produce a competitive advantage for resources with other juveniles (Skoglund et al., 2012; Sternecker et al., 2014). A larger range of egg deposition would likely result in a wider range of emergence from the substrate.

Riverbed scouring caused by hydrological factors can negatively affect egg incubation (Unfer et al., 2011). The HQ2 flood event of December 2018 (see Fig. 4) destroyed every observed redd in the Radersbach that had been constructed prior to the flood. Only the redds dug after the flood provided opportunities for successful egg incubation. This gave credence to the assumption that a longer duration could potentially increase recruitment.

While it was hypothesized that a longer duration of spawning activity would lead to higher recruitment, no evidence that duration in itself had affected recruitment was found. Increased duration of spawning activity corresponds with temporal distribution of eggs, reducing the risk of an environmental event destroying all spawning redds. The duration of spawning activity most likely provides an interaction effect with some other underlying variable. Multivariate linear regression of recruitment using redd density and spawning duration as regressors produced a highly efficient model, however, the sample size was too small to draw any conclusions. Duration of spawning activity could not demonstratively influence recruitment using the collected data, therefore the hypothesis (H_6) could not be accepted. However, it is very likely that this relationship exists and further studies into the interaction between redd density and spawning duration using a larger sample size should be conducted.

6.1.3 Discharge and recruitment

Previous studies have shown that recruitment can be directly impacted by hydrological discharge in the first year of the brown trout life cycle. Observations taken from the Radersbach showed a

strong positive correlation between spawning period discharge and recruitment. Conversely, high flows in the incubation period were found to be negatively correlated with recruitment. These findings were in line with the results that Unfer et al. (2011) reported in a similar catchment. Additionally, maximum discharge in the September immediately prior to stock assessments was negatively correlated with recruitment. This suggested that some of the juveniles may have been washed downstream during elevated discharge levels.

Hydrological discharge influences the morphology of rivers through erosion and sediment transport. The grain size and structure of the substrate is determined by flow velocity. As a gravel spawning species, brown trout reproduction is highly sensitive to the substrate conditions found in spawning areas. For successful reproduction, the interstitial zone requires an adequate throughflow of well-oxygenated water (Grost et al., 1991; Sternecker et al., 2014). Egg incubation and alevin development are contingent upon this interstitial flow (Crisp & Carling, 1989). Accumulation of sand and other small sediments in spawning habitat hinders reproductive success (Sternecker et al., 2014). If these small particles had been flushed from the substrate before egg deposition, recruitment potential is thought to have been increased (Unfer et al., 2011).

After fertilization, the eggs are very sensitive until the 'eyed-egg' stage of development (when eye pigmentation is visible), which occurs after $195-220$ degree-days (Réalis-Doyelle et al., 2016; Santiago, 2017). It is during this early period of incubation that the eggs are susceptible to disruptions to the substrate caused by high discharge levels. Fry emerging from the substrate are also very vulnerable to high flow (Nicola et al., 2009). Sensitivity to discharge decreases as fish grow (Cattanéo et al., 2002), and it is generally accepted that fully developed juveniles are able to seek shelter during high flow events (Unfer et al., 2011).

The following hypotheses were formed to assess the potential influence of hydrological discharge on the recruitment of the brown trout population located in the headwaters of the Piesting. Due to the previously mentioned concerns with the reliability of recruitment values from the Urgersbach and Zellenbach, the hypotheses have been evaluated with the observations taken from the Radersbach.

H_7 - High discharge during the spawning period will increase recruitment

The spawning period had the highest variability of all first-year life stages identified in the study. A strong positive correlation was identified between maximum discharge during the spawning period and recruitment in the Radersbach. While this supported the findings of Unfer et al. (2011), the correlation was not statistically significant with the available data. However, the probability (p-value = 0.069) that they were linked was quite high.

Literature has shown that discharge levels during the period in which spawning activity takes place have a significant role in reproduction success. Fine sediments impede the construction of spawning redds, which are preferably dug in course gravel bars with adequate flow velocities (Grost et al., 1991). Flushing away the tiny particles clogging the gravel bed allows for ample

flow of oxygen saturated water through the spawning redds (Crisp & Carling, 1989). According to Unfer et al. (2011), periods of high discharge immediately preceding or during spawning resulted in increased recruitment. It was speculated that this was due to fine sediments being flushed from the gravel substrate, increasing oxygenation and opening the interstitial spaces for emerging alevins (Unfer et al., 2011).

One area in which this study could have been improved upon was the inclusion of sheer stress data for the river substrate. There exists a critical threshold at which the flow velocity begins to mobilize the substrate. Without having detailed data on the substrate composition and in-stream discharge measurements, this threshold will remain unknown in the study sites. It is only when the discharge exceeds the critical shear stress for sediment motion that it will have an impact on the substrate conditions (Unfer et al., 2011).

As the Radersbach recruitment observations were limited to 8 cohorts, the hypothesis (H_7) could neither be accepted nor rejected with the data available. The inclusion of more cohort data or the discharge at which the substrate was displaced would have greatly enhanced the ability to critically analyze the relationship. However, it was very likely that elevated discharge increased population recruitment as the positive correlation was in agreement with existing literature. Nevertheless, more research must be conducted to confirm these findings.

H_8 - High discharge during the incubation period will decrease recruitment

High incubation period discharge was expected to negatively impact recruitment. There was only one flood event ($HQ1 - 2017$) which took place during the incubation period. However, there were more occurrences of discharge above $5 \times MQ$ than any other period. There was strong negative correlation between recruitment and maximum incubation period discharge. This was in line with the results found in the works of Unfer et al. (2011) and Cattanéo et al. (2002).

The incubation of trout eggs occurs within the interstitial space of the gravel substrate. After egg deposition and fertilization in the spawning redd, the embryo is very sensitive to its environmental conditions until it reaches the eyed-egg stage, upon which it becomes more resilient (Ojanguren & Braña, 2003). After hatching, the alevin remains within the interstitial until it has depleted its yolk sack (Crisp, 2000). While the trout larvae are living in the substrate, their well-being depends on the stability of the riverbed. Cattanéo et al. (2002) found that high discharge during emergence was detrimental to recruitment. These results were corroborated by Unfer et al. (2011), who concluded that high flow during the incubation and emergence periods reduced recruitment.

Trout eggs and alevins are very sensitive to high flow conditions, which may disrupt the gravel substrate in which they reside. If river discharge is high enough, the shear stress of the substrate is surpassed and the eggs and alevins are washed downstream (Unfer et al., 2011). While this may or may not be fatal for the transported individuals, it causes a reduction in recruitment levels of the localized area. Late-stage eggs and alevins may still be viable after being washed away, increasing recruitment levels further down the catchment.

As with the prior hypothesis, with only 8 recruitment observations in the Radersbach, this hypothesis (H_8) could neither be accepted nor rejected with the data available. There was strong indication of a negative relationship between incubation period discharge and recruitment, but more cohort observations were needed before a confident decision could be made.

H_9 - High discharge during the juvenile stages does not have an impact on recruitment

The early-juvenile period saw the highest discharge during the study ($HQ10 - 2014$), while the juvenile period only surpassed $3 \times MQ$ twice. The 10-year flood in 2014 did not seem to have any impact on the recruitment of that cohort. There was no strong evidence of correlation between recruitment and discharge of the early-juvenile or juvenile periods. Literature suggests that shortly after emergence, high flow rates do not significantly affect mortality rates of juvenile fish (Jensen & Johnsen, 1999). In contrast with the above findings, maximum September discharge immediately prior to stock assessments showed very strong negative correlation with recruitment.

Upon emergence from the spawning redd, trout parr are quite hardy but experience very high mortality rates. Deaths are usually caused by intraspecific competition for food, predation or harsh environmental conditions (Scheuerell et al., 2009; Skoglund et al., 2012). Recruitment levels can also be affected by high flows that flush juveniles downstream when no shelter is available (Jensen & Johnsen, 1999; Nicola et al., 2009). Other studies have found that recruitment is not heavily influenced by discharge after emergence (Cattanéo et al., 2002; Unfer & Pinter, 2018). The negative correlation between maximum September discharge and recruitment was most likely a spurious correlation. The fully formed juveniles should easily be able to cope with the low discharge levels observed in September.

There was no conclusive evidence of recruitment being impacted by discharge during the early-juvenile and juvenile life stages. Furthermore, a 10-year flood event in 2014 did not noticeably affect recruitment. The hypothesis (H_9) was accepted as no discernible consequences of high discharge were identified.

6.2 Abiotic conditions

Modeling of the temperature and discharge of the study sites was required as streams of this size are not regularly monitored. The methods used to determine the abiotic conditions provided suitable results in lieu of in situ observations. Regression models provided in stream water temperatures, while the discharge data only allowed for inference of flow conditions.

6.2.1 Temperature

Temperature is known to play a crucial role in the life history of brown trout. This thesis investigated the influence that temperature has on the spawning activity of brown trout in the Piesting catchment. Global temperatures have been predicted to rise in the coming years due to climate change (Perkins-Kirkpatrick & Gibson, 2017). Areas of Austria are expected to be significantly affected by thermal shifts (Ács et al., 2018; Zoboli et al., 2017). As the headwaters

of the Piesting River are located within the Austrian Alps, they may be susceptible to changes in environmental conditions if increases in regional temperature were to occur.

Regression models have been used to overcome the difficulties of monitoring several small streams for the duration of the study period. Despite being based on short-term measurements conducted in winter months, the regression models developed for the investigation sites performed as well as similar models based on long-term measurements available from nearby reference sites. However, longer observation periods of stream temperatures would allow for the inclusion of seasonality in the models. Year-round measurements would allow for multivariate modeling of the temperature, which could further mitigate any bias attributed to seasonal differences throughout the year.

The long-term daily mean temperatures show that the coldest time of the year is late January, near the time spawning activity has completely finished (Fig. 5). Conversely, the highest temperatures are usually found around mid-July. Spawning activity was observed to start in September, and as seen in figure Fig. 5, the water temperature usually begins to decline around this time. This is not surprising as decreasing water temperature is known to be a trigger for spawning migration and activity in several salmonid species (Crisp, 2000; Jonsson & Jonsson, 2009). Deeper investigation into the temperature at which spawning activity begins in the study sites should be considered.

Modeling the temperature from the Gutenstein gauging station made analyzing the in-stream temperature of the investigation streams possible. When analyzing streams of this scale, the temporal differences between the reference station and study site temperatures are small enough to be inconsequential in terms of trout ecology. However, one drawback to linear regression is that the investigated streams all share the same temporal temperature swings as the Kalter Gang, which may not be truly accurate. For example, the models showed that the Radersbach and Zellenbach shared very similar temperature profiles. The Zellenbach, being a slightly larger river, most likely experienced daily temperature fluctuations at a different rate than the Radersbach. These two rivers, as well as the Urgersbach, probably experienced larger temperature variances than observed by the substantially larger Kalter Gang as smaller streams are more affected by air temperature than larger bodies of water (Benyahya et al., 2007). Nevertheless, it must also be considered that as these rivers feed into the Kalter Gang, they all share very similar thermal patterns.

Brown trout are known to exhibit specialized adaptations to their local environments in terms of temperature related behaviors (Jonsson & Jonsson, 2009). Often these traits are related to the latitude or elevation at which the trout population is found. These adaptations are hereditary in nature and have been passed down through generations in order to capitalize on the conditions of the habitat in which the population resides (Fraser et al., 2011). There is little potential for local adaptation for thermal tolerance of the species, however, there is evidence of intraspecific variation in spawning temperature and time (Jonsson & Jonsson, 2009). If the brown trout population found in the study area has become specialized to the local thermal regime, slight

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increases in water temperature may be detrimental to the population even though the temperature remains within the commonly accepted 'safe' range (Álvarez et al., 2006). This is a very important distinction in light of the widely accepted evidence of global climate change and increasing temperatures across central Europe.

The mean annual water temperature records from the Gutenstein gauging station (2005 – 2018) showed an upward trend in the temperature of the Piesting headwaters (see Appendix F). During this 14-year period, the mean annual water temperature rose by a predicted 0.056 °C annually. This alarmingly high rate of temperature increase cannot be accepted at face value, but it is clear that the temperature has been increasing in congruence with relevant literature (Perkins-Kirkpatrick & Gibson, 2017). Temperatures have been predicted to increase and are currently increasing in the study area. Comparing the mean annual temperature (Fig. F.1) together with the 14-rolling mean daily temperature (Fig. F.2) reveals that the water temperature has been getting warmer earlier in the year as the temperatures increase. This earlier warming has the potential to alter the hydrological regime of the study area. The implications that this may have on the health of the trout population is at this point unknown. This research was able to provide insight into how these increasing temperatures will affect the brown trout population in the future. However, more research is needed to better understand the extent of these effects.

6.2.2 Discharge

Brown trout, like all salmonids, are a lithophilic (gravel spawning) fish species. The eggs are deposited within the interstitial zone of suitable gravel banks after excavating a redd in the substrate. When the flow velocity rises to the point that shear stress surpasses its critical level, this substrate can become mobilized. The transportation of sediments caused by high discharge can be both detrimental and beneficial to population recruitment, contingent upon when it occurs within the year.

Flow conditions in the study sites were inferred from discharge observations of the Kalter Gang, which were recorded at the gauging station in Gutenstein. The Kalter Gang was able to be used as a proxy as the scale of the study area was small enough to experience similar weather patterns, and the fact that the study sites are tributaries of the same system (Pattison et al., 2014). Although this method had some limitations, it made possible the ability to assess the impacts of different discharge levels within the investigated streams.

The headwaters of the Piesting tend to follow a pluvial discharge regime, with higher flows occurring early in the calendar year. Winter temperatures are usually low enough for snow accumulation, but warm days can cause this snow to melt, increasing discharge. The high flow events quantified over the duration of the study were sporadic throughout the year, though most occurred in January. The 10-year flood that occurred in May 2014 likely caused a significant amount of sediment transport. Other years also experienced periods of elevated discharge from May to August, but no considerably high discharge occurred between August and December

in any of the observed years. The number of cohort years which experienced discharge above the HQ1 level was surprising low. Discharge levels in 2018 did not even surpass the $5 \times$MQ threshold. These low discharge levels could have had ecological implications regarding spawning habitat access or availability in these small streams. The hydrology of these streams and the resulting sediment transport during elevated discharge levels, or low discharge limiting habitat accessibility has underlying consequences for reproduction of the trout population.

Further investigation into substrate composition of the spawning areas is needed along with discharge measurements recorded in the individual streams. Using the Kalter Gang as a proxy made these analyses possible, but this only provided insight into the general characteristics of the flow conditions and not the actual discharge values of the study sites. Having this additional information would greatly enhance the ability to analyze the hydromorphological conditions of the investigated streams. More knowledge of the shear stress and sediment transport occurring in the study area would provide a better understanding of the interaction between discharge conditions and spawning redds. Future studies should evaluate the individual characteristics of each study site so that a more in-depth analysis of this relationship can be performed.

6.3 Trout population

Two main aspects of the brown trout population were investigated with this research. Spawning activity was monitored with visual observations of redd construction and population dynamics were explained through stock assessments. Regular stock assessments made the Radersbach well represented by the collected data. The Urgersbach and Zellenbach were sampled less frequently, making the analyses less reliable than the Radersbach. An overall decline in population abundance and recruitment was observed in all three study sites. Spawning activity also exhibited a steady decline over the course of the study. A causal link between these declines should be further investigated in the future.

6.3.1 Spawning activity

Visual surveys of redd construction were conducted for the duration of trout spawning within the study sites. These observations made monitoring the spawning activity of the trout population possible. Natural fluctuations in the number of redds dug each year was to be expected, however, a concerning trend found in all three study sites was the steady decline in the number of redds over the duration of the study. Linear regression of the observed redd densities further predicted declines in the future (Appendix G). Identifying the cause of these declines should be the goal of research carried out in the future.

Redd density provided a direct assessment of the level of spawning activity occurring in the streams. The amount of redds constructed in each river gave an indication of the number of adult trout spawning there. The Radersbach consistently contained the highest number of redds despite being the smallest stream. It had much higher redd densities than the other sites due to more

redds being contained in a smaller area. This suggested that either the ratio of suitable spawning habitat was higher in the Radersbach, or that there was a larger population of adult fish making use of the available habitat. The Urgersbach averaged half the number of redds as found in the other sites. This may have been caused by beaver activity which took place in the Urgersbach, but not the other sites. Overall, the redd counts showed a decline in redd density in all three of the investigated streams. This decline was concurrent with decreases in the population abundance of 1+ and 2+ fish.

Density-dependent spawning activity was not assessed in this study and further research is needed to clarify this relationship. A decrease in the number of individuals spawning could have been caused by several factors. Migration obstacles present in the study area are known to become impassable barriers during periods of low discharge (Rottensteiner, 2011). If discharge levels were low just before or during the early spawning period, upstream migration of adult fish looking to spawn may have been hindered. However, as the decrease of redd construction was steady over time, it was unlikely that these barriers were the underlying issue. Therefore, it was likely that the decline in spawning activity was directly related to the decreases in the adult population. The most speculated cause of decline in the adult population was increased predation, which is discussed in the following section.

Using redd counts as a proxy for spawning activity is not without its criticisms (Dunham et al., 2001). Brown trout have been shown to dig multiple redds during spawning (Crisp, 2000). Some female trout will dig redds on top of existing redds (Crisp, 2000). These actions can introduce error into redd counts by increasing or decreasing the number of observable redds. One way to mitigate the problem of redd superimposition is to conduct redd counts more frequently. The Radersbach spawning activity was well documented, but the other sites had less frequent surveys. This may have been a contributing factor in the Radersbach having a higher redd density as the other streams may have had some redds which had gone unnoticed.

A single individual was responsible for performing the redd counts, ensuring that redds were identified consistently throughout the study. This greatly decreased the chance of identification bias which would have occurred if multiple people had been conducting the surveys. However, it also imposed limitations on the frequency of observations due to difficulty in accessing the study sites. As mentioned, the Radersbach had regularly performed redd counts while the other sites were observed less frequently. This did not significantly affect the results aside from one spawning season in the Urgersbach. The 2012 cohort produced parameters deviating from the other cohorts found in the Urgersbach (see section 5.3.2). This deviation was caused by the spawning activity of the 2012 Urgersbach cohort being based on only two redd counts as seen in Appendix A. These limitations were most apparent in the 2012 Urgersbach cohort, but may have introduced slight bias in other redd count calculations as well. More frequent redd observations may have slightly reduced this error, but accessibility and personnel constraints made more frequent redd counts unfeasible.

The decreasing level of spawning activity in the study area is of great concern. This could have a substantial impact on the future of the trout population. Successful reproduction is a core component of a healthy, self-sustaining population. Future research is needed to identify the cause of the declining spawning activity and mitigation efforts must be considered.

6.3.2   Population dynamics

The population dynamics of the trout found in the study area provided insight into the overall health of the population. Natural fluctuations of population structure in response to hydrological conditions were to be expected (Unfer et al., 2011). Years with successful reproduction and high recruitment work to counteract years with unsuccessful reproduction and low recruitment. Seasonal hydrology causes high variance in the density of juvenile fish but does not significantly influence 1+ and larger fish (Cattanéo et al., 2002). The stock assessments of the study sites showed a high degree of variance in the 0+ age-class abundance among the different cohort years. These assessments also found evidence of an overall decline in both the abundance and biomass of the population across all age-classes. Furthermore, these declines were observed in all three of the study sites.

Habitat availability is a limiting factor in trout populations. The small streams studied in this thesis provided little opportunity for adult fish to thrive. This was because the habitat required to support a fish increases with age (Crisp, 2000). The physical size constraints were a limiting factor in both the size of the adult fish and the density of the adult population. The largest fish sampled over the entire duration of the study was only 30.4 cm in length. Small resident adult populations were evident in the Urgersbach and Zellenbach, but absent from the Radersbach. These small streams supplied spawning habitat for adult trout and, in time, acted as nursery habitat for the juvenile fish that emerged from the redds. The limited ability to support larger fish indicated that the Piesting headwaters were used primarily for spawning by adult fish and nursery habitat for juveniles. Larger trout tended to leave the study sites after reaching a certain length, which was probably due to lack of available habitat in these small streams.

Sexually mature trout are known to exhibit 'homing behavior', or returning to the waters in which they originated for spawning (Klemetsen et al., 2003). Female brown trout usually reach sexual maturity while in the 2+ age-class (Avery, 1985). Because the streams are too small to support a large population of resident adults, it was likely that adult trout were migrating into the study sites during the spawning season and then leaving afterward. This was especially evident in the Radersbach, in which no 2+ fish were found during stock assessments. Adults migrated upstream from the Steinapiesting to use the Radersbach for spawning and then migrated back downstream. It was highly probable that this was occurring in the other sites as well, with fish migrating upstream from the Kalter Gang.

While the stock assessments provided plentiful information on the population dynamics of the study sites, they were not without limitations. As with the redd counts, the Radersbach was better

represented than the other study sites. The Radersbach was the only site in which an electrofishing survey was performed in the 2012 cohort year. Additionally, the Zellenbach was also missing the 2018 cohort year. Most of the changes of population structure could be observed, but these missing surveys limited the ability to track the changes in population structure during those years. There were also some concerns that the stock assessments performed in the Urgersbach and Zellenbach were not representative of the entire river. In spite of this, the assessments allowed for a glimpse of the population structure within these sites in terms of age-class and densities.

The observed decline in population abundance and biomass was concerning. The number of adult fish decreased over the duration of the study. The likely cause of this decrease was the Eurasian otter (*Lutra lutra*). The number of otters in Lower Austria has been increasing in recent years (Kofler et al., 2018). A study carried out in the Piesting catchment found that the diet of the local otter population was composed primarily of salmonids, with more than 50% of the diet consisting of brown trout larger than 120 mm in length (Sittenthaler et al., 2019). This must have detrimental effects on the reproductive capability of the trout population. Removal of 1+ and larger trout from the study area would reduce the number of spawning adults in the tributaries. There was a decline in the adult population in all three study sites as well as a reduction in redd density. Otter predation may have contributed to these observations.

While the effects of otter predation on the local trout population have not been studied, it can be assumed that removing fish of spawning size plays a critical role in the dynamics of the population. Small streams, like those in this study, could have their entire breeding stocks depleted by otters. This would reduce the spawning activity and potential recruitment in those streams, further exacerbating the decline. Decreasing spawning activity has been shown to result in less recruitment success. Reduced recruitment then lowers the probability of fish reaching sexual maturity, resulting in a smaller population of spawning adults.

If the otters' food source became too scarce in one area, they would move to another stream in the catchment. The reduced otter pressure would then allow the trout population to rebound. The population of the Radersbach reached its lowest abundance in 2016, but has since been steadily increasing. This level of decline could have been caused by a single otter, with the increase in abundance being the result of the otter seeking out a new source of food in a nearby stream. The otter population is very likely to have contributed to the observed reduction in abundance and biomass of the study sites. Further research on how the otter affects the local trout population should be conducted. If the number of otters in the area continues to increase, it could have had a significant effect on the health of the trout population.

7   Conclusion

This research provided insight into the spawning activity and recruitment of brown trout. The focus was the influence of temperature and discharge on populations in Alpine headwater streams.

Variations in temperature had no detectable influence on the onset or duration of spawning. It was thought that the onset of spawning was determined by inherited phenology traits adapted to local conditions. The duration of spawning was dependent upon adult abundance. Temperature had an inverse relationship with redd density. The validity of this relationship was questioned, as temperatures remained well within tolerance levels. However, some studies suggest that the metabolic rate of trout populations may become locally adapted to their natal streams. The implications this may have had on the observed spawning activity requires further research.

Additionally, redd density was observed to have a substantial role in population recruitment. A higher reproductive effort (in terms of redd density) led to increased YOY abundance. Duration of spawning activity was thought to have had an interaction effect with redd density, with longer duration increasing the odds of successful recruitment. Both redd density and duration of spawning were believed to be dependent upon the abundance of the adult population.

The hydrological regime of the study area had more influence than temperature. Results showed that higher levels of discharge during the spawning period increased reproductive success as YOY abundance was positively correlated with discharge. Conversely, elevated discharge during the incubation period resulted in lower YOY abundance. These findings were in agreement with published literature. There was no indication that post-emergence discharge had any impact on 0+ fish. Upon becoming parr, the YOY were able to effectively cope with elevated discharge.

There was a notable decline in spawning activity during the study. This decline was concerning, as it was compounded by decreases in abundance and biomass of the population. An increasing otter population was implicated in the predation of adult fish, which was thought to significantly reduce the population of spawning fish.

It is important to understand the contributions that nursery habitats make to self-sustaining trout populations. The headwaters of the Piesting are being used for spawning by trout migrating upstream from lower areas of the catchment. In addition to spawning habitat, these small streams provide food and shelter for a high-density juvenile population. A large number of these fish will outgrow this nursery habitat and migrate downstream in search of more suitable territory. There are several external factors exerting influence on the reproductive success of the spawning which occurs in these streams.

Future research should focus on building knowledge of the Radersbach. The analyses performed in this study could be improved with the inclusion of additional years of data. The relationship between the adult population of the Steinapiesting and spawning in the Radersbach should also be investigated. Continued study of the population dynamics and spawning behavior of the trout in the Piesting headwaters will add to understanding the importance of nursery habitat.

8 References

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Appendix A

Annual redd observations

Table A.1. Spawning redd observations of the Radersbach.

Date	Observed redds	Date	Observed redds	Date	Observed redds
2010-11		**2014-15**		**2017-18**	
28-10-2010	1	26-10-2014	3	31-10-2017	4
23-11-2010	13	02-11-2014	5	10-11-2017	10
08-12-2010	13	09-11-2014	8	17-11-2017	7
26-12-2010	26	15-11-2014	13	25-11-2017	12
07-01-2011	14	23-11-2014	17	03-12-2017	12
16-01-2011	6	29-11-2014	10	10-12-2017	6
		07-12-2014	16	17-12-2017	6
Total	73	12-12-2014	8	24-12-2017	3
2011-12		20-12-2014	3	07-01-2018	2
28-10-2011	1	27-12-2014	3		
06-11-2011	9	05-01-2015	1	Total	62
20-11-2011	16			**2018-19**	
04-12-2011	17	Total	87	29-10-2018	2
20-12-2011	40	**2015-16**		07-11-2018	1
26-12-2011	5	24-10-2015	1	18-11-2018	3
05-01-2012	2	31-10-2015	1	26-11-2018	10
		07-11-2015	4	06-12-2018	5
Total	90	14-11-2015	5	18-12-2018	4
2012-13		21-11-2015	6	29-12-2018	3
25-10-2012	1	28-11-2015	8	06-01-2019	1
04-11-2012	2	05-12-2015	6		
11-11-2012	15	12-12-2015	3	Total	29
26-11-2012	23	19-12-2015	6	**TOTAL**	**597**
09-12-2012	31	02-01-2016	4		
25-12-2012	10				
29-12-2012	4	Total	44		
		2016-17			
Total	86	31-10-2016	1		
2013-14		06-11-2016	3		
03-11-2013	2	13-11-2016	6		
09-11-2013	5	20-11-2016	10		
17-11-2013	18	27-11-2016	18		
24-11-2013	9	04-12-2016	14		
01-12-2013	9	11-12-2016	9		
08-12-2013	3	18-12-2016	1		
15-12-2013	6	23-12-2016	5		
22-12-2013	3				
29-12-2013	3	Total	67		
03-01-2014	1				
Total	59				

Appendix A

Annual redd observations

Table A.2. Spawning redd observations of the Urgersbach.

Date	Observed redds	Date	Observed redds	Date	Observed redds
2010-11		**2014-15**		**2017-18**	
12-11-2010	7	01-11-2014	8	11-11-2017	4
08-12-2010	24	15-11-2014	7	18-11-2017	2
09-01-2011	3	27-11-2014	7	26-11-2017	5
		08-12-2014	7	06-12-2017	4
Total	34	22-12-2014	6	15-12-2017	1
2011-12		02-01-2015	2	27-12-2017	1
30-11-2011	26				
18-12-2011	12	Total	37	Total	17
		2015-16		**2018-19**	
Total	38	02-11-2015	4	28-10-2018	3
2012-13		15-11-2015	9	11-11-2018	2
28-10-2012	1	29-11-2015	12	23-11-2018	3
19-11-2012	10	13-12-2015	4	09-12-2018	5
14-12-2012	12			21-12-2018	2
31-12-2012	13	Total	29		
		2016-17		Total	15
Total	36	28-10-2016	2	**TOTAL**	**253**
2013-14		13-11-2016	2		
05-11-2013	2	27-11-2016	18		
14-11-2013	8	14-12-2016	4		
12-12-2013	7				
27-12-2013	3	Total	26		
05-01-2014	1				
Total	21				

Appendix A

Annual redd observations

Table A.3. Spawning redd observations of the Zellenbach.

Date	Observed redds	Date	Observed redds	Date	Observed redds
2011-12		**2014-15**		**2017-18**	
13-11-2011	9	15-11-2014	19	01-11-2017	4
29-11-2011	25	27-11-2014	22	19-11-2017	4
18-12-2011	31	08-12-2014	18	01-12-2017	7
09-01-2012	12	22-12-2014	23	25-12-2017	5
		02-01-2015	4	Total	20
Total	77	Total	86	**2018-19**	
2012-13		**2015-16**		02-11-2018	5
28-10-2012	1	25-10-2015	2	20-11-2018	12
18-11-2012	32	08-11-2015	13	30-11-2018	13
26-11-2012	21	22-11-2015	18	21-12-2018	18
16-12-2012	24	04-12-2015	13	01-01-2019	3
29-12-2012	1	20-12-2015	36	Total	51
Total	79	03-01-2016	7	**TOTAL**	**538**
2013-14		Total	89		
07-11-2013	2	**2016-17**			
18-11-2013	29	27-10-2016	7		
14-12-2013	12	07-11-2016	5		
30-12-2013	11	19-11-2016	21		
07-01-2014	2	03-12-2016	30		
Total	56	17-12-2016	12		
		23-12-2016	5		
		Total	80		

Appendix B

## Maps of annual redd locations
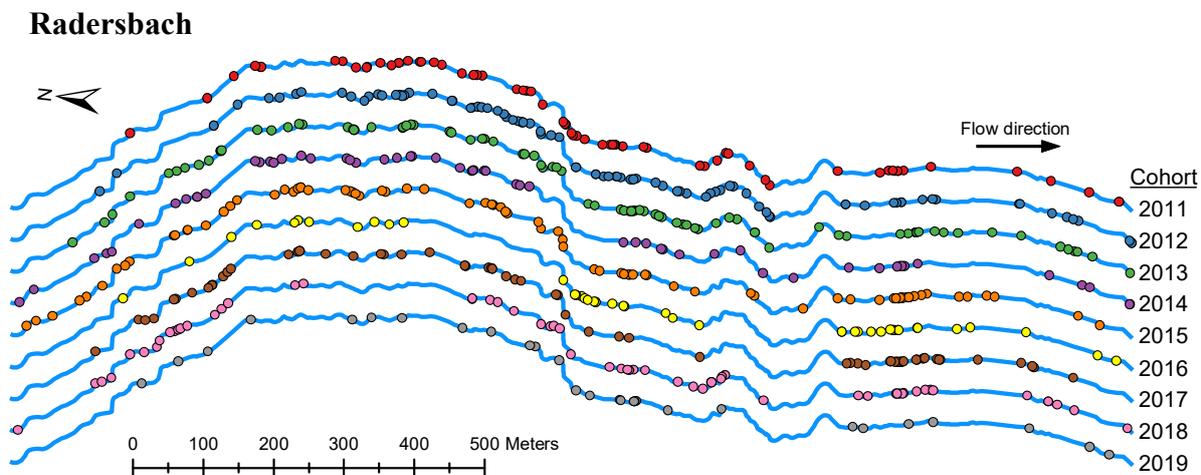
Radersbach

Figure B.1. Location of spawning redds in the Radersbach by annual cohort.
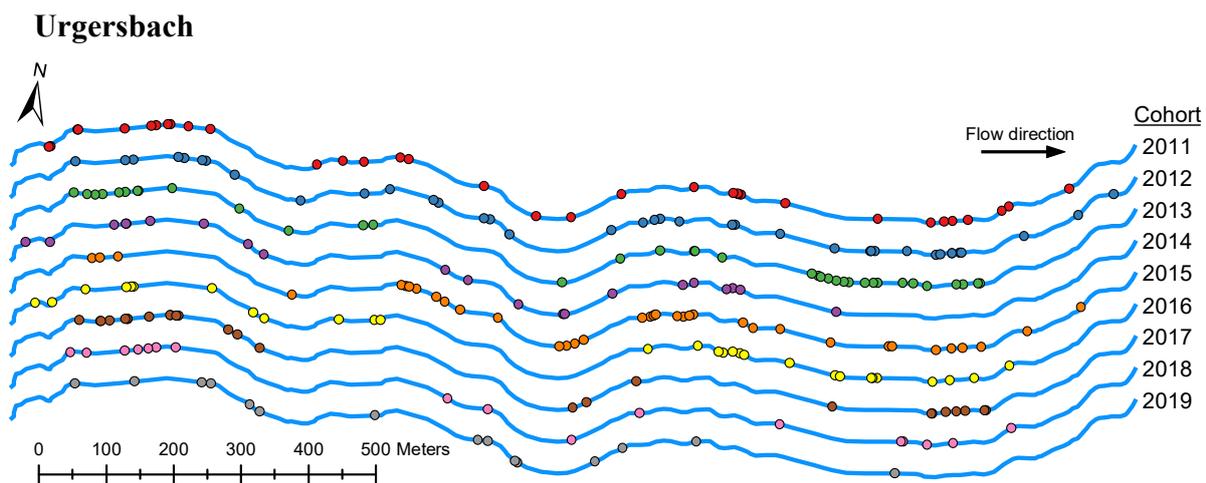
Urgersbach

**Figure B.2.** Location of spawning redds in the Urgersbach by annual cohort.
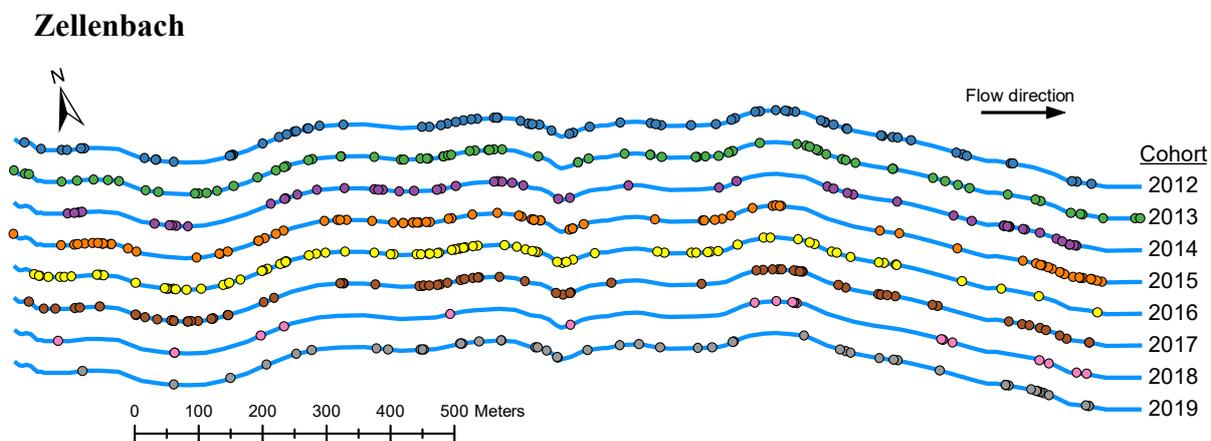
Zellenbach

Figure B.3. Location of spawning redds in the Zellenbach by annual cohort.

Appendix C

Stock assessment records

Table C.1. Radersbach stock assessment record.

Year	Sampled stretch	Date	Length (m)	Width (m)	Age-class 0+	1+	2+
2011	Radersbach I	21-09-2011	40	1.6	26	4	0
	Radersbach II	14-09-2011	53	2.0	52	7	0
	Radersbach III	14-09-2011	50	2.0	93	3	0
	Radersbach IV	14-09-2011	53	2.0	104	0	0
2012	Radersbach I	16-09-2012	40	1.6	9	4	0
	Radersbach II	03-10-2012	53	2.0	42	3	0
	Radersbach III	03-10-2012	50	2.0	54	2	0
	Radersbach IV	03-10-2012	53	2.0	97	1	0
2013	Radersbach I	17-09-2013	40	1.7	9	8	0
	Radersbach II	17-09-2013	53	2.4	52	4	0
	Radersbach III	17-09-2013	50	2.0	59	1	0
	Radersbach IV	17-09-2013	53	2.1	87	2	0
2014	Radersbach I	16-09-2014	40	1.7	14	4	0
	Radersbach II	16-09-2014	53	2.4	30	6	0
	Radersbach III	16-09-2014	50	2.0	42	0	0
	Radersbach IV	16-09-2014	53	2.1	52	1	0
2015	Radersbach I	16-09-2015	40	1.7	33	1	0
	Radersbach II	16-09-2015	53	2.4	53	0	0
	Radersbach III	16-09-2015	50	2.0	57	1	0
	Radersbach IV	16-09-2015	53	2.1	64	1	0
2016	Radersbach I	14-09-2016	40	1.7	13	1	0
	Radersbach II	14-09-2016	53	2.4	6	0	0
	Radersbach III	14-09-2016	50	2.1	15	0	0
	Radersbach IV	14-09-2016	53	2.1	27	1	0
2017	Radersbach I	13-09-2017	40	1.7	5	2	0
	Radersbach II	13-09-2017	53	2.4	37	0	0
	Radersbach III	13-09-2017	50	2.1	14	2	0
	Radersbach IV	13-09-2017	53	2.1	27	0	0
2018	Radersbach I	17-09-2018	40	1.7	18	3	0
	Radersbach II	17-09-2018	50	2.1	33	0	0
	Radersbach III	17-09-2018	50	2.1	25	0	0
	Radersbach IV	17-09-2018	53	2.1	19	0	0

Table C.2. Steinapiesting stock assessment record.

Year	Sampled stretch	Date	Length (m)	Width (m)	Age-class 0+	1+	2+
2012	Steinapiesting I	17-09-2012	60	4.4	13	26	5
	Steinapiesting III	17-09-2012	60	3.9	11	16	0
2014	Steinapiesting I	17-09-2014	60	4.4	20	24	5
	Steinapiesting III	17-09-2014	50	3.9	5	33	4
2016	Steinapiesting I	22-08-2016	60	4.4	17	13	1
	Steinapiesting III	22-08-2016	50	3.9	8	12	1
2018	Steinapiesting I	13-08-2018	60	4.4	34	7	1
	Steinapiesting III	13-08-2018	50	3.9	8	8	1

Appendix C

Stock assessment records

Table C.3. Urgersbach stock assessment record.

Year	Sampled stretch	Date	Length (m)	Width (m)	Age-class 0+	1+	2+
2011	Urgersbach I	29-09-2011	47	2.2	29	31	3
	Urgersbach III	29-09-2011	49	2.1	57	18	2
2012	Urgersbach I	–	–	–	–	–	–
	Urgersbach III	–	–	–	–	–	–
2013	Urgersbach I	25-09-2013	47	2.2	0	12	5
	Urgersbach III	18-09-2013	49	2.1	4	8	1
2014	Urgersbach I	08-10-2014	47	2.2	14	5	1
	Urgersbach III	08-10-2014	49	2.1	57	3	2
2015	Urgersbach I	15-09-2015	52	2.2	15	14	1
	Urgersbach III	15-09-2015	52	2.2	6	14	0
2016	Urgersbach I	14-09-2016	52	2.2	19	7	1
	Urgersbach III	14-09-2016	52	2.2	37	7	0
2017	Urgersbach I	13-09-2017	52	2.2	7	8	1
	Urgersbach III	13-09-2017	52	2.2	47	4	0
2018	Urgersbach I	17-09-2018	52	2.2	5	9	0
	Urgersbach III	17-09-2018	52	2.2	7	4	0

Table C.4. Zellenbach stock assessment record.

Year	Sampled stretch	Date	Length (m)	Width (m)	Age-class 0+	1+	2+
2011	Zellenbach I	15-09-2011	50	2.8	70	18	1
2012	Zellenbach I	–	–	–	–	–	–
2013	Zellenbach I	18-09-2013	50	2.8	14	22	1
2014	Zellenbach I	16-09-2014	50	2.8	17	9	0
2015	Zellenbach I	15-09-2015	50	2.8	10	17	2
2016	Zellenbach I	14-09-2016	50	2.8	54	2	1
2017	Zellenbach I	13-09-2017	50	2.8	17	7	0
2018	Zellenbach I	–	–	–	–	–	–

Appendix D

## Stream temperature regression models
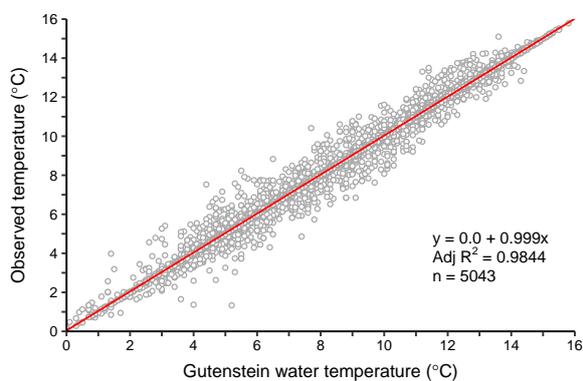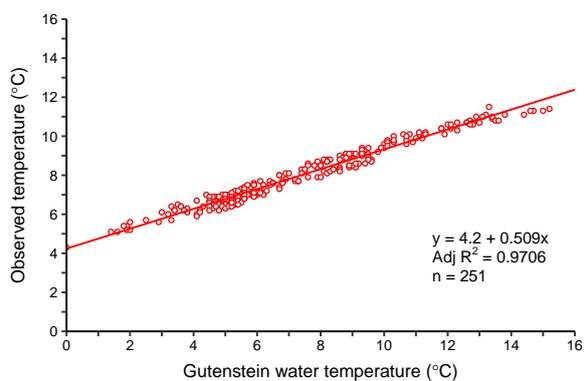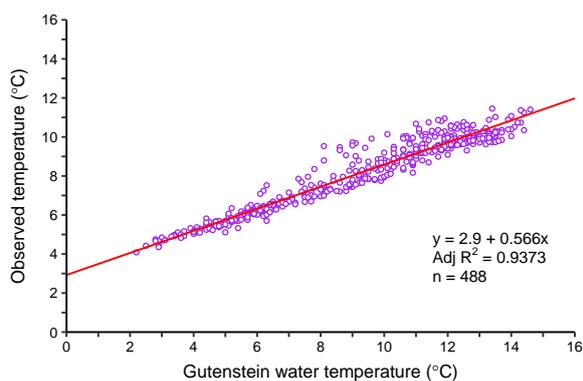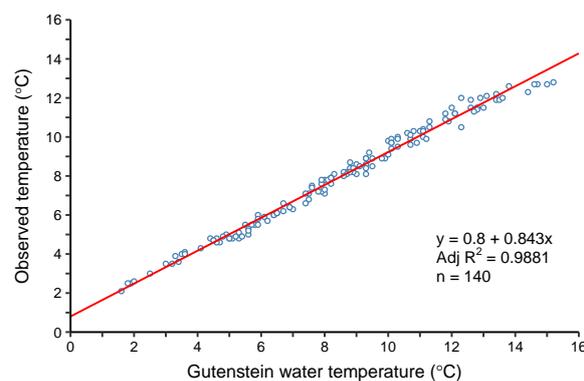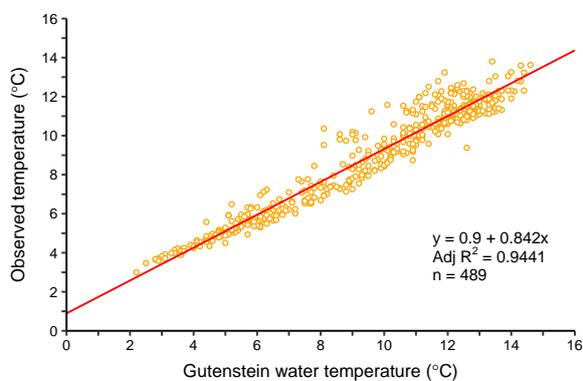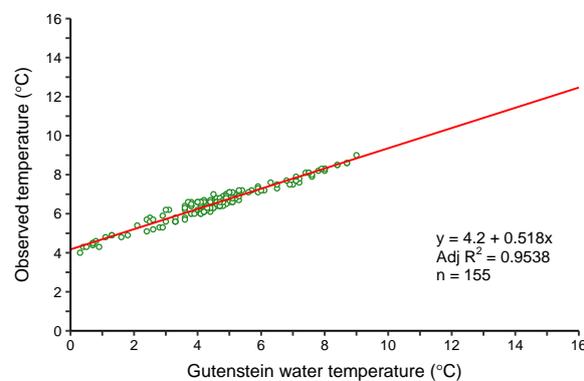
Figure D.1. Linear regression of in-stream temperature monitoring and reported gauging station temperature was used to extrapolate water temperatures of the investigated rivers.

Appendix E

Extrapolated mean water temperature

Table E.1. Kalter Gang mean water temperature for life stages of each cohort year.

		2010 -11	2011 -12	2012 -13	2013 -14	2014 -15	2015 -16	2016 -17	2017 -18	2018 -19
		Mean water temperature (°C)								
Life stage	Temp Summer	12.3	12.1	11.8	12.3	12.1	13.4	12.2	13.2	13.1
	Temp Spawning	5.6	5.7	6.1	6.5	6.9	6.3	5.4	6.6	6.8
	Temp Incubation	5.9	5.1	5.7	6.3	5.7	6.5	6.0	6.3	-
	Temp Early-juvenile	11.2	10.9	11.2	11.1	12.0	11.3	12.0	12.3	-
	Temp Juvenile	12.2	11.2	12.1	11.5	12.9	12.1	12.4	13.0	-
Month	Temp October	8.3	8.6	8.1	9.3	9.5	9.2	8.9	9.3	9.9
	Temp November	7.2	5.6	7.0	7.1	7.9	7.0	6.5	6.9	7.5
	Temp December	3.1	4.5	4.6	5.0	5.4	5.3	4.4	4.8	5.6
	Temp January	3.9	4.0	4.8	4.5	4.7	3.4	2.0	5.4	4.2
	Temp February	4.0	2.3	4.4	4.7	3.8	5.4	4.3	4.1	-
	Temp March	5.3	5.6	4.9	6.2	5.6	5.8	6.4	5.0	-
	Temp April	8.2	7.1	7.6	7.9	7.4	8.4	7.1	9.6	-
	Temp May	9.8	9.5	9.9	8.9	10.1	10.0	10.0	11.5	-
	Temp June	11.6	11.2	11.0	11.4	11.8	11.6	12.6	12.4	-
	Temp July	12.1	12.1	12.7	12.9	14.0	12.4	13.4	13.0	-
	Temp August	12.7	12.0	13.1	12.1	14.1	12.5	13.6	13.9	-
	Temp September	11.7	10.5	11.1	10.8	11.6	11.8	11.1	12.1	-

Table E.2. Radersbach mean water temperature for life stages of each cohort year.

		2010 -11	2011 -12	2012 -13	2013 -14	2014 -15	2015 -16	2016 -17	2017 -18	2018 -19
		Mean water temperature (°C)								
Life stage	Temp Summer	10.5	10.4	10.2	10.5	10.4	11.0	10.4	11.0	10.9
	Temp Spawning	7.1	7.1	7.3	7.5	7.7	7.4	7.0	7.6	7.7
	Temp Incubation	7.2	6.8	7.1	7.4	7.1	7.5	7.3	7.4	-
	Temp Early-juvenile	9.9	9.8	9.9	9.9	10.3	10.0	10.3	10.5	-
	Temp Juvenile	10.4	9.9	10.4	10.1	10.8	10.4	10.5	10.8	-
Month	Temp October	8.4	8.6	8.3	8.9	9.1	8.9	8.8	9.0	9.2
	Temp November	7.9	7.1	7.8	7.8	8.2	7.8	7.5	7.7	8.0
	Temp December	5.8	6.5	6.6	6.8	7.0	6.9	6.5	6.7	7.1
	Temp January	6.2	6.3	6.7	6.5	6.6	6.0	5.2	7.0	6.4
	Temp February	6.3	5.4	6.5	6.6	6.2	7.0	6.4	6.3	-
	Temp March	6.9	7.1	6.7	7.4	7.1	7.2	7.5	6.8	-
	Temp April	8.4	7.8	8.1	8.3	8.0	8.5	7.9	9.1	-
	Temp May	9.2	9.1	9.2	8.8	9.4	9.3	9.3	10.1	-
	Temp June	10.2	9.9	9.8	10.1	10.3	10.1	10.6	10.5	-
	Temp July	10.4	10.4	10.7	10.8	11.4	10.5	11.1	10.9	-
	Temp August	10.7	10.3	10.9	10.4	11.4	10.6	11.2	11.3	-
	Temp September	10.2	9.6	9.9	9.7	10.1	10.2	9.9	10.4	-

Appendix E

Extrapolated mean water temperature

Table E.3. Urgersbach mean water temperature for life stages of each cohort year.

		2010-11	2011-12	2012-13	2013-14	2014-15	2015-16	2016-17	2017-18	2018-19
		Mean water temperature (°C)								
Life stage	Temp Summer	11.1	11.0	10.7	11.1	11.0	12.0	11.0	11.9	11.8
	Temp Spawning	5.5	5.5	5.9	6.2	6.6	6.0	5.4	6.3	6.5
	Temp Incubation	5.7	5.0	5.6	6.1	5.5	6.3	5.8	6.1	-
	Temp Early-juvenile	10.2	10.0	10.2	10.1	10.9	10.3	10.9	11.2	-
	Temp Juvenile	11.1	10.2	11.0	10.4	11.6	11.0	11.2	11.7	-
Month	Temp October	7.7	8.0	7.6	8.6	8.8	8.5	8.3	8.6	9.1
	Temp November	6.9	5.5	6.7	6.7	7.4	6.7	6.3	6.6	7.1
	Temp December	3.3	4.5	4.6	5.0	5.4	5.3	4.5	4.8	5.5
	Temp January	4.0	4.1	4.8	4.6	4.7	3.6	2.4	5.4	4.3
	Temp February	4.2	2.7	4.5	4.7	4.0	5.3	4.4	4.2	-
	Temp March	5.2	5.5	4.9	6.0	5.5	5.6	6.2	5.0	-
	Temp April	7.7	6.7	7.2	7.4	7.0	7.8	6.8	8.9	-
	Temp May	9.1	8.8	9.1	8.3	9.3	9.2	9.2	10.5	-
	Temp June	10.6	10.2	10.0	10.4	10.8	10.6	11.4	11.2	-
	Temp July	10.9	11.0	11.5	11.6	12.6	11.2	12.1	11.8	-
	Temp August	11.4	10.9	11.8	11.0	12.7	11.3	12.3	12.5	-
	Temp September	10.7	9.6	10.2	9.9	10.5	10.7	10.1	11.0	-

Table E.4. Zellenbach mean water temperature for life stages of each cohort year.

		2010-11	2011-12	2012-13	2013-14	2014-15	2015-16	2016-17	2017-18	2018-19
		Mean water temperature (°C)								
Life stage	Temp Summer	10.5	10.4	10.2	10.5	10.5	11.1	10.5	11.0	11.0
	Temp Spawning	7.1	7.1	7.3	7.5	7.7	7.4	7.0	7.6	7.7
	Temp Incubation	7.2	6.8	7.1	7.4	7.1	7.5	7.3	7.4	-
	Temp Early-juvenile	10.0	9.8	10.0	9.9	10.4	10.0	10.4	10.5	-
	Temp Juvenile	10.5	10.0	10.4	10.1	10.8	10.4	10.6	10.9	-
Month	Temp October	8.4	8.6	8.3	9.0	9.1	8.9	8.8	9.0	9.3
	Temp November	7.9	7.0	7.8	7.8	8.2	7.8	7.5	7.7	8.0
	Temp December	5.7	6.5	6.5	6.8	7.0	6.9	6.4	6.7	7.1
	Temp January	6.2	6.2	6.7	6.5	6.6	5.9	5.2	7.0	6.3
	Temp February	6.2	5.4	6.5	6.6	6.1	6.9	6.4	6.3	-
	Temp March	6.9	7.1	6.7	7.4	7.1	7.1	7.5	6.7	-
	Temp April	8.4	7.8	8.1	8.3	8.0	8.5	7.9	9.1	-
	Temp May	9.3	9.1	9.3	8.8	9.4	9.3	9.3	10.1	-
	Temp June	10.2	9.9	9.8	10.1	10.3	10.2	10.7	10.6	-
	Temp July	10.4	10.4	10.8	10.8	11.4	10.6	11.1	10.9	-
	Temp August	10.7	10.4	10.9	10.4	11.5	10.7	11.2	11.3	-
	Temp September	10.2	9.6	9.9	9.8	10.1	10.3	9.9	10.4	-

# Appendix F

Mean annual temperatures
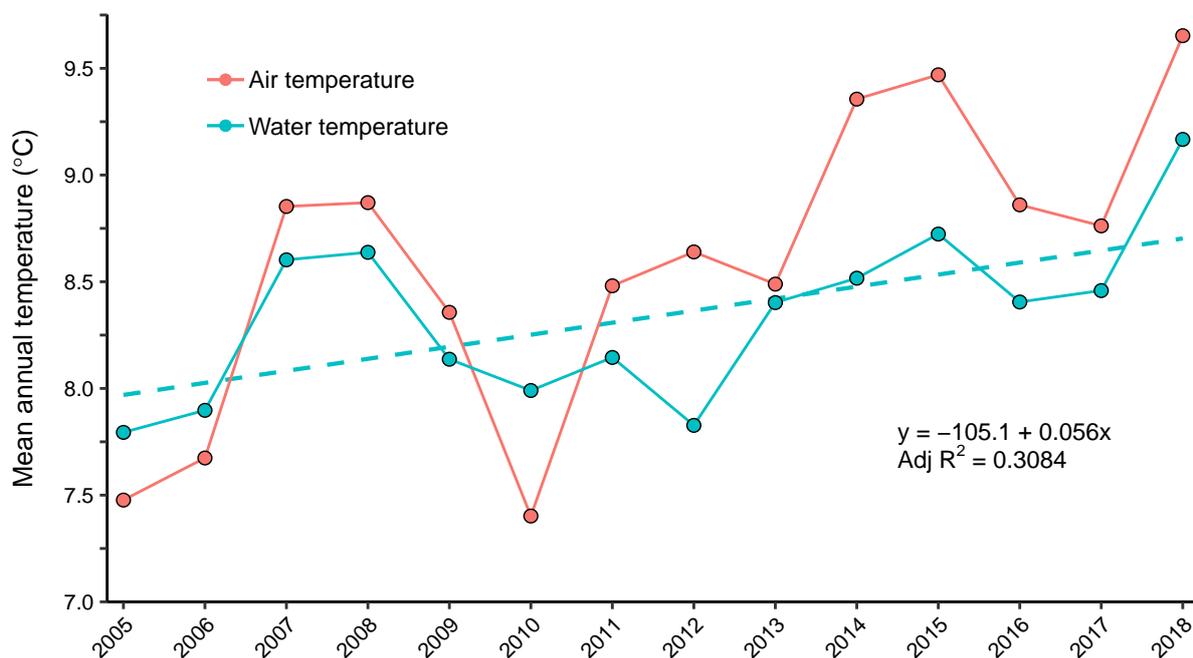
Figure F.1. The mean annual air and water temperatures were recorded at the Gutenstein gauging station. There appeared to be an increase in both temperatures over time from 2005 – 2018. If this trend continues it will pose a risk to the trout populations of the study area.
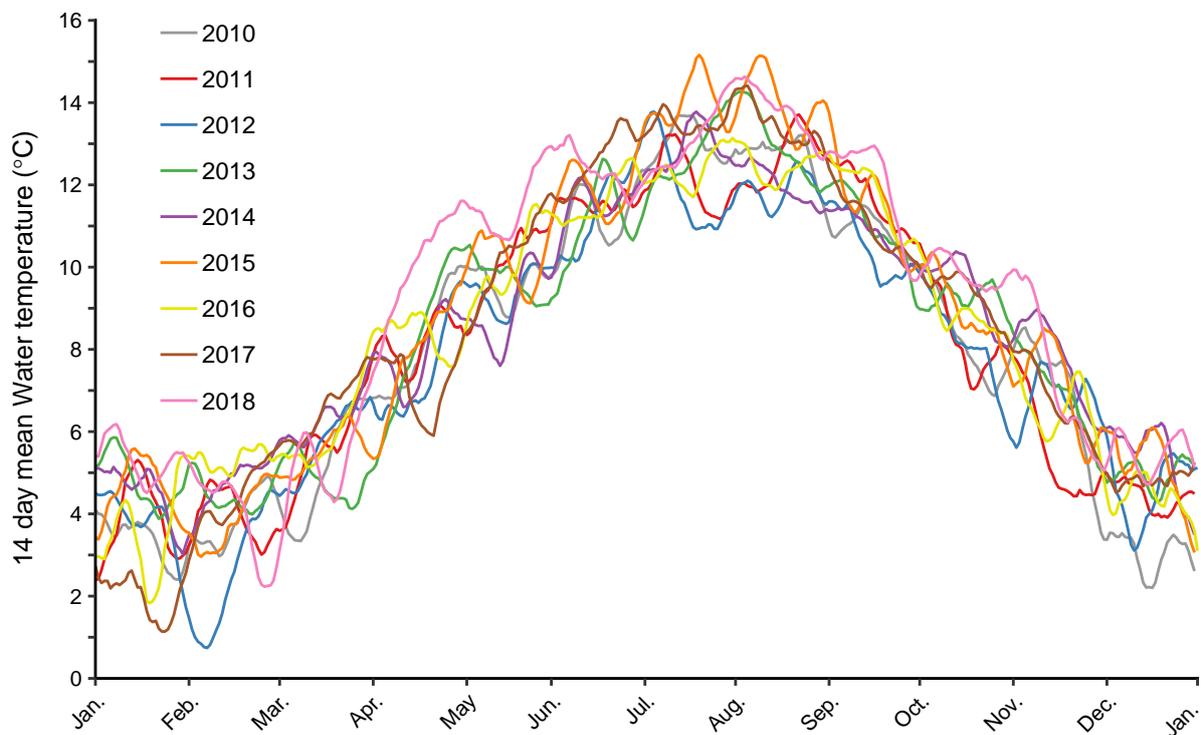

Figure F.2. Yearly 14-day mean water temperature at the Gutenstein gauging station. 2018 had a much warmer spring than the other years.

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Appendix G

Redd density regression
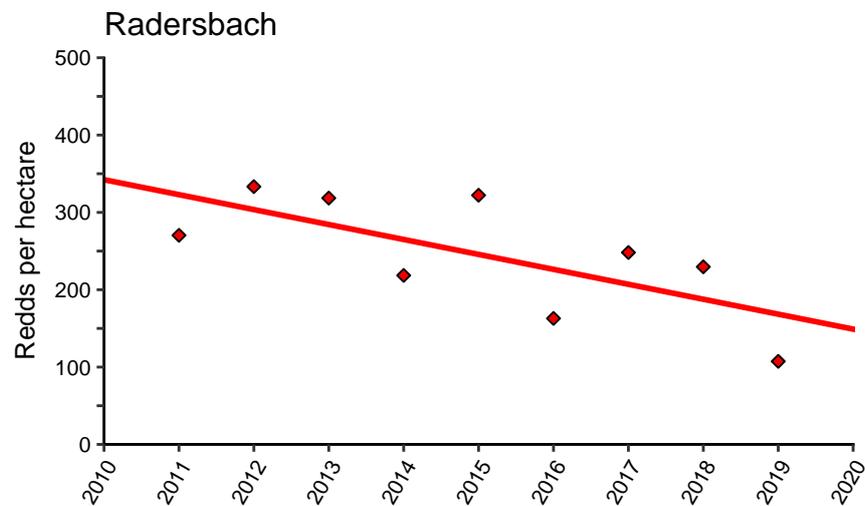
Radersbach

Figure G.1. Linear regression of Radersbach redd density shows a negative trend.
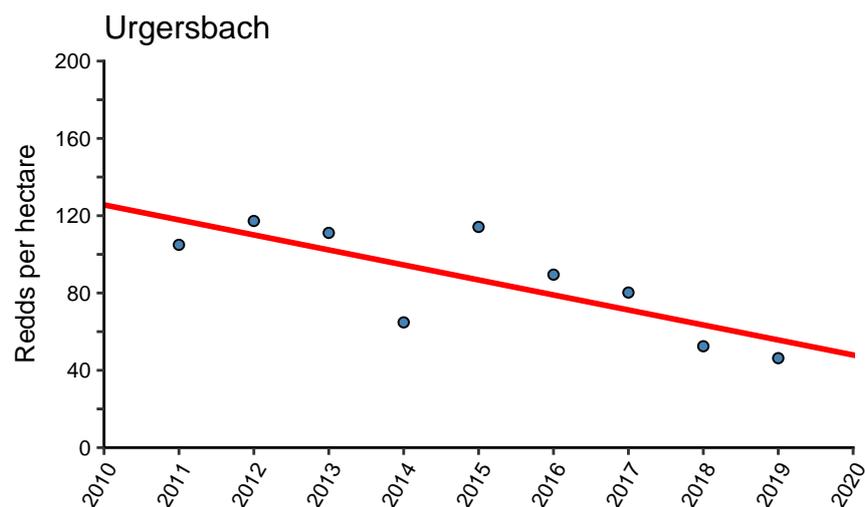
## Urgersbach

Figure G.2. Linear regression of Urgersbach redd density shows a negative trend.
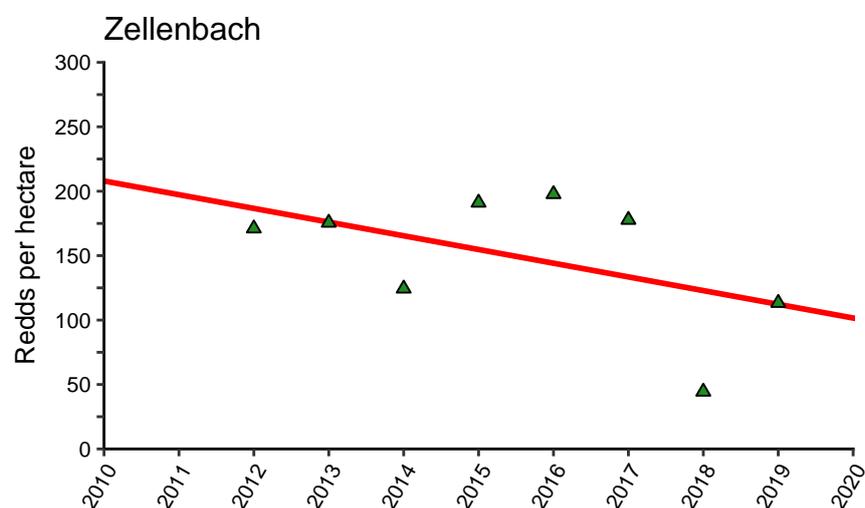
Zellenbach

Figure G.3. Linear regression of Zellenbach redd density shows a negative trend.

Appendix H

Steinapiesting spawning population
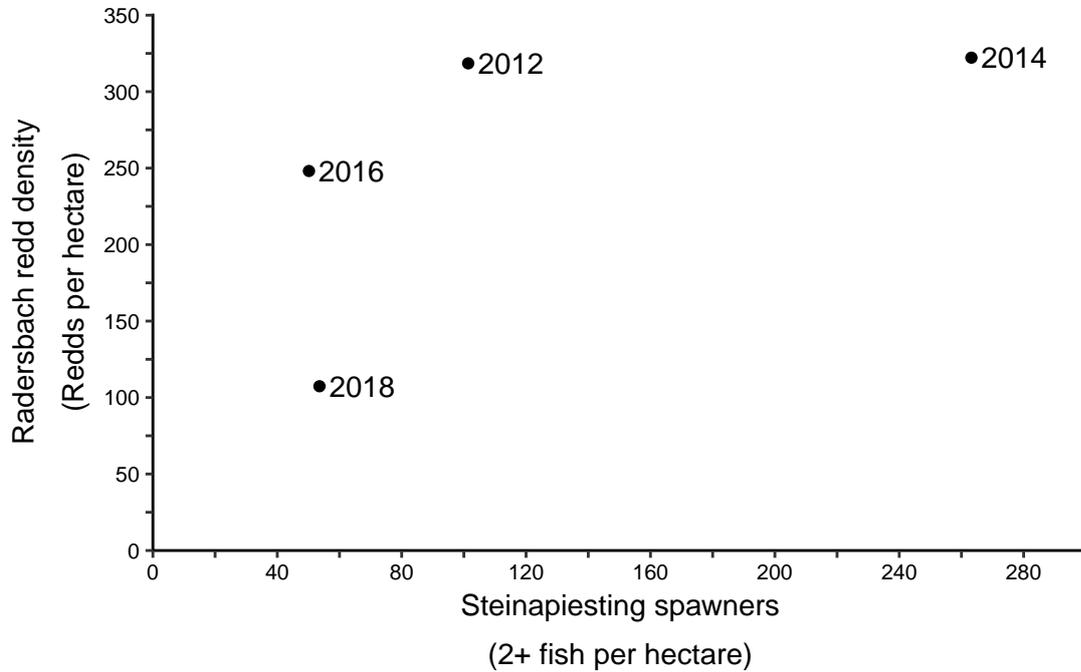
Figure H.1. The spawning population (2+ age-class) of the Steinapiesting was positively correlated with redd density of the Radersbach. This suggested that the adult population of the Steinapiesting used the Radersbach for spawning habitat.
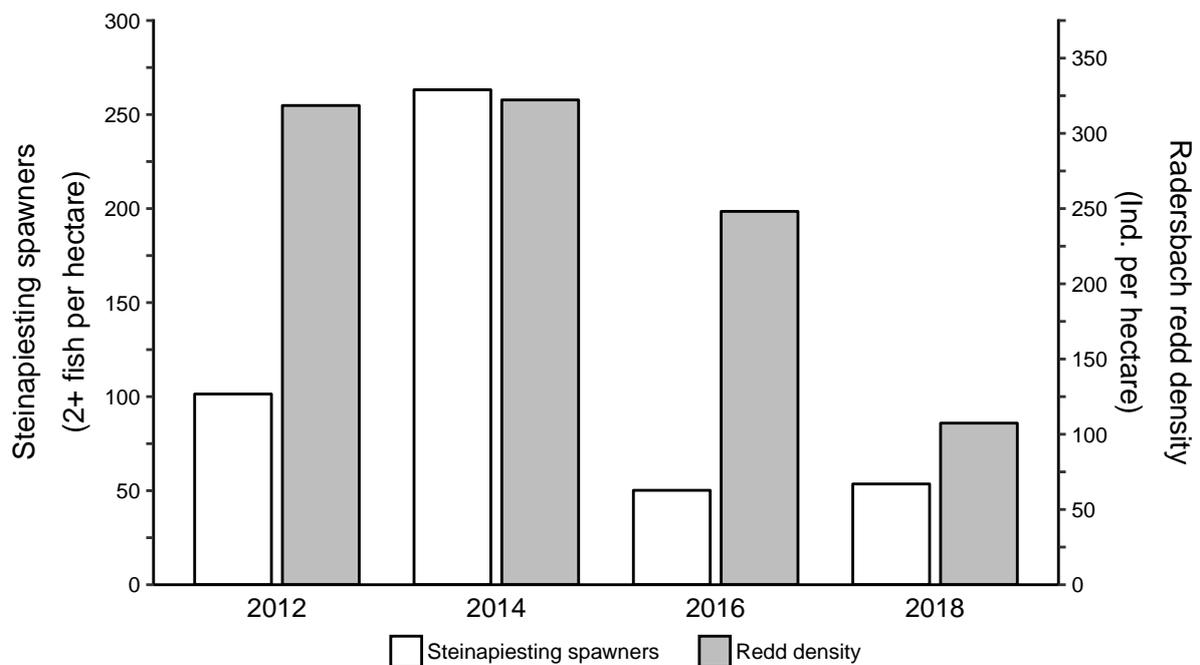

Figure H.2. The abundance of spawners (2+ age-class) in the Steinapiesting showed some evidence of a relationship with the Radersbach redd density. However, the extent of the relation was unclear.