Master Thesis

Effects of management efforts on benthic communities in anthropogenically impacted springs in the Kalkalpen National Park

submitted by

Marc Sonnleitner, BSc

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Supervisor:

Assoc.Prof.Dr. Wolfram Graf

Co-supervisors:

Dipl.-Ing. Dr.nat.techn. Patrick Leitner

Institute of Hydrobiology and Aquatic Ecosystem Management
Department of Water, Atmosphere and Environment

Affidavit

I hereby declare that I have authored this master thesis independently, and that I have not used any assistance other than that which is permitted. The work contained herein is my own except where explicitly stated otherwise. All ideas taken in wording or in basic content from unpublished sources or from published literature are duly identified and cited, and the precise references included.

I further declare that this master thesis has not been submitted, in whole or in part, in the same or a similar form, to any other educational institution as part of the requirements for an academic degree.

I hereby confirm that I am familiar with the standards of Scientific Integrity and with the guidelines of Good Scientific Practice, and that this work fully complies with these standards and guidelines.

Vienna, 24th November 2022   Marc SONNLEITNER *(manu propria)*

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Abstract

Springs are ecotones, not only inhabited by typical spring taxa (crenobionts), but also by groundwater and (spring-)brook elements. Crenobionts are highly specialised organisms which are adapted to the stable abiotic conditions, such as water temperature and discharge. In general, springs are habitats of many small-scale endemic species of the Alps underlining their conservation value. However, their small dimensions make springs vulnerable to disturbances by human cultivation. In the Austrian Kalkalpen National Park, pasture farming, which exposes springs to a multitude of stressors, has been carried out for several centuries. Overgrazing by cattle in particular has pronounced negative impacts on the quality of a habitat. While riparian vegetation is removed, the amount of fine sediments and the organic load are increased and benthic communities are severely altered. To counteract this development, a LIFE project was set up to identify altered spring biotopes and start a monitoring campaign to evaluate management activities. In 2000, emergence traps were set up at four springs in the conservation zone of the National Park. This study analyses the collected data, evaluates the effects of protection fences and investigates how stressors in the surrounding area interfere with the restoration process. The results indicate that protection fences alone are not able to restore near-natural conditions in the investigated springs. In one spring, a high share of specific stoneflies indicative for pre-restoration conditions was observed even 20 years after restoration. Nevertheless, four alpine endemic species and twelve species listed in the Red List of endangered caddisflies (Trichoptera) were documented in these springs, emphasising how important springs are for Austrian biodiversity. These facts underline that springs are vulnerable biotopes which require stringent management activities and a complete removal of stressors.

Kurzfassung

Quellen sind sogenannte Ökotone, die nicht nur von Quellspezialisten (Krenobionten), sondern auch von Grundwasser- und (Quell-)Bachbewohnern beheimatet werden. Krenobionten sind hoch spezialisierte Organismen, die an die konstante Wassertemperatur und -schüttung angepasst sind. Grundsätzlich werden Quellen von einer Vielzahl an Alpenendemiten bewohnt, was ihre naturschutzfachliche Relevanz unterstreicht. Quellen reagieren jedoch aufgrund ihrer Kleinräumlichkeit besonders sensibel auf anthropogene Beeinträchtigungen. Die Flächen des Nationalparks Kalkalpen werden schon seit mehreren Jahrhunderten almwirtschaftlich genutzt, wodurch die darauf befindlichen Quellen stark beeinträchtigt werden. Überweidung im Bereich von Quellen führt zu einem Verlust der Ufervegetation, einem verschlammten Quellabfluss und hoher organischer Belastung. Durch diese Beeinträchtigungen wird auch die aquatische Lebensgemeinschaft der Quelle stark verändert. Um die Managementziele des Nationalparks zu erreichen, wurde im Jahr 2000 ein LIFE-Projekt gestartet. Im Zuge dessen wurden vier beeinträchtigte Quellen mit Schutzzäunen, die den Zutritt von Weidevieh verhindern, und Emergenzfallen, die der biologischen Zustandsüberwachung dienen, ausgestattet. Diese Arbeit untersucht nun die positiven Effekte der Schutzzäune und versucht abzubilden, wie anderweitige Beeinträchtigungen der Quellen den Renaturierungserfolg vermindern. Die Resultate zeigen, dass Schutzzäune allein nicht in der Lage sind, den natürlichen Zustand in Quellen wiederherzustellen. So zeichnete sich beispielsweise die benthische Lebensgemeinschaft einer untersuchten Quelle, selbst 20 Jahre nach der Umzäunung, durch untypische Schlammbewohner aus. Dies unterstreicht, wie sensibel Quellen auf menschliche Eingriffe reagieren und die Notwendigkeit von konsequentem Naturschutz. Weiters zeigen die Funde von vier Alpenendemiten und zwölf Rote-Liste-Arten, welch wichtigen Beitrag Quellen zu Österreichs Biodiversität leisten.

1. Introduction

Springs are "emotionally appealing and fascinating biotopes" (Zollhöfer, 2000). Traditionally, they have been conceived as pure and pristine spots of nature (Cantonati et al., 2006). Furthermore, they are "highly valued by human society" and used for various purposes such as recreational activities, irrigation or drinking water (Barquín & Scarsbrook, 2008). However, these ways of utilisation compromise the natural conditions of springs. As a result, springs belong to the most endangered aquatic habitats (Cantonati et al., 2006). Although spring research has received more attention in the past 50 years, a detailed understanding of the interactions between the biocenoses and relevant human stressors is still missing (Cantonati et al., 2012; Hahn, 2000; Von Fumetti, 2008). It is of utmost importance to bridge this knowledge gap since springs are "important freshwater sites maintaining high biodiversity, especially in mountainous regions" (Berlajolli et al., 2019). This is further underlined by the fact that "springs and subterranean systems support the highest proportion of threatened freshwater species" (Collier et al., 2016).

In addition, headwater streams (1st and 2nd order streams according to the system of Strahler (1952)), "compose over two-thirds of total stream length in a typical river drainage" (Freeman et al., 2007) and thus substantially influence the chemical, biological and hydromorphological conditions of a catchment (Barmuta et al., 2009).

1.1. Springs – A Conceptual Approach

River zonation has been a topic in limnological research for more than a century. Illies and Botosaneanu (1963) summed up attempts of colleagues who tried to arrange "whole water-courses into types", divide them "in sections or zones" or proposed a classification according to patterns of their substrate. They found river zonation based on the encountered fauna to be most fitting, as their biocenotic shift reflects downstream changes of oxygen, temperature and substrate (Illies, 1961). Nevertheless, a holistic approach which includes all organisms (not only fish, e. g. Huet (1949)) was needed. Subsequently, Illies and Botosaneanu used results of entomological investigations in the Fulda river (Illies, 1953) to demonstrate downstream changes of invertebrate communities. As a result, the "rhithron-potamon concept" was developed and has since been continuously used in limnological research (Chovanec, 2022; Roux et al., 1992; Zwick, 1992). The biocenotic distinction of the rithron and potamon can be applied on a global scale, however their respective extent varies depending on the distance to the equator, as this parameter significantly affects the climate (Figure 1, Illies (1961)).

The rhithron-potamon concept (Figure 1) describes the crenon as the uppermost section of running waters, followed by the rhithron and potamon. Illies (1952) suggested that the crenon ends where the annual water temperature amplitude exceeds 5 °C. The point where the monthly mean temperatures differ more than 20 °C was proposed as the lower border of the rhithron (Illies, 1961). The division of the crenon into the eucrenal (immediate area where water emerges) and the hypocrenal (springbrook) zone was first described by Thienemann (1926). In limno- and helocrenes, spatial delineation can be based on the morphological uniqueness of the springmouth (see chapter 1.2). Thus, the eucrenal ends at the point where the run-off forms a channel (i. e. the springbrook). In rheocrenes, however, difficulties arise from the delimitation of the eu- and hypocrenal because their respective morphology is similar. Hence, limnologists have proposed to use water temperature amplitudes (Erman & Erman, 1995) or distance from the spring source (Von Fumetti, 2008) as parameters for spatial delineation.
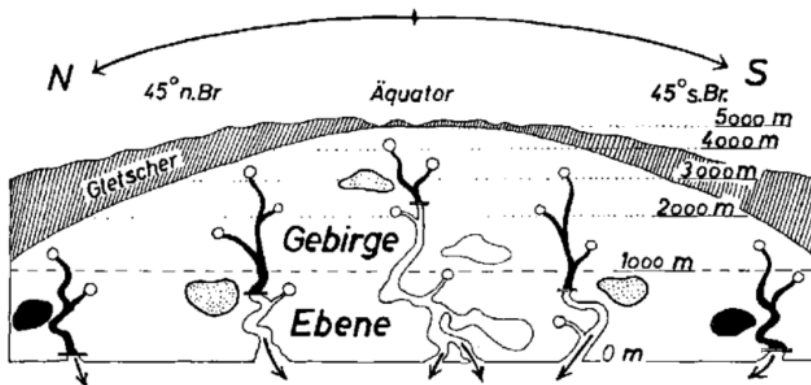
Figure 1: Representation of the "rhithron-potamon concept" showing the three sections of a river: the crenon (white circles), the rhithron (black lines) and the potamon (white lines). It also shows how the extent of the rhithron and the potamon depends on the distance to the equator (Illies, 1961).

The river continuum concept (RCC) was developed by Vannote et al. (1980). It describes how physical gradients, biotic communities, ratio of production and consumption as well as nutrient transport develop along a river system (Figure 2). Additionally, they grouped the biotic communities into those of headwaters, medium-sized streams and large rivers, but did not explicitly mention communities in springs. According to the RCC, headwater streams are highly influenced by riparian vegetation. This manifests itself in high input of coarse particulate organic matter (CPOM) and shading, which "reduces autotrophic production" (Vannote et al., 1980). The functional feeding groups (FFG) of shredders and collectors are expected to dominate the benthic communities since CPOM and fine particulate organic matter (FPOM) respectively are their main food source.
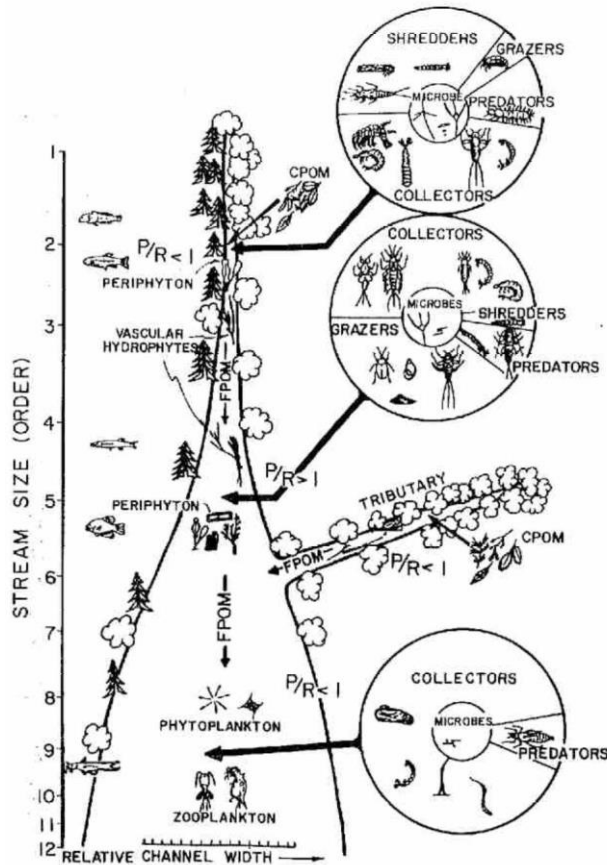
Figure 2: The River Continuum Concept (Vannote et al., 1980).

1.2. Spring Typology

A spring is the immediate area where groundwater surfaces (Cantonati et al., 2006). Its characteristics are governed by the geology and hydrology of the catchment, but since a detailed assessment of the geological situation on-site is often difficult and hydrological long-term records are only rarely available, springs can also be categorised based on the flow pattern at the source (Projektgruppe Aktionsprogramm Quellen, 2004). In this context, Steinmann (1915) and Thienemann (1926) were the first to distinguish between rheocrenes, limnocrenes and helocrenes.

However, this simplified approach fails to capture the typological diversity that actually exists in nature (Di Sabatino et al., 2003; Erman, 2002; Gerecke et al., 2005; Govoni et al., 2018; Stevens et al., 2021). In recent years, limnologists have tried to classify springs using both abiotic and biotic parameters (Bonettini & Cantonati, 1996; Roca & Baltanas, 1993; Von Fumetti, 2008). These works seemingly show "incongruous" results, but in that way "demonstrate the polymorphic character of these biotopes" (Hahn, 2000). Govoni et al. (2018) mentioned further difficulties arising from ambiguity and inconsistency in terminology regarding spring type definition.

For conservation issues, guidelines have been published to help identifying the typology of a spring (Küry et al., 2019; Projektgruppe Aktionsprogramm Quellen, 2004). However, they contain regionally defined definitions and are thus not suitable for operation outside the original region.

Nevertheless, the first-mentioned classification by Steinmann (1915) and Thienemann (1926) is considered to be adequate in the context of this thesis and will be developed in the subsequent paragraphs. This categorisation is also deemed suitable by Reiss et al. (2016) who concludes that this "relatively simple classification is a helpful tool for a first rough assessment of a spring habitat, especially when laypersons are involved", which is commonly the case in nature conservation projects.

Rheocrenes

Rheocrenes (rhéō [greek]: flow; kren-, kreno- [greek]: spring) are "characterised by a single point of outflow" (Biggs et al., 2017), show strong flow (Cantonati et al., 2012) and exhibit a high share of coarse inorganic substrate (Brehm, 1930; Hahn, 2000). Cantonati et al. (2006) describe high current velocity as one of the most important factors in rheocrenes. In low flow sections of forested rheocrenes, accumulations of fallen leaves can develop (Martin & Rückert, 2011).

Limnocrenes

In limnocrenes (límnē [greek]: pond; kren-, kreno- [greek]: spring), discharge emerges "in a natural basin" (Biggs et al., 2017) and forms a stillwater body (Gerecke et al., 2005). Due to missing dynamics due to the low flow velocity in this "pond or lake" (Barquín & Scarsbrook, 2008), the substrate is typically muddy, and abundant macrophyte communities can be observed (Brehm, 1930; Di Sabatino et al., 2003).

Helocrenes

Helocrenes (hélos [greek]: marsh; kren-, kreno- [greek]: spring) are characterised by diffuse emergence of water which creates an extensive swampy zone (Pokorny et al., 2012; Von Fumetti, 2008). Water then runs off through the boggy vegetation (Geissler, 1976). The substrate is dominated by mud which is overlaid by coarse detritus (Martin & Rückert, 2011).

Helocrenes are often referred to as "seepages" (Cantonati et al., 2012; van der Kamp, 1995).

1.3. Crenotypical Characteristics

As opposed to their downstream counterparts, springs in general maintain a typical milieu constancy throughout the year (J. Fischer, 1996). The following paragraphs will focus on the description of typical permanent springs in Austria occurring at the montane level (800 to 1,200 m a.s.l.). In a natural state, these springs are located in beech (submontane) or mixed beech-fir forests (montane, Tappiser (2000)). However, it should be noted that there are springs with completely different conditions (e. g. thermal springs).

Temperature

"Springs are the aquatic ecologist's natural constant temperature laboratory" (Odum, 1971). This figurative phrasing by Odum (1971) holds true for a number of reasons. The low water temperature deviations in springs are mainly due to their strong connection to the nearly isothermic groundwater body (Gräsle & Beierkuhnlein, 1999). In rheocrenes, the small spatial and temporal extent in which atmospheric air can interact with the water body also contributes to nearly constant temperatures (Gräsle & Beierkuhnlein, 1999). As a result, the water temperature typically mirrors the annual average air temperature in the area of the spring (Gerecke, 2016; van der Kamp, 1995). In addition, the strong influence of riparian vegetation reduces the energy input from radiation (Haase, 2003; Vannote et al., 1980).

Oxygen content

As precipitation water is enriched with CO_2 from the atmosphere and the penetrated soil, reduction processes occur within the vadose (unsaturated) zone (van der Kamp, 1995). However, "oxygenation of reduced groundwaters […] occurs rapidly at springheads" (Barquín & Scarsbrook, 2008), causing a steep downstream gradient of oxygen content (Pešić et al., 2016). The constantly low water temperatures of spring water promote high levels of dissolved oxygen.

A study by Von Fumetti and Nagel (2011) revealed that all investigated springs were nearly saturated with oxygen (> 90 %). Hahn (2000), however, observed significantly lower oxygen concentrations in helocrenes than in rheocrenes, which can be explained by the difference in substrate composition and flow patterns. The coarse substrate in rheocrenes causes turbulences, which foster the entry of atmospheric O_2 into the water (Illies, 1961). Furthermore, springs in lowlands typically have lower oxygen contents than springs in alpine regions (Wittrock, 2005).

Hydrology

The hydrological conditions can also be regarded as being stable, but depend on a variety of factors, such as geology, retention capability, size of catchment and precipitation (Hölting & Coldewey, 2013; van der Kamp, 1995). In general, springs are not subjected to bed moving spates (Zollhöfer, 1999).

Permanence and constancy of flow have been described as being the "all-important condition" in "determining community composition" in springs (Erman, 2002; Smith & Wood, 2002). A study into karstic lowland streams suggested that discharge variability had a stronger influence on benthic invertebrate composition than habitat structure (Smith et al., 2003).

Aquatic systems which occasionally dry up are commonly referred to as being intermittent, while those that do not are called permanent (Allan, 2007). In springs, these hydrological differences result in remarkable differences in macroinvertebrate communities. Scarsbrook et al. (2007) discovered that permanent springs not only showed higher taxa richness, but were also inhabited by taxa of "relatively low mobility", while intermittent springs were dominated by multivoltine taxa and species with high mobility.

As a result of the generally low average discharge levels in most springs (< 1 m^3/s), the ability to transport sediments and bedload is low (Hölting & Coldewey, 2013; Zollhöfer, 1999). However, high flow situations may lead to "bed scouring and mass movement of sediment", especially in areas with a high slope gradient (Barmuta et al., 2009).

Production and consumption processes

In forested rheocrenes, shading from riparian vegetation leads to low light conditions, which a "paucity of primary producers" (Anderson & James, 1979). Thus, "that the majority of the energy supplied to the food web derives from organic matter and microbial activity, and mostly originates as terrestrial production outside the stream channel" (Allan, 2007). The influence of bank vegetation as nutrient supply is amplified by the small size of springs (Barquín & Scarsbrook, 2008). In general, nutrient input from riparian vegetation occurs in the form of particulate organic matter (e. g. leaves, woody debris, …) (J. Fischer, 1996; Kauffman & Krueger, 1984) which is broken down by a high share of shredders in the invertebrate community (Barmuta et al., 2009). As CPOM becomes entrapped within small-sized systems, it is "transformed into other organic matter size classes" and then exported as FPOM (Allan, 2007).

Von Fumetti and Nagel (2011) distinguished different types of springs on the basis of their trophic structure and identified three groups: lotic, lentic and mixed systems. In lotic springs with strong flow, leaf litter is transported away, while coarse substrate facilitates the growth of periphyton. These springs were indicated by scraper dominated community. Lentic springs with slow discharge were characterised by "organic substance and clay" where "the input of allochthonous material, which is then converted into CPOM and finally FPOM, is more important and constant" and taken up by filtering collectors (Von Fumetti & Nagel, 2011). In the context of their paper, the intermediate form was limestone springs which are characterised by terraces or calcite stairs. In such springs, the sudden

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release of CO_2 at the springmouth leads to deposition of biogenic (tufa) or abiogenic (sinter) material forming stair-like structures (Projektgruppe Aktionsprogramm Quellen, 2004). Von Fumetti and Nagel (2011) argued that the terraces served as CPOM and FPOM sinks explaining the high share of shredders and collectors. However, these terrace-like structures might also develop in crystalline springs from the naturally present large substrate.

1.4. Crenobiology

Species restricted to crenic habitats are referred to as crenobionts, while those that rarely inhabit other freshwater biotopes are called crenophils (Cantonati et al., 2006). Due to the significant habitat differences among springs (chapter 1.2), crenobionts exhibit individual preferences for specific spring types (Martin & Rückert, 2011). J. Fischer et al. (1998) observed a share of crenobionts and -phils in natural freshwater springs, which amounted to 47.6 %. Other studies, however, found the share of spring-bound organisms to be highly variable (0 to 50 %) (Von Fumetti et al., 2017).

The reasons of stenotopy (see chapter 1.6) towards spring habitats have been a topic in crenobiology for a long time. It was long assumed that many typical spring taxa are cold stenotherms which are adapted to constantly low water temperatures. However, recent studies have shown that constantly low temperatures are only one of several factors contributing to spring stenotopy (J. Fischer, 1996; Von Fumetti et al., 2006; Von Fumetti, 2008) or questioned cold stenothermicity of crenobionts altogether (Wittrock et al., 2007). Other factors contributing to spring stenotopy of organisms are summarised in Table 1.

Table 1: Hypothesised reasons for spring stenotopy of organisms.

Springs are refugial habitats for late glacial relicts (e. g. *Apatania muliebris*)	J. Fischer(1996) and Nielsen (1950)
Outcompetition in rhithral habitats by rithrophils; shift to crenal habitats due to higher tolerance	Nielsen (1950) and Thienemann (1950, pp. 522–528)
Constant presence of wet areas which never freeze (Diptera)	Wagner et al. (1998)
Low density of competing predators (e. g. *Pedicia rivosa*)	J. Fischer (1996)

1.4.1. Aquatic vertebrates

According to Cantonati et al. (2006), with the only exception of strong flowing rheocrenes, fish are completely missing in springs of the Alps. Because fish, which are "important predators of salamander larvae" (Manenti et al., 2009), are absent, springs serve as fitting habitat for the salamander (*Salamandra salamandra*). However, salamander larvae need "springs in medium to low altitudes with

areas of very low currents" and thus preferably inhabit limnocrenes (Cantonati et al., 2006). They most commonly occur within altitudes of 400-700m (Maletzky, 2001).

1.4.2. Aquatic invertebrates

Groups of animals with a high share of real crenobionts are water mites (Hydrachnida) and mud snails (Hydrobiidae) (Cantonati et al., 2006). However, the crenocenosis consists of several other partly discrete cenoses (J. Fischer, 1996).

Regarding the longitudinal gradient, springs constitute the transition zone between groundwater and surface waters. They can thus be defined as ecotones which are inhabited in general by a highly specialised and diversified fauna (Barquín & Scarsbrook, 2008; Di Sabatino et al., 2003; Pešić et al., 2016; Weigand & Tockner, 1996). In particular, species typically living in the bordering habitats of groundwater (phreatobionts = inhabitants of subterranean waters; stygobionts = true groundwater inhabitants; troglobionts = cave inhabitants (Fritsch, 2018)) and the epirhithral can also be found in the crenon (Cantonati et al., 2006; Scarsbrook et al., 2007; Zollhöfer, 1999). Migration or colonisation of these organisms can occur against the current (e. g. the Turbellaria species *Crenobia alpina*) or downstream via drift and upstream via flight for egg deposition (Cantonati et al., 2006; Elliott & Tullett, 1977). Furthermore, Kureck (1967) proved nocturnal migration patterns between underground and surface water for foraging in the Amphipod species *Niphargus aquilex*.

When looking at the cross-section of springs, additional faunal communities can be identified while following the lateral gradient to the terrestrial surroundings. Thienemann (1910) defined the "Fauna Hygropetrica" in areas where stones are constantly overflowed with a thin layer of water. If various other surfaces such as moss or mud are overflowed with a thin water layer, the habitat is called madicolous (Vaillant, 1955). Specialists show adaptations to these particular habitats, such as reduction of swimming hair on the tarsi, specific respiration strategies and feeding on diatoms or organic particles being washed up by the water or sticking to the substrate surface (Brehm, 1930; Graf, 2014; Thienemann, 1910). In Austria, several Diptera families (Psychodidae, Stratiomyidae, Dixidae) and three Trichoptera genera (*Tinodes*, *Stactobia*, *Microptila*) inhabit hygropetric habitats (Graf, 2014; Malicky, 2014). The "Fauna Limnaria" occurring on the semi-aquatic habitat bordering the terrestrial surroundings, which was first described by Feuerborn-Kiel (1922), "mainly consists of leaf-consuming Diptera larvae" (J. Fischer, 1996).

In the vertical dimension, the pore system within the bed sediments, the interstices, can be identified as distinct habitat for invertebrates (Brunke et al., 2015) in addition to the benthic region. As described by Schwoerbel (1964), the hyporheal may act as a refugium from current, which is especially important for the development of eggs and early instars, as well as from temperature fluctuations and predation.

During inhospitable situations on the surface, specialists with slender bodies (e. g. stoneflies of the genera *Leuctra* and *Capnia*) have evolutional advantages to retreat and navigate within the interstitial system. In general, "a large majority of the hyporheic fauna is represented by arthropods: crustaceans, insects and water mites" (Käser, 2010).

However, large mineral substrate, which is typically missing in helocrenes and limnocrenes (see chapter 1.2), is a precondition for the development of interstices (Brunke et al., 2015).

It can be concluded that even though these habitats may occur in other aquatic systems, springs offer them in small spatial dimensions, creating a mosaic-like structure with high microhabitat heterogeneity (Cantonati et al., 2006).

1.4.3. Macrophytes/mosses

Geissler (1976) mentioned that springs are characterised by their moss cover rather than their representative spermatophytes. Byrophytes can develop even under low light conditions as they "are shade adapted", which manifests itself in "very low light compensation and light saturation points" (Barmuta et al., 2009; Glime, 2021b, 2021c).

Mosses create a transitional habitat, serve as shelter, food source and are known to increase biodiversity (Bottazzi et al., 2011; Cummins & Klug, 1979; Glime, 2021a). Typical moss communities of alpine springs are described in Geissler (1976). According to Tomaselli et al. (2011) "the classes *Platyhypnidio-Fontinalietea antipyreticae* and *Montio-Cardaminetea* subsume most of what is regarded as "crenic vegetation". This work also states that crenic vegetation composition depends on alkalinity, pH level, discharge, temperature and the size of the spring.

1.5. Endangered Species and Taxa with Restricted Distribution

To fight the ongoing biodiversity crisis, which is much more pronounced in aquatic than terrestrial ecosystems, already endangered species (Red List) and those with restricted distribution ranges (endemics) require special attention (Cantonati et al., 2012).

Species are classified as being endemic if they occur within a specific area and nowhere else (Gaston, 1994), and thus represent an area's contribution to global biodiversity (Rabitsch et al., 2016). Crenic habitats in particular are inhabited by a large number of endemic species (Cantonati et al., 2012; Di Sabatino et al., 2003). This is mainly due to the insular character of springs which causes "low gene flow and local radiation" (Dudgeon et al., 2006). According to an analysis of five invertebrate groups with the highest amount of endemic species in Austria carried out by Rabitsch et al. (2016), the north-eastern calcareous Alps harbour the highest number of endemics. Out of the 361 species (representing 62 % of endemists in Austria), 75 (21 %) are aquatic.

To provide a tool which monitors the progress towards reaching the goals of the European Union's biodiversity strategy, the International Union for Conservation of Nature (IUCN) Red List was developed. It contains information on the risk for extinction of species on a global or regional level (IUCN, 2012). At the regional level, the classifications "Vulnerable (VU)", "Endangered (EN)" and "Critically Endangered (CR)" were described as "Threatened categories". Species belonging to one of these categories will be referred to as "threatened" in this thesis. Compared to other aquatic biotopes, springs harbour a disproportionately high share of Red List species (Cantonati et al., 2012). In their study from 2011, for example, Martin and Rückert found that 57.5 % of all taxa for which a Red List existed were threatened.

1.6.   Status Assessment Using Biological Indicators

Thienemann (1950) laid the foundation for the utilisation of aquatic organisms as status indicators by recapitulating the concept of ecological valence. He suggested that the distribution and abundance of an organism not only depends on the sum of exogenous conditions, but also on how the organism can use its environment. Every organism can develop in a range of environmental conditions (ranging from a minimum to a maximum), but reaches maximum development at the optimum (Figure 3).

Subsequently, organisms with a broad tolerance range which occur in different biotopes were referred to as being "eurytopic" (generalists), while those with a narrow tolerance range which only occur in similar biotopes were called "stenotopic" (specialists) (Thienemann, 1950).
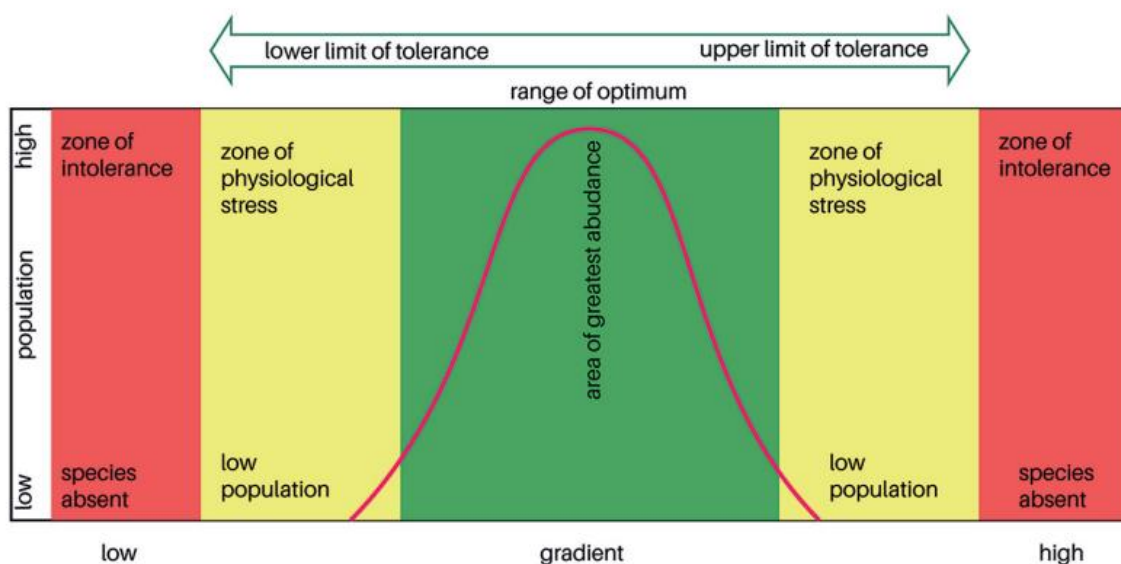

Figure 3: Representation of ecological valence (Ternjej & Mihaljevic, 2017).
The red line shows abundance being greatest in the optimum (green area). Population first decreases (yellow) due to changes in the environment until the limit of tolerance is reached (green arrow above). If conditions are outside the tolerance zone (red area), the species is absent.

Status assessment methods (e. g. Moog and Hartmann (2017)) use this concept to derive prevailing environmental conditions based on the distribution and abundance of certain organisms (Moog & Hartmann, 2017). Austria ("Fauna Aquatica Austriaca" (FAA), Moog (1995)) and Germany ("Ökologische Typisierung der aquatischen Makrofauna", Schmedtje and Colling (1996)) were the pioneers in creating catalogues containing autoecological information on aquatic macroinvertebrates. These methods use numerical classifications to reflect the preferences of an organism to certain conditions (e. g. degree of organic pollution) or their feeding behaviour (Schmidt-Kloiber et al., 2021). The most broadly used point system is the "ten point assignment system" introduced by Zelinka and Marvan (1961) "for the classification of saprobic valences" (Schmidt-Kloiber et al., 2021). Examples are given in Table 2.

Table 2: An example of the numerical classification for the caddisfly Ernodes articularis (EUC = Eucrenal, HYC = Hypocrenal, ERH = Epirhithral, MRH = Metarhithral, HRH = Hyporhithral, EPO = Epipotamal, MPO = Metapotamal, HPO = Hypopotamal, LIT = Littoral, PRO = Profundal; SHR = Shredder; GRA = Grazer, AFIL = Active filter feeder, PFIL = Passive filter feeder, DET = Detritivore, MIN = Miner, XYL = Xylophag, PRE = Predator, PAR = Parasite, OTH = Other; X = Xenosaprob, O = Oligosaprob, b-m = Beta-Mesosaprob, A-M = Alpha-Mesosaprob, P = Polysaprob; Data taken from?? Graf, Grasser, and Waringer (2017)).

Ernodes articularis										
Longitudinal zonation	EUC	HYC	ERH	MRH	HRH	EPO	MPO	HPO	LIT	PRO
Value	9	1	0	0	0	0	0	0	0	0
Functional feeding guild	SHR	GRA	AFIL	PFIL	DET	MIN	XYL	PRE	PAR	OTH
Value	5	0	0	0	5	ß	0	0	0	0
Saprobity class	X	O	B-M	A-M	P					
Value	5	5	0	0	0					

Additionally, recent studies have underlined that benthic invertebrate communities can be used to detect alterations in the hydromorphological regime as well as the composition of sediments (Hering et al., 2004; Lorenz et al., 2004; Ofenböck et al., 2004; Ofenböck et al., 2019; Von der Ohe & Goedkoop, 2013). The following chapters will show how benthic invertebrate communities can be used to draw conclusions on the prevailing conditions of aquatic ecosystems. For this purpose, the biological background of five indicative species traits investigated in this thesis will be presented.

1.6.1. Saprobic valences

In response to high levels of pollution in European riverine systems, biomonitoring at the end of the 19th century focused on bacteriological aspects (Bonada et al., 2006). Kolkwitz and Marsson (1902) played an important role in the development of the saprobic system, which is still commonly used in Central and Eastern Europe (Hartmann, 2011). In their following works, Kolkwitz and Marsson (1908,

1909) described aquatic organisms indicative of clean ("Katharobien") and organically loaded ("Saprobien") waters.

The level of organic pollution is interlinked with oxygen contents since decomposition processes in organically loaded waters consume oxygen (Bonada et al., 2006). However, it is known that benthic invertebrates require different levels of available oxygen. For example, *Tubifex sp.* can withstand low oxygen content as they possess the enzyme haemoglobin and can thus bind available oxygen (Palmer & Chapman, 1970). On the contrary, members of the mayfly family Heptageniidae (e. g. *Rhithrogena sp.*) have immovable gills and thus need strong current and high oxygen content to survive (Bauernfeind & Humpesch, 2001).

Another aspect in relation to available oxygen is flow velocity and turbulence because oxygen is transported with the waves of the moving water and atmospheric O_2 enters water in mixing processes (Allan, 2007; Thienemann, 1950).

1.6.2. Functional feeding guilds (FFGs)

Differentiation of feeding in invertebrates is based on "**how** the food is obtained, rather than [...] **what** food is eaten" (Allan, 2007). The classifications of the FAA are derived from "morphology of mouthparts, feeding behaviour, and food consumed" (Moog, 1995). Descriptions of the functional feeding guilds are given in Table 3. The underlying concept for the FFG distribution within a community is taken from the RCC (Vannote et al. (1980), see chapter 1.1).

Table 3: Functional feeding groups of benthic invertebrates (from Moog (1995); based on Cummins (1973, 1974), Cummins and Klug (1979) and Merritt and Cummins (1984)).

Feeding type	Abbreviation	Sources of food
Shredders	SHR	Fallen leaves, plant tissue, CPOM
Grazers	GRA	Epilithic algal tissues, biofilm, partially POM
Filtering collectors		
active filter-feeders	AFIL	Food in water current is actively filtered
passive filter-feeders	PFIL	Food brought by flowing water current
Detritus feeders	DET	Sedimented FPOM
Leaf borers, miners	MIN	Leaves of aquatic plants
Xylophags	XYL	Woody debris
Predators	PRE	Prey
Parasites	PAR	Host
Other feeding types	OTH	Cannot be classified into this scheme
Omnivorous animals		Diverse

1.6.3. Longitudinal zonation

As noted in chapter 1.1, longitudinal changes along a river can be observed in the faunal communities as temperature regime, substrate composition and flow patterns change. It means that benthic

invertebrates exhibit (more or less specific) individual preferences for water temperatures. Schmidt-Kloiber and Hering (2022) differentiated between cold stenotherm (small range < 10 °C), warm stenotherm (small range > 18 °C) and eurythermic (wide temperature range) aquatic invertebrates. In addition, temperature preferences of aquatic invertebrates can used to "detect and evaluate temperature increases as induced by climate change" (Graf et al., 2008).

Flow velocity is interlinked with substrate. As flow velocity increases, shear stress increases and thus substrate of larger grain size is moved (Allan, 2007). Consequently, water also puts stress on benthic invertebrates, which can be observed in adaptations that enable them to prevail in specific conditions. The mayfly family Heptageniidae is an example of a group that adapted to high currents and coarse substrate. Their large and bent tarsal claws, as well as their dorso-ventrally flattened bodies allow them to stick to the substrate in high currents (Bauernfeind & Humpesch, 2001). Such rheolithophilic taxa were classified by Graf et al. (2021).

1.7. Anthropogenic Impacts

The public associates springs with clean, clear water and untouched nature in mountainous regions (Projektgruppe Aktionsprogramm Quellen, 2004). However, according to the Red List of endangered biotopes in Austria, the number of listed typical springs has either drastically or noticeably declined or is threatened by anthropogenic impacts (Essl et al., 2015). Ecologically, deterioration patterns to aquatic habitats in mountainous areas have created "ecological islands" and resulted in "faunal discontinuity" (Zwick, 1992).

Climate change

Climate change acts as an overarching stressor for all aquatic ecosystem. Climate change is projected to impact the amount and variability of discharge in aquatic ecosystems and lead to an increase of annual mean air temperatures (Alacamo et al., 2007). As a result, the biocenosis in aquatic ecosystems will shift from cold stenotherm taxa towards eurythermic organisms. As springs harbour a high share of cold stenotherm organisms, their suitable habitats (which are already sparse) are lost increasing the risk of extinction (Küry et al., 2016; Tierno de Figueroa et al., 2010). The increase in "periods of desirable weather for tourism" will also amplify touristic activities (Winkler, 2020) with a direct impact on alpine flora and fauna (Negro et al., 2010; Pickering & Hill, 2007).

1.7.1. Pasture farming

Alpine farming has proven its worth as it entails a multitude of potential revenue rendering services including tourism, forestry or hunting, since the primary production of meat and dairy products alone does not ensure profitability (Schönhart, 2015).

Historians suggest that agricultural land use in the Alps dates back to 4000 BC (Gilck & Poschlod, 2019). Jockenhövel (1998) describes an "occupation of the Alps for cultural landscape" in the Bronze Age. From that time, alpine landscape was strongly marked by anthropogenic use (Reitmaier, 2017). Mills, pasture farmed terraces and irrigation systems are remnants of such human activities in mountainous regions. According to Reitmaier (2017), cultivation of alpine areas occurred from the top leading to lower timberlines and an increase in deforested areas. Fire clearance was the prevailing method (Hatzenbichler, 2020).

In addition to the removal of trees for the development of pasture areas, forestry for wood production also leads to an alteration or disappearance of riparian vegetation of springs. This will increase water temperature, alter amount and composition of allochthonous nutrients, increase sediment loads and modify the hydrological regime (Barquín & Scarsbrook, 2008; Erman, 2002; Erman & Erman, 1995; Küry, 2009). However, it has to be mentioned that a decline in pastorally farmed areas and an increase in wooded areas could be observed over the past years (Seher, 1999).

As water is an important resource for livestock and human beings alike, water abstraction for drinking water has played a major role in the history of alpine farming over centuries. Massive culverts were implemented directly at springheads to prevent the input of contaminations (Hölting & Coldewey, 2013; Weigand et al., 2002). Today, only 4.8 % of all springs in the Swiss Jura which were catalogued in the 19th century drain aboveground due to constructed drainage systems for drinking water production (Zollhöfer, 2000). Culverts were also laid to enable the construction of forest roads which were necessary for the logistics of tourism, forestry and pasture management (Küry, 2009; Seher, 1999). As elaborated in chapter 1.3, benthic communities of springs are highly sensitive to changes of the hydrological regime and are thus severely altered when the hydrology is affected.

1.7.2. Grazing

Grazing cattle feeds on riparian vegetation and causes reduced shading (Niedermayr, 2009). Küry (2009) mentioned the input of nitrate and suspended solids as well as the input of organic waste and clippings as main conflicts arising from agricultural land use. In combination, reduced shading and allochthonous input of nutrients lead to high biomasses of primary producers (e. g. algae and macrophytes) (Hill et al., 1995; Sada et al., 2001). Livestock poaching constitutes another major factor as it "erodes spring banks, degrades habitats […] by filling the interstitial spaces around rocks and gravel and by compacting mud and clay" (Barquín & Scarsbrook, 2008; Erman, 2002). This impact is expected to be the most pronounced in the immediate area of a water body as cattle may also use the water for drinking.

In conclusion, overgrazing leads to a high input of nutrients, heavily reduced riparian vegetation and

a substitution of the naturally heterogenous substrate with mud and humus. This results in a homogenised habitat with high shares of fine sediments, stillwater zones caused by depressions and higher temperature fluctuations. Typologically, the rheocrenal character is lost and a helocrenal character is established (see chapter 1.2).

1.8. Spring Management

Although springs in Austria are severely impacted my multiple stressors and are thus at risk, their ecological status is still largely unknown. This is primarily due to the fact that monitoring of water bodies with a catchment smaller than 10 km^2 is not mandatory for national management plans (Ofenböck et al., 2019). Still, the importance of spring management has received worldwide recognition in recent years. As a response, organisations and platforms for information transfer in e. g. the United States (Florida Springs Task Force), Australia (public database on the Great Artesian Basin Springs), Germany (*Cruneocia*) or Switzerland (CRENODAT) were established (Barquín & Scarsbrook, 2008).

Verdonschot (1996) provided a framework for "ecological spring management" consisting of five essential working steps that are required for an ecologically successful spring management (Table 4).

Table 4: Steps of ecological spring management (adapted from Verdonschot (1996)).

1. Measure	Measure both biotic and abiotic parameters
2. Identify	Identify typology, conditional/operating factors, factors of disturbance
3. Choose	Choose a target state, cenotype within the catchment; what needs to be managed?
4. Plan	Plan measures
5. Execute	Execute the measures
6. Evaluate	Monitor and assess the effects of the measures

However, such sustainable management recommendations have not been implemented into national law, which underlines how little attention is paid to these biotopes despite their high importance for global biodiversity. Moreover, methods to assess the ecological status are only available on a regional level (Hotzy & Römheld, 2008; Lubini et al., 2016).

1.8.1. Status Assessment of Springs

As previously mentioned, no generally applicable methods for the assessment of the ecological status of springs are available. Thus, some studies on springs have analysed the overall benthic community

(Berlajolli et al., 2019; Dumnicka et al., 2013), while others focused on specific groups of organisms (e. g. phytobenthos, Cantonati (1999); water mites, Di Sabatino et al. (2003) or caddisflies, Erman and Erman (1995)).

Sufficient ecological information on specific groups of aquatic organisms represents the fundamental requirement for status assessment. It is only against this background that statements on deviations from the naturally expected community can be made. Insects, crustaceans and molluscs are "the best-studied groups" of freshwater invertebrates (Strayer, 2006). It is known, for instance, that the insect orders Ephemeroptera, Plecoptera and Trichoptera (EPT) are the most intolerant groups of aquatic insects. They are particularly sensitive to impairments in aquatic systems (Lenat, 1993; Ofenböck et al., 2004; Wallace et al., 1996).

In Austria, however, only a single mayfly species (*Rhithrogena taurisca*) mainly inhabits springs (Bauernfeind et al., 2017). Stone- and caddisflies show a stronger stenotopy towards spring habitats. 11 % (17 taxa) of all Plecoptera species and 15 % (48 taxa) of all Trichoptera species in Austria can be classified as being crenobionts (see chapter 2.4, Moog and Hartmann (2017)). Additionally, Erman (2002) observed stone- and caddisflies in nearly all investigated springs during a 20-year-long study programme. Stoneflies were only missing in intermittent springs.

The suitability of Plecoptera and Trichoptera as status indicators of spring biotopes is supported by the fact that both are scientifically well researched groups. Overall, 135 stonefly and 314 caddisfly species were recorded in Austria. For Plecoptera, Graf and Schmidt-Kloiber (2008) only described the area in the Federal State of Salzburg as relatively unexplored. For Trichoptera, Lunz am See is the best investigated area, which has been intensely sampled by Hans Malicky (Malicky, 2009). For the rest of Austria, Malicky (2009) describes uneven states of knowledge, while the areas of Upper Austria and Vorarlberg are rather well explored.

Plecoptera

Due to diverse ecological needs of individual species, Plecoptera are well-suited indicators for the ecological status of aquatic systems (Konar, 1997). They are typical inhabitants of alpine brooks with strong flow, coarse substrate and low temperature fluctuations (Graf & Schmidt-Kloiber, 2008). 39 % of all European Plecoptera taxa can be classified as being cold stenotherm, while 10 % are associated exclusively with the crenic zone (Tierno de Figueroa et al., 2010). Due to the high density of cold springs and lakes (36 species), many Plecoptera species occur in the mountainous regions of Central Europe (Fochetti & Tierno de Figueroa, 2008; Graf & Schmidt-Kloiber, 2008). Out of the 17 crenobionts in Austria, 29 % are classified as predators (e. g. *Dictyogenus fontium*) (frequency value for predatory feeding type > 5) and 29 % are classified as shredders (*Nemoura sp.*). The remaining taxa are

opportunistic feeders (e. g. *Leuctra sp.*) (Graf, Grasser, & Weinzierl, 2017).

Specific stonefly species were described as "freshwater ubiquitists" (*Nemurella pictetii* or *Nemoura cinerea*) which occur in high abundance only in areas where other stonefly species are missing (Eckstein, 1994; Lieske, 2005; Zwick, 2004). Zwick (2004) mentioned that *Nemurella pictetii* is not tolerant to pollution, while being common in swampy springs. Equally common in springs is *Nemoura cinerea*, which prefers mud, sludge and decaying plant material (Gerecke et al., 2005). Another crenophilous stonefly is *Leuctra nigra*, which shows a preference for the silty parts of springs and small streams (Elliott, 1987).

A striking characteristic of stoneflies is , that their "ecological requirements greatly limit the dispersal capacity of the nymphs", while the reduced flight ability of the adult stage further contributes to a high share of endemism (Fochetti & Tierno de Figueroa, 2008). For example, the potamal stonefly fauna (e. g. *Marthamea vitripennis*) has already gone extinct in large parts of Central Europe as a result of anthropogenic alterations (Zwick, 1992). This underlines the need for conservation and protection of stonefly habitats to prevent further extinction. Zwick (2004) described species of the genera *Brachyptera*/*Protonemura* (Mediterranean) and *Perla*/*Siphonoperla* (West Palaearctic Region) as groups with high endemism.

Trichoptera

With just a few exceptions, Trichoptera inhabit all aquatic systems and are ideal for the quality assessment of aquatic ecosystems (Malicky, 2014). Taxa of several families, in particular taxa belonging to the genera *Barea*/*Ernodes* (Beraeidae), *Synagapetus* (Glossosomatidae), *Microptila*/*Stactobia* (Hydroptilidae) and *Crunoecia* (Lepidostomatidae) are typical inhabitants of springs (Waringer & Graf, 2011). Thus, they can provide fundamental information on the ecological status of springs. Fischer (2003), for instance, proved that two *Synagapetus* (Glossosomatidae) species show preference for a high share of stony substrate, high oxygen content as well as low amounts of organic pollution.

However, there are also crenobiontic species which prefer conditions atypical for rheocrenes – an example is *Beraea pullata* (Beraeidae) which inhabits helocrenes with fine sediment accumulations; it is classified as a detritivore (Graf, Grasser, & Waringer, 2017). Another, example is *Parachiona picicornis*. As Malicky (2014) described, their larvae do not develop in the spring run-off itself, but rather in mud accumulated in between herbaceous vegetation.

In Austria, endemic caddisflies are restricted to springs and streams, while the highest endemics diversity can be observed in an altitude of 1,000 to 1,200 m a.s.l. (Rabitsch et al., 2016). A majority of Austrian endemics belong to the genera *Rhyacophila*, *Consorophylax* and *Drusus* (Appendix 1, Rabitsch et al. (2016)). According to the Red List on Trichoptera in Austria (Malicky, 2009), 51 % of Austrian

caddisfly species are classified as being threatened, while the author expects and increase in the coming years. Malicky (2009) mentioned river-engineering work in densely populated areas and intensive agriculture as the main threats for Austrian caddisfly populations.

1.8.2. Sampling techniques

As mentioned in Table 4, analysing the biotic parameters before and monitoring them after the implementation of restoration measures is an integral part of spring management. Now, it is of utmost importance to carefully consider which sampling tools are the most adequate for spring biotopes (Barquín & Scarsbrook, 2008). Due to the fragility of spring ecosystems, Erman (2002) proposed to limit substrate sampling in order to reduce disturbances to the habitat. However, studies on the consequences of such activities are still missing (Berlajolli et al., 2019). Nonetheless, substrate samples tend to underestimate the overall species diversity, because they only provide a snapshot of the current faunistic assemblage living in the benthos (Erman & Erman, 1995; Malison et al., 2010). For example, semi-aquatic insects are missing from the benthos during some part of the year and are thus also missing in substrate samples (Berlajolli et al., 2019).

Another possible sampling procedure consists of emergence traps which capture adults of organisms with semi-aquatic life cycles. The taxonomy of these is much more "detailed and better known" than for immature instars (Lemke & Mattson, 1969). If deployed throughout the year, emergence traps can capture all emerging insects thus compensating for the high variability of seasonal emergence patterns (Baxter et al., 2005). Besides, they are cheap, timesaving and gentle on the surrounding flora and fauna (Erman, 2002; Weigand et al., 1998).

However, emergence traps only allow for qualitative analyses because they do not only catch animals from the covered area below. Malicky (2002a, 2002b) discussed that he found adults which could not be found in the streams as larvae, aged ovipositing females (indicated by empty abdomens) and even terrestrial insects.

1.8.3. Restoration

To counteract the degradation of freshwater ecosystems, restoration measures have frequently been implemented, however with a strong focus on rivers and lakes (Lehosmaa et al., 2017). Restoration measures aim at returning ecosystems to near-natural conditions by eliminating stressors and ensuring natural dynamics.

However, as springs in mountainous areas are of high importance for pasture farming, utilisation can only rarely be stopped altogether. Consequently, compromises must be made. For example, if abstraction measures cannot be removed completely, restoration should ensure that water is only diverted in times of need (Barquín & Scarsbrook, 2008). To eliminate the damages of trampling from

cattle in pastorally farmed areas, Hotzy and Römheld (2008) proposed to erect a fence with at least 5 m distance to the spring. In helocrenes, carefully monitored and regulated extensive grazing should be upheld to foster natural conditions and prevent strong growth of the most competitive vegetation (Barquín & Scarsbrook, 2008).

1.8.4. Colonisation patterns

Restoration measures should aim to "result in drastic changes of the environmental conditions for benthic invertebrates" by improving water quality and generating new habitats (Winking et al., 2016). The original habitat is then lost for the pre-restoration community.

Now, recolonisation by a more natural benthic community depends on a variety of factors, such as land use in the catchment, persistence of original stressors or the lack of certain habitats outside the restored area which are required by some taxa (Sundermann et al., 2011). Additionally, the "distance to [recolonisation] sources and in-stream barriers are key areas requiring attention for restoration projects" (Tonkin et al., 2014). On the one hand, because the dispersal ability of hololimnic organisms is limited to migration within the inhabited watercourse (Zwick, 1992). On the other, because the dispersal capacity of merolimnic organisms (i. e. the flying adult stage) can be limited (e. g. reduced flight ability in Plecoptera; Fochetti and Tierno de Figueroa (2008)).

According to Zollhöfer (1999), recolonisation first occurs by fast colonisers (within the first 30 days), followed by intermediate (1-12 months) and slow colonisers (> one year). However, in his study in Switzerland, Zollhöfer discovered that invertebrate densities recovered to reference levels, while the number of taxa remained low and certain spring specialists were still lacking even after several years.

1.9.   National Parks

According to the IUCN, national parks are "large natural or nearly natural areas set aside to protect large-scale ecological processes, along with the complement of species and ecosystems characteristic of the area, which also provide a foundation for environmentally and culturally compatible spiritual, scientific, educational, recreational and visitor opportunities" (IUCN, 2022). Human interventions to the natural environment must be prohibited in at least 75 % of the National Park area. This area is called core or nature zone (Umweltbundesamt, 2022). The remaining area may be disclosed as conservation area. Therein, high-value cultural landscape can be sustained (Haseke & Gärtner, 2003). It shall nevertheless be ensured that land use "will not adversely affect the primary management objective" (IUCN, 2022).

In Austria, there are six National Parks (Table 5), covering a total area of 2,382 km^2 (Umweltbundesamt, 2022).

Table 5: Area and year of establishment of the six National Parks in Austria (Umweltbundesamt, 2022).

National Park	Area [km^2]	Year of formation
Hohe Tauern	1,857	1981 / 1984 / 1991
Neusiedler See – Seewinkel	96	1993
Donau-Auen	96	1996 / 1997
Kalkalpen	209	1997
Thayatal	14	2000
Gesäuse	110	2002

1.10. Kalkalpen National Park

When plans for the development of a hydropower plant and military testing grounds were published in the 1970s and 80s, local initiatives laid the foundation for the establishment of a nature conservation area in the Kalkalpen. In 1997, the organisation and financing of the National Park were contractually settled between the Austrian government and the Federal State of Upper Austria (Seher, 1999). Today, the National Park covers the Sengsengebirge in the West and the Reichraminger Hintergebirge in the East, extending over an area of 209 km^2 (Bundesministerium für Land- und Forstwirtschaft, Umwelt und Wasserwirtschaft, 2002). The National Park ranges from 385 to 1,970 m a.s.l., while half of the area (50 %) is located in the mid-montane level (800 to 1,200 m a.s.l.) (Fuxjäger et al., 2016). Geologically, the area is dominated by Main Dolomite (45 %) and Wetterstein Formation (32 %) with water mainly emerging at lower altitudes due to strong karst formation (Haseke, 2004; Stadler, 2017). About 780 different springs are situated in the Kalkalpen National Park (Weigand & Tockner, 1996).

Intensive alpine farming has been pursued in the Kalkalpen National Park for several centuries. Clearings for pasture farming date back to the 13th century – only four centuries later, almost all pasture privileges had been granted (Hatzenbichler, 2020). About a third (1,786 ha) of the unforested area is cultivated by 21 pasture farms (Hatzenbichler, 2020). They are located in the conservation area (*Bewahrungszone*, Figure 4), which makes up for 11 % of the National Park territory (Haseke & Gärtner, 2003).
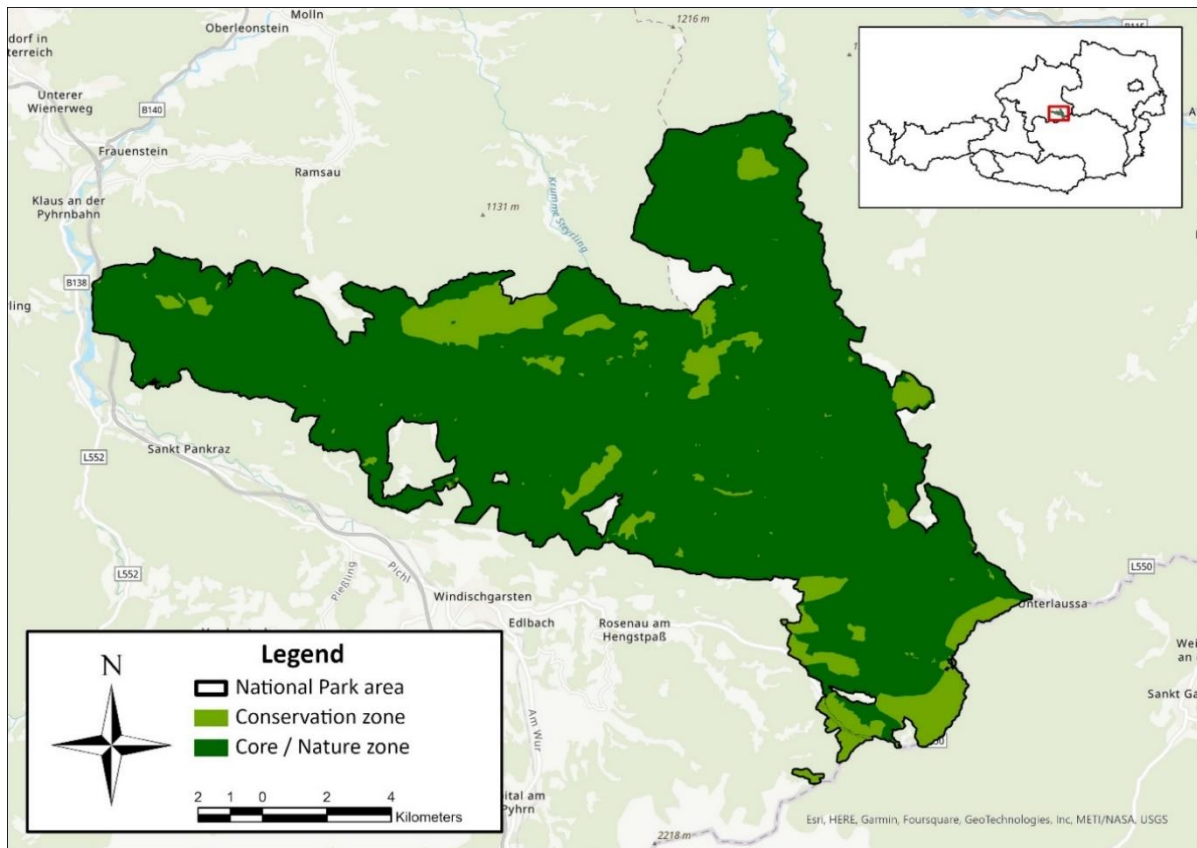
Figure 4: Location of the Kalkalpen National Park in Austria (top right) and the spatial distribution of the conservation and core / nature zone.

Farmers in the National Park are contractually obliged ("Vertragsnaturschutz") to adjust their agricultural processes to be in line with the nature conservation and protection aims of the National Park management. Compensation is paid to balance financial loss incurred from 1) limitations of intensive farming, 2) complete abstinence from use or 3) active landscape conservation (Seher, 1999).

Nonetheless, the results of a large mapping campaign in the National Park indicated that springs in pastorally farmed areas are subject to high organic load and structural devastation. To ensure that the main objectives of the National Park, such as maintaining natural biotic communities and contributing to regional ecological processes, are achieved, a LIFE project (LIFE99NAT/A/5915) was started in 1999 in which several springs were equipped with protection fences. This thesis will use findings of this project as basis and investigate new developments using recently gathered data.

To sum up, this thesis will…

- analyse the development of changes of the benthic communities in anthropogenically impacted springs in a timeframe of 20 years after the start of restoration.
- evaluate, whether protection fences can help to restore the natural conditions in springs while other stressors in the surroundings are still active.

1.11. Research Questions and Hypotheses

Conceptual background
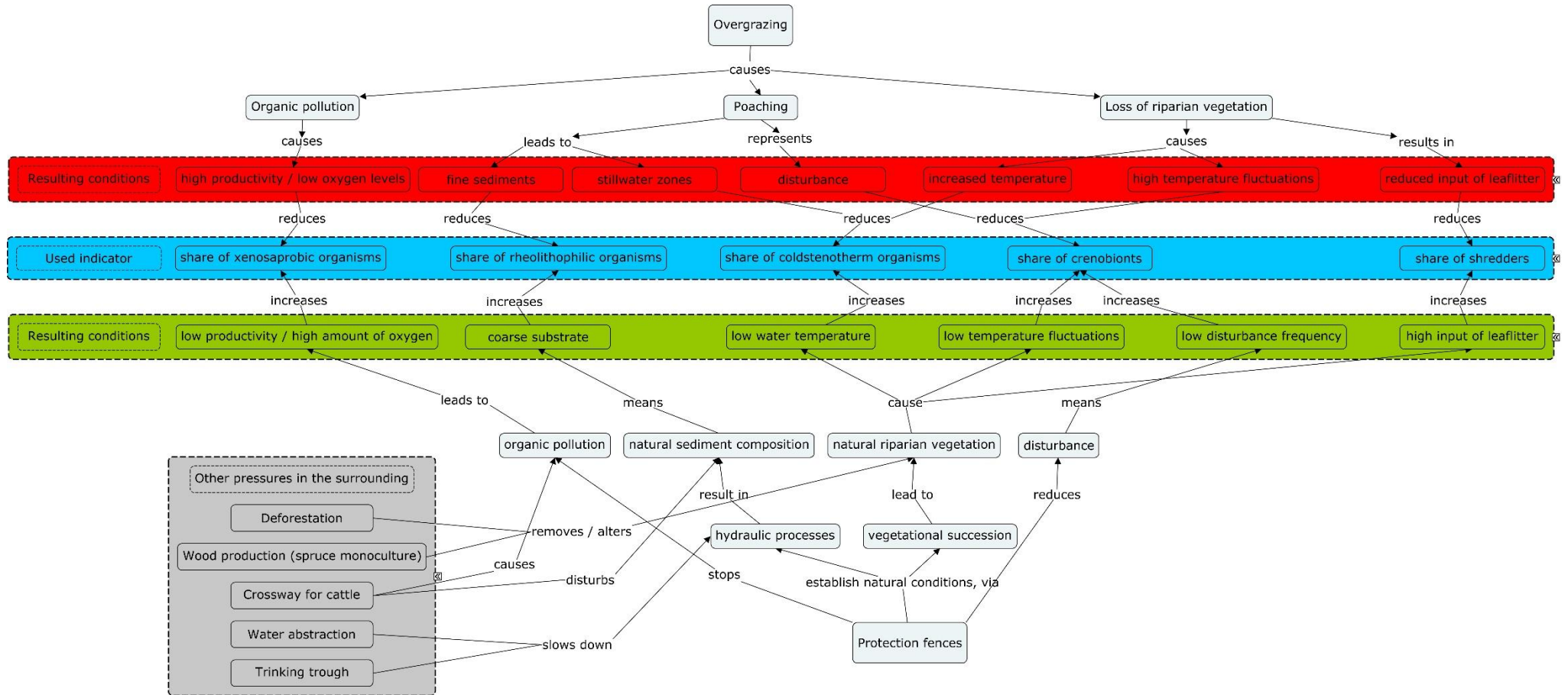
Figure 5: Concept map of impacts of overgrazing (light blue rectangles in the top two rows) and resulting conditions in an impacted spring biotope (red rectangles). The positive effects of protection fences are shown in the lower section of chart. The resulting, more natural conditions are shown in green rectangles. Used metrics are given in the centre (blue rectangle), while expected changes are shown on the arrow pointing to each metric. Prevalent stressors at the investigated springs are described in grey rectangles at the bottom left. The effects of these pressures are indicated by the arrows. This concept map was created using CmapTools (Cañas et al., 2004).

Research questions and hypotheses

Based on these aims, the following research questions and hypotheses are derived:

1. **Do protection fences contribute to establishing a near-natural character in rheocrenic springs by**

   a. *decreasing the amount of organic pollution?*

   H₁: Due to the absence of allochthonous input of cattle excrements, which constitute organic pollution, the share of xenosaprobic organisms increases.

   b. *allowing a natural riparian vegetation to develop?*

   H₂: Due to the protection fences, a natural deciduous vegetation which provides allochthonous CPOM develops and thus, the share of specialised shredders increases.

   H₃: Due to the protection fences, a natural deciduous vegetation which provides shading develops and thus, the share of cold stenotherm taxa increases.

   c. *allowing a natural sediment composition to develop?*

   H₄: Due to the protection fences, natural hydraulic dynamics will reduce fine sediments and result in a high share of mineral substrate. Thus, the share of rheolithopilic taxa will increase (Graf et al., 2021).

   d. *establishing naturally constant conditions?*

   H₅: Due to the protection fences, a near-natural character with constantly low water temperatures and substrate stability is established which provides suitable habitat for a high share of crenobionts.

2. **Is restoration success impaired if other pressures are still prevalent in the immediate surrounding of the spring run-off area?**

   H₆: A combined analysis of all metrics reveals whether stressors in the surrounding area of the spring are still active.

   H₇: If stressors in the surrounding area are active, change towards a typical rheocrene community occurs at a slower rate.

2. Materials and Methods

2.1. The LIFE Project

The LIFE project aimed at increasing the number and extent of sensitive aquatic biotopes by preventing main disturbance factors through pasture farming pattern management (Haseke & Gärtner, 2003). A number of moors and springs (as of 2020: 20, Hatzenbichler (2020)) were fenced. To examine the effects of these protection fences, four springs were equipped with emergence traps and monitored on basis of their benthic communities (Figure 6). These springs are the subject of this thesis.

2.2. Study Sites

The description of the current situation of the investigated sites is based on a field inspection which took place on August 4, 2022. Earlier conditions are described using the documentation (Haseke & Gärtner, 2003; Weigand & Graf, 2002; 1996) of the National Park as well as photographs and notes provided by Dr. Erich Weigand. Limnological characterisation of the springs is taken from Weigand and Tockner (1996) and Weigand and Graf (2002). A summary of all basic parameters for each spring is shown in Table 6. The abiotic conditions reflect the situation in 2022.

Table 6: Summary of basic parameters of the investigated springs
(Used coordinate system: WGS 1984; abbreviations: mil = microlithal (2–6.3 cm), akl = akal (0.2–2 cm), psm = psammal (0.063–0.2 cm)).

Site	EBA	JÖA	SCHA3	SCHÜ
Location				
Elevation [m a.s.l.]	1120	785	1205	1125
Coordinates (Easting)	14,4166811°E	14,4344939°E	14,4186477°E	14,4128206°E
Coordinates (Northing)	47,8001074°N	47,7822253°N	47,7886720°N	47,7866654°N
Exposition	SW-NE	NWW-SEE	NE-SW	NE-SW
Avg. slope [%]	13,71	24,67	34,69	35,74
Abiotic Conditions				
Water depth [cm]	10	10	20	15
Channel width [cm]	40	200	30	30
Shading [%]	100	80	100	50
Choriotope distribution	80% akl, 20% psm	50% akl, 25% mil, 25% psm	50% akl, 32% psm, 18% mil	50% akl, 30% mil, 20% psm
Protection fence				
Fence type	Wooden fence	Game fence	Barbed wire fence	Barbed wire fence
Month of errection	August 2001	October 1999	August 2000	May 2000
Fence length [m]	180	100	350	100
Area [m2]	300	100	500	100
Fully fenced	No	Yes	No	Yes
Persisting impacts	Abstraction / Drinking trough	Game	Abstraction / Drinking trough	Spruce monoculture / clearing

Due to several reasons explained in chapters 2.2.1 to 2.2.5, the protection fences were not continuously in place throughout the observed period (Table 8).

All investigated springs are located in the conservation zone of the National Park (Figure 6). Furthermore, all investigated springs were typologically classified as rheocrenes.
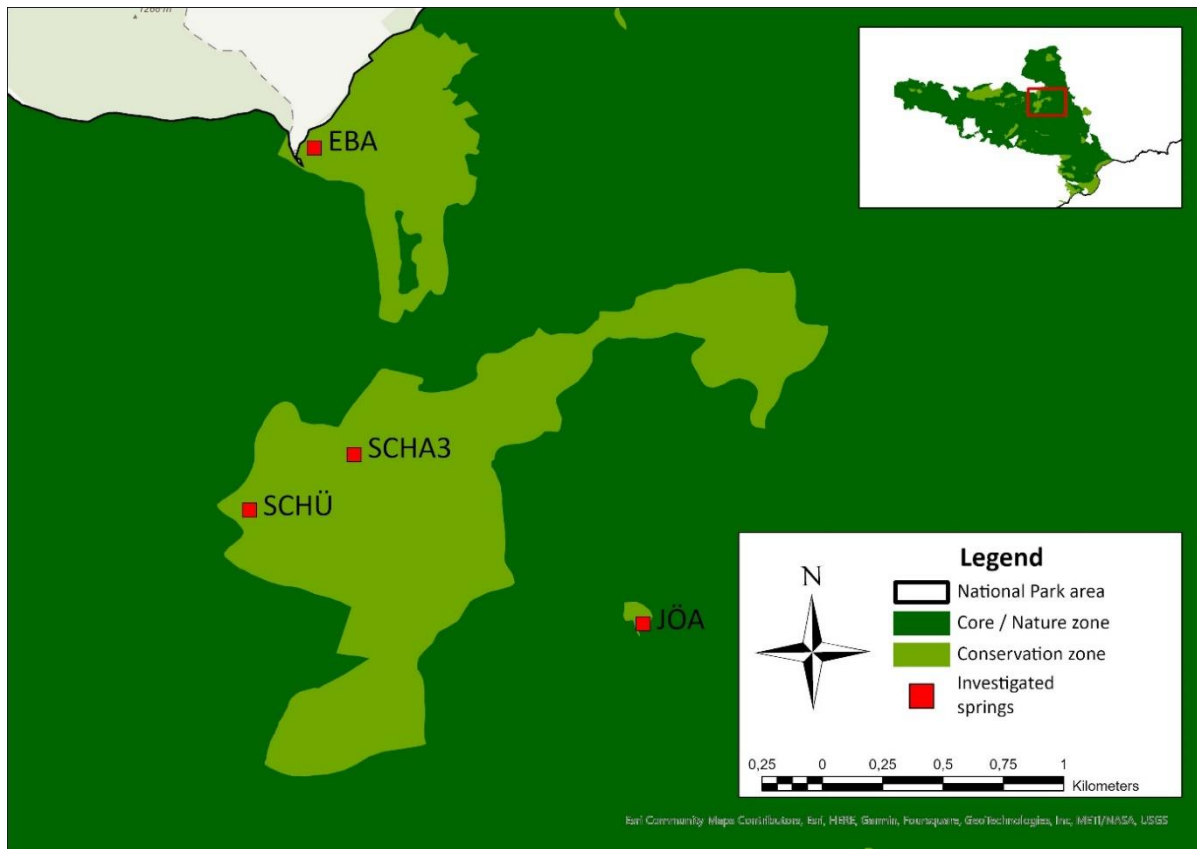

Figure 6: Investigated springs in the National Park Kalkalpen.

2.2.1. Ebenforstalm spring (EBA)

EBA is located in the eastern part of Ebenforstalm cultivated for several centuries. The spring runs off with a low slope at an altitude of 1,120 m a.s.l. and is cut off by a forest road after approximately 70 m.

For pasture farming, trees in the area were removed several centuries ago. Additionally, a drinking trough below the springmouth was installed. This section (approx. 5 m^2) was fenced by farmers to protect the drainage construction (Figure 7, ①). The discharge flowed through the drinking trough and formed the springbrook below. The area of the spring was heavily frequented by cattle leading to severe trampling and organic pollution from excrements in the immediate and adjacent area of the drinking trough. Furthermore, woody vegetation (e .g. alders and beeches) was continuously suppressed by grazing and only allowed for herbaceous vegetation to develop. Hence, the run-off was subjected to intense radiation.

Before the management, the springmouth was characterised by stony substrate covered by epilithic algae. The springbrook was marked by a high share of fine sediment, while moss cover was low (< 10 %).

The protection fence was erected in August 2001 and covers (in addition to the fenced area at the springmouth) 60 m of the springbrook. A space of 3 m in between ensures that cattle can cross and access the drinking trough. A wooden chute was installed to guarantee run-off into the springbrook (Figure 7, ①). This drinking trough was in use during the whole observation period.
The emergence traps were installed 1 m (E1), 10 m (E2) and 40 m (E3) below the springmouth. E1 had to be relocated closer to E2 after farmers repeatedly carried out diggings to ensure an optimal functioning of the drinking trough (Figure 7, ②). As a result, the traps were renamed (E1 -> E2/1; E2 -> E2/2).

Situation in 2022:

The run-off was characterised by a thin layer of gravel (80 % akal, 20 % psammal) on top of a humus layer. The channel was surrounded by thick walls of humus (15 cm) and completely shaded by herbaceous plants (Figure 7, ③ and ④). At half of the fenced area, a PVC pipe was noticed which drained water to a drinking trough at the forest road. The surrounding area of the last 20 m was densely covered with stinging nettle.

Figure 7: Conditions at the Ebenforstalm spring (EBA): (1) Drinking trough with wooden chute in the ground and crossway for cattle; 2008. (2) Relocation of E1 closer to E2 in response to diggings at the springhead; 2008. (3) Dense herbaceous vegetation in the fenced area; 2021. (4) Current situation: channel is accompanied by humus walls, thin layer of gravel forming bed sediment; 2022.

2.2.2. Jörglalm spring (JÖA)

JÖA is located in the Jörglgraben at an altitude of 785 m a.s.l., while run-off occurs towards south-west.

Conventional pasture farming was stopped after the pasture hut had been abandoned several decades ago. Thereafter, the area was used for hunting purposes as the open space represented attractive feeding grounds for game.

To ensure open space for hunting purposes, a large elm tree, which shaded the spring area, was cut down in 1993 (Figure 8, ①). Additionally, logging activities for wood production caused severe input of CPOM (spruce branches and needles). Additionally, a PVC pipe with riprap for water abstraction was installed in 1996. This concentrated the flow forming a central channel and exposing substrate. The combination of strong radiation and the input of organic matter from excrements promoted algal growth in the run-off area. As a result, the substrate was overgrown with green and blue algae (Figure 8, ②).

The protection fence was erected and the PVC pipe and riprap removed in July 2000. In addition, a construction was put in place to ensure shading of the springmouth (Figure 8, ①). The protection fence was devastated by heavy snowfall in 2008 and was removed completely thereafter.

The emergence traps were installed directly at the springmouth (E1) and 5 m (E2) and 10 m (E3) downstream.

Situation in 2022:

The run-off area was dominated by coarse substrate with diverse size distribution (50 % akal, 25 % microlithal, 25 % psammal). Additionally, several rivulets developed in between the large substrate, while larger emersed stones were densely covered in mosses (Figure 8, ④). The area was shaded by a mixture of coniferous (spruces) and deciduous (beech) trees.

Figure 8: Conditions at the Jörglalm spring (JÖA): (1) Game fence and construction below the springhead for shading purposes. The spring emerges below the tree stump (large elm); 2005. (2) Accumulation of green algae; spring 2006. (3) Situation during a high flow event; 2006. (4) Run-off occurs between large rocks via several channels which take up several metres; 2021.

2.2.3. Schaumbergalm

The Schaumbergalm extends over an area of 170 km^2 and is situated at an altitude of 1,100 to 1,400 m a.s.l. (Hatzenbichler, 2020; Seher, 1999). To the north, the area is constrained by a mountain called "Trämpl" with its peak at 1,426 m a.s.l (Figure 9). The area has been cultivated for several centuries, although intensity of cultivation decreased since industrialisation (Erich Weigand, personal communication).

Figure 9: Orthophoto showing the location of the springs SCHA3 and SCHÜ and the "Trämpl" peak in the north of the cultivated area.

2.2.4. Schaumbergalm spring (SCHA3)

SCHA3 is located on the southern slope of the Trämpl at an altitude of 1,205 m a.s.l. Thus, run-off occurs along a steep slope towards the south-west.

For pasture cultivation, trees in the surrounding area were removed. Additionally, three drinking troughs were installed in the immediate vicinity of the spring run-off area. Thus, the area was heavily frequented by grazing cattle, which formed several heavily compacted traverses. The mineral substrate was burrowed and caused input of fine sediments into the springbrook (Figure 10, ①). Despite continuous grazing, green alder shrubs grew on the left of the channel (Figure 10, ②). On the right side, however, grazing and high organic load from cattle excrements facilitated the development of herbaceous vegetation. Furthermore, the channel was concentrated as a result of the proceeding root penetration. Strong radiation was also a result of the missing vegetational cover, leading to the development of algae in the run-off. In some areas, algal clumps were observed.

The area was fenced in August 2000 and consisted of two parts. The first part of the fenced area covers 40 m downstream from the springmouth. After 3 m, to provide space for cattle to cross the springbrook, the fenced area covers another 40 m downstream (Figure 10, ③). In the course of the management programme, the drinking troughs were relocated to below the fenced area.

In 2004-2006, a new alpine cabin (Schaumbergalm) was built. Several diggings were carried out at the springmouth and a concrete construction was erected to supply drinking water (Figure 10, ②). However, the water could not be used due to high bacterial contamination, which is why it was assumed that the hydrological regime was not adversely affected. However, it cannot be ruled out that the impervious bedrock was damaged, which would reduce surface run-off.

The emergence traps were originally placed at the springmouth (E1), 10 m later in a small pool (E2), and immediately before (E3; this area has occasionally fallen dry) and after (E4) the crossway (Figure 10, ③). However, E1 had to be removed due to the drainage construction in 2006.

Situation in 2022:

Run-off occurred via cascades forming small pools below the sills. The pools were dominated by fine sediment (80 % psammal, 20 akal), while regular run-off was characterised by coarser substrate (60 % akal, 25 % microlithal, psammal 15 %). The whole run-off area was shaded by a dense grey alder population. Fallen leaves were sporadically observed in the upper fenced area, while being common in the lower fenced area (Figure 10, ④).

Figure 10: Conditions at the Schaumbergalm spring (SCHA3): (1) Situation in the lower fenced area (E4) immediately after the management measures. The channel is characterised by high share of fine sediment and accompanied by herbaceous vegetation; 2002. (2) Water abstraction construction at the springhead and accompanying green alders to the left of the run-off; 2006. (3) Heavily trampled crossway between the fenced areas. Dense vegetation on both sides of the run-off; 2009. (4) The run-off in the lower area is now characterised by coarse substrate (akal), partly covered by leaves; 2021.

2.2.5. Schaumbergalmhütte spring (SCHÜ)

SCHÜ is located close to an abandoned alpine hut in a spruce farm at an altitude of 1,125 m a.s.l. on the south-western slope of the Trämpl. The spring with its run-off extends over 100 m and is then cut off by a logging road leading up to the Schaumbergalm (alpine cabin).

Especially the upper part of the spring area (approx. 30 m downstream of the springmouth) is located in an intensely cultivated spruce monoculture (Figure 11, ①). Thus, the run-off was heavily shaded by the surrounding spruces. This also caused strong input of CPOM (spruce cones and needles), which suppressed natural flow. It was first assumed that the dense spruce stock made the area difficult to access for grazing cattle and thus organic pollution and trampling in this area would be low.

The lower part, however, was regularly frequented by cattle and was missing woody vegetation. Trampling and organic pollution created an extended swamp zone, which was subject to strong radiation. The bed sediments largely consisted of humous fine sediment, while the low share of mineral substrate was covered by epilithic brown algae.

The area from the springmouth to the logging road was fenced in May 2000. A report from 2003 mentioned that the upper area was frequented more often than it was assumed at first, which was proven by traces of cattle along the protection fences. In the years 2009 and 2010, almost all trees in the upper area were removed in response to bark beetle infestation (Figure 11, ②). Additionally, the protection fence was removed in 2013. In the years following the clearance, the upper area was subject to intense radiation, which allowed for a dense herbaceous vegetation to develop along the run-off in the subsequent years (Figure 11, ③).

The emergence traps were deployed in the forested area (E1, close to the springhead; E2, strong CPOM accumulation; E3, in a pool) and in a cleared area (E4, 10 m above the logging road). In 2018, a farmer removed E1 and installed a water abstraction for drinking water supply. However, this farmer put up a protection fence which now covers the area from E2 down to the logging road.

Situation in 2022:

The bed sediment was dominated by coarse substrate (50 % akal, 30 % microlithal, 20 % psammal), while emersed stones were covered by mosses (Figure 11, ④). The run-off occurred through deadwood (tree trunks) and herbaceous vegetation (Figure 11, ③). The uppermost 30 m of the run-off were shaded by sparsely occurring spruces, while the lower section ran through a dense spruce stock.

Figure 11: Conditions at the Schaumbergalmhütte spring (SCHÜ). (1) Situation in the upper area (E1). The spring runs off in a dense spruce stock almost entirely covering the spring with spruce CPOM with heavy shading; 2002. (2) Situation after the clearing in response to bark beetle infestation; 2011. (3) Herbaceous vegetation developed in the following years; 2021. (4) Current situation of the channel: high share of mineral substrate with diverse size classes (microlithal, akal, psammal). Emersed stones partly overgrown with mosses; 2021.

2.3. Sampling Procedure

Biotic data

In the context of the LIFE project, the investigated springs were equipped with emergence traps. The dimensions of the triangular base cone were 55 x 55 x 40 cm, covering an area of 0.1 m^2 (Figure 12, ①). At the top part of the emergence trap, a ring construction with a depression was installed (Figure 12, ②). This depression was filled with the preservative consisting of 66 % ethylene glycol, 19 % isopropanol, 14 % distilled water and 1 % detergent. This ring construction was closed with a plastic container.

Figure 12: Emergence trap at the third section of the Schaumbergalm spring (SCHA3 – E3) (Weigand, 2021).

In each spring, three to four traps were set up at a distance of approx. 10 m. The uppermost trap was placed directly at the springmouth. Each trap was installed on the dominant microhabitat in the respective area. The traps were named E1 to E4, with E1 being the one at the springmouth and E4 being the lowermost trap.

The traps were emptied several times a year, with the first samples being taken as early as in February and the last in October. During each sampling run, the ring construction containing the insects was emptied, repaired if necessary and refilled with the preservative.

The insect orders Plecoptera (stoneflies) and Trichoptera (caddisflies) exhibit a semi-aquatic lifecycle and are therefore captured with emergence traps. As remarked in chapter 1.8.1, they show a relatively high share of crenobionts and are highly sensitive to organic pollution and deteriorations to the hydrological regime.

The captured individuals were preserved in 80 % alcohol and subsequently sent to Assoc. Prof. Dr. Wolfram Graf who conducted the identification. Identification was done on the lowest taxonomic level with additional determination of sex. The individuals were counted and entered into datasheets.

Physico-chemical data

In addition, hydrochemical parameters were measured in the context of the LIFE project and the spring monitoring programme of the Kalkalpen National Park. Measurements were taken throughout the year (February to November) at irregular intervals and time periods (Table 7) and thus only serve to give a general idea on water temperatures and discharge regime at each spring. Water temperature was measured directly at the springhead using a WTW conductivity meter. Discharge was estimated.

Table 7: Time periods and number of measurements of the two parameters. (N = Number of samples).

Spring	First measurement	Last measurement	Parameter	N
EBA	17.10.2001	07.04.2020	Temperature	45
			Discharge	43
JÖA	18.10.2000	09.07.2013	Temperature	25
			Discharge	23
SCHA3	19.10.2000	31.05.2005	Temperature	12
			Discharge	12
SCHÜ	09.05.2000	08.10.2019	Temperature	36
			Discharge	36

2.4. Data Preparation and Mathematical Analyses

2.4.1. Data preparation

Due to the individual nature of each spring (hydrology, slope, past and present impacts and differing time frames of the protection fences), statistical comparison between the sites was not carried out. Each site was rather looked at individually to discover trends over time. Due to high heterogeneity in the database, only descriptive statistics were used. To start with, years with sufficient data were identified (Table 8). To depict all emerged individuals, all captured individuals per year were accumulated. All subsequent analyses were done with these accumulated values.

Additionally, for taxa which could not be identified down to species level, classifications of corresponding species found at the respective sites were used (e. g. *Nemoura marginata-group -> Nemoura marginata*; *Sericostoma sp. -> Sericostoma personatum*).

Table 8: Data availability in each spring (green checkmark = data is available; red cross = data is missing, brown dotted line = years in which the spring area was surrounded by a protection fence).

Site \ Year	2000	2001	2002	2004	2005	2006	2007	2008	2009-2019	2020	2021
EBA	✓	✓	✗	✓	✗	✓	✓	✓	✗	✓	✓
JÖA	✓	✓	✓	✗	✓	✓	✓	✓	✗	✓	✓
SCHA3	✓	✓	✓	✗	✓	✓	✓	✓	✗	✓	✓
SCHÜ	✓	✓	✓	✗	✓	✓	✓	✓	✗	✓	✓

2.4.2. Statistical analysis

To depict the development of FFGs, longitudinal zonation and saprobity classes, ECOPROF 5.0 was used – underlying formulas are provided in the software manual (Moog et al., 2018).

However, these calculations do not render information regarding the share of specialists (e. g. share of xenosaprobic taxa), but rather a weighted relative share of taxa with classification points in a specific trait (ten point classification, see chapter 1.6). Therefore, xenosaprobists, specialist shredders and spring specialists were classified manually (Table 9). Moreover, the share of cold stenotherm taxa was investigated using classifications from freshwaterecology.info (Schmidt-Kloiber & Hering, 2022) – 54 out of 73 taxa (74 %) were classified. The classifications of rheolithophilic taxa were taken from Graf et al. (2021) and complemented for the remaining taxa by Assoc. Prof. Dr. Wolfram Graf.

For these analyses the dominance was calculated using the formula provided below (Figure 13).

$$Dominance\ of\ species\ X\ (\%) = \frac{Abundance\ of\ species\ X}{Overall\ abundance} * 100$$

Figure 13: Formula used to calculate the dominances.

Metric	Xenosaprobists	Shredders	Crenobionts	Cold stenotherms	Rheolithophils
Source	FAA	FAA	FAA	Freshwaterecology.info	Graf et al. (2021)
Threshold	SI <1	SHR > 5	EUC + HYC > 6	Cold stenotherm = 1	Rheolithophil = 1

Community changes

To identify changes in the community, the five most dominant taxa were depicted in bar charts. Additionally, the Renkonen index was calculated between the first sampled year at a spring and the following years (e. g. 2000/2001, 2000/2002,…; Figure 14). The Renkonen index portrays the concordance of dominance and respective species distribution. It ranges between 0 and 1, whereas a value of 1 indicates the same distribution of dominance and species.

$$P = \sum min(p_1; p_2)$$

P = Renkonen Index

Min (p1; p2) = Lower value of relative abundance of taxa shared between sample A and B

Figure 14: Formula for the calculation of the Renkonen index (Renkonen, 1938).

To indicate the expected return (from a helocrenal) to a rheocrenal character, five indicator taxa were chosen based on the expert judgement of Assoc. Prof. Dr. Wolfram Graf. The chosen taxa are: *Nemurella pictetii*, *Nemoura cinerea*, *Leuctra nigra*, *Parachiona picicornis* and *Beraea pullata*. These taxa are crenobionts/-phils, but prefer conditions typical for those found in helocrenes (see chapter 1.8.1).

Taxa with particular relevance for nature conservation

Information on the risk of extinction of caddisflies was taken from the Red List Austria (Malicky, 2009). Currently, no such list exists for stoneflies. Taxa endemic to the Alps were identified using information from freshwaterecology.info (Schmidt-Kloiber & Hering, 2022).

Analysis of physico-chemical data

The box plots and descriptive statistics were generated in Microsoft Excel using the "Real Statistics Resource Pack Software 7.6" (Zaiontz, 2020).

2.4.3. Qualitative analysis regarding stressors in the surrounding area

To answer the second research question, a qualitative analysis of the persisting pressures in the surrounding area of the observed springs was carried out (Table 10). Information on active stressors at each spring was gathered from past reports of the National Park and communication with Dr. Erich Weigand. Direct organic pollution means direct pollution from the excrements of cattle, while indirect organic pollution means the input of organic material from the outside (e. g. if the surrounding fence of a spring has gaps to provide a crossing for cattle and organic material can thus enter the run-off below the crossing). Poaching was split in equal subgroups to account for the differences of direct poaching by cattle and the attenuated effects below a cattle crossing. Hydrological impairment was split into two subgroups to image the different deterioration levels if water is completely missing (abstraction) or flows through a drinking trough and is thus not removed but rather reduces hydraulic dynamics. Impacts on the riparian vegetation were divided into "removal" (due to cattle or clearing) and "alteration" (e. g. spruce monoculture for wood production). This was done to capture the extenuated negative effects of altered riparian vegetation, as it still provides shading so that the natural situation is not completely lost.

Table 10: Acting stressors in the investigated area (0.5 = moderate level of impact is expected, 1 = high level of impact is expected).

Stressor		Value
Organic pollution	Direct	1
	Cattle trail	0.5
Poaching	Cattle	1
	Cattle trail	0.5
Hydrological impairment	Abstraction	1
	Drinking trough	0.5
Riparian vegetation	Removal	1
	Alteration	0.5

The values were then accumulated for each spring and per year. Subsequently, the resulting values were classified and visualised with symbols (Table 11).

Table 11: Thresholds for the combined value of stressors and the used symbol.

Value	0-1	1.5-2	>2
Symbol	✅	➖	❌

Combination of the investigated metrics

A classification based on dominance classes (Engelmann, 1978) was used for the combined analysis of the five investigated metrics. Table 12 shows the thresholds for each dominance class and the assigned values.

Table 12: Dominance class thresholds used for the classification of each metric.

Dominance class	Eudominant	Dominant	Subdominant	Recedent	Subrecedent
Percentage of community	100–32 %	< 32–10 %	< 10–3.2 %	< 3.2–1 %	< 1 %
Value for calculation	5	4	3	2	1

Subsequently, the values of the five metrics were accumulated yielding a maximum value of 25. Finally, the resulting values were used for a grading system (Table 13).

Table 13: Thresholds for the grading system of the combined metrics analysis. All metrics mentioned in Table 9 were used.

Value	25–23	22–20	19–18	17–15	< 15
Grade	1	2	3	4	5

3. Results

In the following chapters, the results of the analyses for the stone- and caddisfly communities will be described for each spring separately. At first, an overall list of all found species and their densities will be shown. The results of ECOPROF relating to longitudinal distribution, functional feeding guilds and saprobity classes will be explained. The dominances of species with indicative traits as well as the observed community changes will be described. Thereafter, the results of the physico-chemical measurements and the qualitative stressor analysis will be summarised for all four springs. The results of the combined analysis of all investigated metrics will be shown in the same manner. Lastly, the occurrence of caddisflies endangered according to the Red List Austria and endemics of the Alps is given.

3.1. Ebenforstalm Spring (EBA)

3.1.1. Taxa list

Table 14: Calculated abundances [Ind. / m²] of sampled species at the Ebenforstalm spring (EBA).

Species	Abundance [Ind. / m²]							
	2000	2001	2004	2006	2007	2008	2020	2021
Amphinemura standfussi	3,3	0	4,2	7,2	0,3	0	0,3	1,6
Nemoura cinerea	0,7	2,3	0,7	4,2	0,7	0	5,5	1,3
Nemoura marginata	0	0	0	1,3	0	0,7	1,0	0,3
Nemoura minima	0	0,7	0	0,3	0	0	0	0
Nemoura sp.	0,7	0,7	0,7	1,3	1,0	0,7	1,0	0,3
Nemurella pictetii	10,4	46,9	2,9	28,6	43,0	11,1	13,3	15,0
Protonemura auberti	8,5	9,8	3,3	5,9	9,8	13,0	2,9	0,3
Leuctra armata	4,2	49,5	4,2	15,3	1,6	2,6	15,6	2,3
Leuctra braueri	0,3	0	0	1,0	0,3	0	0	0,00
Leuctra handlirschi	1,0	87,6	1,6	13,0	4,9	0,3	1,0	0
Leuctra helvetica	0	0	0	0	0,3	0	0	0
Leuctra major	0	0	0,3	0	0	0	0	0
Leuctra nigra	1,6	15,3	1,0	7,2	3,3	1,0	19,9	31,3
Rhyacophila hirticornis	0	0	0	0	0	0,7	1,0	0
Wormaldia occipitalis	0	0	0	0,7	0	0	0	0
Plectrocnemia conspersa	0	0,3	0,3	0,7	2,9	0	0	0
Allogamus uncatus	0	0	0,7	0,3	0	0	0	0
Chaetopteryx major	0	0	0,3	0	0	0	0	0
Parachiona picicornis	0	1,0	0,7	0,7	1,3	0	1,0	0,3
Potamophylax nigricornis	0	0	0	0	0,7	0,7	0,3	0
Pseudopsilopteryx zimmeri	0	0	0	0,7	0	0	0	0
Rhadicoleptus alpestris	0	0	0	0,3	0	0	0	0
Lithax niger	0	0	0	0	0	0	0,3	0
Crunoecia kempnyi	0,7	0,3	0	0,7	0,3	0,3	0	0
Beraea pullata	0	0	0	0	0,7	0,3	0	0
Overall abundance	31,3	214,2	20,8	89,2	71,0	31,2	63,2	52,7

3.1.2. Longitudinal distribution

The longitudinal distribution analysis (Figure 15) shows the eucrenal share, which ranges between 21.1 % (2001) and 33.2 % (2007), while the hypocrenal share fluctuates between 18.4 % (2007) and 31.9 % (2001). The overall highest dominance was observed for the share of epirhithral in 2001 (33.9 %). Cumulatively, the crenic zone is represents the highest share in 2020 (59.4 %) and the lowest in 2021 (51.5 %). The share of the littoral zone fluctuated, but showed a trend towards an increase, while it reached the highest value in 2021 (15.3 %).
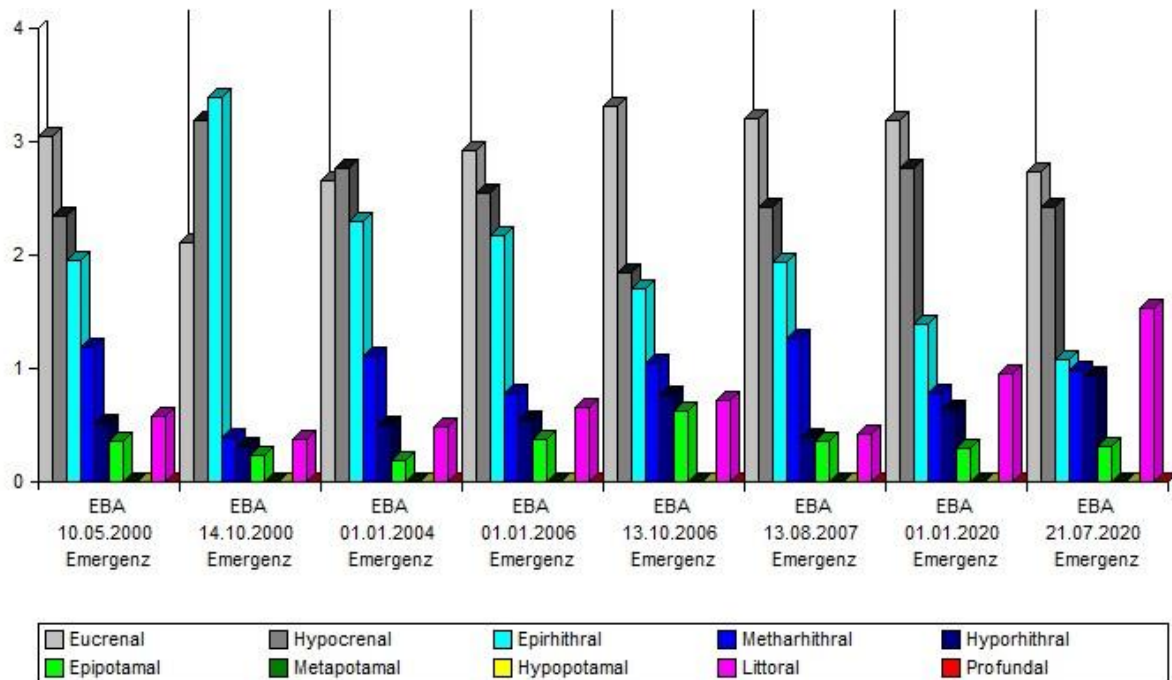

Figure 15: Results of the longitudinal distribution analysis at the Ebenforstalm spring (EBA) using ECOPROF. The y-axis shows the relative shares in % (1 = 10 %). The dates on the y-axis indicate the different sampling periods. The second time frame (starting on 14/10/2000) e. g. represents the sampling year 2001.

3.1.3. Functional feeding guilds

The ECOPROF analysis of the FFGs (Figure 16) does not show a clear trend, but rather a constant distribution of shredders, grazers and detritivores. The biggest increase of shredders occurred from 2007 (26.7 %) to 2008 (36.4 %) – and the biggest decrease of detritivores (41.2 % -> 33.1 %) in the same period.
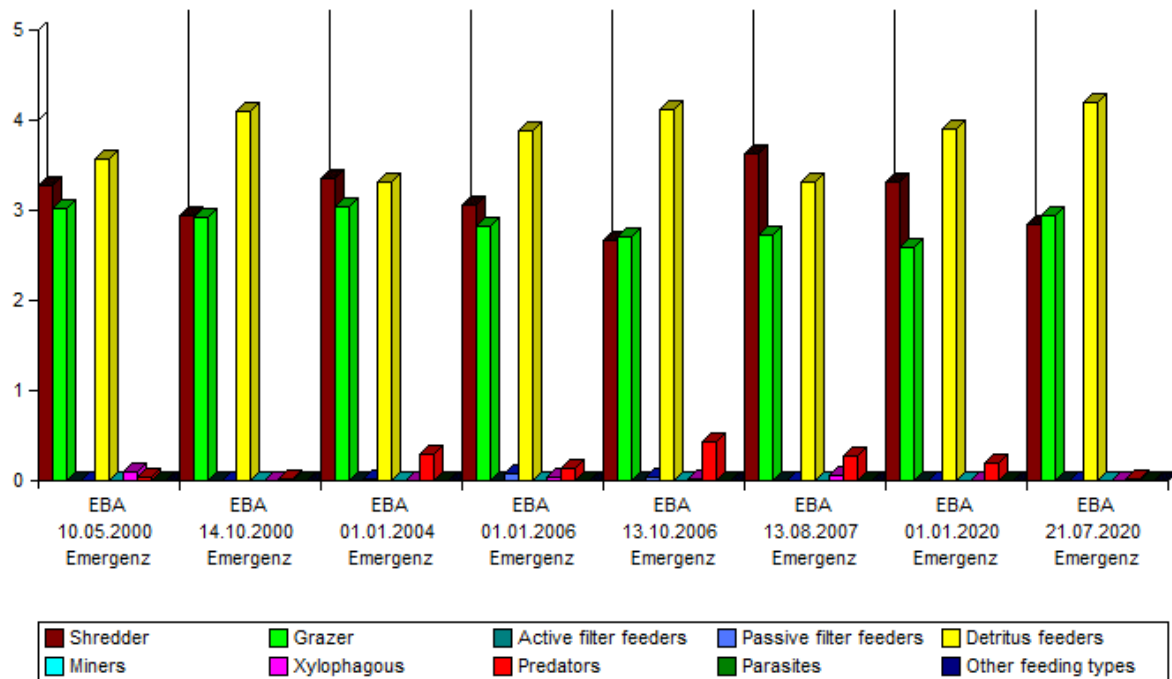

Figure 16: Results of the distribution of FFGs at the Ebenforstalm spring (EBA) using ECOPROF. The y-axis shows the relative shares in % (1 = 10 %). The dates on the y-axis indicate the different sampling periods. The second time frame (starting on 14/10/2000) e. g. represents the sampling year 2001.

3.1.4. Saprobity classes

The share of xenosaprobic taxa fluctuated between 38.9 % and 49.4 % in the first observed period (2000-2008) and thereafter drastically decreased to the lowest value in 2021 (14.3 %; Figure 17). This development is mirrored in the share of beta-mesosaprobic taxa, however reversely. It fluctuates between 10 % and 2.2 % in the first observed period (2000-2008) and heavily increases thereafter to its maximum in 2021 (35 %).
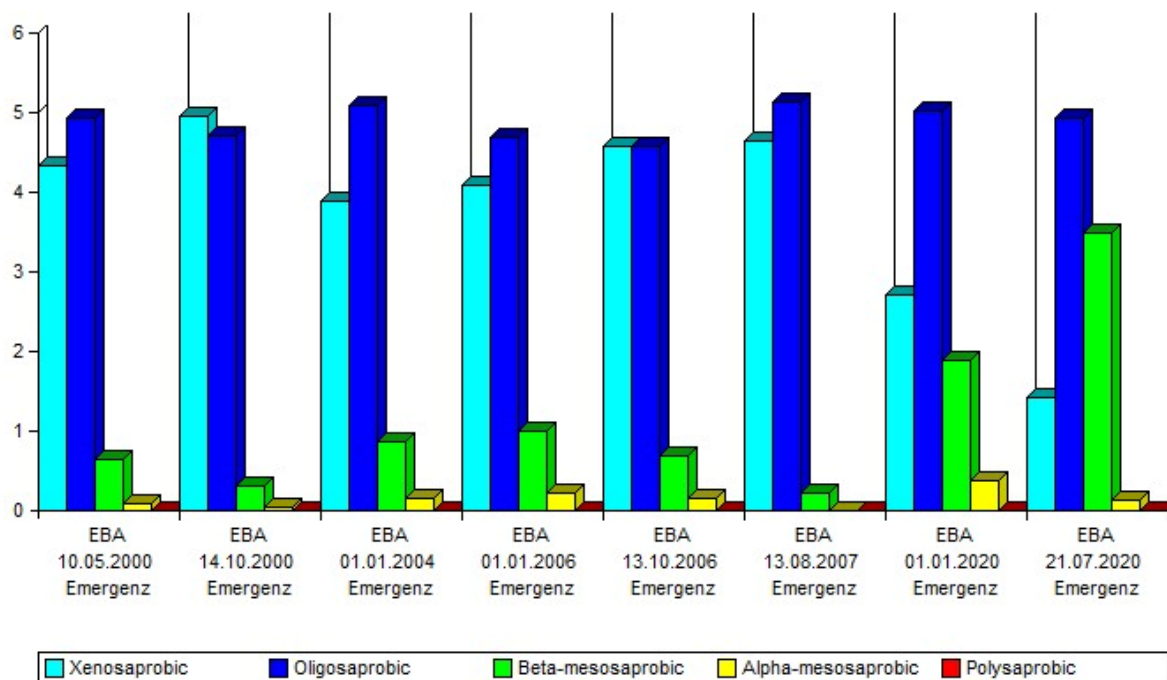

Figure 17: Results of the distribution of saprobity classes at the Ebenforstalm spring (EBA) using ECOPROF. The y-axis shows the relative shares in % (1 = 10 %). The dates on the y-axis indicate the different sampling periods. The second time frame (starting on 14/10/2000) e. g. represents the sampling year 2001.

3.1.5. Dominance of species with indicative traits

The dominance of shredders fluctuates between 1.67 % (2001) and 12.37 % (2020; Figure 18). In 2021 (3.7 %), this value was lower than it was two years before the protection fence was erected (2000; 4.17 %). The share of species indicating xenosaprobic conditions was highest in 2004 (70.31 %) and lowest in 2021 (8.64 %). Species requiring constantly low water temperatures were most dominant in 2004 (67.19 %) and made up the lowest share of the community in 2021 (8.64 %). Rheolithophil species were only found in 2006 (0.73 %), 2008 (2.08 %) and 2020 (2.06 %). Crenobionts were most dominant in 2020 (30.41 %) and least dominant in 2021 (5.56 %). The second highest share of crenobionts was observed in 2001 (23.71 %).
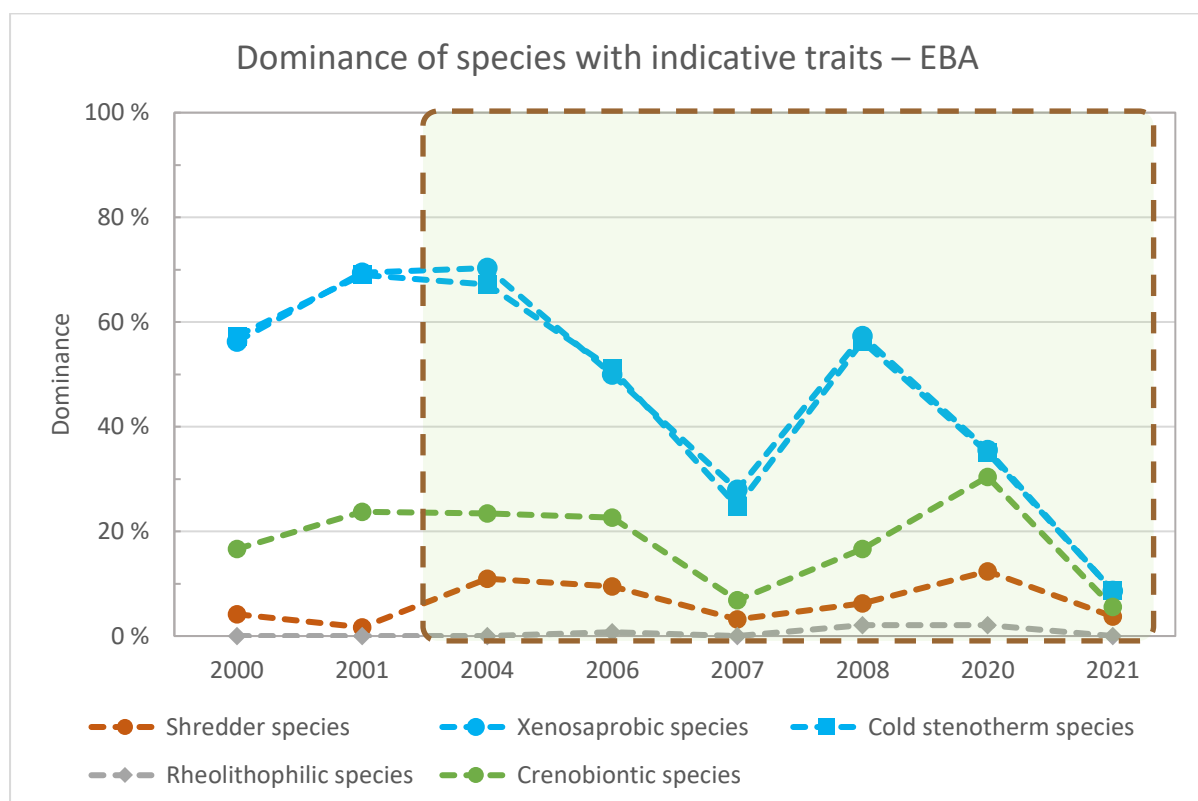

Figure 18: Development of species with indicative traits over time at the Ebenforstalm spring (EBA). Brown dashed rectangle indicates the period with a protection fence.

3.1.6. Community changes

Development of the five most abundant taxa and similarity

At EBA, one taxon (*Nemurella pictetii*) was found every year, with the highest dominance in 2007 (60.55 %; Figure 19). This was also the highest overall dominance recorded. *Leuctra armata* was not among the five most dominant taxa in but one year (2007) and exhibited a dominance between 4.32 % (2021) and 24.74 % (2020). Taxa with dominances > 10 % (≙ dominance class "dominant", see Table 12), are *Amphinemura standfussi* (2000), *Leuctra handlirschi* (2001, 2006) and *Protonemura auberti* (2000, 2004, 2007 and 2008). The remaining taxa made up a share between 2.43 % (2001) and 21.88 % (2004).

Similarity in comparison to the first investigated year (2000) was highest in 2008 (P = 0.76). In both years, *Nemurella pictetii* and *Protonemura auberti* were the two most abundant taxa. The lowest similarity was observed in 2021 (P = 0.44) when the community was dominated by *Leuctra nigra* (59.26 %).
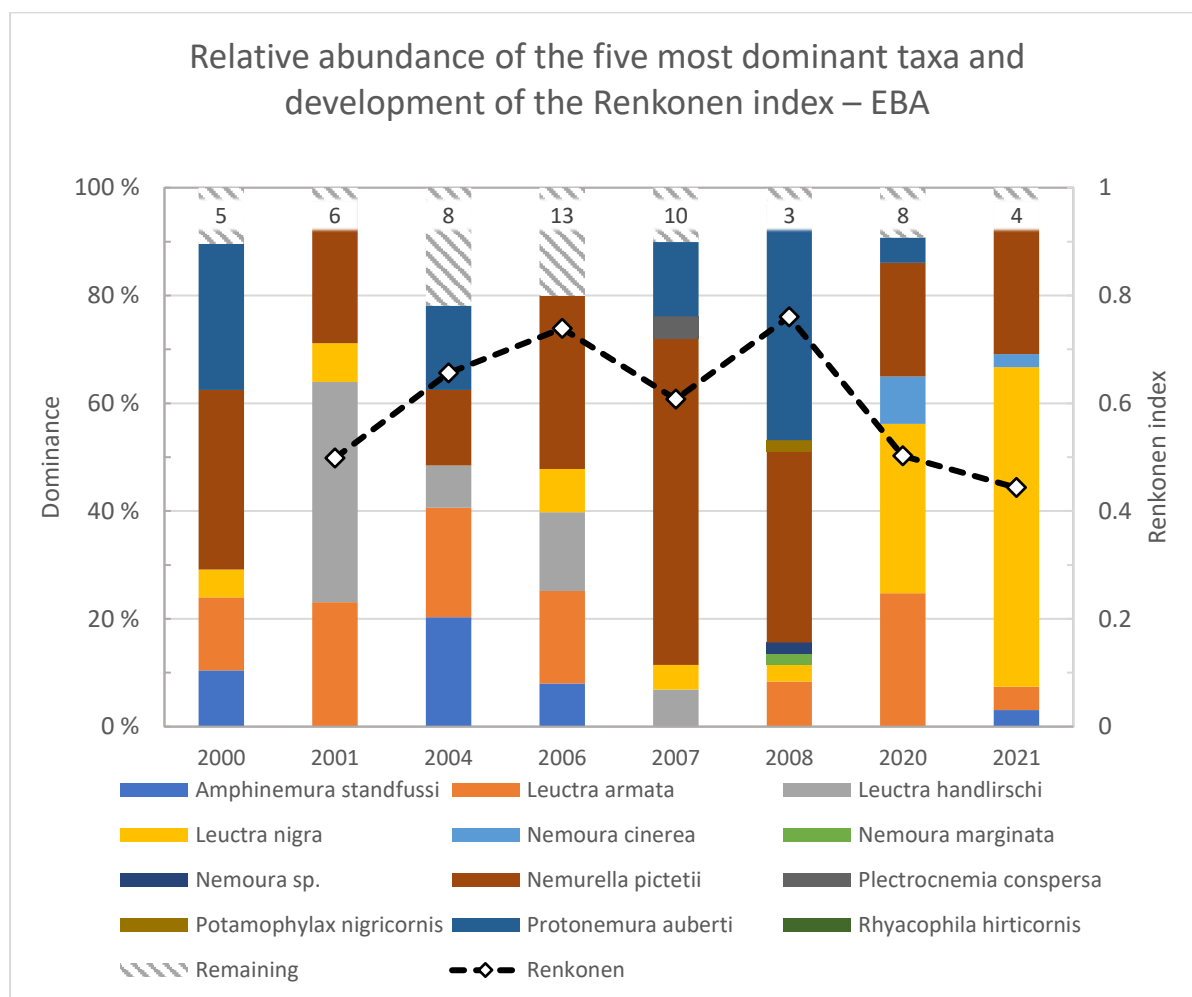
Figure 19: Dominance of the five most dominant taxa at the Ebenforstalm spring (EBA) (y-axis1). If multiple taxa showed the same dominance, more than five taxa were displayed. The Renkonen index shows the similarity between the first and each consecutive year thereafter (y-axis2). The number on top of the bar shows the taxa number of the share, not covered by the five most abundant taxa ("Remaining").

Development of taxa, indicative of a helocrenal character

At EBA, all five taxa which are typical for helocrenal conditions were found. *Nemurella pictetii* developed the highest dominance in 2007 (60.55 %). A comparably high dominance was observed for *Leuctra nigra* (59.26 %; 2021). *Nemoura cinerea* was found in every year except 2008 and developed the highest dominance in 2020 (8.76 %). *Parachiona picicornis* was found in all but two years (2000 and 2008) and was most dominant in 2004 (3.13 %). The crenobiont *Beraea pullata* was only found in 2007 and 2008 (~ 1 %).

Figure 20: Development of the dominance of five taxa, indicative of a helocrenal character at the Ebenforstalm spring (EBA).

3.2. Jörglalm Spring (JÖA)

3.2.1. Taxa list

Table 15: Calculated abundances [Ind. / m²] of sampled species at the Jörglalm spring (JÖA).

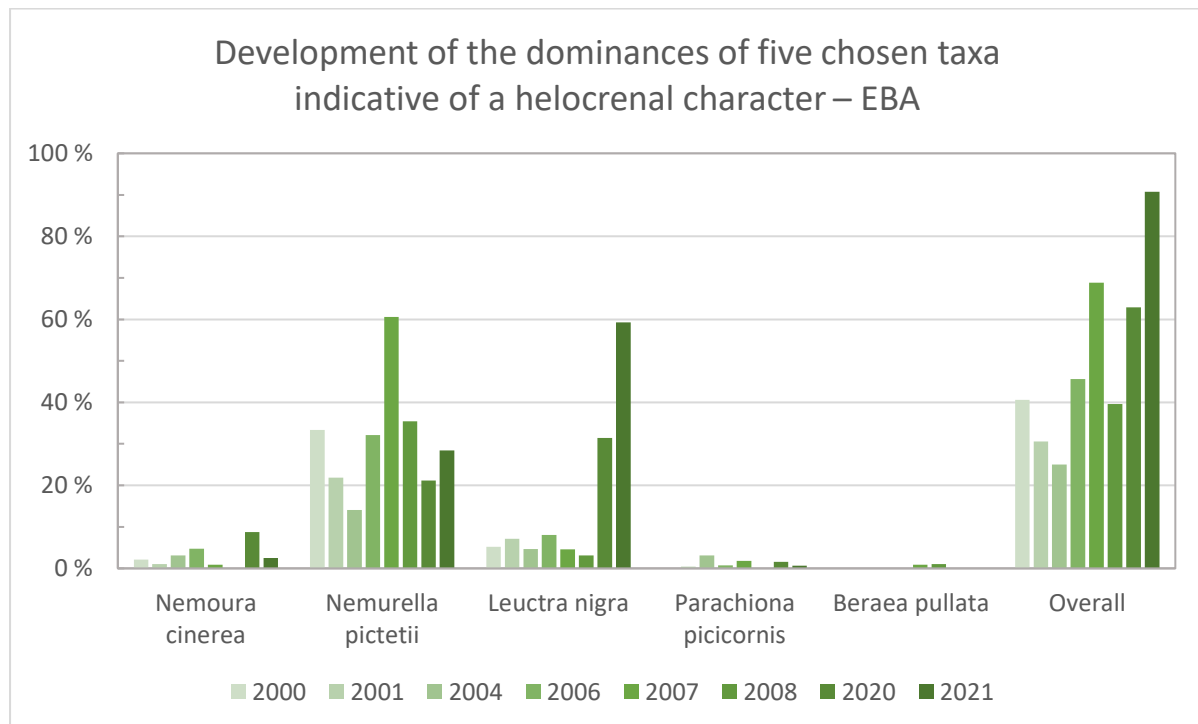| Species	Abundance [Ind. / m2]								
	2000	2001	2002	2005	2006	2007	2008	2020	2021
Dictyogenus alpinum	0	0	0	0,7	0	0	0	0	0
Dictyogenus fontium	15,6	34,5	0,7	2,6	2,9	0,3	6,2	3,9	1,0
Isoperla goertzi	0	0	0	0	0	0	0	0	0,3
Isoperla sp.	0	0	0	0	0	0	0,3	0	0
Perlodes intricatus	0	0	0	0	0,3	0	0	0	0
Perla grandis	0	0,3	0	0	0	0	0	0	0
Amphinemura standfussi	0	0	0	0	0	0	0,3	0	0
Nemoura marginata	0	0	0,3	1,3	0	0	0	0	0,3
Nemoura minima	3,3	9,4	5,9	8,5	4,6	2,9	6,2	5,5	9,1
Nemoura mortoni	0	0	0	0	0	0,3	0,3	1,0	3,3
Nemoura sp.	1,3	2,6	0	2,6	2,9	0,3	2,9	2,0	3,6
Protonemura auberti	4,2	13,3	4,6	14,3	16,0	2,3	7,5	13,0	2,9
Protonemura hrabei	0	0	0	0	0	0,3	0	0	0
Protonemura nitida	0	0	0	0	0	0,3	0	0	0
Protonemura sp.	0,3	0	0	0	0	0	0	0	0
Capnioneura nemuroides	0	0	0	0	0	0	0	0,3	0
Leuctra alpina	0	0	0,3	0	0	0	0	0	0
Leuctra armata	1,0	14,0	11,4	23,1	8,5	9,4	20,5	21,8	27,3
Leuctra autumnalis	4,2	1,3	0	7,5	8,8	0,7	3,3	11,4	0
Leuctra braueri	5,9	7,5	0	43,9	9,4	1,6	13,7	26,7	0
Leuctra cingulata	0	0	0	0	0	0,7	0	0,3	0
Leuctra handlirschi	0	0,3	0	0	0	0	0	0	0
Leuctra helvetica	0,3	0	0	0	0	0	0	0	0
Leuctra moselyi	0	0	0	0	0	0	0	0	0,3
Leuctra nigra	0	0,3	0	0	0	0	0	0	0
Leuctra pseudosignifera	0	0,3	0	0	3,3	0	0	0	0
Leuctra rosinae	0	0,3	0	0	0	0	0	0	0
Leuctra sp.	0	0,7	0	0	0	0	0	0	0
Rhyacophila producta	0,7	7,8	3,9	3,6	7,2	4,6	5,5	5,5	6,2
Rhyacophila vulgaris	1,3	0,7	0	1,6	0	0,3	1,0	1,6	0
Glossosoma conformis	0	0	0	0,3	0	0	0	0	0
Synagapetus iridipennis	9,8	3,3	0	6,2	0,7	0	5,5	0	9,4
Synagapetus krawanyi	5,2	4,6	0	3,6	6,2	0	5,9	10,1	4,2
Synagapetus iridipennis / krawanyi	0,7	7,2	0	0	0	0	11,4	4,2	0,3
Philopotamus ludificatus	0	2,9	8,1	3,6	2,6	0,3	5,5	9,4	2,6
Wormaldia copiosa	1,3	0	0	0	0	0	0	0,3	0,3
Wormaldia occipitalis	0,3	0,3	0,3	3,3	0,7	1,0	1,6	4,9	0,3
Hydropsyche sp.	0	0	0	0,3	0	0	0	0	0
Plectrocnemia conspersa	0	0	0	0	0	0	0	0,3	0
Tinodes dives	30,3	11,4	3,3	11,4	5,9	1,0	50,1	16,9	5,2
Micrasema morosum	0,7	1,0	0,3	0,7	0,3	0	1,6	0	0,3
Allogamus uncatus	0,7	0,3	0	0,7	0,7	0,3	0,3	0,7	0
Chaetopteryx major	0	0	0	0,3	0	0	0	0	0
Drusus monticola	0	2,0	3,3	0,3	0,7	1,6	4,9	2,0	1,3
Melampophylax melampus	0	0	0	0	0	0,3	0	0,7	0
Potamophylax cingulatus	0	0	0	0,3	0	0	0,7	0	0
Pseudopsilopteryx zimmeri	0,3	2,0	0	0	3,6	2,6	0,3	0,7	0
Overall abundance	87,2	128,3	42,3	140,6	85,0	31,3	155,6	143,2	78,5

3.2.2. Longitudinal distribution

The longitudinal distribution analysis shows a eucrenal share ranging from 17.5 % (2002) to 32.8 (2021), while the hypocrenal share fluctuates at a higher level between 35.6 % (2006) and 44 % (2008; Figure 21). Additionally, the share of the epirhithral is equally high with a maximum of 42.1 % in 2002. Cumulatively, the crenic zone is represented the most in 2021 (69.3 %) and the least in 2002 (53.2 %).
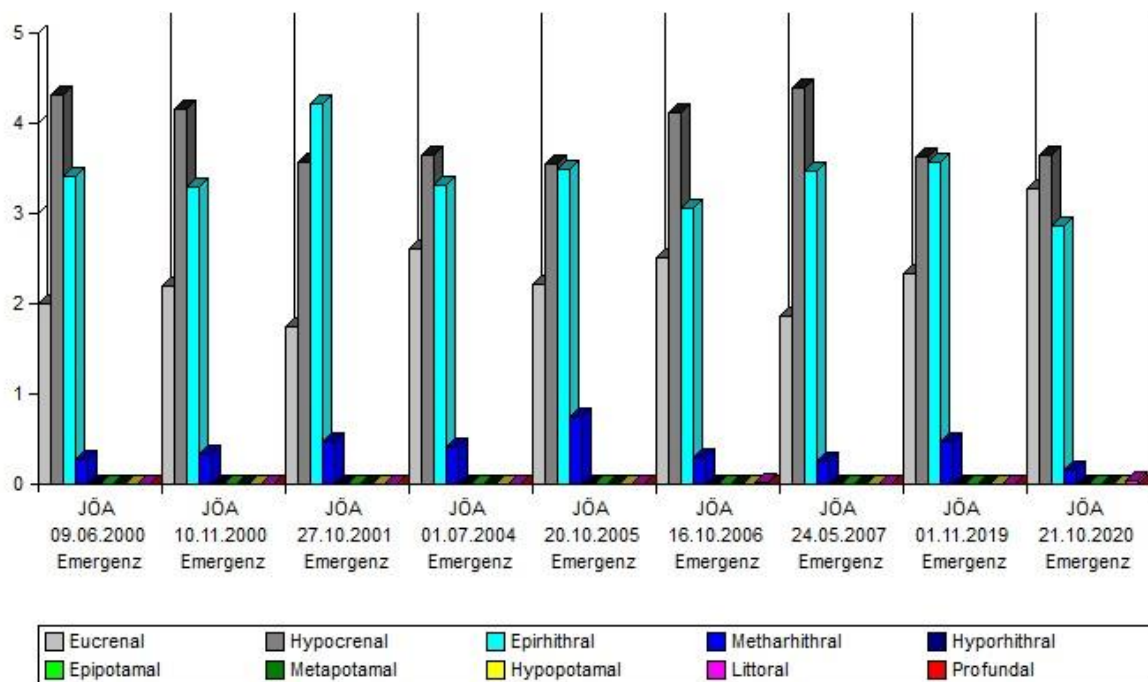

Figure 21: Results of the longitudinal distribution analysis at the Jörglalm spring (JÖA) using ECOPROF. The y-axis shows the relative shares in % (1 = 10 %). The dates on the y-axis indicate the different sampling periods. The second time frame (starting on 10/11/2000) e. g. represents the sampling year 2001.

3.2.3. Functional feeding guilds

The ECOPROF analysis of the FFGs at JÖA (Figure 22) shows five feeding guilds being represented in each year. In six of the nine investigated years, grazers were the most dominant feeding guild. By far the highest dominances occurred in 2000 (48.2 %) and 2008 (49.5 %). In the remaining years, the predators (34.3 %; 2001) or shredders (24.9 %; 2002 / 31.4 %; 2007) were most dominant. The share of detritivores was lowest in 2000 (15 %) and highest in 2005 (28.3 %). Additionally, passive filter feeders were found in all investigated years and were most dominant in 2002 (20.9 %).

Figure 22: Results of the distribution of FFGs at the Jörglalm spring (JÖA) using ECOPROF. The y-axis shows the relative shares in % (1 = 10 %). The dates on the y-axis indicate the different sampling periods. The second time frame (starting on 10/11/2000) e. g. represents the sampling year 2001.

3.2.4. Saprobity classes

The share of xenosaprobic taxa was lowest in 2008 (34.3 %) and highest in 2021 (49.3 %; Figure 23). Oligosaprobic taxa were most dominant in 2008 (54.6 %) and least dominant in 2001 (46.4 %), while the share of beta-mesosaprobic taxa fluctuated between 3.8 % (2021) and 12.9 % (2005). Alpha-mesosaprobic taxa were found in 2007–2021, however their share was below 1 %.

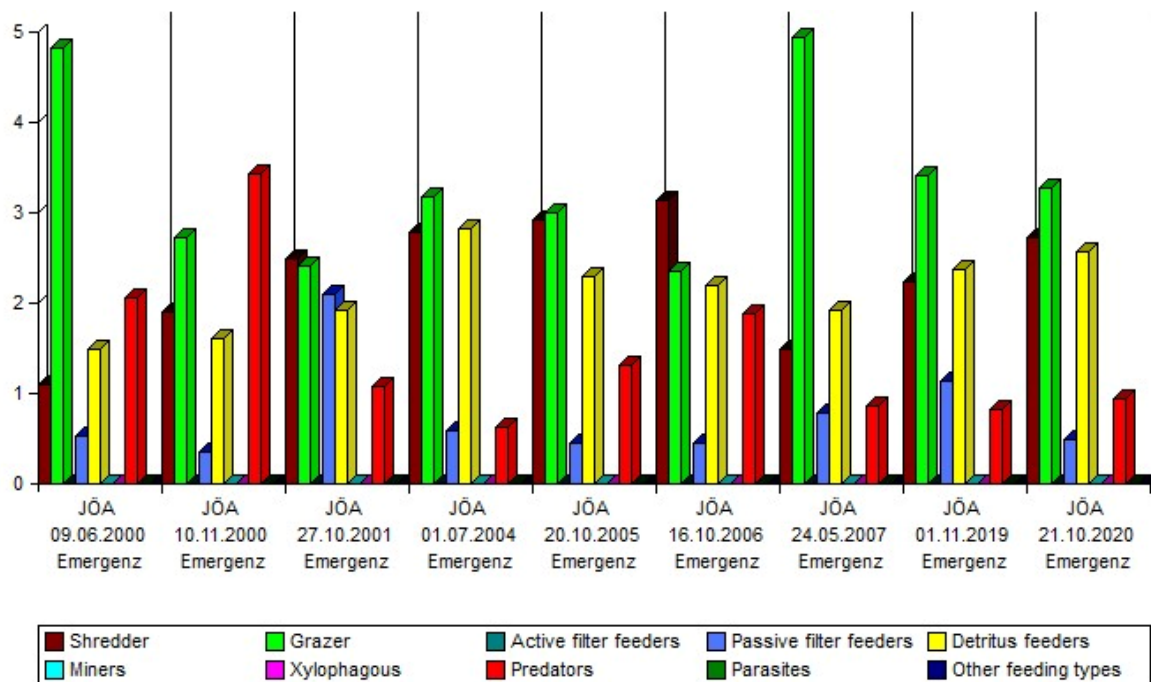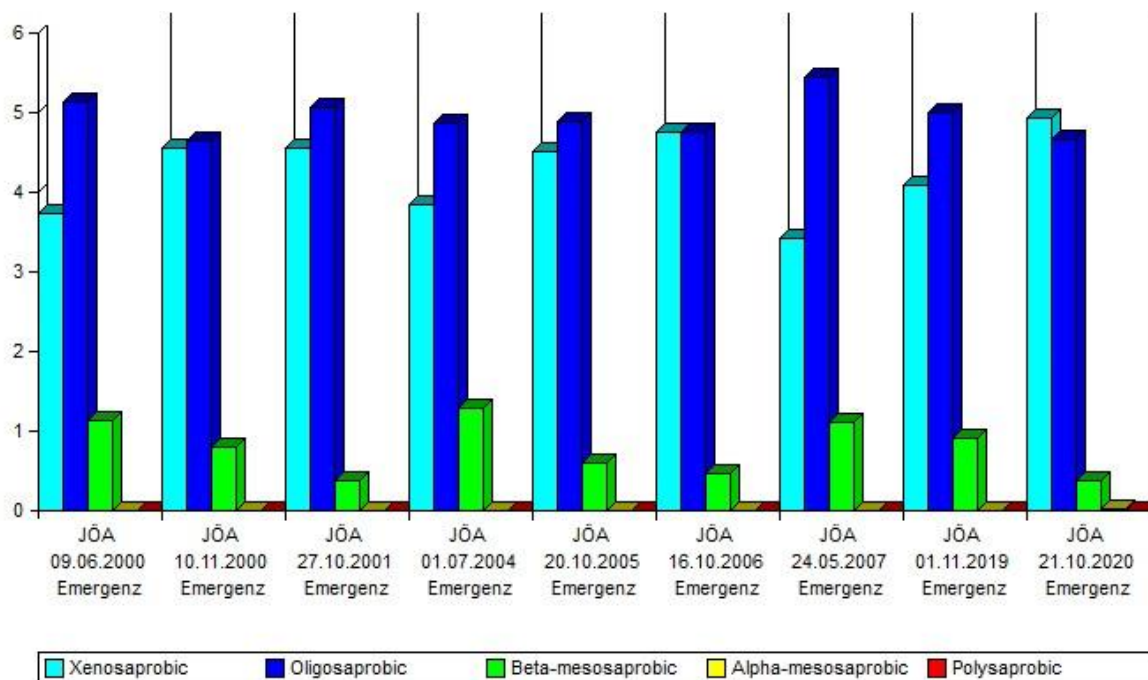*Figure 23: Results of the longitudinal distribution analysis at the Jörglalm spring (JÖA) using ECOPROF. The y-axis shows the relative shares in % (1 = 10 %). The dates on the y-axis indicate the different sampling periods. The second time frame (starting on 10/11/2000) e. g. represents the sampling year 2001.*

3.2.5. Dominance of species with indicative traits

The dominance of specialist shredders increased from 6.34 % in 2000 up to 21.88 % in 2007 (Figure 24). In 2021, the second highest value (20.75 %) was observed. In 2000 (55.22 %), 2005 (56.02 %) and 2008 (56.07 %), the lowest dominances of xenosaprobists were observed. On the other hand, the highest share was observed in 2002 (90.77 %), followed by 2007 (87.50 %) and 2021 (83.82 %). Cold stenothermic taxa were most dominant in 2007 (88.54 %). The lowest (2008; 60.04 %) and second lowest (2000; 60.07 %) dominance value were both observed in the fenced period. Rheolithophil species made up the highest share of the community in 2000 (73.88 %). Until 2002, they decreased by 46.19 % and only made up 27.69 %. Thereafter, the share of these species stagnated until 2007 and rose thereafter to 60.46 % in 2008. The share of spring specialists fluctuated between 53.64 % (2006) and 80.96 % (2008).
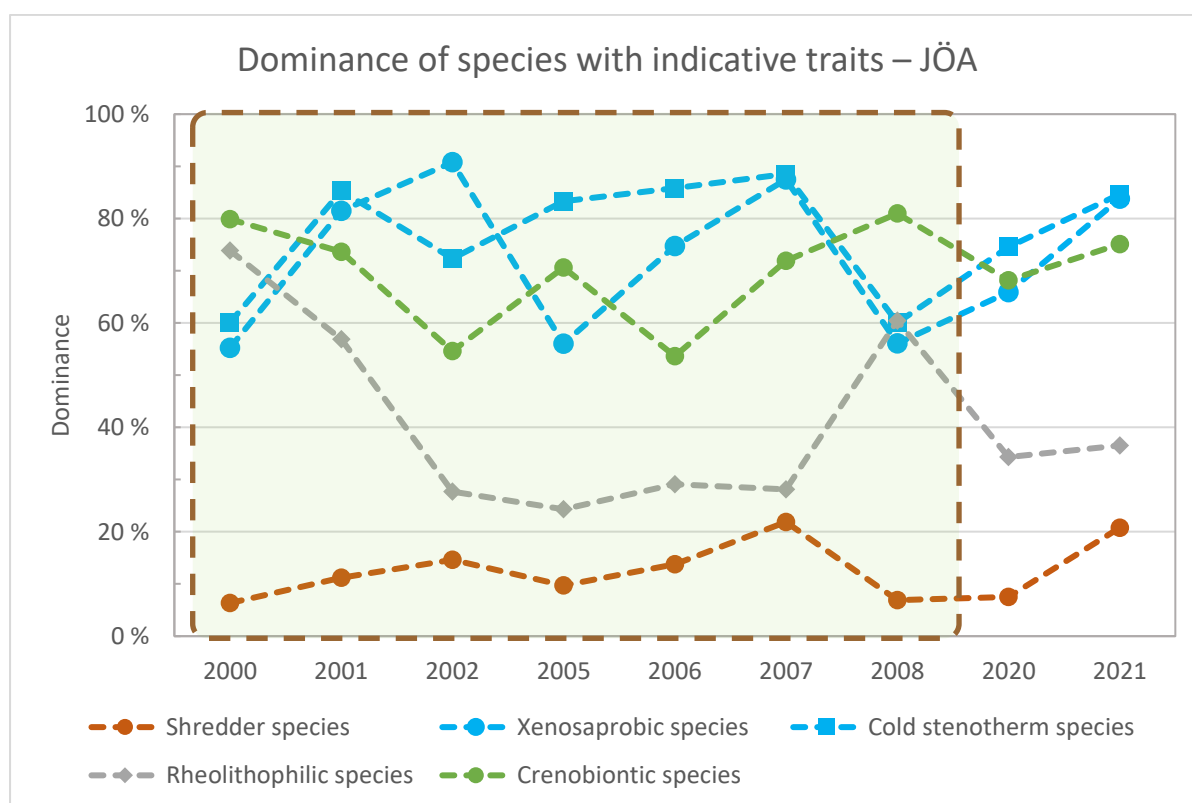
Figure 24: Development of species with indicative traits over time at the Jörglalm spring (JÖA). Brown dashed rectangle indicates the period with a protection fence.

3.2.6. Community changes

Development of the five most abundant taxa and similarity

From 2001 onwards, *Leuctra armata* continuously showed a dominance > 10 % and also represented the overall highest dominance in 2021 (34.85 %; Figure 25). Only one other taxon (*Tinodes dives*) was eudominant (> 32 %; 2008). The share not covered by the five most dominant taxa fluctuated between 20 % (2002) and 41.4 % (2006) and was made up by 7 (2002) to 20 taxa (2001).

Similarity to the community in 2000 was lowest in 2002 (P = 0.21), mainly due to the drastic differences regarding the dominance of *Dictyogenus fontium* (17.9 % -> 1.5 %), *Leuctra armata* (1.1 % -> 26.9 %), *Philopotamus ludificatus* (0 % -> 19.2 %) and *Tinodes dives* (34.7 % -> 7.7 %). The highest similarity to 2000 was observed in 2008 (P = 0.66) when *Tinodes dives* in particular occurred in similar dominances (34.7 % ≈ 32.2 %).
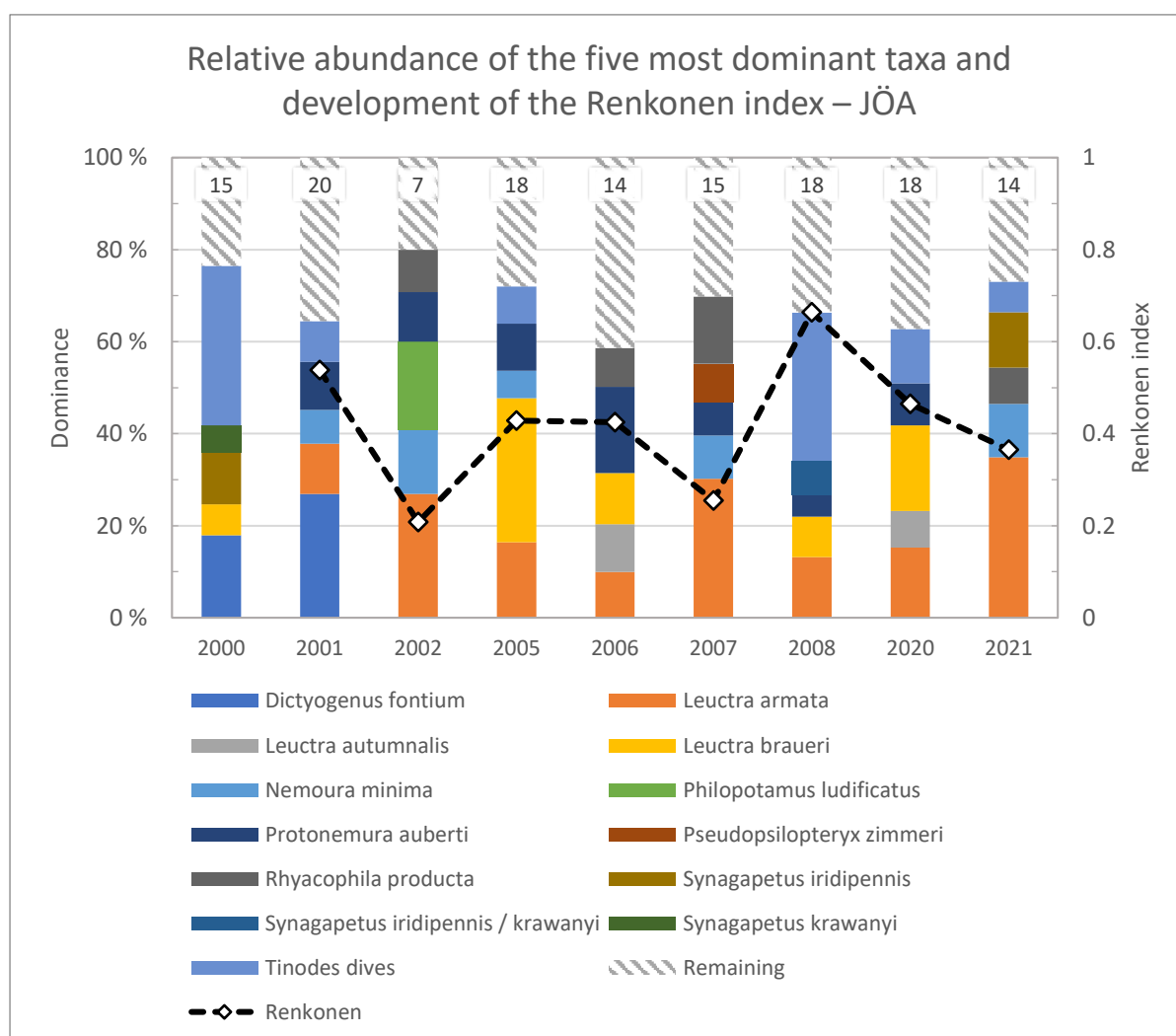
Figure 25: Dominance of the five most dominant taxa at the Jörglalm spring (JÖA) (y-axis1). If multiple taxa showed the same dominance, more than five taxa were displayed. The Renkonen index shows the similarity between the first and each consecutive year thereafter (y-axis2). The number on top of the bar shows the taxa number of the share, not covered by the five most abundant taxa ("Remaining").

Development of taxa, indicative of a helocrenal character

At JÖA, only *Leuctra nigra* was found. In 2001, it had a dominance of 0.25 %.

Figure 26: Development of the dominance of five taxa, indicative of a helocrenal character at the Jörglalm spring (JÖA).

3.3. Schaumbergalm spring (SCHA3)

3.3.1. Taxa list

Table 16: Calculated abundances [Ind. / m²] of sampled species at the Schaumbergalm spring (SCHA3).

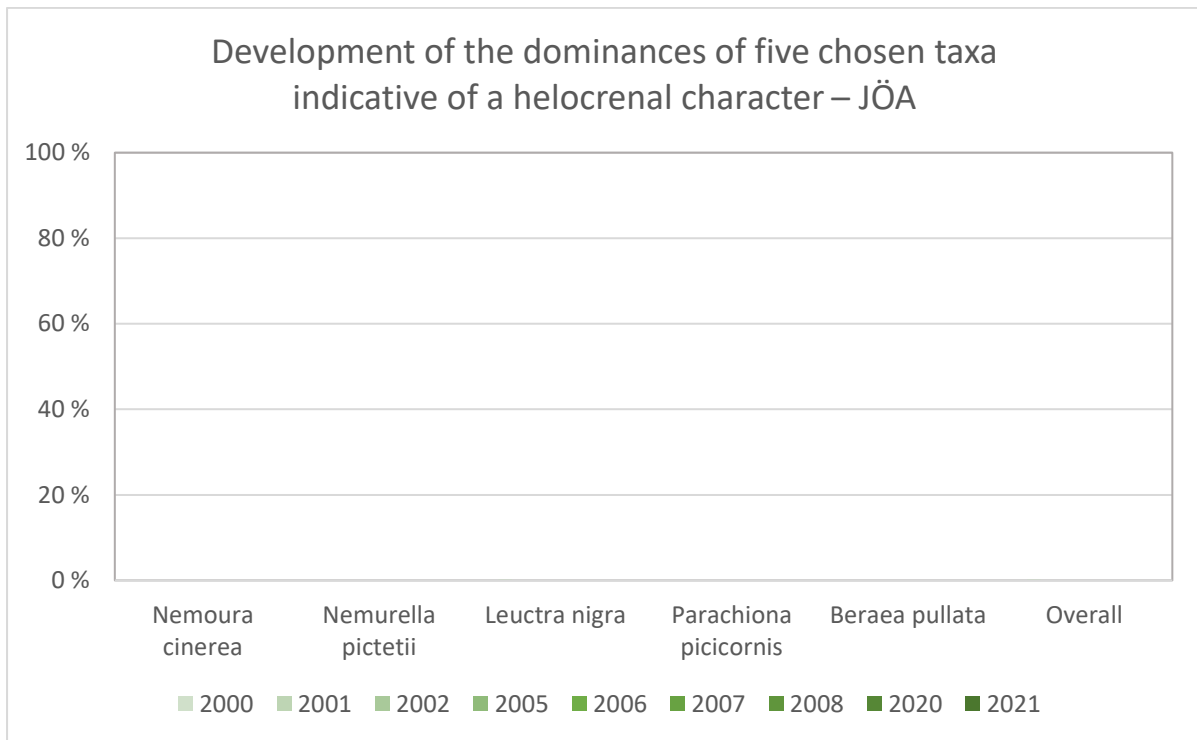| Species	Abundance [Ind. / m^2]								
	2000	2001	2002	2005	2006	2007	2008	2020	2021
Amphinemura standfussi	0	5,2	5,2	0	0	5,4	9,0	1,0	4,6
Nemoura cinerea	1,0	1,3	0,3	0	0,7	0	0,5	0	0
Nemoura marginata	0	0	0	4,9	3,6	7,3	0,7	7,5	7,2
Nemoura minima	0,3	0,3	0	0,3	0	4,9	0,2	0,3	0,3
Nemoura obtusa	0	0	0	0	0	0	0,2	0	0
Nemoura sp.	0,3	2,9	2,6	2,0	3,3	14,9	1,7	8,1	1,3
Nemurella pictetii	7,5	13,7	6,2	2,0	0,7	4,2	2,7	4,2	2,3
Protonemura auberti	0,3	0,3	0	0,7	4,6	11,5	0	51,1	26,4
Leuctra albida	0	1,0	1,0	0,3	0	0	0	0,3	0
Leuctra armata	5,9	6,8	1,0	10,1	110,0	27,8	10,7	6,8	22,5
Leuctra braueri	0	13,7	13,7	0	0	10,5	27,3	28,3	113,3
Leuctra handlirschi	17,9	18,2	0,3	9,1	11,1	12,2	3,7	3,3	8,8
Leuctra sp.	0	0,3	0,3	0	0	0	0	0	0
Rhyacophila hirticornis	0,3	0,3	0	0	0,3	0,5	0,5	6,8	2,0
Philopotamus ludificatus	0	0	0	0,7	0,3	0	0	0	0
Wormaldia copiosa	0	0	0	0	0	0	0,2	0	0
Wormaldia occipitalis	0	0,3	0,3	0	0	0,2	1,0	0	0,3
Plectrocnemia conspersa	0	0,7	0,7	0	0	0,5	0,5	1,0	2,9
Tinodes dives	0	0	0	0	0,3	2,0	0	2,6	1,6
Chaetopteryx major	0	0	0	0	0	0	0,2	0	0
Drusus chrysotus	0	0	0	0,3	0	0	0,2	0,3	0
Leptotaulius gracilis	0	0	0	0	0,3	0,5	0	0	0
Limnephilus extricatus	0	0	0	0	0	0	0	0	0,3
Limnephilus sparsus	0	0	0	0	0	0	0,2	0	0
Melampophylax melampus	0	0	0	0	0	0	0,2	0	0,3
Potamophylax nigricornis	0,3	0,3	0	1,0	0	1,2	1,0	0,7	0,3
Pseudopsilopteryx zimmeri	0	0,7	0,7	0	0	0	1,2	0	0
Lithax niger	0	0	0	0,3	1,6	0,7	0,7	0	1,3
Crunoecia kempnyi	0	1,0	1,0	0	0	2,9	1,2	1,0	1,6
Sericostoma personatum	0,3	0,3	0	0,3	0	0,2	1,2	0,7	0,7
Beraea pullata	0	0	0	0	0	0,5	0,2	0	0,3
Ernodes vicinus	0	0	0	0	0	0,2	0	0	0
Overall abundance	34,2	67,4	33,2	31,9	136,7	108,2	65,7	124,0	198,2

3.3.2. Longitudinal distribution

The longitudinal distribution analysis at SCHA3 (Figure 27) shows the highest eucrenal share in 2002 (36.3 %) and a downward trend from then on. Thus, the lowest value was observed in 2021 (19.3 %). The hypocrenal share follows an equal trend: The highest dominance was observed in 2002 (38.9 %) and lowest thereafter in 2020 (32.2 %). The share of the epirhithral reached equally high dominances and fluctuates between 23.5 % in 2002 and 39.1 % in 2021.

Figure 27: Results of the longitudinal distribution analysis at the Schaumbergalm spring (SCHA3) using ECOPROF. The y-axis shows the relative shares in % (1 = 10 %). The dates on the y-axis indicate the different sampling periods. The second time frame (starting on 05/11/2000) e. g. represents the sampling year 2001.

3.3.3. Functional feeding guilds

The ECOPROF analysis of the FFGs at SCHA3 (Figure 28) shows no clear trends for any of the observed guilds. However, shredders were the most dominant group in five of the nine investigated years, while detritivores were the most dominant in the remaining four. The share of grazers fluctuates between 19.8 % (2020) and 29.1 % (2006). Additionally, predators were most abundant in 2007 (2.2 %) and passive filter feeders in 2001 (2.4 %). Xylophags (*Crunoecia kempnyi*) were observed in 2000, from 2005 to 2008 and in 2020 with the highest share recorded in 2005 (1.4 %).

Figure 28: Results of the distribution of FFGs at the Schaumbergalm spring (SCHA3) using ECOPROF. The y-axis shows the relative shares in % (1 = 10 %). The dates on the y-axis indicate the different sampling periods. The second time frame (starting on 05/11/2000) e. g. represents the sampling year 2001.

3.3.4. Saprobity classes

The share of xenosaprobic taxa at SCHA3 was lowest in 2008 (32.3 %) and highest in 2021 (49.4 %, Figure 29). Oligosaprobic taxa were most dominant in 2002 (57 %) and least dominant in 2001 (43.1 %). They were the most dominant share in every year, with the exception of 2000 and 2021. The share of beta-mesosaprobic taxa was highest in 2008 (22.1 %) and second highest in 2006 (19.2 %).
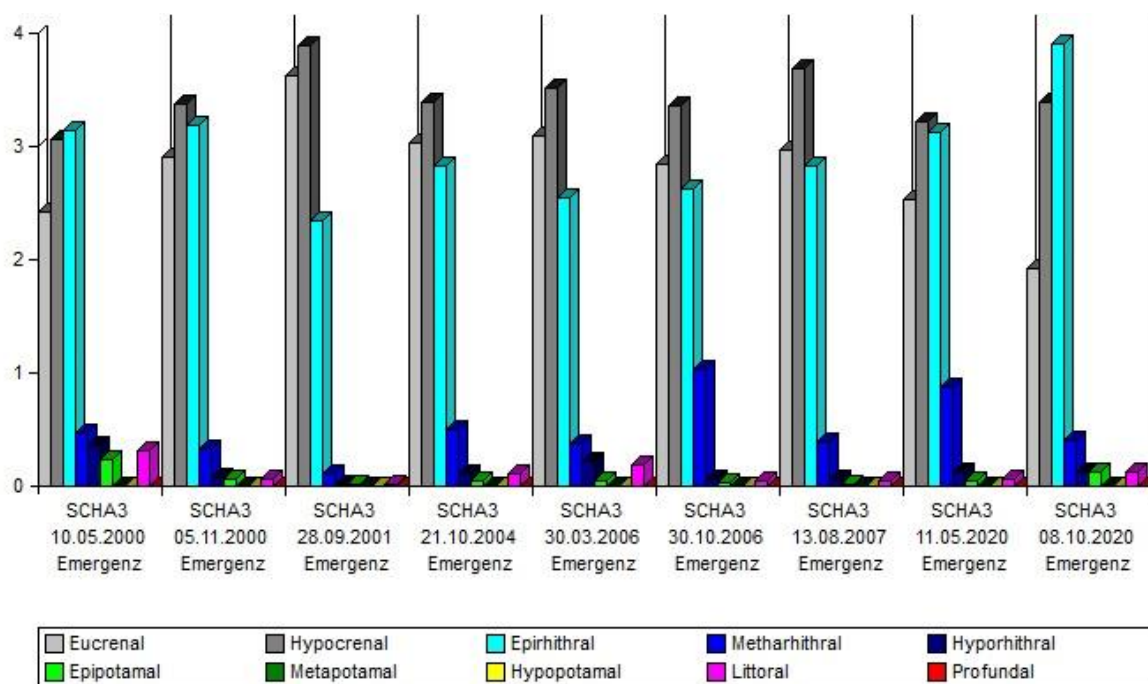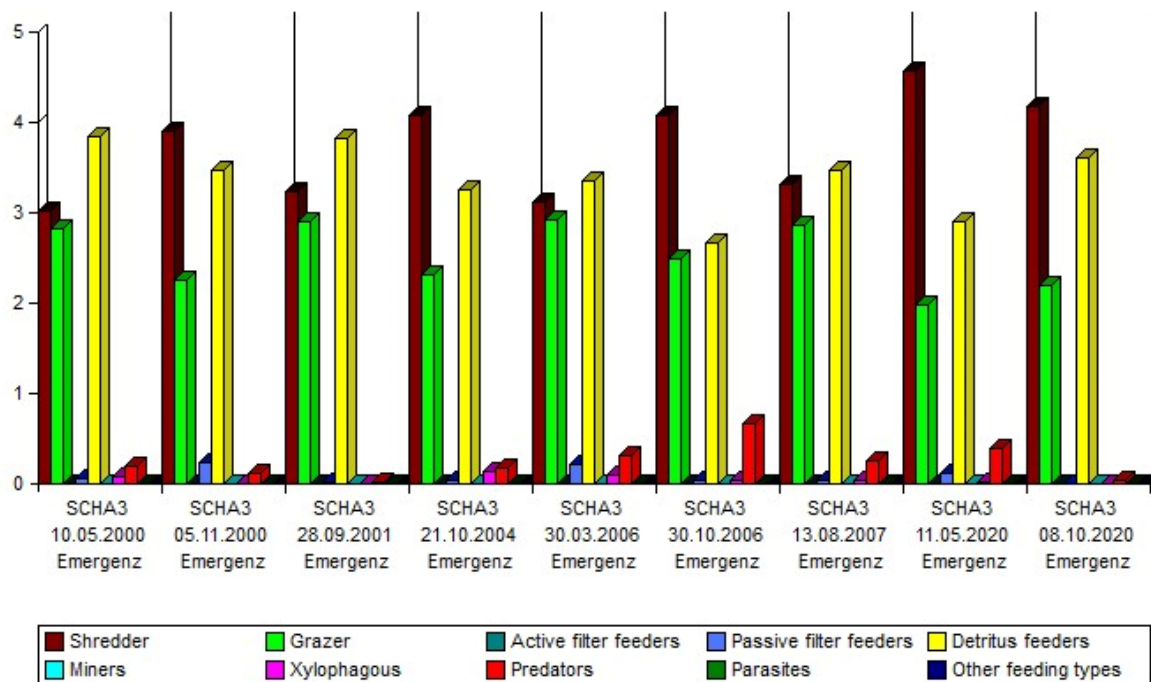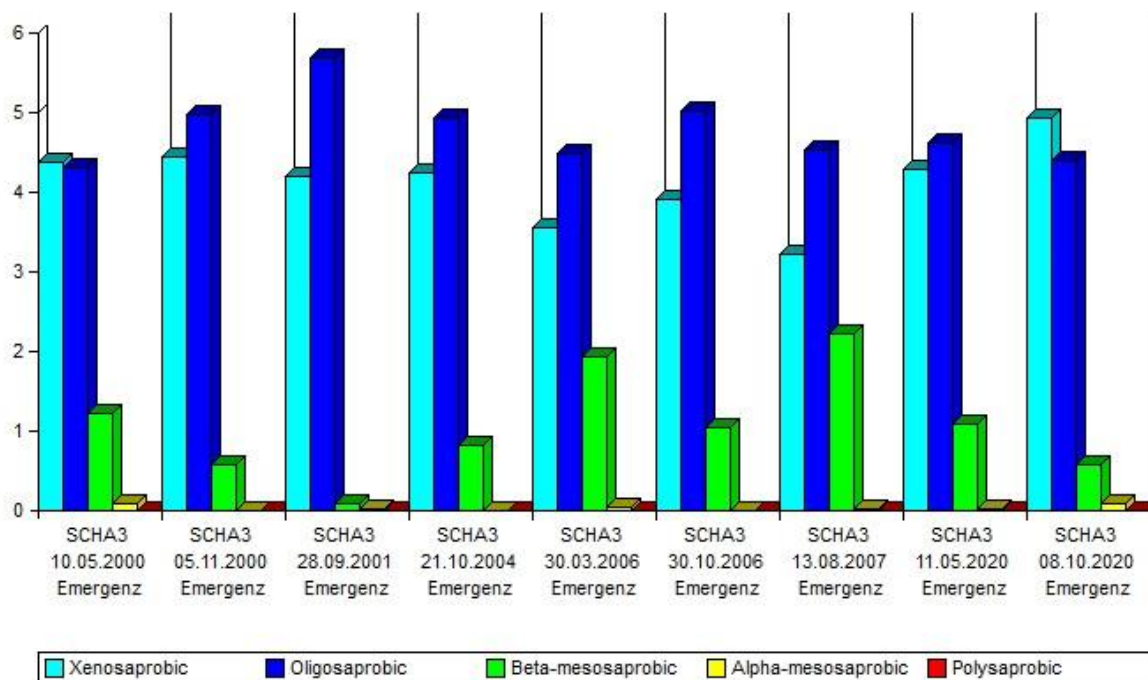

Figure 29: Results of the distribution of saprobity classes at the Schaumbergalm spring (SCHA3) using ECOPROF. The y-axis shows the relative shares in % (1 = 10 %). The dates on the y-axis indicate the different sampling periods. The second time frame (starting on 05/11/2000) e. g. represents the sampling year 2001.

3.3.5. Dominance of species with indicative traits

The share of specialised shredders fluctuated between 5.09 % (2008) and 33.33 % (2020, Figure 30). From 2000 (49.76 %) to 2002 (93.81 %), the share of xenosaprobic organisms increased to by 44.05 %. The lowest value was observed six years later (34.65 %). The second lowest dominance of cold stenotherms was observed in 2000 (70.53 %) before the protection fence was put up. After that, dominance rose up to 96.19 % in 2002 and stayed at high levels (78.10 % to 94.91 %) until 2008. The lowest value (68.14 %) was recorded in 2020. The share of species requiring fast currents and mineral substrate increased from 0.97% in 2000 to 7.87 % in 2007. Afterwards, the share of these species declined, and none of them was observed in 2021. The share of specialists was lowest in 2021 (23.16 %) and highest in 2002 (85.00 %).
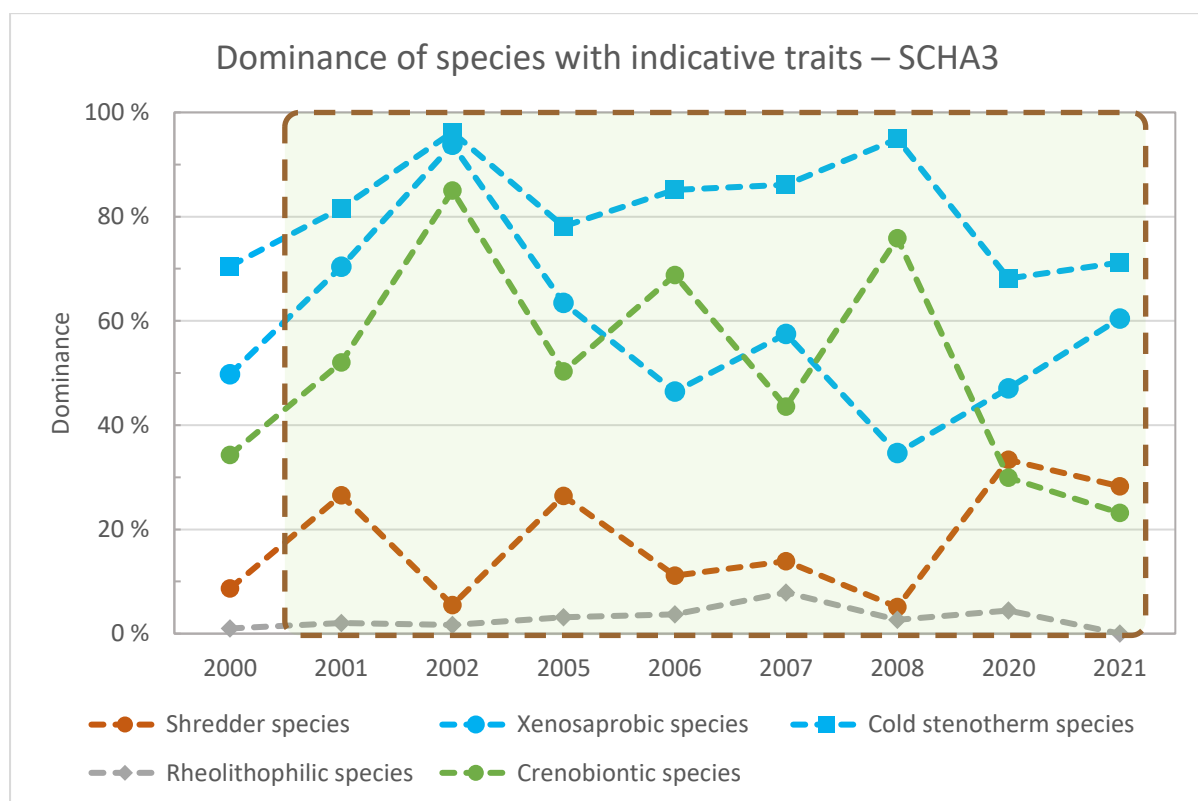
Figure 30: Development of species with indicative traits over time at the Schaumbergalm spring (SCHA3). Brown dashed rectangle indicates the period with a protection fence.

3.3.6. Community changes

Development of the five most abundant taxa and similarity

The overall highest dominance was observed in *Leuctra armata* (2002, 80.48 %; Figure 31). The taxa which belonged to the five most dominant taxa in all but one year were *Leuctra armata* (2020) and *Leuctra handlirschi* (2007). Additionally, *Leuctra braueri* had dominances > 10 % (≙ dominant) in 2000, 2006–2008 and 2020. The only caddisfly species detected in this analysis was *Rhyacophila hirticornis* (2007, 5.51 %).

The lowest similarity to the first year was observed in 2002 (P = 0.22) which is due to drastic differences in the dominance of *Leuctra armata* (10.1 % -> 80.5 %). The community in 2006 was the most similar to the community in 2000 (P = 0.57). In that year, the biggest differences were observed in *Leuctra handlirschi* (27.1 % -> 5.6 %) and *Leuctra braueri* (20.3 % -> 41.6 %).
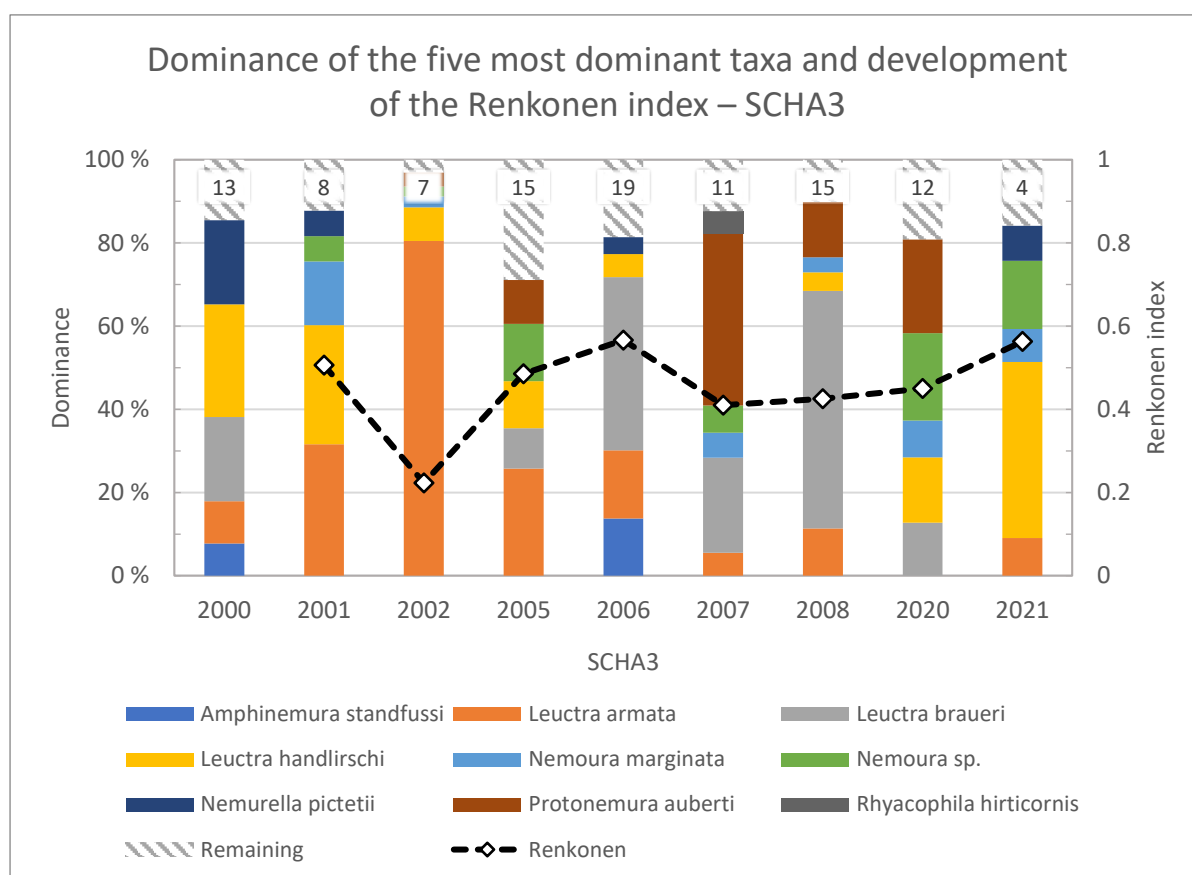
Figure 31: Dominance of the five most dominant taxa at SCHA3 (y-axis1). If multiple taxa showed the same dominance, more than five taxa were displayed. The Renkonen index shows the similarity between the first and each consecutive year thereafter (y-axis2). The number on top of the bar shows the taxa number of the share, not covered by the five most abundant taxa ("Remaining").

Development of taxa, indicative of a helocrenal character

The dominance of *Nemurella pictetii* decreased from 2000 (20.29 %) to 2001 (0.48 %). Thereafter, its dominance fluctuated between 1.15 % and 8.47 %. *Nemoura cinerea* was found in 2000, 2002, 2006 and 2021 when it reached its highest dominance (2.26 %). Lastly, *Beraea pullata* was found in three years, while its dominance remained below 0.5 %.

Figure 32: Development of the dominance of five taxa, indicative of a helocrenal character at the Schaumbergalm spring (SCHA3).

3.4. Schaumbergalmhütte spring (SCHÜ)

3.4.1. Taxa list

Table 17: Calculated abundances [Ind. / m²] of sampled species at the Schaumbergalmhütte spring (SCHÜ).

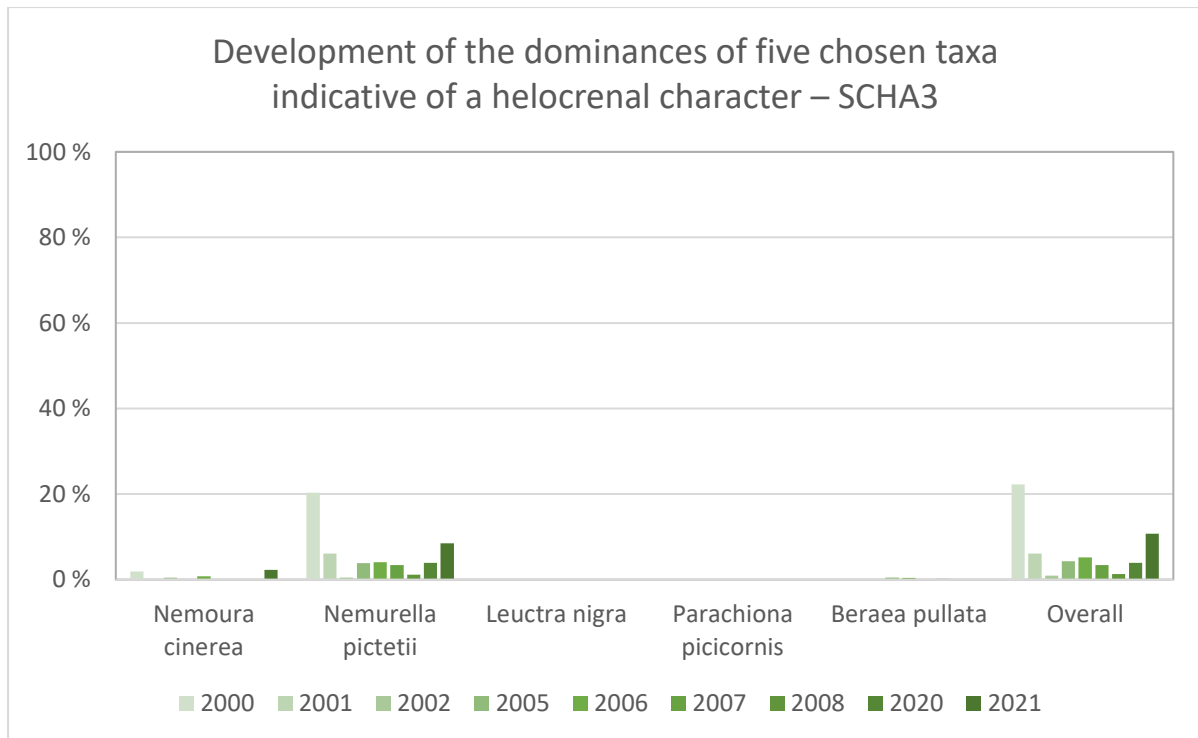| Species	Abundance [Ind. / m^2]								
	2000	2001	2002	2005	2006	2007	2008	2020	2021
Dictyogenus fontium	0	0	0	0,2	0	0	2,0	1,0	2,0
Isoperla rivulorum	0	0	1,5	0	0	0	0	0	0
Isoperla sp.	0	0	1,2	0	0	0	0	0,7	0,7
Amphinemura standfussi	1,0	0	0,5	0	0	0	0	0	0
Nemoura cinerea	0	1,3	0	0	0	0	0	0	0
Nemoura marginata	5,9	4,6	1,0	3,7	1,0	0	1,0	0,3	0,7
Nemoura minima	0	0	2,7	1,2	0,7	0	0	2,6	8,5
Nemoura mortoni	0	0	0,5	4,6	1,2	7,8	2,0	0	1,0
Nemoura sp.	14,0	9,4	8,5	5,1	3,2	2,9	6,8	4,6	5,9
Nemurella pictetii	2,6	4,9	1,0	0	0	3,9	2,0	4,2	4,2
Protonemura auberti	15,0	4,2	3,4	0,7	2,9	0	2,9	10,4	4,6
Protonemura austriaca	0	0	0	0,7	0	2,9	0	0,3	0,7
Protonemura hrabei	0	0	0	0	0,2	0	0	0	0,3
Protonemura sp.	0	0	0	0,2	0	0	0	0	0
Leuctra armata	2,3	5,2	18,1	33,2	12,0	14,6	33,2	19,2	13,7
Leuctra autumnalis	0	0	3,2	0	1,2	20,5	0	0	0
Leuctra braueri	8,5	2,6	48,3	0	5,1	2,9	3,9	8,8	0,3
Leuctra handlirschi	10,4	24,4	32,0	1,5	0	0	0	3,3	12,4
Leuctra major	0	0	0	0	0	2,0	0	0	0
Leuctra nigra	0	0	0,2	0	0	0	0	0	0
Leuctra prima	0	0	0	0	0	0	6,8	0	0
Rhyacophila producta	0	0	0	0,2	0,2	1,0	2,0	2,0	2,0
Rhyacophila stigmatica	0	0	0,5	0	0	0	0	0	0
Rhyacophila tristis	1,6	0	0	0	0	0	0	0	0
Rhyacophila vulgaris	0	0	0	0	0	1,0	0	0	0
Synagapetus iridipennis	0	0	0,2	0	0	2,9	3,9	39,4	3,3
Synagapetus krawanyi	0	0	0,2	0	0	1,0	0	0	0
Philopotamus ludificatus	0,3	0	0	0	0	0	0	0	0
Wormaldia occipitalis	0,3	0	0	0	0,2	0	0	0,3	1,6
Plectrocnemia conspersa	0,7	0	0	0	0	0	0	0	0
Tinodes dives	1,0	0	2,9	0	0	0	0	1,0	0,7
Micrasema morosum	0	0	0,2	0	0	0	0	0,3	0,3
Allogamus uncatus	0	0	0,5	0	2,0	0	1,0	0,7	0
Chaetopteryx major	0	0	3,2	0	0,2	0	9,8	0	0
Drusus monticola	0	0	0,7	0	0	1,0	0	0	0
Leptotaulius gracilis	0	0	0	0	0	1,0	0	0	0
Melampophylax melampus	0	0	0	0	1,0	0	0	0	0
Parachiona picicornis	0	0	0	0,2	0	0	0	0	0
Potamophylax nigricornis	1,3	1,0	0	0	0	0	1,0	0,3	0,7
Pseudopsilopteryx zimmeri	0	0	0	0	1,2	0	0	0	1,6
Lithax niger	0	0	0	0	0	1,0	0	0	0
Crunoecia kempnyi	0,3	0	0,7	0	0,5	43,9	10,7	0	0,3
Sericostoma personatum	1,0	0	0,2	0	0	0	0	0	0,3
Beraea pullata	0	0	0,2	0	0	0	0	0	0
Ernodes vicinus	0,3	0	0	0	0	0	0	0	0
Overall abundance	66,4	57,6	131,8	51,8	33,0	110,4	88,9	99,3	65,4

3.4.2. Longitudinal distribution

The longitudinal distribution analysis at SCHÜ (Figure 33) shows the highest eucrenal share in 2007 (47.2 %) and the lowest in the first investigated year (21.4 %). The hypocrenal share remains fairly constant (35.2 %–37.9 %) until 2006 and decreases to 23.1 % in 2007. After that, it rises again to 35.7 % in 2021. The two highest shares of the epirhithral were recorded in the first (2000; 38.4 %) and last investigated year (35.4 %). In between, it fluctuated between 20.7% and 28.1 %. The share of the littoral was highest in 2001 (3%) and that of the metarhithral in 2007 (5.1 %).

Figure 33: Results of the longitudinal distribution analysis at the Schaumbergalmhütte spring (SCHÜ) using ECOPROF. The y-axis shows the relative shares in % (1 = 10 %). The dates on the y-axis indicate the different sampling periods. The second time frame (starting on 09/12/2000) e. g. represents the sampling year 2001.

3.4.3. Functional feeding guilds

The ECOPROF analysis of the FFGs at SCHÜ (Figure 34) does not show clear trends for any of the observed guilds. The year with the markedly lowest share of shredders was 2020 (21.7 %). In the remaining years, their share fluctuated between 32.1 % and 44.3 %. After reaching its maximum with 36.7 % in 2001, the share of detritivores decreased with the lowest value recorded in 2007 (21 %). The markedly highest dominance of grazers was observed in 2020 (46.9 %). An equally remarkable maximum was observed in xylophaghs (*Crunoecia kempnyi*), which was highest in 2007 (19.9 %).
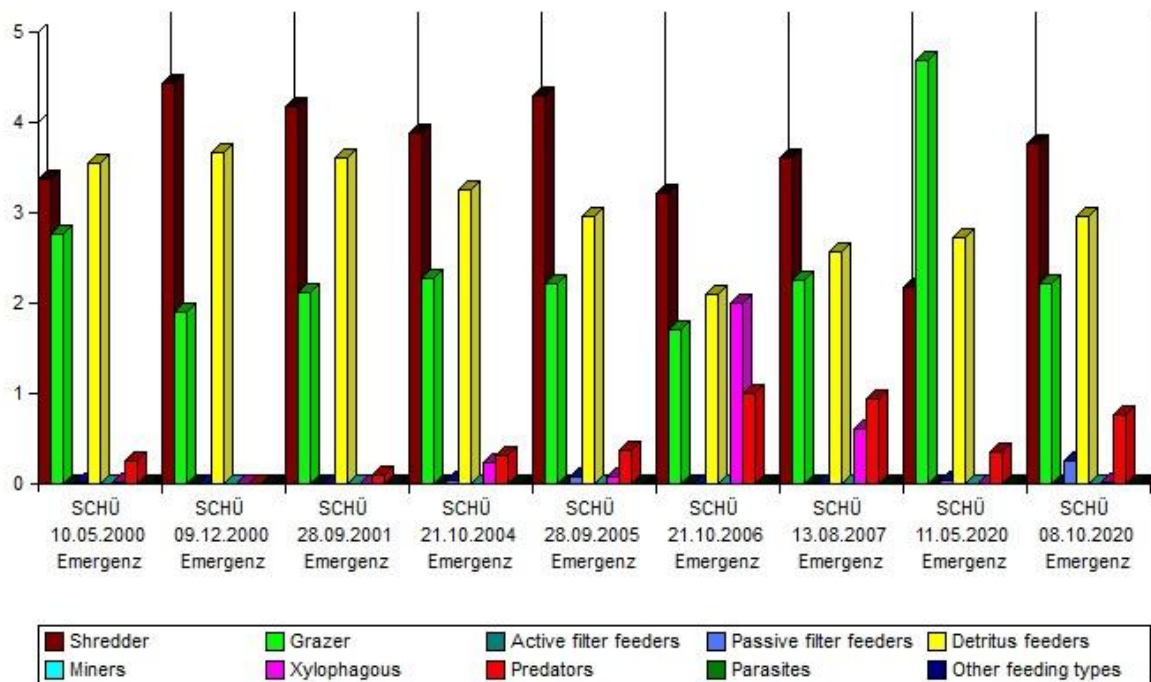
Figure 34: Results of the distribution of FFGs at the Schaumbergalmhütte spring (SCHÜ) using ECOPROF. The y-axis shows the relative shares in % (1 = 10 %). The dates on the y-axis indicate the different sampling periods. The second time frame (starting on 09/12/2000) e. g. represents the sampling year 2001.

3.4.4. Saprobity classes

The share of xenosaprobic taxa at SCHÜ remained at a constant level from 2000 to 2006 (38-39 %; Figure 35). Thereafter, it heavily rose to 57.6 %. An equally high value was observed 13 years later (56.9 %; 2020). The share of oligosaprobic taxa showed no such trend and fluctuated between 39.7 % and 57.2 %. The share of beta-mesosaprobic taxa was highest in 2000 (14.2 %) and lowest in 2007 (2.4 %).
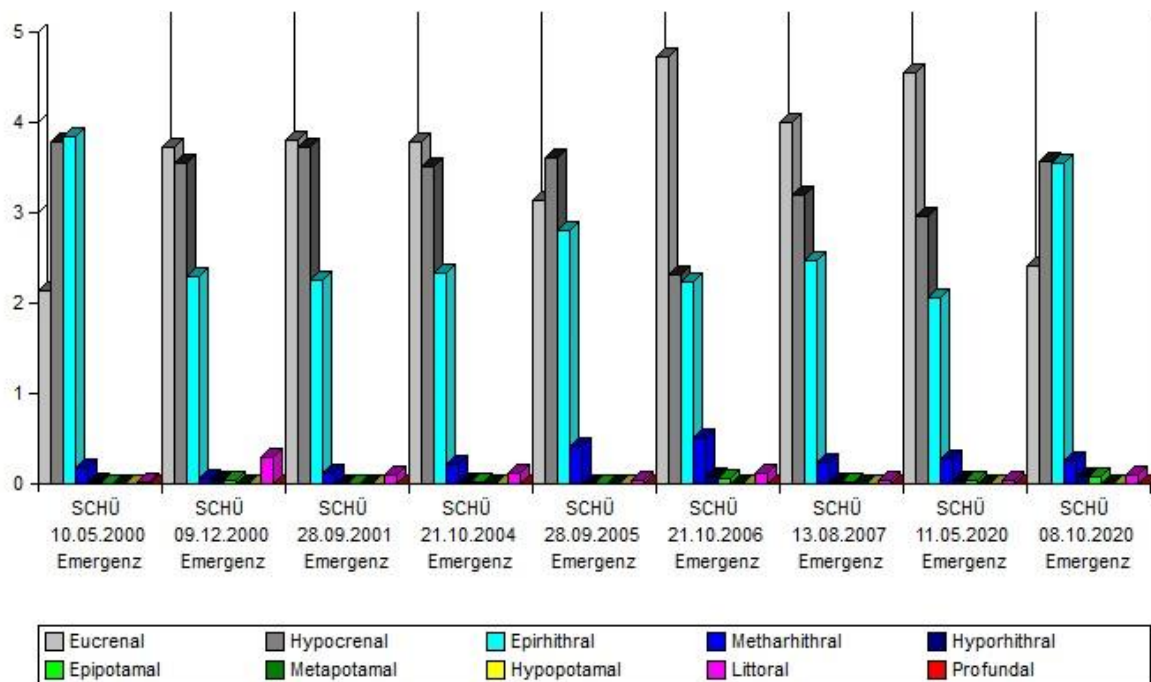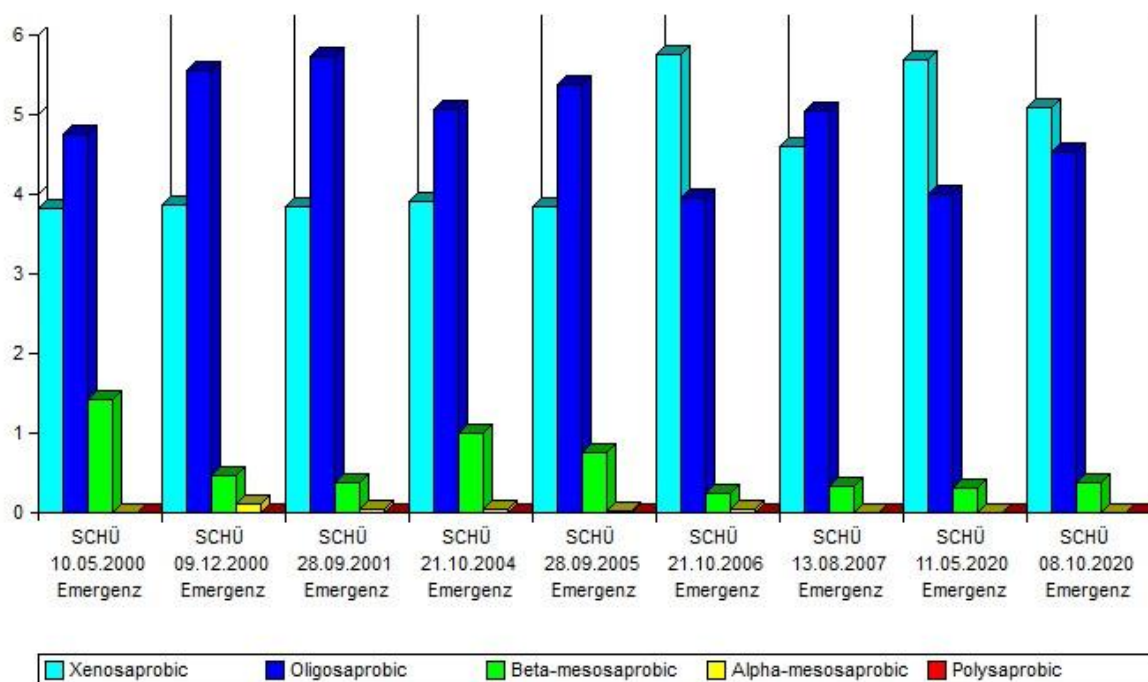

Figure 35: Results of the distribution of saprobity classes at the Schaumbergalmhütte spring (SCHÜ) using ECOPROF. The y-axis shows the relative shares in % (1 = 10 %). The dates on the y-axis indicate the different sampling periods. The second time frame (starting on 09/12/2000) e. g. represents the sampling year 2001.

3.4.5. Dominance of species with indicative traits

The dominance of specialist shredders was highest between 2001 (36.56 %) and 2006 (31.85 %; Figure 36). The lowest dominance was observed in 2020 (8.52 %). Xenosaprobic species were least dominant in 2000 (49.07 %). After that, their share increased and reached its maximum in 2007 (81.42 %). The second highest value was observed in 2020 (80.33 %). Between 2000 and 2007, the share of cold stenothermic taxa fluctuated between 85.93 % and 91.15 %. The lowest share was observed in the following year (2008; 78.02 %). During the first fenced period, the share of rheolithophils ranged between 0 % in 2001 and 8.79 % in 2008. A drastic increase up to 44.92 % was observed in 2020. The lowest dominance of specialists was recorded in 2021 (41.79 %) and the highest in 2001 (81.72 %).
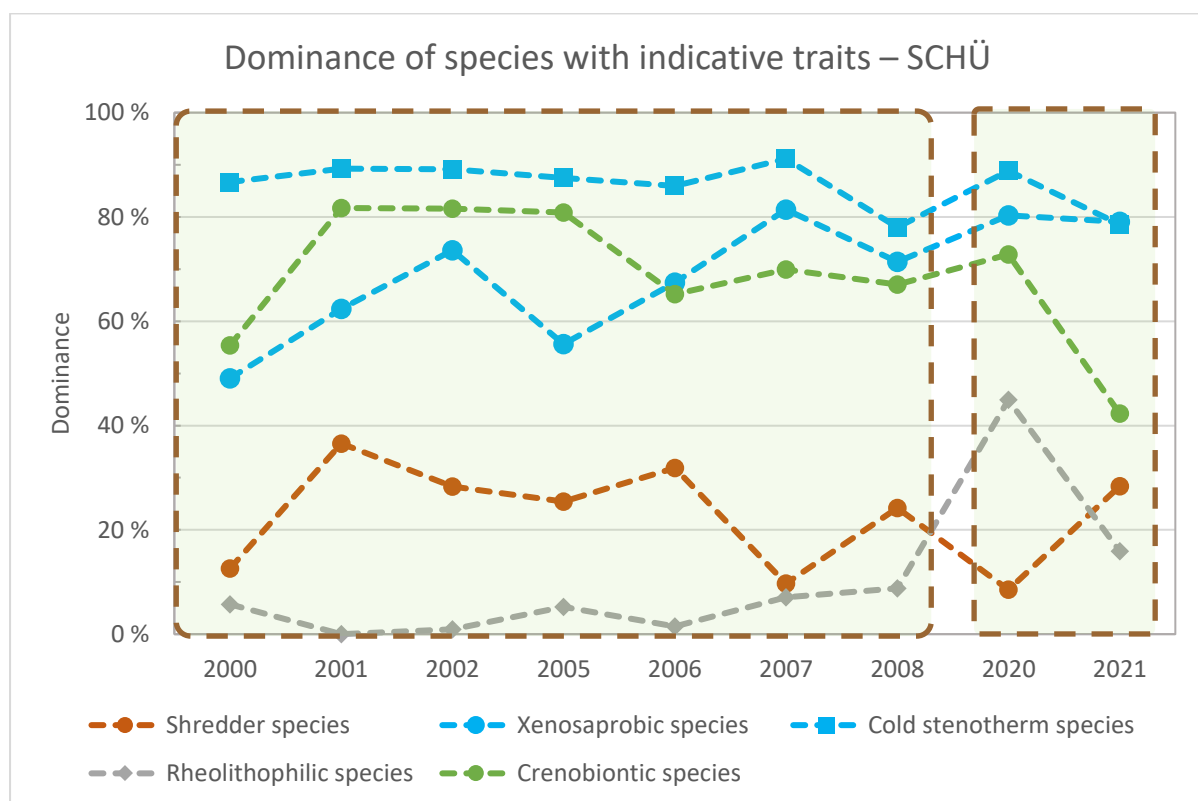
Figure 36: Development of species with indicative traits over time at the Schaumbergalmhütte spring (SCHÜ). Brown dashed rectangle indicates the period with a protection fence.

3.4.6. Community changes

Development of the five most abundant taxa and similarity

Leuctra armata was eudominant (> 32 %) from 2001 to 2006 and in 2008, while it was dominant (> 10 %) in the remaining years (Figure 37). It was most dominant in 2002 (64.15 %). *Cruneocia kempnyi* (2007), *Leuctra braueri* (2000) and *Synagapetus iridipennis* (2020) were eudominant in one year each. *Nemoura mortoni* belonged to the five most dominant taxa in 2001 (24.73 %), 2002 (8.96 %), 2005 (8.54 %) and 2007 (7.08 %).

The lowest similarity (P = 0.24) was calculated for 2007, which is due to the large differences in the dominance of *Leuctra braueri* (36.67 % -> 2.65 %), *Leuctra handlirschi* (24.26 % -> 0 %) and *Crunoecia kempnyi* (0.56 % -> 39.82 %). The highest similarity occurred in 2005 due to *Leuctra braueri* (36.67 % -> 18.96 %) and *Leuctra armata* (13.7 % -> 37.29 %).
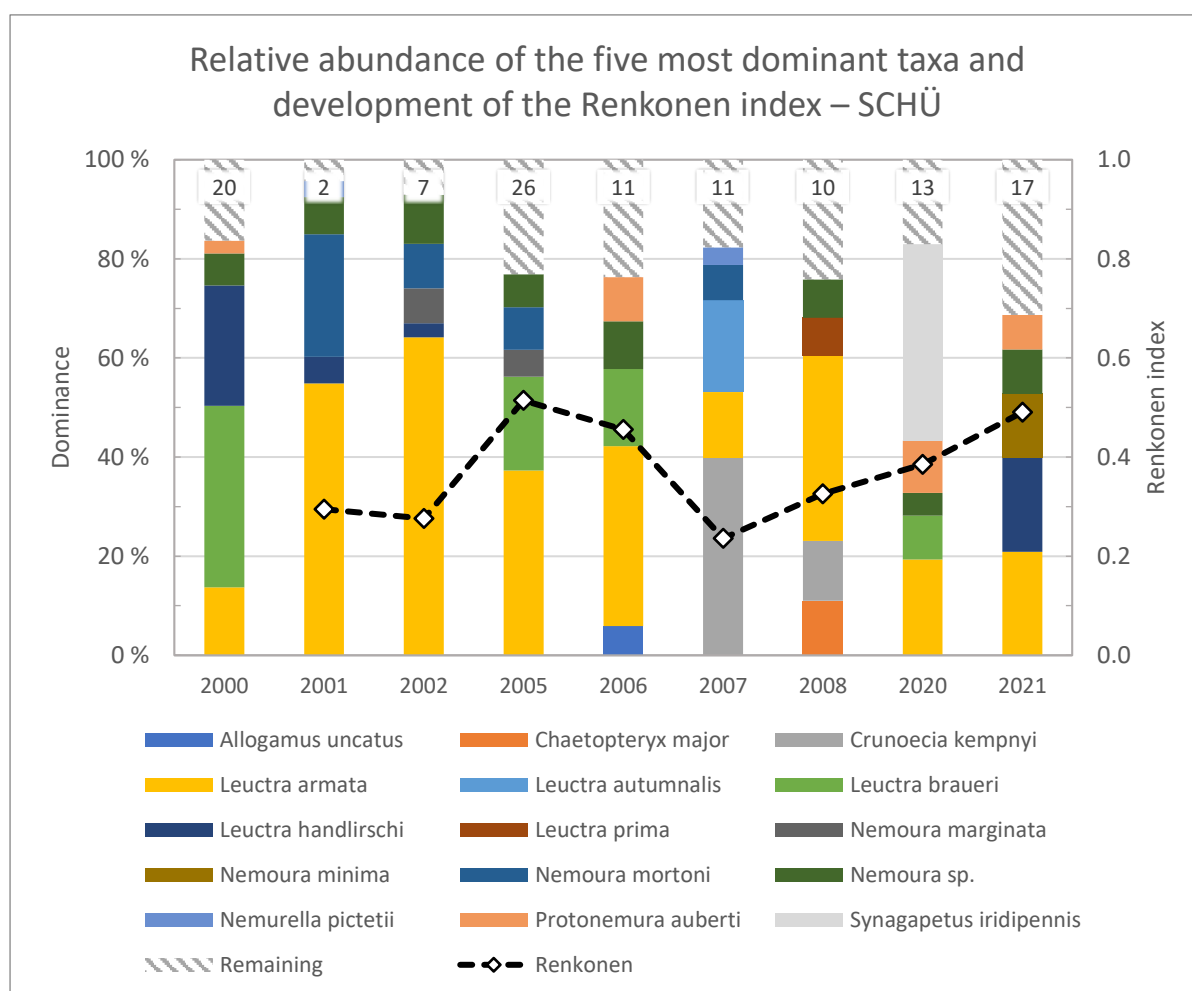
Figure 37: Dominance of the five most dominant taxa at the Schaumbergalmhütte spring (SCHÜ) (y-axis1). If multiple taxa showed the same dominance, more than five taxa were displayed. The Renkonen index shows the similarity between the first and each consecutive year thereafter (y-axis2). The number on top of the bar shows the taxa number of the share, not covered by the five most abundant taxa ("Remaining").

Development of taxa, indicative of a helocrenal character

At SCHÜ, *Nemoura cinerea* (2005), *Leuctra nigra* (2000), *Parachiona picicornis* (2005) and *Beraea pullata* (2000) were only found in a single year, while their recorded dominances were low (< 0.5 %). *Nemurella pictetii*, however, was found in all years except 2002 and 2006. The highest dominance was observed in 2021 (6.47 %).
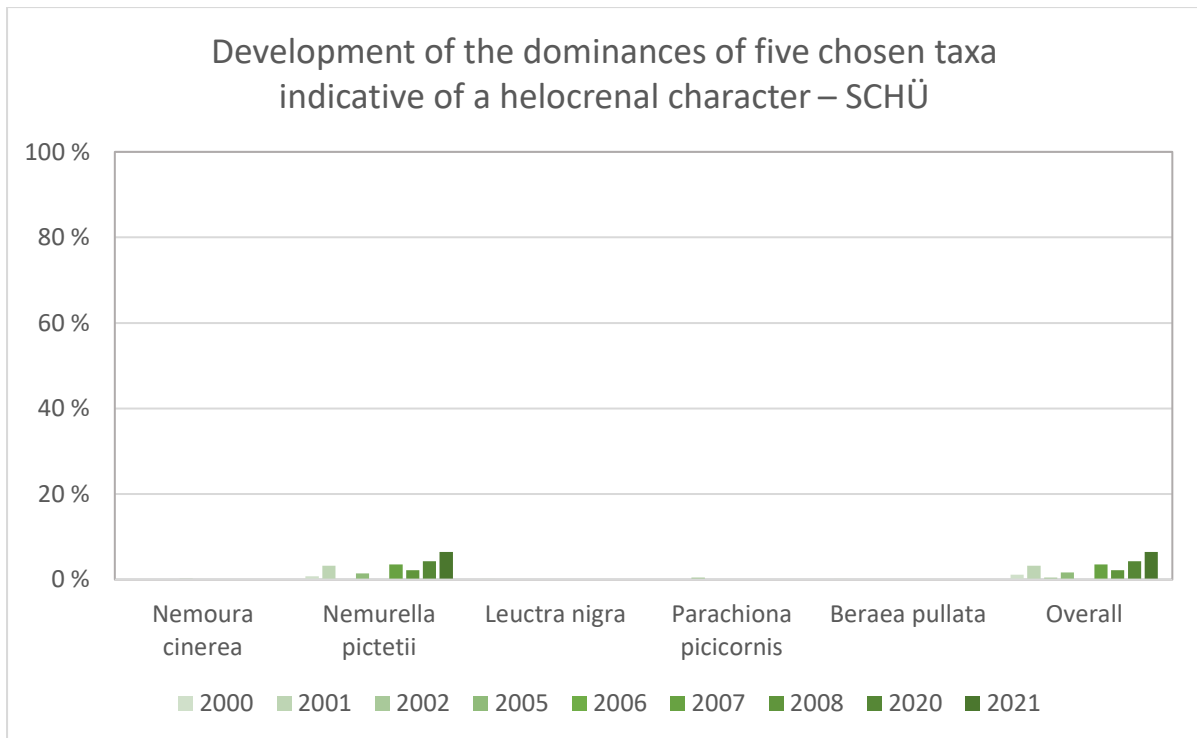
Figure 38: Development of the dominance of five taxa, indicative of a helocrenal character at the Schaumbergalmhütte spring (SCHÜ).

3.5. General Results Regarding All Investigated Springs

3.5.1. Physico-chemical parameters

Water temperature

On average, water temperature was highest at SCHA3 (7.77 °C) and lowest at SCHÜ (6.38 °C; Figure 39). JÖA (standard deviation (SD) = 0.34 °C) and SCHÜ (SD = 0.38 °C) showed a narrow range of water temperature with 1.5 °C (JÖA) and 2 °C (SCHÜ). In contrast, EBA showed the second largest (4.01 °C) and SCHA3 the largest range (5.5 °C). The highest water temperature was measured at SCHA3 with 11.7 °C.
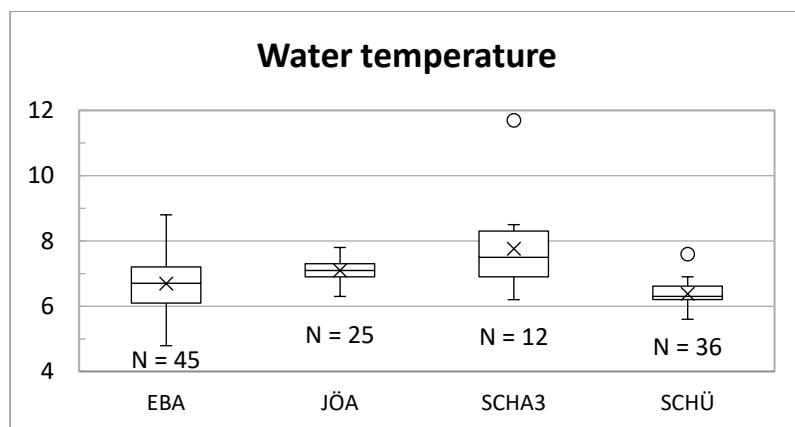
Figure 39: Box plots of water temperatures at each spring (x = average; ∘ = outlier, N = number of measurements).

Discharge

EBA showed the lowest average discharge (0.91 l/s) and JÖA the highest (16.66 l/s). The lowest values (0.1 l/s) were recorded at EBA and SCHA3. On the one hand, discharge fluctuated between 0.01 l/s and 3 l/s at SCHA3, which is the narrowest range observed. On the other, the largest range was observed at JÖA (99.75 l/s). Peak discharge levels were measured there in September 2002 (100 l/s) and February 2002/May 2005 (50 l/s).
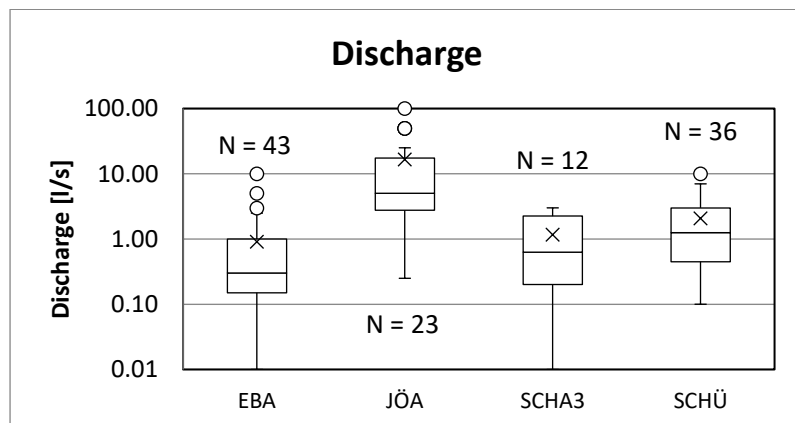
Figure 40: Box plots of discharge at each spring (x = average; ∘ = outlier, N = number of measurements).

3.5.2. Active stressors

The qualitative assessment indicates the strongest impact at EBA before the protection fence was erected (2000 and 2001; Table 18). Organic pollution from cattle, poaching and the removal of riparian vegetation (cattle) were the main stressors. Although these impacts were mitigated by the protection fences, the drinking trough and water abstraction remained active during the fenced period. Furthermore, organic material and poached sediments still entered the run-off below the crossway. In contrast, JÖA was not impacted during the investigated period as the pasture hut was abandoned. SCHA3 was as heavily impacted as EBA in 2000 and 2001, but there was no water abstraction. Until 2005 all stressors, besides the negative results of cattle trails were mitigated. From 2006 on, however, a water abstraction at the springmouth adversely impacted the spring run-off. Apart from the altered riparian vegetation (spruce monoculture), no stressors were active at SCHÜ until 2008. After that, the area had to be cleared in response to bark beetle infestation, which resulted in a complete removal of the riparian vegetation. In addition, the protection fence was removed for several years in this time frame, which exposed the spring to the negative effects of cattle.

EBA

Stressor		Value	2000	2001	2002	2004	2005	2006	2007	2008	2009-2019	2020	2021
Organic pollution	Cattle	1	X	X									
	Cattle trail	0,5			X	X	X	X	X	X	X	X	X
Poaching	Cattle	1	X	X									
	Cattle trail	0,5											
Hydrological impairment	Abstraction	1	X	X	X	X	X	X	X	X	X	X	X
	Drinking trough	0,5	X	X	X	X	X	X	X	X	X	X	X
Riparian vegetation	Removal	1	X	X									
	Alteration	0,5											
Accumulated Values			4,5	4,5	2	2	2	2	2	2	2	2	2

JÖA

Stressor		Value	2000	2001	2002	2004	2005	2006	2007	2008	2009-2019	2020	2021
Organic pollution	Cattle	1											
	Cattle trail	0,5											
Poaching	Cattle	1											
	Cattle trail	0,5											
Hydrological impairment	Abstraction	1											
	Drinking trough	0,5											
Riparian vegetation	Removal	1											
	Alteration	0,5											
Accumulated Values			0	0	0	0	0	0	0	0	0	0	0

SCHA3

Stressor		Value	2000	2001	2002	2004	2005	2006	2007	2008	2009-2019	2020	2021
Organic pollution	Cattle	1	x										
	Cattle trail	0,5		x	x	x	x	x	x	x	x	x	x
Poaching	Cattle	1	x										
	Cattle trail	0,5											
Hydrological impairment	Abstraction	1						x	x	x	x	x	x
	Drinking trough	0,5											
Riparian vegetation	Removal	1	X										
	Alteration	0,5											
Accumulated Values			3	0,5	0,5	0,5	0,5	1,5	1,5	1,5	1,5	1,5	1,5

SCHÜ

Stressor		Value	2000	2001	2002	2004	2005	2006	2007	2008	2009-2019	2020	2021
Organic pollution	Cattle	1									x		
	Cattle trail	0,5											
Poaching	Cattle	1									x		
	Cattle trail	0,5											
Hydrological impairment	Abstraction	1											
	Drinking trough	0,5											
Riparian vegetation	Removal	1									x		
	Alteration	0,5	x	x	x	x	x	x	x	x			
Accumulated Values			0,5	0,5	0,5	0,5	0,5	0,5	0,5	0,5	3	0	0

Table 19 shows the classified accumulated values of the stressors for each year per spring. A high level of impact is only reached at EBA and SCHA3 before the area was fenced, and at SCHÜ from 2009 to 2019 because the area was cleared and the protection fence removed. The level of impact at EBA (2002–2021) and at SCHA3 from 2006 onwards was moderate. JÖA was not subjected to any pressures in the investigated time period.

Table 19: Qualitative assessment of active stressors for each spring and per year (thresholds for the symbols are given in Table 11)

Site \ Year	2000	2001	2002	2004	2005	2006	2007	2008	2009-2019	2020	2021
EBA	✖	✖	—	—	—	—	—	—	—	—	—
JÖA	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
SCHA3	✖	✔	✔	✔	✔	—	—	—	—	—	—
SCHÜ	✔	✔	✔	✔	✔	✔	✔	✔	✖	✔	✔

3.5.3. Combined analysis of the investigated metrics

The analysis of the combined metrics (see chapter 2.4.3) shows the lowest accumulated value at EBA in 2021 (Table 21). In general, the low share of shredders and rheolithophil organisms resulted in continuously low values at EBA. Moreover, the low shares of xenosaprobic (8.64 %), cold stenotherm (8.64 %) and crenobiont (5.55 %) taxa were responsible for the lowest value in 2021. At JÖA, the overall highest accumulated value (24) was recorded twice (2001 and 2021). The minimum at JÖA was recorded in 2005 (22, grade 2) because the low share of shredders and rheolithophilic taxa lead to point reduction. At SCHA3, the two lowest values were observed in 2021 (18) and 2000 (19). In both years, the share of rheolithophilic taxa wase below 1 %. This is also true for SCHÜ in the years 2001 and 2002 which also led to the lowest recorded value (20) in the mentioned years. The highest values were calculated for 2020 and 2021 (23).

Table 20 shows the resulting grades of each spring for the investigated years. EBA achieved the poorest grade (5) in 2007 and 2021, while JÖA had the best grade (1) in all but one year (2005). Additionally, grade 1 was calculated for SCHÜ in 2020 and 2021. SCHA3 achieved grade 3 in the first (2000) and last year (2021) of investigation. In between, it was continuously graded with 2.

Table 20: Resulting grades of the combined analysis of the metrics for each spring and year.

Site \ Year	2000	2001	2002	2004	2005	2006	2007	2008	2009-2019	2020	2021
EBA	4	4		3		3	5	3		2	5
JÖA	1	1	1		2	1	1	1		1	1
SCHA3	3	2	2		2	2	2	2		2	3
SCHÜ	2	2	2		2	2	2	2		1	1

Table 21: Dominance of taxa with a specific trait and the derived values using dominance classes. Accumulated values are calculated in the last row.

EBA

	2000	2001	2002	2004	2005	2006	2007	2008	2009-2019	2020	2021
Shredders	4,16 % -> 3	1,67 % -> 2		10,93 % -> 4		9,48 % -> 3	3,21 % -> 3	6,24 % -> 3		12,37 % -> 4	3,7 % -> 3
Xenosaprobic	56,25 % -> 5	69,45 % -> 5		70,31 % -> 5		49,99 % -> 5	27,98 % -> 4	57,29 % -> 5		35,56 % -> 5	8,64 % -> 3
Coldstenotherm	57,29 % -> 5	68,99 % -> 5		67,18 % -> 5		51,09 % -> 5	24,77 % -> 4	56,24 % -> 5		35,05 % -> 5	8,64 % -> 3
Rheolithophils	0 % ->0	0 % ->0		0 % ->0		0,72 % -> 1	0 % ->0	2,08 % -> 2		2,06 % -> 2	0 % ->0
Specialists	16,66 % -> 4	23,7 % -> 4		23,43 % -> 4		22,62 % -> 4	6,88 % -> 3	16,66 % -> 4		30,41 % -> 4	5,55 % -> 3
Accumulated value	17	16		18		18	14	19		20	12

JÖA

	2000	2001	2002	2004	2005	2006	2007	2008	2009-2019	2020	2021
Shredders	6,34 % -> 3	11,16 % -> 4	14,61 % -> 4		9,72 % -> 3	13,79 % -> 4	21,87 % -> 4	6,9 % -> 3		7,49 % -> 3	20,74 % -> 4
Xenosaprobic	55,22 % -> 5	81,47 % -> 5	90,76 % -> 5		56,01 % -> 5	74,71 % -> 5	87,5 % -> 5	56,06 % -> 5		65,9 % -> 5	83,81 % -> 5
Coldstenotherm	60,07 % -> 5	85,27 % -> 5	72,3 % -> 5		83,33 % -> 5	85,82 % -> 5	88,54 % -> 5	60,04 % -> 5		74,54 % -> 5	84,64 % -> 5
Rheolithophils	73,88 % -> 5	56,85 % -> 5	27,69 % -> 4		24,3 % -> 4	29,11 % -> 4	28,12 % -> 4	60,46 % -> 5		34,31 % -> 5	36,51 % -> 5
Specialists	79,85 % -> 5	73,6 % -> 5	54,61 % -> 5		70,6 % -> 5	53,63 % -> 5	71,87 % -> 5	80,96 % -> 5		68,18 % -> 5	75,1 % -> 5
Accumulated value	23	24	23		22	23	23	23		23	24

SCHA3

	2000	2001	2002	2004	2005	2006	2007	2008	2009-2019	2020	2021
Shredders	8,69 % -> 3	26,53 % -> 4	5,47 % -> 3		26,41 % -> 4	11,15 % -> 4	13,91 % -> 4	5,09 % -> 3		33,33 % -> 5	28,24 % -> 4
Xenosaprobic	49,75 % -> 5	70,4 % -> 5	93,8 % -> 5		63,43 % -> 5	46,46 % -> 5	57,48 % -> 5	34,64 % -> 5		47,05 % -> 5	60,45 % -> 5
Coldstenotherm	70,53 % -> 5	81,63 % -> 5	96,19 % -> 5		78,1 % -> 5	85,13 % -> 5	86,08 % -> 5	94,9 % -> 5		68,13 % -> 5	71,18 % -> 5
Rheolithophils	0,96 % -> 1	2,04 % -> 2	1,66 % -> 2		3,16 % -> 2	3,71 % -> 3	7,87 % -> 3	2,62 % -> 2		4,41 % -> 3	0 % ->0
Specialists	34,29 % -> 5	52,04 % -> 5	85 % -> 5		50,33 % -> 5	68,77 % -> 5	43,56 % -> 5	75,86 % -> 5		29,9 % -> 4	23,16 % -> 4
Accumulated value	19	21	20		21	22	22	20		22	18

SCHÜ

	2000	2001	2002	2004	2005	2006	2007	2008	2009-2019	2020	2021
Shredders	12,59 % -> 4	36,55 % -> 5	28,3 % -> 4		25,41 % -> 4	31,85 % -> 4	9,73 % -> 3	24,17 % -> 4		8,52 % -> 3	28,35 % -> 4
Xenosaprobic	49,07 % -> 5	62,36 % -> 5	73,58 % -> 5		55,62 % -> 5	67,4 % -> 5	81,41 % -> 5	71,42 % -> 5		80,32 % -> 5	79,1 % -> 5
Coldstenotherm	86,66 % -> 5	89,24 % -> 5	89,15 % -> 5		87,49 % -> 5	85,92 % -> 5	91,15 % -> 5	78,02 % -> 5		88,85 % -> 5	78,6 % -> 5
Rheolithophils	5,74 % -> 3	0 % ->0	0,94 % -> 1		5,2 % -> 3	1,48 % -> 2	7,07 % -> 3	8,79 % -> 3		44,91 % -> 5	15,92 % -> 4
Specialists	55,37 % -> 5	81,72 % -> 5	81,6 % -> 5		80,83 % -> 5	65,18 % -> 5	69,91 % -> 5	67,03 % -> 5		72,78 % -> 5	42,28 % -> 5
Accumulated value	22	20	20		22	21	21	22		23	23

3.5.4. Taxa with particular relevance for nature conservation

In the following two chapters, findings of endangered and endemic species, which are particularly important for nature conservation, will be described (chapter 1.5).

3.5.5. Occurrence of threatened caddisflies

Between 2000 and 2002, twelve caddisfly species classified in one of the "threatened categories" were found. The highest number of threatened caddisfly species was found at SCHÜ (8). The only critically endangered species was *Sericostoma personatum* (Table 22). It was found at SCHA3 in every year except 2002 and at SCHÜ in 2000 and 2021. The two species which are classified as endangered are *Drusus monticola* (JÖA, 2001; SCHÜ, 2007) and *Leptotaulius gracilis* (SCHA3, 2002/2005; SCHÜ, 2007). Only one species was found consecutively in all investigated years (*Rhyacophila producta* at JÖA). At SCHÜ, it was found from 2002 on. *Parachiona picicornis* was found at SCHÜ (2002) and EBA where it was caught in all years except 2000 and 2008.

Table 22: Years with findings of caddisfly species classified in a "Threatened category" (findings are indicated by X; CR = Critically Endangered, EN = Endangered, VU = Vulnerable; information taken from (Malicky, 2009))

Taxon	Category	EBA								JÖA									SCHA3									SCHÜ								
		2000	2001	2004	2006	2007	2008	2020	2021	2000	2001	2002	2005	2006	2007	2008	2020	2021	2000	2001	2002	2005	2006	2007	2008	2020	2021	2000	2001	2002	2005	2006	2007	2008	2020	2021
Rhyacophila producta	VU									1	1	1	1	1	1	1	1	1												1	1	1	1	1	1	1
Rhyacophila tristis	VU																									1										
Glossosoma conformis	VU												1																		1					
Plectrocnemia conspersa	VU		1	1	1	1											1		1			1	1	1	1	1										
Chaetopteryx fusca	VU																														1					
Chaetopteryx major	VU				1								1										1					1			1	1		1		
Drusus monticola	EN										1																						1			
Leptotaulius gracilis	EN																				1	1											1			
Parachiona picicornis	VU		1	1	1	1		1	1																					1						
Potamophylax cingulatus	VU												1			1																				
Rhadicoleptus alpestris	VU			1																																
Sericostoma personatum	CR																		1	1		1	1	1	1	1		1								1
Overall Red - List taxa		0	2	3	3	2	0	1	1	1	2	1	4	1	1	2	2	1	2	1	1	3	3	2	2	3	0	2	0	2	4	2	3	2	1	2
Overall taxa		10	11	13	18	15	11	13	9	20	25	12	23	19	20	23	23	19	18	13	12	20	24	17	20	17	9	25	7	12	31	16	16	15	18	22

3.5.6. Endemic taxa

Endemics species which were found in the investigated springs are listed in Table 23. In all investigated springs, at least one endemic taxon was found. SCHÜ harboured the highest number of endemics (3), namely *Isoperla lugens*, *Rhyacophila stigmatica* and *Leptotaulius gracilis*. *Leuctra helvetica* was only found at EBA and JÖA.

Table 23: List of endemic species found in the investigated springs.

Taxon	Category	EBA 2000	2001	2004	2006	2007	2008	2020	2021	JÖA 2000	2001	2002	2005	2006	2007	2008	2020	2021	SCHA3 2000	2001	2002	2005	2006	2007	2008	2020	2021	SCHÜ 2000	2001	2002	2005	2006	2007	2008	2020	2021
Isoperla lugens	VU																														X					
Leuctra helvetiva	VU					X				X																										
Rhyacophila stigmatica	VU																											X								
Leptotaulius gracilis	VU																				X	X											X			

4. Discussion

In the following paragraphs, the results of all analyses carried out will be discussed.

4.1. Analyses of Indicative Species Traits Over Time

As mentioned in chapter 0, this thesis used the development of dominances of species with indicative traits to draw conclusions on the effects of the protection fences. The results will be discussed in the following chapters.

4.1.1. Shredding species

No clear continuous increase in shredders, but strong fluctuations were observed in the four investigated springs. However, a drastic increase was measured at SCHA3 from 2008 to 2020 (Figure 30), which might correlate with the increasing density of alder bushes in the fenced area (chapter 2.2.4). The occurrence of *Sericostoma personatum*, which is classified as specialised shredder (SHR = 9) in every year (except 2002 and 2021, Table 16), indicates high availability of leaves at SCHA3. Elliott (1969) found the highest density of its mature larvae in areas with aquatic macrophytes and deciduous leaves, while "most larvae had only eaten plant material". In addition, Anderson and James (1979) stated that shredding activity required areas with low flow velocity where leaf packs were able to accumulate. Such areas were available at SCHA3 due to its morphological character defined by terrace-like sections (chapter 2.2.4).

Regularly occurring high flow situations (Figure 40), which mobilise leaf litter (Ortiz, 2004), could explain the relatively low share of shredders at JÖA.

The concept of FFGs provides a rough outline for the general feeding behaviour of benthic invertebrates. Anderson and James (1979) elaborated that "most aquatic invertebrates are opportunistic feeders and thus cannot be rigidly placed in a single functional group". In the context of this thesis, a threshold of > 5 was used to classify "specialised shredders". This excluded 80 % of all species found. However, among those excluded species, several taxa are able to take up CPOM (e. g. *Leuctra sp.*, *Protonemura sp.* or *Ernodes vicinus*). Despite being "facultative shredder-collectors", they are still able to maintain a high "efficiency of food conversion to growth" when taking up CPOM (Cummins & Klug, 1979). Thus, the method used in this thesis might underestimate the availability of allochthonous CPOM from riparian vegetation.

4.1.2. Xenosaprobic species

SCHÜ was the only spring in which a trend towards an increase in xenosaprobic taxa was determined, which supports the second hypothesis. Here, the high dominances of *Leuctra armata* (2002–2008),

Nemoura minima and *Leuctra handlirschi* (2020–2021) indicate reduced levels of organic pollution (Table 17). At JÖA, the share of xenosaprobic taxa fluctuated markedly. The low values are due to high dominance of *Leuctra braueri* (2005) and *Tinodes dives* (2008). However, high abundance of *Leuctra braueri* was also observed in springs with very low content of organic material (Staudacher & Füreder, 2005).

At SCHA3 and EBA, strong decrease occurred two years after the springs had been fenced, while high shares of *Nemurella pictetii* were observed. Regarding saprobity classes, this taxon is not classified in the FAA (Graf, Grasser, & Weinzierl, 2017), but was regarded as "not resistant to organic pollution" by Zwick (2004).

In conclusion, in three of the four springs, no clear increase in xenosaprobic taxa was observed, even after the main stressor of organic pollution (cattle excrements) had been excluded.

4.1.3. Cold stenotherm species

No increase, but rather a consistently high share of cold stenotherm taxa was observed at SCHÜ (Figure 36). In the first period (2000–2008), the spring was surrounded by a dense spruce stock heavily shading the area. The high share in the second period (2020–2021) underlines the development of dense herbaceous vegetation, which is seemingly able to provide enough cover from radiation (chapter 2.2.5). The high abundance of *Synagapetus iridipennis* (2021) underlines the constantly low water temperatures, as it is a cold stenotherm caddisfly (Fischer, 2003).

At SCHA3 and JÖA, strong fluctuations occur, but no clear trends could be determined, even though both run-off areas are shaded by natural vegetation.

Nonetheless, low values at JÖA are due to high dominances of *Tinodes dives*, a taxon which is not classified regarding its temperature preference (Graf, Murphy, et al., 2022). However, the regular occurrence of *Drusus monticola*, a typical inhabitant of cold springs in high altitudes (Malicky, 2009), underlines the constantly low water temperatures in this particular spring.

At SCHA3, the low value in 2000 is due to a high dominance of *Nemurella pictetii*, a eurythermic stonefly (Graf, Murphy, et al., 2022). This might indicate high water temperature fluctuations caused by missing vegetation along the run-off (chapter 2.2.4).

At EBA, consistently high dominances of *Leuctra nigra, Nemurella pictetii* and *Nemoura cinerea* (all three are eurythermic stoneflies, (Graf, Lorenz, et al., 2022)) were observed (Figure 20). This is indicative of high water temperature fluctuations, which might be due to a combination of several factors. The exposition and reduced hydrological dynamics are likely to add to the effects of radiation, while the low slope increases the influence of air temperature by lengthening the retention period of water.

It can be concluded that the protection fences did not generally lead to an increase of cold stenotherm organisms.

4.1.4. Rheolithophilic species

The share of rheolithophils was constantly low at EBA and SCHA3 (Figure 18 and Figure 30).

Low dominance (≤ 1 %) of *Rhyacophila hirticornis* in only two years, a rhithrobiont caddisfly (Botosaneanu, 1999), confirms the reduced flow velocity and disturbed sediment regime at EBA.

At SCHA3, the occurrence of *Lithax niger*, which builds "stony cases […] with laterally incorporated larger grains" (Waringer & Graf, 2011), is indicative of areas with coarse substrate. Still, their abundance remains low (< 8 %), which suggests a run-off largely dominated by low flow velocity and fine substrate. Low flow velocities and fine sediments are also indicated by the regular occurrence of *Plectrocnemia conspersa*, which typically inhabits such mesohabitats (Waringer & Graf, 2011).

At SCHÜ, rheolithophils were sparse until 2008. Apparently, drastic changes in the habitat occurred until 2020, as high dominance of *Synagapetus iridipennis* was observed (Table 17). This grazing caddisfly is "absent from sandy or muddy areas" and is a typical grazer which feeds on epilithic algae (Waringer & Graf, 2011). Thus, its high abundance indicates a high share of mineral substrate and strong flow in the second investigation period.

Although strong fluctuations of rheolithophils were observed at JÖA, the generally high abundance and diversity within this group indicate a natural distribution of sediments and high flow velocities (Table 15). In addition to the rheophilous grazers *Synagapetus iridipennis/krawanyi* and *Drusus monticola*, the filter-feeder *Wormaldia occipitalis* (Wagner, 2002) strongly suggests an undisturbed sediment and flow regime.

Overall, the share of rheolithopils did not increase in all springs after the run-off area was fenced. Therefor, it can be concluded that the protection fences alone, were not able to restore a natural sediment and flow regime.

4.1.5. Crenobiontic species

At EBA, the share of crenobionts did not markedly increase after the run-off area had been fenced. The community was dominated by two crenophilous stonefly species, namely *Nemurella pictetii* and *Leuctra nigra* (Figure 20). As elaborated in chapter 1.8.1, these stoneflies commonly occur in helocrenes and thus indicate conditions atypical for unimpaired rheocrenes. This suggests that the protection fence could not restore natural conditions.

At SCHA3, the share of crenobionts with a disproportionately high dominance of stoneflies fluctuated markedly. However, the share of real crenobiontic caddisflies (e. g. *Rhyacophila hirticornis*) remained low. This suggests that the run-off only scarcely provided structures and conditions typical of natural

rheocrenes.

The same development was determined at SCHÜ in the first investigation period. However, the drastic increase in *Synagapetus iridipennis* in 2020 suggests more natural conditions thereafter.

At JÖA, the constantly high dominance of crenobionts, such as *Rhyacophila producta* and *Synagapetus iridipennis* (Table 15), indicates crenotypical conditions regarding temperature, substrate and food availability. The regular occurrence of *Tinodes dives*, a semi-hygropetric caddisfly, which typically inhabits small brooks and avoids areas with fine sediments (Waringer & Graf, 2011), completes the picture of a natural rheocrene with high microhabitat heterogeneity.

In conclusion, it can be stated that the share of crenobionts did not increase in any of the investigated springs after the protection fences had been erected.

4.2. Active Stressors and Restoration Success

The combined analysis of the metrics clearly shows that EBA is in the worst condition, which coincides with the multitude of stressors in the surrounding area. The resulting grade of the combined metric analysis (4, Table 20) for the years 2001 and 2002 (before the area was fenced), indicates the pronounced effects of overgrazing. However, even after restoration, helocrene-typical species made up at least 25 % of the community (Figure 20), which is indicative of a severely altered sediment and flow regime. Additionally, low similarity to the pre-restoration community was simply due to a shift from one species indicative of deteriorated conditions to another (*Nemurella pictetii -> Leuctra nigra*, Figure 19). As mentioned in chapter 1.8.1, these stoneflies typically inhabit sandy and muddy areas. The reasons why restoration apparently failed to succeed are manifold. The crossway for cattle still in place after restoration seems to foster allochthonous input of organic material and fine sediments. Additionally, the drinking trough and water abstraction reduce the hydraulic dynamics, which could have reduced the share in fine sediments. Reduced dynamics let a thick humus layer develop, which provides optimal conditions for dense herbaceous vegetation preventing the growth of higher vegetation. These factors in combination with the exposition and low slope (Table 6) of the Ebenforstalm spring drastically reduce the success of its restoration.

At SCHA3, the pronounced effects of overgrazing are indicated by the worst grade in 2000 (3, Table 20). Thereafter, sediments were no longer poached and the share of fine sediments was reduced, which is indicated by the increasing share of rheolithophils. Aditionally, the drastically higher dominance of *Nemurella pictetii* before the area had been fenced suggests that the share of fine sediments sustainably declined as a result of the protection fence. However, the share of rheolithophils remains at low levels from 2006 on, which suggests disturbances to the hydrological regime. As mentioned, a water abstraction was erected below the springmouth in that year

(chapter 2.2.4). This underlines that disturbances to the hydrological regime in springs severely impact benthic communities (Von Fumetti & Nagel, 2012).

SCHÜ was located in a densely stocked spruce monoculture in the first investigated period (chapter 2.2.5). For one part, this leads to naturally low (and constant) water temperatures (indicated by a high share of cold stenotherms, Figure 36). For the other, dense stocks of cornifers causes high input of slowly decaying needles, which hinder run-off and cover the substrate (Küry, 2009). Thus, the share of rheolithophils remained low. Waringer and Graf (1996) observed abundant populations of *Crunoecia kempnyi* in a well shaded springbrook on fine sediments with pine needle accumulations. This caddisfly was also found at SCHÜ (especially in 2005, Table 17) and supplements the aforementioned elaborations. The clearances in response to bark beetle infestation (2009) produced pronounced changes in the surrounding area. These were also visible in the benthic community, as the share of rheolithophils increased by the factor of five (Figure 36), which indicates a more natural run-off allowing water to freely run through the substrate. A low similarity between the communities of the first (2000) and last (2021) investigated years underlines the effect of clearances on the benthic community (Figure 37).

The Jörglalm spring (JÖA) is situated in an area where pastoral farming was abandoned several decades ago (chapter 2.2.2). As expected, this unimpacted spring achieved the best grade (grade 2 only in 2005, Table 20) throughout the observed period. Even though the share of rheolithophils was comparatively low from 2002 to 2007, this guild remains dominant (> 10 %, Table 21). In the years with the lowest dominance of crenobionts, the remaining community consisted of typical inhabitants of undisturbed brooks and streams. Examples are: *Philopotamus ludificatus*, *Nemoura minima* and *Protonemoura auberti* (Graf, Grasser, & Weinzierl, 2017; Remschak et al., 2016). This could be due to the highly dynamic hydrological regime at the JÖA spring (see chapter 3.5.1), which creates conditions more typical for the epirhithral. This is in line with other studies which found that dynamic rheocrenes are inhabited by a larger number of rhithrobionitc taxa than other types of springs (Von Fumetti & Nagel, 2012; Zollhöfer, 2000).

In conclusion, this multi-metric approach is able to show the differences in communities of springs with and without stressors in their surroundings. It further indicated that external stressors severely hamper the success of restoration. It stresses that proper spring restoration demands an approach that considers the whole spring catchment and enforces the unconditional exclusion of stressors. The near-natural community of the Jörglalm spring further suggests that the return to a completely natural community might even take several decades without any stressors in the surroundings.

However, it must be mentioned that the underlying approach of this thesis needs to be applied on a larger scale as only four springs were investigated providing a low sample size. The qualitative assessment of stressors does not capture the differing intensity of the specific stressors at a single spring. If applied to other spring types, different metrics and thresholds must be used as their communities will strongly differ, even when in a natural state (Martin & Rückert, 2011).

4.3. Data Collection and Availability

As detailed in chapter 1.6, there are six integral elements of ecological spring management (Verdonschot, 1996). Four of them should be executed before restoration measures are implemented, with the most important one being the measurement of biotic and abiotic parameters. In this study, samples from the period before protection fences were erected are sparse (EBA, SCHA3) or missing altogether (JÖA, SCHÜ). For future studies, it is strongly recommended to start sampling before the restoration to

1. depict the community of altered spring ecosystems,
2. analyse community changes caused by restoration,
3. allow for clearer statements on the effects of protection fences.

In theory, emergence traps collect the emerging hemilimnic benthic community when active throughout the year. However, the samples provided for this study were not taken consistently throughout the years. In addition, the time periods in which the samples were taken in the individual years differed. The fact that some traps were relocated or removed (chapter 2.2) during the years under investigation adds to the reduced comparability of each sampling year.

Using SCHÜ as an example, sampling times and consequential biases will be described in the following. The emergence traps were deployed on May 10th, 2000, at a time when *Nemoura mortoni*, which was abundant in 2001, is on the wing (from March to June) (Graf & Schmidt-Kloiber, 2008). A drastic decline of *Synagapetus iridipennis* was observed from 2020 to 2021. The traps were last emptied on June 24th, 2021, with *Synagapetus iridipennis* being on the wing from April to October (Waringer & Graf, 2011).

However, it should be mentioned that high costs, a significant time effort and the poor accessibility of remote springs (in this study especially JÖA) represent limiting factors for continuous monitoring at equal periods (Berlajolli et al., 2019). The monitoring process of springs in pastorally farmed areas was made even more difficult because farmers involved ignored existing regulations. The mentioned relocation or removal of traps was only done in response to their activities, such as digging or construction works.

5. Conclusion and Recommendations

Due to their small spatial scale and naturally low dynamics, springs are highly sensitive ecosystems. While crenobiologists have recognised the importance of protecting these habitats, the public is hardly aware of their contribution to biodiversity.

Unimpaired springs are characterised by a high number of specialised and rare organisms and thus require consistent restoration actions and persistent management. As indicated by the findings of the thesis, the return to a natural state via protection fences, which only exclude one stressor (overgrazing), was not achieved. This demonstrates that even supposedly minor stressors severely impact the cenosis in spring ecosystems and underline how sensitive these peculiar biotopes really are. Although consequent nature protection of springs is difficult to implement in practice, which is mostly due to their exploitation taken for granted, the high shares of highly specialised and rare organisms and the drastic decline of these biotopes should encourage ongoing discussions of this topic. The overall aim should be to implement protection and restoration of these outstanding habitats into national conservation legislation. Decisive contributions to species and biotope protection would then be feasible and gathered data could shed light on topics of crenobiology rather unexplored so far.

This thesis impressively documented that springs are inhabited by a large number of endemics and endangered Red List species (Barquín & Scarsbrook, 2008). In the four springs under investigation, already four endemics and twelve endangered caddisfly species were found (Table 22 and Table 23). Especially, the regular occurrence of the critically endangered caddisfly *Sericostoma personatum*, stresses how important it is to sustain the management of these springs.

As a last point, the value and significance of the LIFE project, which provided the basis for this thesis, cannot be overestimated. Long-term studies on the ecological status of springs in Europe had not been carried out before, making this project the first of its kind. It could and should serve as a role model for future spring studies. The dataset aggregated for this study also allows for other analyses not considered in this thesis. Long-term analyses of seasonal emergence patterns or species interaction shall be mentioned as examples. Since the emergence traps were positioned on a longitudinal setup, the dataset can also provide insights into downstream community changes within spring ecosystems.

6. References

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