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The effects of global change on the quality of thermal habitat for Salmonids with an emphasis on trout (*Salmo marmoratus* and *Salmo trutta*) within the Upper Soča watershed in Slovenia

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Final report - December 2022

Contents

Preface

Project Podnebne spremembe – vpliv na temperature vode in ribe (PO – TEM RIBE), cofounded by European Union and Republic of Slovenia through Maritime and Fisheries Fund ends with this Report.

In the frame of the Project, we collected temperature data on 18 locations in Upper Soča River catchment. The final Report also includes historic data from these locations and data from 7 additional locations, which were not included in this Project. Additional locations are: Tolminka, Kozjak, Godiča, Dabršček, Hotenja, Sevnica and lower part of Idrijca Spring.

Historic data were collected in the frame of Marble trout repopulation programme in Upper Soča River catchment lead by Biological Station Tour du Valat in cooperation with Tolmin Angling Association. We thank them for the allowance to use these data in our Report.

Some historic data were collected under different names for some locations, compared to ones used in our Project. These locations are named under old names in our Report. Locations with old names are: Podbreg – old name Upper Volarja, Upper Podmlaka – Upper Brinta, Lower Podmlaka – Lower Brinta.

Authors are responsible for the content of the Report.

Tolmin, December 2022

Executive summary

This project aims at reviewing the main effects of the global change on mountain watercourses and on their associated fish fauna, especially Salmonids, through the increase of water temperature. Temporal data series of water temperature collected at various locations in the Upper Soča river basin since several years (earliest from 1996) were analyzed to assess any trends as potential effects of the global change. Different temperature metrics were calculated to study more specifically eventual impacts on trout species known as present in the target sites: the endemic marble trout (*Salmo marmoratus*), the exotic brown trout (*Salmo trutta*) and hybrid trout (*Salmo marmoratus x Salmo trutta*). A general warming of water temperatures over the entire Upper Soča basin is here reported, with cold periods (temperatures less than 5°C) tending to shorten and extreme hot temperatures becoming more frequent, especially during summer. Most of the time, thermal conditions remain favorable for salmonids in all sites. However, in some sites, temperatures above 15°C or even 19°C are increasingly recorded, enhancing short periods with stressful conditions for Salmonids, at first for the highly patrimonial *S. marmoratus*.

1 Introduction

Two essential observations have nourished the motivation to realize the present study: the water temperature is a major factor of influence for the aquatic life, and, because of global warming, water temperature is one of the main physical factors likely to significantly change.

1.1 Influence of water temperature on freshwater fish ecology

Temperature is considered one of the most important physicochemical parameter to describe aquatic habitat attributes and the overall health of river ecosystems (Coutant, 1999; Caissie, 2006), particularly because it is a key determinant for metabolic and biological processes (Brown et al., 2004). It directly influences the biology and ecology of aquatic species by affecting their physiology and growth rates, by modifying their breeding periods, altering their behavior and, in fine, their spatial distribution. Temperature also indirectly impacts the biological compartment, having a strong influence on other aspects of water quality, such as the concentration of dissolved oxygen and the ability of organisms to assimilate it, as well as increasing the toxicity of various pollutants (Verneaux, 1977; Vannote et al., 1980; Webb, 1996; Giller and Malmqvist, 1998; Chu and Jones, 2010; Govedič, 2018).

Particularly due to their economic importance as a source of food and of recreational activities (Elliott and Elliott, 2010; Giller and Malmqvist, 1998; FAO, 2016), fish are one of the best-known dwellers of river systems, and are often included into riverine ecosystem health assessment (e.g. the European Water Framework Directive 2000/60/EC) as they are sensitive to anthropogenic perturbations. As the majority of freshwater fauna, fish are poikilothermic organisms. That means that they can't physiologically generate or retain heat, therefore their body heat depends exclusively from the external environment (Brett, 1956; Giller and Malmqvist, 1998). Temperature requirements have long been studied and are increasingly well understood for many fish species and the different stages of their life cycle (Coutant, 1977; Alabaster and Lloyd, 1980; Daufresne and Boët, 2007). For instance, growth, which involves temperature-dependent underlying metabolic processes, requires species- and stage-specific temperature window (Meynard et al., 2012; Neuheimer and Taggart, 2007; Wolter, 2007). The most suitable temperatures for growth generally concern a narrower part of this window (Elliott and Hurley, 1998a). Outside this temperature window, especially when temperatures exceed the upper limit, individuals are under physiological stress which can directly affect their fitness (Hemmer-Brepson et al., 2014) or even their survival (Elliott and Elliott, 2010; Miller and Stillman, 2012). Moreover, most behaviors, such as foraging, migratory movements and reproduction, are triggered by thermal thresholds (Kottelat and Freyhof, 2007) or the duration of specific thermal conditions (Nunn et al., 2007). Hence, characterizing the thermal environment is a key factor to determinate whether a habitat is appropriate for one fish species (Magnuson et al., 1979). It enables to produce cartography of favorable areas for different species and assemblages (Daufresne and Boët, 2007).

1.2 Consequences of water temperature increase in the context of climate change

Climate change has already modified rivers' thermal regime and has been predicted as a major stressor for the coming decades at both local and global scales (Bates et al., 2008; IPCC, 2021; Mohseni et al., 2003; Mohseni and Stefan, 2001; Vörösmarty et al., 2000; Woodward et al., 2010). Many cases of increased water temperature have already been documented in Europe (Arora et al., 2016; Bonacci et al., 2008; Orr et al., 2015; Tibaldi et al., 2010; Webb and Nobilis, 2007), up to near 0.1°C per year (Basarin et al., 2016; Markovic et al., 2013) and further warming is expected (Calbó, 2010; Tibaldi et al., 2010; van Vliet et al., 2011).). Heat exchange processes at the water surface,

which stem from the atmospheric conditions, are highly important in the river's thermal behavior (Pletterbauer et al., 2018; Caissie, 2006). Air temperature has been shown to be a very strong predictor of riverine temperature (Webb and Nobilis, 2007) and can describe up to 80% of the water temperature variability (Markovič et al., 2013; Basarin et al., 2016). It is then a question of being able to quantify locally the temperature increase while identifying the particularities inherent to each tributary, since the thermal balance of a river is the sum of several components¹ varying at different scales (Webb, 1996; Caissie, 2006; Webb et al., 2008; Chu and Jones, 2010; Basarin et al., 2016).

Biological reactions related to heated water may include heat shocks, stress responses and changes to enzyme system function or to genetic structure (Angilletta, 2009 ; Alabaster and Lloyd, 1980; McCullough et al., 2009; Simčič et al., 2015; Pletterbauer et al., 2018). An organism may be differently affected by water warming depending on its thermal tolerance (survival) and sub-lethal effects (e.g. growth), all determined by genetic potential (Alabaster and Lloyd, 1980; Wenger et al., 2011; Killen et al., 2008; McCullough et al., 2009; McCarthy and Houlihan, 1997). The tolerance to higher temperature is especially linked to stage of development, prior thermal acclimation, water chemistry (e.g. dissolved oxygen), pollution, season and the extent to which water is heated (Alabaster and Lloyd, 1980; Pletterbauer et al., 2018). Closer observations of several species spotted behavior reactions during high temperature events, such as seeking thermal refugees. In thermally heterogeneous environments, fish tend to move to thermally adequate microhabitats such as coldwater tributaries or deeper pools (Kottelat and Freyhof, 2007; Ebersole et al., 2001; 2003; Sutton et al., 2007; McCullough et al., 2009). Climate-induced thermal variability can lead to decline in the number and size of areas of suitable thermal niches for most fish species, all having negative effects on population viability (abundance, productivity or genetic diversity, Pletterbauer et al., 2018; Pörtner and Knust, 2007; Comte et al., 2013) and forcing changes in distributional range (Carlson et al., 2017; Lyons et al., 2010). Distribution contractions and shifts to higher altitude or latitude have already been reported for many species (Hari et al, 2006; Almodóvar et al., 2012; Comte et al., 2013; Hickling et al. 2006; Govedič, 2018). Comte and Grenouillet (2015) found that suitable habitat loss tend to be faster compared to fish response and revealed differences in vulnerability of local populations within species distributions. Besides, a warmer environment is suggested to allow alien fish species to faster expand their distribution range and to offer more opportunities for new species to invade (Rahel and Olden, 2008). Climate change is also suspected to alter food web dynamics, leading to feeding changes or even food shortage (Alabaster and Lloyd, 1980; Pletterbauer et al., 2018).

Another important consequence of climate change is that the increase of temperature accelerates the metabolism of parasites and enhances their proliferation. There is also a nonnegligible health risk for fish (Maire, 2021) and in particular for cold-water species that are likely to be infected more frequently and intensely than species tolerating higher temperatures (Marcos-López et al., 2010).

1.3 Climate change and fish context for the Upper Soča river basin

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In Slovenia, surface waters (including rivers) recorded a mean warming trend of 0.19°C per decade for the period of 1953-2015, in Upper Soča river basin 0.15 – 0.20 °C per decade. The greatest temperature increase was observed during the spring and summer season (Vertačnik et al., 2018; Draksler et al., 2018).

 $¹$ Such as, for instance, radiation, evaporation and condensation, air/water transfer, conduction through the</sup> riverbed, friction, precipitation transfer, hyporheic and groundwater exchanges, tributaries, riparian vegetation, and so on.

Warming projections for the Upper Soča river basin are expected to result in changed temporal pattern of mean monthly values of precipitations (warmer and wetter winters and hotter and drier summers), increased actual evapotranspiration, reduced snow amount, decreased summer groundwater recharge, and alternated monthly average discharges (Janža, 2013), all likely to be responsible for additional water warming and thermal variability. All this climate-induced effects are expected to be exacerbated with multiple anthropogenic stressors, such as flow modifications (Ormerod, 2009; Vörösmarty et al., 2000).

The Upper Soča river basin is inhabited by 14 fish species (RIBKAT, 2022) and the effect of climate change raised concern especially for their future conservation (Appendix 1). Fish fauna from the Salmonidae family have already been heavily impacted by human activities, especially stocking for recreational purposes. The native marble trout (*Salmo marmoratus*) is threatened by both the introduced rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*). The result of genetic pollution (hybridization) of marble trout with brown trout is the presence of hybrid trout (*Salmo marmoratus x Salmo trutta)* in many waters (Berrebi et al. 2000, 2022; Fumagalli et al. 2002; Stankovic et al. 2015; Vincenzi et al. 2016, 2018, 2019). On the list of alien species could also be added the European grayling (*Thymallus thymallus*). Indeed, recent genetic analyses identified the Soča grayling population as a hybrid swarm between the Adriatic grayling and the European grayling (*Thymallus aeliani x Thymallus thymallus,* Bravničar et al., 2020; Bravničar, 2021). Salmonids are accompanied with other rheophilic species such as bullhead (*Cottus gobio*), large spot barbel (*Barbus balcanicus*), Cavedano chub (*Squalius squalus*), Italian barbel (*Barbus plebejus*), Italian riffle dace (*Telestes muticellus*), Varione (*Telestes souffia*), Italian minnow (*Phoxinus lumaireul*), tench (*Tinca tinca*) and exotic European Chub (*Squalius cephalus*) (RIBKAT, 2022; BiosWeb, 2022).

Salmonids are cold-water stenothermal (limited thermal tolerance) species with high metabolic rate and oxygen demand and are particularly affected by increases in temperature, especially those that may occur during periods of heat, with the risk of exceeding optimal temperatures or even reaching lethal thresholds (Elliot, 1994; Giller and Malmqvist, 1998). *S. marmoratus* has lower and more restricted thermal preferences than *S. trutta* and is therefore likely to be more affected by rising temperatures. Furthermore, the endemic *S. marmoratus* has a restricted distribution within the Adriatic drainage basin and any change in the quality and availability of its suitable thermal habitat may have important repercussions on its populations and conservation in the long term.

Monitoring water temperature over time and assessing the direction and extent of changes enable to survey how may evolve the spatial distribution of species and to predict how it could further evolve under different scenarios. The finer scale is the monitoring, the better will be identified the most sensitive and vulnerable sectors or those which could be used as refuge. Such information is essential to propose management actions adapted to the local characteristics of the targeted zones.

Within the Upper Soča river basin, a consequent monitoring of water temperature has been progressively deployed on 25 watercourses since 1996. Some streams have thus a data set of more than 25 years which allows to start identifying trends in a robust way. Others, where monitoring was set up more recently, have data series of at least ten years. If this duration is still too short to establish individual solid conclusions, the trends identified on these sites can however consolidate the overall conclusions on a regional scale, while bringing valuable information on the local specificities of these watercourses.

1.4 Objectives

The aim of this study is (i) to provide a detailed spatial description of the thermal specificities of the three main rivers (Soča, Bača and Idrijca) and multiple other headwater streams of the Upper Soča river basin, (ii) to assess and quantify the changes over time and (iii) to evaluate the potential repercussions on the two representative trout species, the marble trout and the brown trout. The spatial and temporal variability of the thermal characteristics among watercourses are examined to distinguish the regional trends from the local specificities.

2 Material & Methods

2.1 Geography and climatic context of the study area

The Upper Soča river basin is located in the southern edge of the south-eastern Alps (Julian Alps) in the north-western part of Slovenia. The northern, alpine part of the area has been strongly formed by glacial erosion and accumulation process (Bavec et al., 2004; Janža, 2013; Rojšek, 1991). Above deeply eroded river valleys are peaks and ridges that exceed the tree line (around 1700 m of altitude). Water circulation in the southern part represented by the Dinaric plateau (highlands with a maximum altitude of around 1000 m) is highly complex due to karst processes and river erosion (Rojšek, 1991; Janža, 2013; Knez and Kranjc 2009).

The Upper Soča river basin interacts with three climatic types: mountain, sub-Mediterranean and temperate continental. The mountain climate with cold winter and cool summer prevail in the alpine part, whereas the temperate continental climate (hot summer and cold winter) is noticeable lower in the valleys and more characteristic in the central and southern part of the study area. The heat of the Adriatic Sea (sub-Mediterranean climate) extends from the Soča river's mouth along the valley up to the town Tolmin and even higher towards headwater parts (Ogrin, 1998; Janža, 2013; Rojšek, 1991).

The Julian Alps and the Dinaric barrier have a strong influence on the precipitation regime. When the wet south-westerly winds from the sea cross the Dinaric-Alpine barrier, most of the precipitation falls in the upwind side, explaining why the Upper Soča river basin is one of the wettest of Europe (Zupančič, 1998; Cegnar et al., 1996). The highest daily precipitation has been recorded above 400 mm and total annual precipitation is more than 2500 mm, exceeding 3000 mm in the mountainous part with the most pronounced maximum in autumn (Zupančič, 1998; Kolbezen and Pristov, 1998). The Upper Soča river basin is hence exposed to frequent heavy precipitations, also above 100 mm per hour (Zupančič, 1998). The Soča catchment is characterized by a nival-pluvial river regime down to the confluence with the Idrijca (Kolbezen and Pristov, 1998).

2.1.1 Sites of the water temperature monitoring

The temperature of the rivers was measured at 25 sites in total, distributed into three watersheds feeding the Soča River: the Upper Soča (named as Soča hereafter), the Bača and the Idrijca rivers (Figure 1). Three of the monitored sites are located in the lowlands, on the main rivers of the three basins, while the other 22 are located on headwater streams, at more or less high altitudes. The main characteristics of the monitored stations and the Salmonid species in presence are provided in Table 1. The first monitoring was set up in 1996 in two streams of the Bača basin (Zakojška and Gorska), then the network was progressively extended in the whole study area (Table 1). Since 2019, the temperature monitoring has been maintained at 18 sites only (Table 1). Detailed information and photographs of each site are providing in the Appendix 3 available online.

Figure 1. Map of water temperature monitoring sites. The colors of the points correspond to their catchment area (brown: Soča basin, pink: Bačabasin, green: Idrijca basin).

Table 1: Monitored watercourses, associated drivers and Salmonid species in presence

2.1.2 Water temperature measurements

Water temperature is measured at each site with a waterproof data logger (©HOBO). To maximize the logger security in case of a flash flood event, it is placed inside a long metal tube, which is attached to a rock. The tube extremity, where the logger is placed, is punctuated with several holes to ensure the circulation of water and the evacuation of fine sediments. The tube is placed underwater, often below a big rock which can protect it from eventual logjams. Furthermore, the localization is chosen so that the logger is insured to be maintained as much as possible underwater throughout the year. Despite all precautions, some data logger were lost due to important flood events or found out of the water. This explains why some missing data exist in the data series. The change of loggers has occurred once or twice a year until 2018 (in June and/or in September) and only once in September since 2019.

Each logger is parametered for a mean water temperature measurement every 2 hours, which enables to spare both its battery and its storage capacity. These temperature measurements at time *i* are noted hereafter 'T_i'.

2.2 Characterisation of the thermal habitats of *S. marmoratus, S. trutta and S. marmoratus x S. trutta*

Stream temperature can be characterized by simple statistical descriptors (e.g. mean, minimum, maximum) summarizing annual, seasonal or monthly measurements of mean daily temperature. This was done largely to analyze past and future water temperature trends in the context of climate change (Webb et al., 2008). Modelizing temperature curves can bring additional descriptors of the annual thermal regime of the watercourses, allowing to compare easily streams behavior with a reduced number of parameters (Tasker and Burns, 1974; Maheu et al., 2016). Nevertheless, all these simple descriptors give little information of the finer spatial and temporal variability of temperature experienced by organisms (Caissie, 2006) and many metrics, more biologically significant, can be proposed to describe the timing, duration and frequency of certain events or thermal conditions (Dunham et al., 2005; Arismendi et al., 2013). These metrics can be refined with the known preferences of the target species or communities related to their range of tolerance (Eaton et al., 1995; Dunham et al., 2005). Here, we sought to describe the thermal conditions within the selected streams and possibly to identify some spatial or temporal variations between sites and years. The heat requirements of *S. marmoratus* and *S. trutta* are summarized hereafter (with rounded values) according to the different known phases and periods of the life cycle. For hybrid trout, we used the same heat requirement as for *Salmo trutta*.

2.2.1 Reproduction and spawning

The passage below of a certain threshold (10-14°C or 6-12°C depending of the hydrological conditions, Gouraud et al., 2014) triggers an upstream migratory movement to spawn for *S. trutta* which seems to be absent in *S. marmoratus* (Kottelat and Freyhof, 2007). Spawning season generally starts in November of year *n-1* for both species and ends in January of year *n* for *S. trutta* (Cattanéo et al., 2002; Elliott and Hurley, 1998a; Gouraud et al., 2014; Hari et al., 2006; Keith et al., 2020; Kottelat and Freyhof, 2007; Ovidio, 1999) and for *S. marmoratus* (Kottelat and Freyhof, 2007; Povz et al., 1996; Povz, 1989). The water temperatures have to be lower than 12°C for *S. trutta* (optimal at 5- 6°C) or 6°C for *S. marmoratus* (optimal at 4-6°C, Bruslé and Quignard, 2001; Kottelat and Freyhof, 2007; Povz et al., 1996). The rainbow trout is spawning in February-March and emerge in July (Crivelli, unpublished data).

2.2.2 Embryonic development and Hatching

For *S. trutta*, hatching is documented as occurring between February and early March (Elliott, 1994; Gouraud et al., 2014) and its timing is closely related to the water temperature (Crisp, 1981;

Elliott and Hurley, 1998a). In one hatchery experiment, the larvae of *S. trutta* hatched at 415 degree days, *S. marmoratus* larvae at 464 degree days and hybrid larvae (*S. marmoratus x S. trutta*) at 420- 435 degree days (Simčič et al., 2017). For the marble trout, at a constant temperature of 10°C eyed eggs were observed after 260-280 day degrees and hatching success at 460-480 day degrees (Simčič et al., 2015). In rivers, hatching is then assumed to require approximately 400 degree days after spawning for both species, or about 40 to 45 days (Keith et al., 2020; Vignes and Heland, 1995; Kottelat and Freyhof, 2007). The embryonic development is optimal for *S. trutta* between 1 and 12°C (cf. Vigier and Caudron, 2007). If the temperature is too cold (< 4-5°C) during the incubation period, the recruitment of 0+ may be compromised for *S. marmoratus* (Crivelli, pers. comm.).

2.2.3 Emergence

The emergence corresponds to the fry stage (i.e. when the individuals leave the redd, Elliott, 1994). It can occur around April (Cattanéo et al., 2002; Elliott and Hurley, 1998a; Gouraud et al., 2014) with a variation range of 2 months (Elliott and Hurley, 1998a, 1998b) or even more under high latitudes (Kottelat and Freyhof, 2007). It requires between 520 (Vignes and Heland, 1995) to nearly 800 degree days after spawning (Bruslé and Quignard, 2001; Keith et al., 2020) for *S. trutta* and about 500 (Specchi et al., 2004) or 592-632 degree days at 10-12°C (Ocvirk, 1994; Povz et al., 1996) or 59-63 days at 10°C for *S. marmoratus* (Kottelat and Freyhof, 2007).

2.2.4 Optimum of temperature and tolerance range

Because these species are poikilotherms, their metabolism remains dependent on ambient temperature for their whole life. The optimums as well as the limits of their tolerance range vary with age.

At the fry stage of *S. trutta*, the temperature preferences are between 1 and 15°C. At the juvenile stage, the tolerance range is from 4 to 19°C (cf. Gouraud et al., 2014), or even up to 22-25°C (Elliott and Elliott, 2010), with a preferendum of 17.6°C (Coutant, 1977). During the adult life, the optimal range of *S. trutta* is given between 7 and 19°C with a preferendum at 13.8°C. While lower critical limit for tolerance is near 0°C, avoidance occurs at 20°C and temperature can become lethal beyond that value: survival is for 1 week above 25°C and 10 minutes above 30°C. Growth ceases below approximatively 3°C and above 19.5° and is optimal around 13.5°C (Hari et al., 2006; Coutant, 1977; Vigier and Caudron, 2007; Bruslé and Quignard, 2001; Keith et al., 2020; Cianfrani et al., 2015).

The tolerance range of *S. marmoratus* seems to be slightly narrower than that of *S. trutta*: the lower limit is 5°C (Keith et al., 2020) or below 5 to 0°C (Vincenzi et al., 2008; Povz et al., 1996) and the upper limit at 14°C (Vincenzi et al., 2008) or 15°C (Keith et al., 2020; Povz et al., 1996; Kottelat and Freyhof, 2007).

2.2.5 Diseases (Proliferative Kidney Disease)

One of the most common diseases in salmonids, the Proliferative Kidney Disease (PKD), has been identified as one potential cause for the decline of fish stocks in several places in Great Britain, in Switzerland and in the French Savoie region (Burkhardt-Holm et al., 2002; Feist et al., 2002; Vigier and Caudron, 2007; Wahli et al., 2002). The severity of the disease and its prevalence are higher in warm than cold environments (Bailey et al., 2017; Debes et al., 2017). The cause of PKD is the myxozoan pathogen (*Tetracapsuloides bryosalmonae*) which uses bryozoans (also known as the moss animals) as final hosts. They release masses of actinospores when water temperature reaches 14°C (Debes et al., 2017) insuring the dispersion of the pathogen and fish infestations. Clinical symptoms and trout mortality generally appear when the temperature exceeds 15°C (Sudhagar et al., 2020; Gay et al., 2001; Wahli et al., 2002).

To date, no cases have been diagnosed in the Slovenian study area. Because PKD is a concern in the neighboring alpine regions, we take this into account while exploring data to assess the health risk in case of accidental introduction of the pathogen.

2.3 Selected thermal metrics

This section describes the metrics chosen to describe the thermal regime of each stream and the thermal habitat of *S. marmoratus* and *S. trutta* (Table 2). Most of these metrics were inspired from the literature (Arismendi et al., 2013; Cianfrani et al., 2015; Dumoutier et al., 2010; Hari et al., 2006; Vigier and Caudron, 2007). Some of the metrics were calculated from the 2 hours temperature measurements (T_i) , which, in particular, enabled to identify the extreme thermal situations experienced by the fish on a daily basis. Mean daily values (T_i) were calculated from the T_i values in order to compute more general metrics allowing to describe the thermal evolution during the last two decades (Table 2).

Following Maheu (2015), metrics were computed only if less than 10% of data in the reporting period was missing (e.g. at least 329 daily measurements were needed to compute a metric over a one-year period, or at least 82 daily measurements for a period of 3 months). All these metrics could have been calculated on the whole T_i or T_i data series of each year and each stream, but when only part of the year was sufficient, we chose to refine the periods concerned in order to limit the number of potential missing values (thus for example; a lack of measurements in summer could no longer prevent the calculation of metrics concerning the cold period).

Table 2 : List of metrics calculated on each water temperature time series

3 Results

3.1 Overview on monitoring records

All mean daily values are presented in Figure 2 and the annual proportions of cumulative durations for the main temperature classes relevant to trout biology (<5°C; 5-15°C; 15-19°C; >19°C) are shown in Figure 3. These data will be explored in a first part for the three main lowland rivers (Soča, Bača and Idrijca) and then for all the monitored sites.

Figure 2. All recorded daily averages per site. Sites are color-coded according to their watershed (Bača, Idrijca or Soča), and classed per altitude. Floods that led to changes in the riverbed were noted in the field (blue diamonds) or identified from the maximum flows (see Figure 6; blue triangles).

Figure 3. Proportion of the number of hours per year with the temperature distributed between different ranges of *values (<5°C; 5-15°C; 15-19°C; and > 19°C). The pie charts represent the averages for each stream/river. The percentage of cumulative time when the temperature is favorable to S. marmoratus (5-15°C) is noted on the pie charts.*

3.2 Main rivers (Soča, Bača and Idrijca)

3.2.1 General thermal description

1

The Soča and Idrijca rivers have been thermally monitored since fall 2007 and the Bača river since fall 2009. With an average annual temperature of 9.4°C, the Soča River is the coldest of the three main rivers studied. The Soča thermal amplitude is also relatively low, 90% of the measurements taken since 2008 being between 5.3°C and 14.7°C, which correspond to the preferential thermal range both for *S. marmoratus* and for *S. trutta*. The cumulative duration when temperature is favorable² for both species (between 5 and 15°C; 'ND_Ti_5_15') is on average 338 days per year (Figure 4).

\blacksquare ND_Ti_sup19 \blacksquare ND_Ti_15_19 \blacksquare ND_Ti_5_15 \blacksquare ND_Ti_inf5

Figure 4. Average annual proportions of temperature classes for each river. The percentage of 'ND_Ti_5_15' is written in black into the bars.

The Bača River is next, with a water temperature of 10.3°C on average and a slightly higher amplitude (90% of the measurements between 4.9°C and 16.4°C). The cumulative duration when temperature is favorable for both species is on average 287.5 days per year.

The Idrijca River is a less steep-sided, wider and longer river than the Bača and therefore has more time to warm up. It is the warmest of the three (11.1°C on average), with the greatest thermal amplitude (90% of measurements between 4 and 19.4°C). The Figure 2 shows clearly that the Idrijca river have the highest mean daily values, often above 19°C in summer. The Idrijca river logger is the only one of the three main rivers where no value below or equal to 0°C was recorded. Thermal conditions here are more favorable for *S. trutta* (90% of the time) than for *S. marmoratus* because 21% of the measurements are above 15°C. The cumulative duration when temperature is favorable for both species is on average 237.8 days per year. It is also the river with the highest recorded temperature: 23.5°C, which remains below the 1-week lethal threshold of 25°C for *S. trutta* but

² The thermal environment is favorable for *S. marmoratus*, and therefore for *S. trutta* which has a wider range of tolerance, when the temperature is between 5 and 15°C. This also corresponds to the conditions that limit PKD-related symptoms (if the pathogen is present). We therefore consider that the conditions are favorable for both species in terms of thermal and sanitary preferences.

above its avoidance upper limit of 20°C. The Idrijca has hence the most thermally stressful conditions for *S. trutta* with an average accumulation of hours above 19°C ('ND_Ti_sup19') equivalent to 16.6 days per year, whereas this represents generally less than 1 day per year for the two other rivers. The maximum cumulative duration above this threshold observed were 1.07 days in the Bača river (in 2010), 1.27 in the Soča river (2018) and 35.72 days in the Idrijca river (2012).

The annual cumulative duration of heat stress for *S. marmoratus* (above 15°C; 'ND_Ti_sup15') is on average 81.2 days in the Idrijca river (maximum of 108 days in 2011) and 38 days in the Bača river (maximum of 53 days in 2018), while it is only 7.8 days in the Soča river (maximum of 30 days in 2018). The duration of the observed periods when the temperature is continuously above 15°C ('N_max_Ti_csh_sup15') is much longer in the Idrijca river (37.4 days on average, maximum of 86.6 days in 2012) than in both the Soča and Bača rivers (respectively 1.7 and 6.5 days on average). In these last two rivers this duration has just exceeded 2 weeks for only one year during the monitoring (in 2018). This duration of 2 weeks is supposed to be necessary for the development of the PKD for the rainbow trout *Oncorhynchus mykiss* (Vigier and Caudron, 2007). The Idrijca river is therefore rather thermally less favorable for *S. marmoratus* due to prolonged exposure to temperatures above its Upper tolerance limit (in the absence of thermal refuges) and potentially favorable to the development of diseases such as PKD (which may present a risk if the pathogen is introduced).

3.2.2 Thermal trends

Years

Figure 5. Trends of annual mean temperature for the three rivers (Soča, Bača and Idrijca) tested with Mann-Kendall test and quantified with Sen's slope.

The Figure 5 shows graphical increasing trends of the annual mean temperatures ('Tmp') for the three rivers between 2008 and 2020. However, this trend is statistically significant only for the Soča river using the Mann-Kendall test (P=0.001) with an increase of 0.044°C per year. For this river, both increases in summer temperatures (0.22°C per year, P=0.016) and in annual maxima ('Ti_max', 0.24°C per year, P=0.009) are significant. In this river, the increase in annual mean temperatures is

hence associated with an increase in the number of days with temperature above 15°C ('ND_Ti_sup15', 0.9 days per year, P=0.032).

At the seasonal level, no significant changes in average temperatures ('Tmp_spring', 'Tmp_summer', 'Tmp_fall_winter') is observed for the Idrijca River (Figure 12). Nonetheless, both a significant increase in annual minima ('Ti_min', 0.15°C per year, P=0.016) and a significant decrease in the length of the cold period ('DUR_cold_inf5', -4.67 days per year, P=0.002) are noted.

For the Baca River, a marginal significant increase in average for summer temperatures (0.05°C per year, P=0.1) is obtained. It is also noted a significant decrease of 2.34 days per year with temperatures below 5°C (P=0.034, 'ND Ti inf5'), which may enhance more favorable thermal conditions for trout growth during the winter period.

3.2.3 River flows with maximal and minimal trends

Figure 6. Minimum and maximum flows recorded since the beginning of the 1940s in the three rivers (ARSO, 2019). The dotted horizontal line corresponds to a morphogenic flood flow (A. Crivelli; Comm. Pers.). The Sen's slope is given with the

significance of the Mann-Kendall test for each data set. The lines are thickened over the period corresponding to the temperature monitoring of these rivers.

Maximum river flows show a significant upward trend in the Idrijca river and especially in the Soča river, where peak flows almost systematically exceed 500 $\text{m}^3\text{/s}$ in the most recent period. This can be explained by a coupling between a precipitations increase instead of snowfall and an earlier snowmelting (particularly in the Soča watershed), and is consistent with the hypothesis of a transition toward a more pluvial regime (Kolbezen and Pristov, 1998; EEA, 2009). The low water flows do not show any significant trend, except for a slight decrease in the Bača River. Thus, although the trends are still rather weak, a progression towards wetter winters and drier summers can be observed through these three rivers long flow data time series.

3.3 Headwater streams

3.3.1 General thermal description and habitat quality

The mean annual temperature ('Tmp') of all streams ranges from 7.6°C (Gačnik) to 10.2°C (Dabrček). The annual maximum temperatures ('Ti_max') observed on all the streams are on average 16.3°C and range from 12.4°C (Trebuščica) to 18.95°C (Gačnik). The average of 'Ti_max' over the years is below 19°C for most streams; only the Lower Volarja, which in fact correspond to a lowland river section, is an exception with 19.8°C. Stressful thermal conditions for *S. trutta* are therefore rare in these streams. The cumulative number of hours with temperature above 19°C ('ND_Ti_sup19') is on average always less than 1 day for each site, except in the Lower Volarja (1.7 days in average, up to 8.4 days in 2018).

The thermal habitat is mostly favorable for the growth of trout species in all rivers and streams, especially in the Tolminka, Upper Volarja, Sevnica and Zadlaščica streams with temperatures less than 15°C more than 90% of the time (see 'ND_Ti_5_15' in the Figure 7). The Lower Volarja displays a contrasting thermal behavior with the lowest proportion of measurements between 5 and 15°C, which is related to a relatively high proportions of measurements both below 5°C ('ND_Ti_inf5'; 18.3%) and above 15°C (18.2%, Figure 2 and Figure 7).

Despite its high altitude, Gačnik displays strong thermal variation between summers, which can be sometimes very hot (especially in 2018) and winters, which are often very cold. It is known that small, shallow and exposed rivers are more sensitive to atmospheric exchanges compared to larger, deeper and more in the shade ones (Torgersen et al., 2001; Zwieniecki and Newton, 1999). Gačnik stream is located on a gently sloping highland and fed by springs that can be sometimes very low. It is therefore subject to strong cooling in winter and strong warming in summer due to these low flows and velocities. Also, the absence of riparian vegetation on large part of the stream make it more exposed to sunlight, accentuating the summer heating (Johnson, 2004). Tolminka and Upper Volarja streams have a more constant temperature throughout the seasons. This results from strong flow all year round, especially for Tolminka. Tolminka maintains cool summer temperatures throughout the summer: this river is particularly steep and has little exposure to the sun along most of its course. Upper Volarja, whose catchment area is very steep with high mountain peaks, maintains relatively cool temperatures at winter (Figure 2).

The vast majority of sites are concerned by temperatures above the upper tolerance limit for *S. marmoratus* (15°C), and for a potential PKD development (in case of introduction of the pathogen). However, the cumulative durations of these periods are relatively short: from 16.8 days on average for Kozyak up to 66.5 days for Lower Volarja. Only two sites, Trebuščica and Upper Volarja, were not subject to temperatures above 15°C values (shown in white in the Figure 12). The duration of the observed periods when the temperature is continuously above 15°C ('N_max_Ti_csh_sup15') exceeds 2 weeks only in 2 sites, Zakojca and Lower Volarja, for at least 3 years of their monitoring.

3.3.2 Reproduction and Spawning

The spawning dates of *S. marmoratus* that were observed in the field between 2005 and 2012 are shown as dashed rectangles in Figure 8. They range from early November to early January and vary between streams and basins. On the same graph, the distribution of days when the temperature falls below 6°C ('D_SpawnSma_inf6'), over the years at the sites concerned, is shown.

Effective spawning theoretically occurs at least from the day 'D_SpawnSma_inf6', but has been systematically observed delayed from this date in the Huda grapa, Lipovšček or Zadlaščica streams. Both the 'D SpawnSma inf6' days and the observed spawning date are the latest and the most variable for the Upper Volarja. The day 'D_SpawnSma_inf6' (estimated here from a single point temperature measurement in the streams) might not be sufficient on its own to accurately explain the onset of spawning, but it does help to define when spawning can occur.

Figure 8. Distribution of spawning dates for S. marmoratus and S. trutta observed in the field between 2005 and 2012 (dashed rectangles) or estimated by the date of passage below the 6°C ('D_SpawnSma_inf6') within the same years (2005 to 2012) threshold (boxplots).

In some sites 'D SpawnSma inf6' already shows a significant tendency to become later in time (Gorska, Huda, Zakojca, Sevnica, Upper Volarja, Upper and Lower Idrijca, Zadlaščica and the Bača river, Figure 12). It can therefore be expected that the spawning dates in these sites will shift over time.

3.4 Spatial variations

3.4.1 Altitude, an important thermal driver

Overall, the annual mean river temperature ('Tmp') decreases with the altitude of the monitored point (Pearson correlation = -0.57; Figure 9a). Tolminka, in the Soča basin, is at low altitude and has lower mean temperatures than the other streams, which suggests the influence of additional factors specific to this basin (e.g. snowmelt water supply). While in the Bača and Idrijca basins the number of cold measurements ('ND_Ti_inf5') tends to increase with altitude, this is not the case for the Soča basin (Figure 7). These results illustrate that several factors can act as sources of water temperature variations.

Figure 9. Plot of annual mean temperature for each stream and year of the record as a function of: a) altitude (m) and b) total pool area (m²). The coefficients of the general linear regression are given in grey above the figures with R². The Pearson correlation coefficient (r) is noted in black.

Another result that may be of interest but must be interpreted with care for this same reason and for the numerous possible interactions between factors influencing thermal regimes: the total area of pools in the river monitored sections is negatively correlated with mean temperatures (Figure 9b) and not correlated with altitude (Kendall's tau = 0.21, P=0.23). The presence of pools reflects the existence of deeper areas in the streams where the temperature may remain cooler, especially if the pools are shaded. This is generally the case in deep valleys dominated by forests, except for example in Zadlaščica where the pools are rather exposed to the sun. The mean temperature ('Tmp') of this stream is on average higher for a given pool surface compared to other sites (points above the regression line, Figure 9b).

3.4.2 Comparison of thermal characteristics of streams between the three basins

Overall, the diversity of streams, in terms of thermal characteristics, is similar between the three basins. Nevertheless, some significant differences between the three basins were statistically revealed (Figure 10).

The streams of the Idrijca watershed have on average colder temperatures compared to the two other watersheds (Figure 10a). Streams in the Idrijca basin have more days with temperatures below 5°C than those in the Soča basin (Figure 10c) and the duration of the cold period tends to be longer in the Idrijca basin than in the Soča one (but the post-hoc test is non-significant at the 5% level; Figure 10h). The thermal amplitude is significantly higher in the streams of the Idrijca basin than in the Bača basin (Figure 10d). The day of crossing below the 6°C threshold ('D_SpawnSma_inf6') is earlier in the streams of the Idrijca basin than in those of the Soča basin (Figure 10f). The first day when the smoothed temperature exceeds the annual mean temperature is earlier in the streams of the Idrijca watershed (Figure 10g). The heat peak is earlier in the Idrijca streams than in the Bača ones (Figure 10e).

*Figure 10. (a - h) boxplots of 8 meaningful metrics calculated per year and stream here grouped by Basin. Kruskal-Wallis test (p-value in black) and Tukey's non-parametric post-hoc (arrows and significance in blue; p<0.001, '***' ; p [0.001;0.01], '**' ; p [0.01;0.05], '*'; p [0.05,0.1], "." ; p>0.1, 'n.s.'). The average proportions of the different temperature classes among all streams per watershed are shown in the last barplot.*

The temperatures remain very favorable to both trout species in the three watersheds. The average proportions of temperature classes are indeed very close between the streams of the three watersheds and particularly favorable for *S. marmoratus* (high proportion of 5-15°C class; Figure 10h). Streams in the Idrijca watershed tend to have fewer days with favorable temperature for *S. trutta* (Figure 10b), but post-hoc differences are only significant compared to the Soča streams. It must be noted that in most of the sites, only hybrid trouts (*S. marmoratus x S. trutta*) are present, except in the Upper Volarja stream where the only genetically pure population of *S. trutta* has been found (Berrebi et al., 2000, Table 1).

3.4.3 Regional coherence

The regional coherence between the time series of daily mean temperatures is assessed via the square of the correlation coefficient (r^2) between each site and the mean of the other sites (Hari et al., 2006). A high value therefore indicates a synchrony between the temperature variations of the site under consideration and those of the other 24 sites. The factors influencing the temperature of the rivers can then be considered as homogeneous at the regional scale.

Four correlations are calculated for each site on the set of real measured temperatures (Ti) over the whole chronicle ('Tot') or selected on the periods of the chronicle corresponding to fall-winter, spring or summer. The distribution of the squares of these coefficients is represented by season and watershed (Figure 11). The r² are high for the total daily averages in the three watersheds, indicating a regional synchrony in the temperature variations of the rivers and therefore probably an overall predominant climatic influence.

Figure 11. Regional coherence: r² between the temperature time series of each site and the average of the other sites.

The lowest $r²$ are observed in summer for the three watersheds. Flows are then generally lower and stream temperatures are more sensitive to local conditions (e.g. shading, type of substrate, slope of the land, land use), the regional coherence is then partly masked by local conditions. In spring, some streams of the Soča watershed, where are the highest altitude summits, may be fed by snowmelting water and therefore have a colder temperature than other streams, which may explain the observed low r².

3.5 Temporal variations

3.5.1 Trend analysis

The inter-annual trends of each metric per site are analyzed using the non-parametric Mann-Kendall test (Esterby, 1996; Hirsch et al., 1982; Webb, 1996). The slopes of the trends found to be significant are estimated using the Sen method which represents the median slope calculated from all observations (Arismendi et al., 2013; Sen, 1968). The results of the trend analysis on all calculated metrics are summarized in the Figure 12. Trends are significant for at least half of the sites for a total of 8 metrics.

Figure 12. Results of trend tests (Mann-Kendall test and Sen's slopes) on all metrics. In color, the result of the Mann-Kendall test is significant, in orange/red the Sen's slope is positive, in blue it is negative. The number of metrics showing at least a marginal significant trend for each site is noted in parentheses after the site name. The number of sites where each metric shows at least a marginal significant trend is noted in the margin on the right. The average Sen's slopes (of sites where the Mann-Kendall test is at least marginal significant) for each metric are given in parenthesis.

The following major points are emphasized:

- The mean annual temperatures ('Tmp') increase by 0.04°C per year in average (from 0.02°C to 0.13°C per year for Studenc and Dabrček respectively);
- The mean fall-winter temperatures ('Tmp_fall_winter') increase by 0.05°C per year in average (from 0.04°C per year for Lipovšček, Driselpoh and Upper Idrijca by 0.08°C per year for Gorska);
- The mean summer temperatures ('Tmp_summer') increase by 0.11°C per year in average (from 0.06 to 0.22°C per year for respectively Upper Volarja and Lower Idrijca);
- The maximal temperatures ('Ti_max') increase by 0.17°C per year in average (from 0.09°C and 0.41°C per year for respectively Stopnikarca and Gačnik);
- The cumulative number of hours with temperatures above 15°C increases by 1.59 days per year in average ('ND_Ti_sup15', from 0.21 to 3.54 days per year for respectively Lipovšček and Hotenja);
- The trends are significantly decreasing for at least half of the sites for only one metric: the duration period with temperatures below 5°C ('DUR_cold_inf5'; from -2.5 to -8.5 days per year for Gačnik and Bača river respectively). The shortening of this cold period is explained either by a delayed drop below the 5°C threshold in late autumn or early winter (i.e. the start date of the cold period; 'Dd_Tmj_inf5'), by an earlier rise above this threshold in late winter

or early spring (i.e. the end date of the cold period; 'Df_Tmj_inf5'), or by both combined (e.g. in Gorska, Stopnikarca, Sevnica where the upward trend in 'Dd_Tmj_inf5' and the downward trend in 'Df Tmj inf5' are at least marginally significant).

The increase in mean temperatures at the monitored sites is quantitatively comparable to that reported in the literature (e.g. Basarin et al., 2016; Bonacci et al., 2008; Orr et al., 2015; Webb and Nobilis, 2007). Also, the seasonal shifts observed are consistent with the earlier spring warming and increase in summer heat already documented elsewhere (Arora et al., 2016; Markovic et al., 2013). The next three figures detail the changes in average temperatures for all sites, grouped by watershed.

Figure 13. Evolution of the annual mean temperature of all the sites of the Soča basin. See Figure 5 for legend details.

Figure 14. Evolution of the annual mean temperature of all the sites of the Bača basin. See Figure 5 for legend details.

Figure 15. Evolution of the annual mean temperature of all the sites of the Idrijca basin. See Figure 5 for legend details.

3.5.2 "Precocity" or "lateness"

The day when the temperature drops below 6°C (expected to be reliable to the triggering of spawning for *S. marmoratus*) appears later in the autumn-winter season for 9 sites ('D_SpawnSma_inf6'; Figure 12). The first day of the cold period ('Dd_Tmj_inf5') is found significantly later for 7 sites, while the final day of the cold season ('Df_Tmj_inf5') is observed earlier for 8 sites.

These shifts appear related to the general increase in temperature and not to a prolongated warm period. Indeed, the day of passage under the mean temperature of the year ('Df_Tmj_supTmp') does not show significant tendency in any site, but the day of passage under a reference temperature (average of all temperatures of the site) is significantly increasing for 9 sites ('Df_Tmj_supTm'). The day when the smoothed temperature goes over the annual mean temperature ('Dd_Tmj_supTm') happens earlier in 2 sites, which is consistent with the general increase in overall temperatures (but not generalizable because of the small number of sites involved). On the contrary, 'Dd_Tmj_supTmp' is increasingly late in 5 other sites, mainly in the Soča basin. In this case, this is consistent with the hypothesis of a prolonged influence of the snowmelt (cold water) feeding of these rivers.

3.6 Some concrete examples

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As an example, the temperatures measured at the beginning and end of the monitoring are given for three sites³ : Gačnik (Idrijca basin), Gorska (Bača basin) and Lower Brinta (Soča basin). All these 3 sites correspond to small streams with low flows and water levels. While the Gačnik stream is slightly sloping, located on a high plateau and relatively exposed to the sunlight, the Gorska stream is very steep and sheltered from the sun by a dense canopy. The Lower Brinta site is rather open and less steep compared to the Gorska stream.

 3 Graphs for all sites are provided in the Appendix 2.

Figure 16. Comparison between the temperatures of the first 4 (1998-2001) and last 4 years (2018-2021) of monitoring for the station of Gačnik (Idrijca river basin). In white: the range of daily values for the considered period. In black: the average of daily temperatures over this period (and its smoothing over 3 months to determine the days of crossing thresholds). The number of days below the 5°C threshold and over the 6 and 10°C thresholds are calculated from the smoothed curve. Those above 15 and 19°C are calculated from the first and last days when a temperature above these thresholds was observed.

For Gačnik, the changes involve a marginally significant shortening of the duration of the cold season ('DUR_cold_inf5'; Figure 12) with generally high temperatures at the end of the year over the recent period. Moreover, an increase in both average (general rise of the smoothed curve) and maximum temperatures can be observed (crossing of the 19°C threshold, and longer duration above the 15°C threshold in the recent period). Fish (in the present case *S. marmoratus*) may thus find themselves more frequently in a situation of physiological stress due to warmer summer, in duration and intensity, especially if there is no thermal refuges.

Figure 17. Comparison between the temperatures of the first 4 and last 4 years of monitoring for the station of Gorska grapa (Bača river basin).

Concerning Gorska, the evolution is coherent with that of Gačnik but the temperatures remain favorable to both species in the recent period (with nevertheless the appearance of some rare unfavorable situations for *S. marmoratus*). One can also note the disappearance of the cold period with the rise of the low temperatures.

Figure 18. Comparison between the temperatures of the first 4 and last 4 years of monitoring for the station of Lower Brinta (Soča river basin).

For the Lower Brinta site, the changes show a decrease in intensity, but not in duration, of the cold period, and a general rise in temperatures with the average temperatures exceeding the 15°C threshold and a longer duration above this threshold. It can be noted in this case that only 8 years separate the two periods whereas for the two previous sites these periods were 18 years apart. The evolution for the Lower Brinta has been therefore relatively rapid.

For all the other sites, the number of days above the 6, 10 and 15°C thresholds is significantly greater in the recent period than in the former period (Wilcoxon test), and only marginally significant for the 19°C threshold.

4 Discussion

4.1 Spatio-temporal variations of water temperature

Having conducted a multi-site study with a large number of monitored sites allows us to appreciate the generalizability of the observed processes. Here, significant trends for more than half of the considered streams (Figure 12) indicate a general warming of water temperatures over the entire Upper Soča basin. This water warming is highlighted through 5 main points:

- 1. The annual mean temperature ('Tmp') is significantly increasing for most sites ;
- 2. The cold period is shortening (decrease of 'DUR_cold_inf5') and less frequent (decrease of 'ND Ti $inf5'$) ;
- 3. Extreme hot temperatures are more and more frequent ('Ti_max') ;
- 4. The increase in temperatures is twice as fast in summer ('Tmp_summer', on average 0.11°C per year) as in fall-winter (0.05°C per year) and as inter-annually (0.06°C per year). Only few sites are concerned by a significant increase of spring temperatures;
- 5. The period with temperature between 15 and 19°C, above the upper limit for adult of *S. marmoratus*, is more and more frequent (increase of 'ND_Ti_15_19').

The evolution of the annual mean temperatures ('Tmp') for all sites in Figure 19 summarizes the overall observed increase of water temperature. Before 2003, the number of sampled sites is relatively low and the relationship between 'Tmp' and time is therefore not very robust. From 2003 to 2008, about 12 sites were sampled, and then almost twice as many from 2009 onwards, which provides a better picture of the regional trend in 'Tmp' over the last 10 to 16 years. The relationship shows a clear increase in the observed median 'Tmp' (black dots) compared to the overall mean 'Tmp' (corrected by altitude; blue line, Figure 9).

Figure 19. Evolution of the distribution of the 'Tmp' of all the sites per year (thin lines: min and max; thick lines: quantiles 0.25 and 0.75, points: medians). The number of sites sampled per year is indicated inside the points. The blue line shows predicted temperature as a function of mean altitude for sites sampled per year (based on the general linear regression model of 'Tmp' on altitude across all sites and years; parameters noted above the graph).

A large majority of the monitored sites ($n=18$ out of 24) are concerned by an increase in the mean annual temperature ('Tmp'). The Upper Brinta stream was excluded from most of the tests due to a too short time series, since its monitoring only started in 2018. The sites exhibiting a nonsignificant trend are also among the last sites where the temperature monitoring was set (Figure 20), so probably with too few data to observe any trend.

In a more general way, the number of metrics showing a significant trend is particularly variable between sites (Figure 12) and the number of metrics for each site where the trend is significant is negatively correlated with the first year of monitoring (Pearson's r=-0.77, P<0.001; Figure 20). The duration of the monitoring appears therefore as fundamental to identify modifications in the thermal regime of the rivers.

Figure 20. Relationship between the number of metrics with a significant trend and the first year of monitoring for each site.

On Figure 20, some sites are particularly far from the regression line (absolute value of residuals above 4): Upper Idrijca and Lower Idrijca (black-circled). These two sites above the regression line present a higher number of metrics where the evolution is significant, taking into account the duration of the monitoring, compared to the other sites. They then seem to be more subject to changes in their thermal regime.

4.2 Quality of the thermal habitat for trout

4.2.1 Suitable habitat

The main finding from the temperature monitoring is that the thermal habitat is generally favorable for both trout species at the scale of the Upper Soča river basin. The 3 rivers and 22 streams present at least two thirds (and nearly 80% on average) of thermal situations between 5 and 15°C ('ND Ti 5 15'). At first sight this proportion of favorable thermal range has remained stable over the years in most of the sites, and has even increased in 4 of them (Gorska, Lipovšček, Trebuščica and Upper Idrijca).

If this observation seems optimistic, it must nevertheless be considered in the light of the evolution of other aspects of the thermal habitat. First of all, it can be linked to a regression of cold situations ('ND_Ti_inf5' or 'DUR_cold_inf5') due to the shift of all the temperature curves upwards, and thus to a better superposition of the temperature curves with the preference window of *S. marmoratus* (Appendix 2). This generalized rise in temperature also implies the appearance of increasingly frequent thermally stressful situations for *S. marmoratus* ('ND_Ti_sup15'), and the same for *S. trutta* ('ND_Ti_sup19'). If the deployment of a substantial multi-site monitoring has allowed the identification of robust general trends, it also allows the identification of local particularities.

So far, the thermal habitat of the Soča River appears still particularly favorable for both species (94% proportion of 'ND Ti 5 15', Figure 3). Nonetheless, some streams in the Soča catchment area already exhibit some considerable percentage of temperatures above 15°C (Kozjak, Godiča, Lower Brinta and especially Lower Volaria, Figure 3). These percentages are likely to increase over the years since, although these sites have some of the shortest data series (except Lower Volarja), they are all already showing increasing trends in summer temperatures and are consequently expected to be progressively less favorable for both trout species. On the other hand, the Upper Volarja and Tolminka streams exhibit the highest percentages of the 5-15°C favorable range among all sites (respectively 96% and 97%; Figure 3). In addition, the water temperatures of both sites remain well below the 15°C limit (Appendix 2). In case of degradation of the thermal quality of the Soča River and of surrounding streams, these two sites could be suitable refuges for *S. marmoratus*.

Within the Bača and Idrijca basins, although the sites located at high altitudes are the coldest (Figure 9), it appears that some headwater streams can present stressful thermal conditions for *S. marmoratus* ('ND Ti sup15'). These streams generally have low thermal inertia due to low flow rates. The Gačnik stream, for instance, exhibits low slope, low flow rate and relative exposure to the sunlight due to a reduced riparian vegetation. This stream appears particularly sensitive to summer warming and thus to the development of stressful thermal conditions, despite its relative high altitude.

In the context of global change, summers are expected to be hotter and drier. As a result, headwater streams would be more sensitive to heating due to low flows and high air temperatures. This would reduce the quality of thermal habitat, which would limit the amount of habitat available in the headwaters and thus the potential for altitudinal refuges of trout species. The Idrijca River already presents stressful conditions for trout species, especially during the summer. Most of the streams in this watershed could already be considered as thermal refuges during the warm season, nonetheless boundaries prevent most of the time an upstream migration of fish. Furthermore, this hosting potential may evolve according to the modifications of hydrology and vegetation cover.

4.2.2 Phenology

Another aspect related to the increase in temperatures concern the reproductive success. On the field, from 2005 to 2012, it has been observed that the reproductive success was very low or even null when cold situations (<5°C) were prolonged. The temperature monitoring shows that the duration of the cold season has been shortened and winters have become milder, thus that the conditions are becoming more favorable to growth, and even to reproduction. In some cases, the increase in temperature can also be accompanied by a shift in the crossing of thermal thresholds that can affect phenology. In 4 sites, the date when the temperature falls below 6°C, threshold favorable for spawning, has significantly increased during the monitoring and it can be expected that the breeding season will be shifted.

The metrics identifying a date ('D_SpawSma_inf6', 'Dd_Tmj_inf5' and 'Df_Tmj_inf5)' are subject to high variability due to punctual events that may occur within a short period (despite the use of temperatures smoothing to identify these dates). Hence, these metrics are considered sensitive compared to other ones, such as the annual mean temperature ('Tmp') or the cumulative duration of temperatures above 15°C, which by contrast will inherently buffer exceptional events. It is therefore more difficult to conclude about potential changes in phenology over time, but the fact that trends are appearing at some sites suggests that an evolution is underway (Figure 12). The fact the 'D SpawnSma inf6' metric is highly correlated with the mean fall-winter temperature ('Tmp_fall_winter', Figure 21) seems to confirm a regional trend towards a later breeding, since this seasonal temperature significantly increase for a large number of sites (n=14, Figure 12). The confirmation of such hypothesis require however longer data sets, especially in streams subject to strong hydrological variations.

Figure 21. Plot of the date of crossing below the 6°C threshold ('D_SpawnSma_inf6') as a function of the average temperature in fall-winter ('Tmp_fall_winter').

4.3 Perspectives

The complexity of the processes and their interactions highlight the interest of multi-site and long-term monitoring to extract significant information. The continuity of the temperature monitoring will enable to better quantify trends with more robustness and to specify the fine modifications of the thermal regimes. Further analyses could be conducted to assess the implications of other local or regional factors in the observed thermal regime modifications (e.g. hydrology, type of riparian and watershed vegetation, precipitation regimes). For example, discharge is, like temperature, a major parameter that can influence migratory or phenological behaviors (e.g., reproduction) as well as the survival of individuals during extreme events such as droughts or major floods (Wenger et al., 2011). It also directly influences the thermal regime of the rivers. Discharge monitoring on rivers for a better consideration of hydroclimatic variables would increase the interest of the present study.

The present study makes a fundamental contribution to the knowledge of aquatic systems and their response to global changes. It also constitutes a key step in the conservation of species and the management of natural environments. This work, initiated more than 25 years ago, has now provided an assessment of the evolution of the thermal habitat for two species of trout in a context of global changes. A similar analysis could be carried out with the species present in the study area that prefer warmer waters.

From 1996 to 2018, most of the sites equipped with temperature loggers were surveyed once or twice a year with a scientific fishing protocol designed to assess the dynamics of the local trout populations. Capture-Mark-Recapture programs were hence set up on the long-term, and enabled to assess the evolution of the survival, growth and reproduction of each population, in relation to biotic (e.g. density-dependence, trophic resources) and abiotic (e.g. temperature, habitat capacity, extreme

events) factors. Considering the significant increases in water temperature from year to year, it would be of major interest to start again these fishing surveys for at least a period of 5 years to be able to assess the evolution of the population dynamics, in comparison with previous periods. Such surveys would enable to assess how the trout species cope with thermal changes.

References

- Adamicka, P., 1991. Schicksal einer durchschnittlichen Koppe (Cottus gobio L.) im Lunzer Seebach. Österreichs Fischerei 44:162-164
- ARSO Environmental Agency of the Republic of Slovenia, 2019. Hydrological data archive [\(http://vode.arso.gov.si/hidarhiv/\)](http://vode.arso.gov.si/hidarhiv/)
- Alabaster, J.S., Lloyd, R., 1980. Water Quality for Fresh Fish. Butterworts, London. 283 p.
- Almodóvar, A., Nicola, G.G., Ayllón, D., Elvira, B., 2012. Global warming threatens the persistence of Mediterranean brown trout. Global Change Biology. 18, 1549–1560.
- Arismendi, I., Johnson, S.L., Dunham, J.B., Haggerty, R., 2013. Descriptors of natural thermal regimes in streams and their responsiveness to change in the Pacific Northwest of North America. Freshw. Biol. 58, 880– 894. https://doi.org/10.1111/fwb.12094
- Arora, R., Tockner, K., Venohr, M., 2016. Changing river temperatures in northern Germany: trends and drivers of change: Changing River Temperatures in Germany. Hydrol. Process. 30, 3084–3096. https://doi.org/10.1002/hyp.10849
- Angilletta, M.J., 2009. Thermal sensitivity. In: Angilletta MJ Jr (ed.) Thermal adaptation: a theoretical and empirical synthesis. Oxford University Press. New York. 35–87
- Baensch, H. A., Riehl, R., 1991. Aquarien atlas. Bd. 3. Melle: Mergus, Verlag für Natur-und Heimtierkunde, Germany : 1104 p.
- Bailey, C., Schmidt-Posthaus, H., Segner, H., Wahli, T., Strepparava, N., 2017. Are brown trout *Salmo trutta* fario and rainbow trout *Oncorhynchus mykiss* two of a kind? A comparative study of salmonids to temperature-influenced *Tetracapsuloides bryosalmonae* infection. 41, 191–198.
- Basarin, B., Lukić, T., Pavić, D., Wilby, R.L., 2016. Trends and multi-annual variability of water temperatures in the river Danube, Serbia: Danube Water Temperature Trends in Serbia. Hydrol. Process. 30, 3315– 3329. https://doi.org/10.1002/hyp.10863
- Bates, B.C., Kundzewicz, Z.W., Wu S., Palutikof J.P., 2008. Climate Change and Water. Technical Paper of the Intergovernmental Panel on Climate Change, IPCC Secretariat, Geneva. 210 pp.
- Bavec, M., Tulaczyk, S.M., Mahan, S.A., Stock, G.M., 2004. Late Quaternary glaciation of the Upper Soca River Region (Southern Julian Alps, NW Slovenia). Sed Geol. 165, 3–4, 265–283.
- Berrebi, P., Povz, M., Jesensek, D., Crivelli, A.J., 2000. The genetic diversity of native, stocked and hybrid populations of Marble trout in the Soca River, Slovenia. Heredity, 85, 277-287.
- Berrebi P., Jesenšek, D., Martin, D., Laporte, M., Crivelli, A.J., 2022. Restoring marble trout genes in the Soča River (Slovenia). Two decades of monitoring the introgression. Conservation Genetics, in press
- Bertoli, M., Pizzul, E., Devescovi, V., Franz, F., Pastorino, P., Giulianini, P. G., Ferrari, C., Nonnis Marzano, F., 2019. Biology and distribution of Danube barbel (*Barbus balcanicus*) (Osteichthyes: Cyprinidae) at the Northwestern limit of its range. The European Zoological Journal, 86, 1: 280-293
- BiosWeb Biološka zbirka podatkov Zavoda za ribištvo Slovenije, 2022. www.biosweb.org
- Bonacci, O., Trninić, D., Roje-Bonacci, T., 2008. Analysis of the water temperature regime of the Danube and its tributaries in Croatia. Hydrol. Process. 22, 1014–1021. https://doi.org/10.1002/hyp.6975
- Bravničar, J., 2021. Populacijska genomika in varstvo jadranskega lipana *Thymallus aeliani* (VALENCIENNES, 1848) v reki Soči. Dokt. disertacija. Ljubljana, Univerza v Ljubljani, Biotehniška fakulteta. 151 p.
- Bravničar, J., Palandačić, A., Sušnik Bajec, S., Snoj, A., 2020. Neotype designation for Thymallus aeliani Valenciennes, 1848 from a museum topotype specimen and its affiliation with Adriatic grayling on the basis of mitochondrial DNA. ZooKeys, 999, 165–178.
- Brett, J.R., 1956. Some Principles in the Thermal Requirements of Fishes. Q. Rev. Biol. 31, 75–87.
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a metabolic theory of ecology. Ecology 85, 1771–1789. https://doi.org/10.1890/03-9000
- Bruslé, J., Quignard, J.-P., 2001. Biologie des poissons d'eau douce européens. Lavoisier.
- Burkhardt-Holm, P., Peter, A., Segner, H., 2002. Decline of fish catch in Switzerland. 64, 36–54.
- Caissie, D., 2006. The thermal regime of rivers: a review. Freshw. Biol. 51, 1389–1406. https://doi.org/10.1111/j.1365-2427.2006.01597.x
- Calbó, J., 2009. Possible Climate Change Scenarios with Specific Reference to Mediterranean Regions, in: Water Scarcity in the Mediterranean. pp. 1–13. https://doi.org/10.1007/698_2009_28
- Carlson, A.K., Taylor, W.W., Schlee, K.M., Zorn, T.G., Infante, D.M., 2017. Projected impacts of climate change on stream salmonids with implications for resilience-based management. Ecol. Freshw. Fish. 26, 190– 204. https://doi.org/10.1111/eff.12267
- Cattanéo, F., Lamouroux, N., Breil, P., Capra, H., 2002. The influence of hydrological and biotic processes on brown trout (*Salmo trutta*) population dynamics 59, 12–22.
- Cegnar, T., Sušnik, A., Mekinda-Majaron, A., 1996. Climate of Slovenia. Cegnar, T. (eds.). Hydrometeorological Institute of Slovenia, Ljubljana. 70 p.
- Chu, C., Jones, N.E., 2010. Do existing ecological classifications characterize the spatial variability of stream temperatures in the Great Lakes Basin, Ontario? J. Gt. Lakes Res. 36, 633–640. https://doi.org/10.1016/j.jglr.2010.08.006
- Cianfrani, C., Satizábal, H.F., Randin, C., 2015. A spatial modelling framework for assessing climate change impacts on freshwater ecosystems: Response of brown trout (*Salmo trutta* L.) biomass to warming water temperature. Ecol. Model. 313, 1–12. https://doi.org/10.1016/j.ecolmodel.2015.06.023
- Comte, L., Buisson, L., Daufresne, M., Grenouillet, G., 2013. Climate-induced changes in the distribution of freshwater fish: observed and predicted trends. Freshwater Biology. 58, 625-639. https://doi.org/10.1111/fwb.12081
- Comte, L., Grenouillet, G., 2015. Distribution shifts of freshwater fish under a variable climate: comparing climatic, bioclimatic and biotic velocities. Diversity Distrib. 21, 1014-1026. https://doi.org/10.1111/ddi.12346
- Coutant, C.C., 1999. Perspectives on Temperature in the Pacific Northwest's Fresh Waters (No. ORNL/TM-1999/44). Oak Ridge National Lab. (ORNL), Oak Ridge, TN (United States). https://doi.org/10.2172/9042
- Coutant, C.C., 1977. Compilation of Temperature Preference Data. J. Fish. Res. Board Can. 34, 739–745. https://doi.org/10.1139/f77-115
- Crisp, D.T., 1981. A desk study of the relationship between temperature and hatching time for the eggs of five species of salmonid fishes. Freshw. Biol. 11, 361–368. https://doi.org/10.1111/j.1365- 2427.1981.tb01267.x
- Daufresne, M., Boët, P., 2007. Climate change impacts on structure and diversity of fish communities in rivers. Glob. Change Biol. 13, 2467–2478. https://doi.org/10.1111/j.1365-2486.2007.01449.x
- Debes, P.V., Gross, R., Vasemägi, A., 2017. Quantitative Genetic Variation in, and Environmental Effects on, Pathogen Resistance and Temperature-Dependent Disease Severity in a Wild Trout. Am. Nat. 190, 244–265. https://doi.org/10.1086/692536
- DIREKTIVA SVETA 92/43/EGS z dne 21. maja 1992 o ohranjanju naravnih habitatov ter prosto živečih živalskih in rastlinskih vrst
- Draksler, A., Frantar P., Savić V., 2018. Trendi temperatur površinskih in podzemnih voda do leta 2015 v Sloveniji. Temperature trends in surface and groundwaters in Slovenia up to 2015. Ujma. 32, 139-146.
- Dumoutier, Q., Vigier, L., Caudron, A., 2010. Macro Excel d'Aide au Calcul de variables thermiques appliquées aux Milieux Aquatiques Salmonicoles.
- Dunham, J., Chandler, G., Rieman, B., Martin, D., 2005. Measuring stream temperature with digital data loggers: a user's guide (No. RMRS-GTR-150). U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ft. Collins, CO. https://doi.org/10.2737/RMRS-GTR-150
- Dussling, U., Berg, R., Klinger, H., Wolter, C., 2004. Assessing the Ecological Status of River Sytems Using Fish Assemblages. In: Handbuch Angewandte Limnologie: Grundlagen - Gewässerbelastung - Restaurierung - Aquatische Ökotoxikologie - Bewertung – Gewässerschutz. Steinberg, C., Klapper W., Klapper H., Wilken R-D. (eds.). Edition 20. Erg.Lfg. Ecomed: 1-84 p. 10.1002/9783527678488.hbal2004006.
- Eaton, J.G., McCormick, H., Stefan, H.G., Hondzo, M., 1995. Extreme Value Analysis of a Fish/Temperature Field Database. Elsevier Sci., Ecological Engineering 289–305.
- Ebersole, J.L., Liss, W.J., Frissell, C.A., 2001. Relationship between stream temperature, thermal refugia and rainbow trout *Oncorhynchus mykiss* abundance in arid-land streams in the northwestern United States. Ecology of Freshwater Fish. 10, 1–10.
- Ebersole, J.L., Liss, W.J., Frissell, C.A., 2003. Cold water patches in warm streams: physicochemical haracteristics and the influence of shading. Journal of the American Water Resources Association. 39, 355–367.
- EEA, 2009. Regional climate change and adaptation : the Alps facing the challenge of changing water resources (No. 8). European Environment Agency, Copenhagen. 143 p.
- Elliot, J.M., 1981. Some aspects of thermal stress on freshwater teleosts. IIn: Stress and fish. Pickering A.D. (ed.). London, Acafemic Press: 209-245
- Elliott, J.M., 1994. Quantitative Ecology and the Brown Trout. Oxford University Press, USA.
- Elliott, J.M., Elliott, J.A., 2010. Temperature requirements of Atlantic salmon *Salmo salar*, brown trout *Salmo trutta* and Arctic charr *Salvelinus alpinus*: predicting the effects of climate change. J. Fish Biol. 77, 1793–1817. https://doi.org/10.1111/j.1095-8649.2010.02762.x
- Elliott, J.M., Hurley, M.A., 1998a. An individual-based model for predicting the emergence period of sea trout fry in a Lake District stream. J. Fish Biol. 53, 414–433. https://doi.org/10.1111/j.1095- 8649.1998.tb00990.x
- Elliott, J.M., Hurley, M.A., 1998b. Predicting fluctuations in the size of newly emerged sea-trout fry in a Lake District stream. J. Fish Biol. 53, 1120–1133. https://doi.org/10.1111/j.1095-8649.1998.tb00468.x
- FAO (Ed.), 2016. The state of world fisheries and aquaculture, Contributing to food security and nutrition for all. Rome.
- Feist, S.W., Peeler, E.J., Gardiner, R., Smith, E., Longshaw, M., 2002. Proliferative kidney disease and renal myxosporidiosis in juvenile salmonids from rivers in England and Wales. J. Fish Dis. 25, 451–458.
- Fishbase, 2022. https://fishbase.net.br/search.php
- Fumagalli, L., Snoj, A., Jesensek, D., Balloux, F., Jug, T., Duron, O., Brossier, F., Crivelli, A.J., Berrebi, P., 2002. Extreme genetic differentiation among the remnant populations of marble trout (*Salmo marmoratus*) in Slovenia. Molecular Ecology, 11, 2711-2716.
- Gay, M., Okamura, B., de Kinkelin, P., 2001. Evidence that infectious stages of *Tetracapsula bryosalmonae* for rainbow trout *Oncorhynchus mykiss* are present throughout the year. Dis. Aquat. Organ. 46, 31–40. https://doi.org/10.3354/dao046031
- Giller, P.S., Malmqvist, B., 1998. The Biology of Streams and Rivers, Oxford University Press. ed. Oxford.
- Gouraud, V., Baran, P., Bardonnet, A., Beaufrère, C., Capra, H., Caudron, A., Delacoste, M., Lascaux, J.M., Naura, M., Ovidio, M., Poulet, N., Tissot, L., Sabaton, C., Baglinière, J.-L., 2014. Sur quelles connaissances se baser pour évaluer l'état de santé des populations de truite commune (*Salmo trutta*) ? Hydroécologie Appliquée 18, 111–138. https://doi.org/10.1051/hydro/2014001
- Govedič, M., 2018. Kako s(m)o skuhali reko Savo. Ribič, 9, 246-250
- Hari, R.E., Livingstone, D.M., Siber, R., Burkhardt-Holm, P., Güttinger, H., 2006. Consequences of climatic change for water temperature and brown trout populations in Alpine rivers and streams: CLIMATE CHANGE, RIVER TEMPERATURES AND BROWN TROUT. Glob. Change Biol. 12, 10–26. https://doi.org/10.1111/j.1365-2486.2005.001051.x
- Hemmer-Brepson, C., Replumaz, L., Romestaing, C., Voituron, Y., Daufresne, M., 2014. Non-stressful temperature effect on oxidative balance and life history traits in adult fish (Oryzias latipes). J. Exp. Biol. 217, 274–282. https://doi.org/10.1242/jeb.096172
- Hickling, R., Roy, D.B., Hill, J.K., Fox R., Thomas, C.D., 2006. The distributions of a wide range of taxonomic groups are expanding polewards. Global Change Biology. 12, 450–455.
- IPCC, 2021: Summary for Policymakers. In: Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Masson-Delmotte, V., P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J.B.R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu and B. Zhou (eds.)]. Cambridge University Press. 3949 p.
- Janža, M., 2013. Impact assessment of projected climate change on the hydrological regime in the SE Alps, Upper Soča River basin, Slovenia. Nat Hazards. 67, 1025–1043. (https://doi.org/10.1007/s11069-011- 9892-7)
- Johnson, S.L., 2004. Factors influencing stream temperatures in small streams: substrate effects and a shading experiment. Can. J. Fish. Aquat. Sci. 61, 913–923. https://doi.org/10.1139/f04-040
- Keith, P., Poulet, N., Denys, G., Changeux, T., Feunteun, E., Persat, H., 2020. Les Poissons d'eau douce de France - 2ème édition - Biotope éditions, Biotope Editions-Muséum National d'Histoire Naturelle. ed.
- Killen, S.S., Brown, J.A., Gamperl, A.K., 2008. Lack of metabolic thermal compensation during the early life stages of ocean pout Zoarces americanus (Bloch & Schneider): a benthic, cold-water marine species. Journal of Fish Biology, 72: 763-772. https://doi.org/10.1111/j.1095-8649.2007.01735.x
- Knez, M., Kranjc, A., 2009. Karst. In: Pleničar M, Ogorelec B, Novak M (eds). The geology of Slovenia. Geološki zavod Slovenije, Ljubljana: 563–574
- Kolbezen, M., Pristov, J., 1998. Površinski vodotoki in vodna bilanca Slovenije = Surface streams and water balance of Slovenia. Ljubljana, Ministrstvo za okolje in proctor, Hidrometeorološki zavod Republike Slovenije. 98 p.
- Kobolt, M., Ulaga, F., 2012. Hidrološko stanje voda in podnebna spremenljivost. In OKOLJE, v katerem živimo. Cegnar T. (ed). Ljubljana, Ministrstvo za kmetijstvo in okolje, Agencija Republike Slovenije za okolje. 61-71. ISBN 978-961-6024-59-4
- Kottelat, M., Freyhof, J., 2007. Handbook of European Freshwater Fishes, Kottelat, Cornol, Switzerland and Freyhof. ed. Berlin, Germany.
- Lyons, J., Stewart, J.S., Mitro, M., 2010. Predicted effects of climate warming on the distribution of 50 stream fishes in Wisconsin, U.S.A. J. Fish Biol. 77, 1867–1898. https://doi.org/10.1111/j.1095- 8649.2010.02763.x
- Magnuson, J., Crowder, L., Medvick, P., 1979. Temperature as an Ecological Resource. Integr. Comp. Biol. 19, 331–343. https://doi.org/10.1093/icb/19.1.331
- Maheu, A., 2015. Développement d'outils de caractérisation et de modélisation du régime thermique des rivières naturelles et régulées. Université du Québec.
- Maheu, A., Poff, N.L., St-Hilaire, A., 2016. A Classification of Stream Water Temperature Regimes in the Conterminous USA: Classification of Stream Temperature Regimes. River Res. Appl. 32, 896–906. https://doi.org/10.1002/rra.2906
- Maire, A., 2021. Synthèse du programme de recherche Thermie-Hydrobiologie 2016-2020. EDF R&D.
- Marcos-López, M., Gale, P., Oidtmann, B.C., Peeler, E.J., 2010. Assessing the Impact of Climate Change on Disease Emergence in Freshwater Fish in the United Kingdom: Climate Change and Disease Emergence in Freshwater Fish. Transbound. Emerg. Dis. 57, 293–304. https://doi.org/10.1111/j.1865- 1682.2010.01150.x
- Markovic, D., Scharfenberger, U., Schmutz, S., Pletterbauer, F., Wolter, C., 2013. Variability and alterations of water temperatures across the Elbe and Danube River Basins. Clim. Change 119, 375–389. https://doi.org/10.1007/s10584-013-0725-4
- McCarthy, I.D., Houlihan, D.F., 1997. The effect of temperature on protein metabolism in fish: the possible consequences for wild Atlantic salmon (*Salmo salar* L.) stocks in Europe as a result of global warming. In: Wood CM, McDonald DG (eds.). Global warming: implications for freshwater and marine fish. Cambridge University Press, Cambridge. 51–78
- McCullough, D.A., Bartholow, J.M., Jager, H.I., Beschta, R.L., Cheslak, E.F., Deas, M.L., Ebersole, J.L., Foott, J.S. , Johnson, S.L., Marine, K.R., Mesa, M.G., Petersen, J.H., Souchon, Y., Tiffan, K.F., Wurtsbaugh, W.A., 2009. Research in Thermal Biology: Burning Questions for Coldwater Stream Fishes, Reviews in Fisheries Science. 17,1, 90-115. DOI: 10.1080/10641260802590152
- Meynard, M., Testi, B., Veslot, J., Carrel, G., 2012. Facteurs hydroclimatiques et taille des poissons juvéniles Etude thermique du Rhône Phase IV 86.
- Miller, N.A., Stillman, J.H., 2012. Physiological Optima and Critical Limits. Nat. Educ. Knowl. 3, 10.
- Mohseni, O., Stefan, H.G., 2001. Water budgets of two watersheds in different climatic zones under projected climate warming. Climate Change. 49, 77–104.
- Mohseni, O., Stefan, H.G., Eaton, J.G., 2003. Global warming and potential changes in fish habitat in U.S. streams. Climatic Change. 59, 389–409.
- Neuheimer, A., Taggart, C., 2007. The growing degree-day and fish size-at-age: The overlooked metric. Can. J. Fish. Aquat. Sci. 64, 375–385. https://doi.org/10.1139/F07-003
- Nunn, A.D., Harvey, J.P., Cowx, I.G., 2007. Variations in the spawning periodicity of eight fish species in three English lowland rivers over a 6 year period, inferred from 0+year fish length distributions. J. FISH Biol. 70. https://doi.org/10.1111/j.1095-8649.2007.01415.x
- Ocvirk, J., 1994. Vzreja in program repopulacije soške postrvi (*Salmo marmoratus* Cuvier, 1817) v Sloveniji (English: Artificial propagation and reintroduction of Mable trout (*Salmo marmoratus* Cuvier, 1817) in Slovenia (Thesis). Univerza v Ljubljani, Veterinarska fakulteta: 199 p.
- Ogrin, D., 1998. Podnebje. In: Fridl, J., Kladnik, D., Orožen Adamič M., Perko, D. (eds.). Geografski atlas Slovenije, Država v prostoru in času. DZS, Ljubljana: 110–111 p.
- Orr, H.G., Simpson, G.L., des Clers, S., Watts, G., Hughes, M., Hannaford, J., Dunbar, M.J., Laizé, C.L.R., Wilby, R.L., Battarbee, R.W., Evans, R., 2015. Detecting changing river temperatures in England and Wales. Hydrol. Process. 29, 752–766. https://doi.org/10.1002/hyp.10181
- Ovidio, M., 1999. Cycle annuel d'activité de la truite commune (*Salmo trutta* L.) adulte : Étude par radio-pistage dans un cours d'eau de l'Ardenne belge. Bull. Fr. Pêche Piscic. 1–18. https://doi.org/10.1051/kmae:1999017
- Pletterbauer, F., Melcher, A., Graf, W., 2018. Climate Change Impacts in Riverine Ecosystems. In: Schmutz S., Sendzimir J. (eds). Riverine Ecosystem Management. Aquatic Ecology Series, 8, 203-232. https://doi.org/10.1007/978-3-319-73250-3_11
- Pörtner, H.O., Knust, R., 2007. Climate change affects marine fishes through the oxygen limitation of thermal tolerance. Science, 315, 95–97.
- Povz M., 1989. Distribution and biometric Characteristics of the Marble Trout (*Salmo marmoratus* Cuvier 1817) in Slovenia. Ichthyos, 8, 1-6: 29-36
- Povz, M., Jesensek, D., Berrebi, P., Crivelli, A.J., 1996. The Marble Trout *Salmo trutta marmoratus*, Cuvier 1817 In the Soca River basin, Slovenia. Publications de la Tour du Valat. 65 p.
- Pravilnik o ribolovnem režimu v ribolovnih vodah (Uradni list RS, št. 99/07 in 75/10)

Pravilnik o uvrstitvi ogroženih rastlinskih in živalskih vrst v rdeči seznam (Uradni list RS, št. 82/02 in 42/10)

Rahel, F.J., Olden, J.D., 2008. Assessing the effects of climate change on aquatic invasive species. Conserv Biol. 22, 3, 521-33. doi: 10.1111/j.1523-1739.2008.00950.x. PMID: 18577081.

- RIBKAT Ribiški kataster, 2022: Baza podatkov o sladkovodnem ribištvu (https://www.zzrs.si/page/ribiskikataster/)
- Riehl, R., Baensch H. A., 1991. Aquarien Atlas. Band. 1. Melle: Mergus, Verlag für Natur-und Heimtierkunde, Germany : 992 p.
- Rojšek, D., 1991. Naravne znamenitosti Posočja. Ljubljana, Državna založba Slovenije. 206 p.
- Simčič, T., Jesenšek, D., Brancelj, A., 2015. Effects of increased temperature on metabolic activity and oxidative stress in the first life stages of marble trout (*Salmo marmoratus*). Fish Physiol Biochem. 41, 1005-1014. DOI 10.1007/s10695-015-0065-6
- Simčič, T., Jesenšek, D., Brancelj, A., 2017. Metabolic characteristics of early life history stages of native marble trout (*Salmo marmoratus*) and introduced brown trout (*Salmo trutta*) and their hybrids in the Soča River. Ecol Freshw Fish. 26, 141-149. https://doi.org/10.1111/eff.12264
- Specchi, M., Battistella, S., Amirante, G.A., Sigalotti, G.M., Tibaldi, E., Pizzul, E., 2004. Il ricupero della trota marmorata nel Friuli Venezia Giulia. Sintesi di 10 anni di studi e ricerche. Ente Tutela Pesca del Friuli Venezia Giulia. Manzano, Grafiche Manzanesi. 57 p.
- Stankovic, D., Crivelli A.J., Snoj A., 2015. Rainbow trout in Europe: Introduction, Naturalization, and Impacts. Reviews in Fisheries Science & Aquaculture, 23, 39-71.
- Sudhagar, A., Kumar, G., El-Matbouli, M., 2020. The Malacosporean Myxozoan Parasite *Tetracapsuloides bryosalmonae*: A Threat to Wild Salmonids. Pathogens 9, 16. https://doi.org/10.3390/pathogens9010016
- Sutton, R.J., Deas, M.L., Tanaka, S.K., Soto, T., Corum, R.A., 2007. Salmonid observations at a Klamath River thermal refuge under various hydrological and meteorological conditions. River Res. Applic. 23, 7, 775- 785. https://doi.org/10.1002/rra.1026
- Tasker, G.D., Burns, A.W., 1974. Mathematical Generalization of Stream Temperature in Central New England1. JAWRA J. Am. Water Resour. Assoc. 10, 1133–1142. https://doi.org/10.1111/j.1752- 1688.1974.tb00633.x
- Tibaldi, S., Cacciamani, C., Pecora, S., 2010. Il Po nel clima che cambia. Biol. Ambient. Biologia Ambientale, 24 (1): 21-28, 2010. Atti XVIII congresso S.It.E., Parma 1-3 settembre 2008, 21–28.
- Torgersen, C.E., Faux, R.N., McIntosh, B.A., Poage, N.J., Norton, D.J., 2001. Airborne thermal remote sensing for water temperature assessment in rivers and streams. Remote Sens. Environ. 76, 386–398. https://doi.org/10.1016/S0034-4257(01)00186-9
- Uredba o posebnih varstvenih območjih (območjih Natura 2000) (Uradni list RS, št. 49/04, 110/04, 59/07, 43/08, 8/12, 33/13, 35/13 – popr., 39/13 – odl. US, 3/14, 21/16 in 47/18)
- Uredba o zavarovanih prosto živečih živalskih vrstah (Uradni list RS, št. 46/04, 109/04, 84/05, 115/07, 32/08 odl. US, 96/08, 36/09, 102/11, 15/14, 64/16 in 62/19)
- van Vliet, M.T.H., Ludwig, F., Zwolsman, J.J.G., Weedon, G.P., Kabat, P., 2011. Global river temperatures and sensitivity to atmospheric warming and changes in river flow. Water Resour. Res. 47. https://doi.org/10.1029/2010WR009198
- Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., Cushing, C.E., 1980. The River Continuum Concept. Can. J. Fish. Aquat. Sci. 37, 130–137. https://doi.org/10.1139/f80-017
- Verneaux, J., 1977. Biotypologie de l'écosystème "eau courante". Déterminisme approché de la structure biotypologique. Comptes Rendus L'Académie Sci. Paris 77–79.
- Vertačnik, G., Bertalanič, R., Draksler, A., Dolinar M., Vlahović, Ž., Frantar, P., 2018. Podnebna spremenljivost Slovenije v obdobju 1961–2011: Povzetek. Ministrstvo za okolje in prostor, Agencija Republike Slovenije za okolje, Ljubljana. 23p.
- Vigier, L., Caudron, A., 2007. ETUDE DE LA QUALITE THERMIQUE DU FORON DE GAILLARD -Etude de l'impact du lac de Machilly- 21.
- Vignes, J.C., Heland, M., 1995. Comportement alimentaire au cours du changement d'habitat lié à l'émergence chez le saumon atlantique *Salmo salar* L. et la truite commune *Salmo trutta* L., en conditions seminaturelles. Bull. Fr. Pêche Piscic. 207–214. https://doi.org/10.1051/kmae:1995023
- Vincenzi, S., Crivelli A.J., Jesensek D., Campbell E., Garza, J.C., 2019. Effects of species invasion on population dynamics, vital rates and life histories of the native species. Population Ecology. 61, 25-34.
- Vincenzi, S., Jesensek D., Crivelli, A.J., 2018. A framework for estimating the determinants of spatial and temporal variation in vital rates and inferring the occurrence of unobserved extreme events. Royal Society Open Science. 5, 171087. doi.org/10.1098/rsos.171087.
- Vincenzi, S., Mangel, M., Jesensek, D., Garza, J.C., Crivelli, A.J., 2016. Within and among-population variation in vital rates and population dynamics in a variable environment. Ecological Applications. 26, 2086-2102.
- Vincenzi, S., Crivelli, A.J., Jesensek, D., De Leo, G.A., 2008. Total population density during the first year of life as a major determinant of lifetime body-length trajectory in marble trout. Ecol Freshw Fish. 17, 515–519
- Vörösmarty, C. J., Green, P., Salisbury, J., Jammers, R.B., 2000. Global water resources: vulnerability from climate change and population growth. Science. 289, 284–288.
- Wahli, T., Knuesel, R., Bernet, D., Segner, H., Pugovkin, D., Burkhardt-Holm, P., Escher, M., Schmidt-Posthaus, H., 2002. Proliferative Kidney Disease in Switzerland. J. Fish Dis. 25, 491–500. https://doi.org/10.1046/j.1365-2761.2002.00401.x
- Webb, B.W., 1996. Trends in stream and river temperature. Hydrol. Process. 10, 205–226. https://doi.org/10.1002/(SICI)1099-1085(199602)10:2<205::AID-HYP358>3.0.CO;2-1
- Webb, B.W., Hannah, D.M., Moore, R.D., Brown, L.E., Nobilis, F., 2008. Recent advances in stream and river temperature research. Hydrol. Process. 22, 902–918. https://doi.org/10.1002/hyp.6994
- Webb, B.W., Nobilis, F., 2007. Long-term changes in river temperature and the influence of climatic and hydrological factors. Hydrol. Sci. J. 52, 74–85. https://doi.org/10.1623/hysj.52.1.74
- Wenger, S.J., Isaak, D.J., Luce, C.H., Neville, H.M., Fausch, K.D., Dunham, J.B., Dauwalter, D.C., Young, M.K., Elsner, M.M., Rieman, B.E., Hamlet, A.F., Williams, J.E., 2011. Flow regime, temperature, and biotic interactions drive differential declines of trout species under climate change. Proc. Natl. Acad. Sci. 108, 14175–14180. https://doi.org/10.1073/pnas.1103097108
- Woodward G., Perkins, D. M., Brown Lee, E., 2010. Climate change and freshwater ecosystems: impacts across multiple levels of organization. Phil. Trans. R. Soc. B, 365, 2093–2106.
- Wolter, C., 2007. Temperature influence on the fish assemblage structure in a large lowland river, the lower Oder River, Germany. Ecol. Freshw. Fish 16, 493–503. https://doi.org/10.1111/j.1600- 0633.2007.00237.x
- Zupančič, B., 1998. Podnebje. In: Fridl, J., Kladnik, D., Orožen Adamič, M., Perko, D. (eds). Geografski atlas Slovenije, Država v prostoru in času. DZS, Ljubljana:. 98-99
- Zwieniecki, M.A., Newton, M., 1999. Influence of Streamside Cover and Stream Features on Temperature Trends in Forested Streams of Western Oregon. West. J. Appl. For. 14, 106–113. https://doi.org/10.1093/wjaf/14.2.106

Appendices

Appendix 1. Fish fauna in the selected sectors in the Upper Soča River basin with national and international conservation status according to the applicable regulations (summarized after RIBKAT, 2022; BIOSWEB, 2022; Dussling et al., 2004).

*Data missing - summarized after the most similar species: S. marmoratus after S. trutta; T. aeliani after T. thymallus; B. plebejus after B. balcanicus, when missing both after B. barbus except the migration distance; S. *muticellus* after *T. souffia; P. lumaireul* after *P. phoxinus.*

** In the Annex 1 and Annex 2 of the Decree on protected wild animal species is listed also Italian riffle dace.

*** Rules on fishing regime (Article 16, paragraph 2): The minimum fishing measures and conservation periods do not apply to alien fish species, if they are defined as invasive species in the fisheries management plans and in it (unofficial translation).

****Angling associations may implement more restricted rules on fishing regimes which can also change between seasons.

Legend

Decree = Decree on protected wild animal species (Uradni list RS, št. 46/04, 109/04, 84/05, 115/07, 32/08 - odl. US, 96/08, 36/09, 102/11, 15/14, 64/16 in 62/19)

Annex 1A (Z) Autochthonous species which are protected with the conservation regime for specimens and populations (unofficial translation).

Habitat directive = COUNCIL DIRECTIVE 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora (Habitat Directive of the European Commission)

Red list of Slovenia = Rules on the inclusion of endangered plant and animal species in the Red List (Uradni list RS, št. 82/02 in 42/10)

Decree on special protection areas (Natura 2000 areas) (Uradni list RS, št. 49/04, 110/04, 59/07, 43/08, 8/12, 33/13, 35/13 – popr., 39/13 – odl. US, 3/14, 21/16 in 47/18)

Rules on fishing regime (Uradni list RS, št. 99/07 in 75/10) for the Adriatic River basin.

Habitat guild (summarized after Dussling et al., 2004)

Reproductive guilds (summarized after Dussling et al., 2004)

Migration-distance guilds (summarized after Dussling et al., 2004)

Appendix 2 : Comparison of water temperatures between the first years of monitoring (former period) and the most recent years (recent period) per site. Since the monitoring timing varies between sites, periods may differ depending on the site.

