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THERMAL REGIME OF MOUNTAIN STREAMS: DRIVERS AND ECOLOGICAL EFFECTS ON THE AQUATIC BIOTA

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Les montagnes partagent les eaux
et unissent les hommes

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Abstract

Temperature has been recognized as a pivotal factor shaping ecosystem structure and functioning; nevertheless, there is still a lack of systematic water temperature monitoring in rivers. Most of the data are scattered and have been measured sporadically providing rough estimations of the water thermal regime, especially in mountain streams where fluctuations are not negligible. Moreover, field studies investigating the relationship between water temperature and the aquatic biota rarely address the role of intra annual variability and not always disentangle the effects of other environmental factors. Given these gaps, this thesis presents six pieces of work regarding the water thermal regime and its effect on the aquatic biota.

First, since the thermal regime varies depending on the type of watercourse, the water temperature of 16 mid-altitude stream sites was monitored, and the daily and seasonal patterns were described. The results show that the interaction of different water sources and the presence of reservoirs promote a high stream thermal heterogeneity within the watershed, outlining important ecological implications. Then, hydroelectric plants powered by flowing water can affect the water thermal regime, but their impacts have not yet been considered, despite their widespread distribution. Thus, the water temperature was monitored along a sequence of riverine stretches subjected to water diversion. The analysis of the thermal regimes revealed that within the by-passed stretches, due to the low flow, the rate of warming doubles the natural gradient while in the diverted channel the water temperature remains almost constant. Overall, a cascade system of run of river plants shifts the longitudinal riverine thermal profile from continuous to "stepped".

In the following studies, the relationship between the water thermal regime and the aquatic biota was investigated by combining a systematic literature review focusing on the effects of water temperature on freshwater macroinvertebrates with three field studies carried out on biofilm, macroinvertebrates, and fish, respectively. A one-year survey with monthly samplings of biofilm and macrobenthos across streams with different annual thermal variability allowed to examine the spatiotemporal patterns of the communities, disentangling the effect of the water thermal regime from other environmental variables. The results showed that water temperature promotes a change in the dominance of periphyton groups and macroinvertebrate taxa through the year. The annual thermal variability induces a phenological desynchronization among the populations of some macroinvertebrate taxa inhabiting the different streams. Lastly, since climate change is one of the first threats to mountain lotic systems, the *Salmo trutta* habitat suitability of a regulated river was assessed under different climatic scenarios and a deterioration was pointed out especially driven by the temperature increase.

Overall, this thesis contributed to the field of thermal research, with a particular focus on mid-altitude mountain streams, filling gaps in the characterization of the water thermal regime, its drivers, and the effects on aquatic taxa and communities.

Keywords

Water temperature, reservoirs, hydropower plants, biofilm, macroinvertebrates, fish, bioassessment, climate change

Riassunto

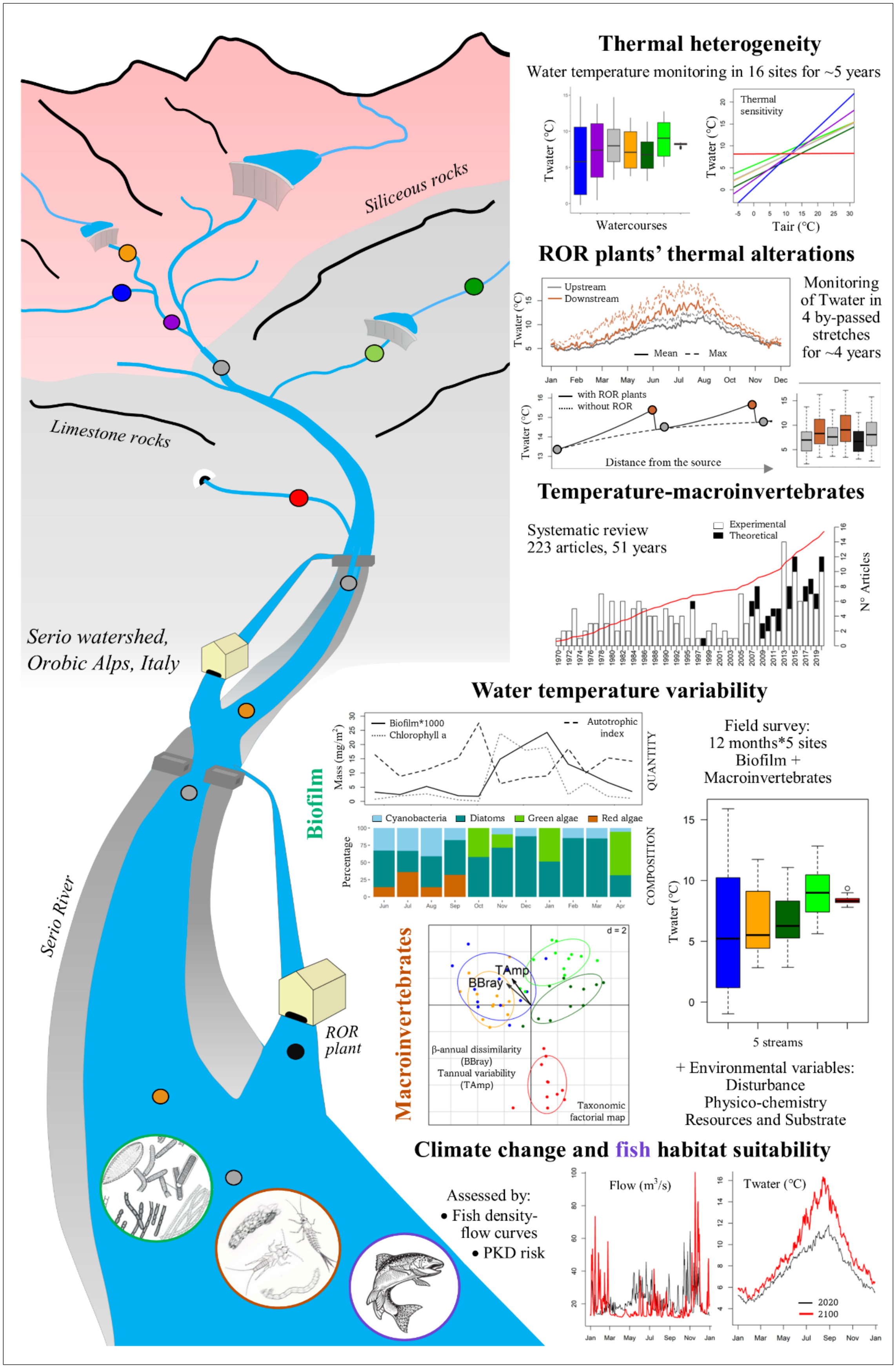
La temperatura è un fattore cruciale che influenza la struttura e il funzionamento degli ecosistemi; tuttavia, manca ancora un monitoraggio sistematico di tale parametro nei fiumi. La maggior parte dei dati riguarda misure sporadiche e sparse che forniscono stime approssimative del regime termico dell'acqua, soprattutto in montagna dove le fluttuazioni non sono trascurabili. Inoltre, gli studi in campo che indagano la relazione tra la temperatura e il biota acquatico raramente affrontano il ruolo della variabilità intra-annuale e non sempre disgiungono gli effetti di altri fattori ambientali. Date queste lacune, questa tesi presenta sei lavori riguardanti il regime termico dell'acqua e il suo effetto sul biota.

Innanzitutto, dato che il regime termico varia a seconda del tipo di corpo idrico, è stata monitorata la temperatura dell'acqua in 16 siti situati in torrenti montani e sono state descritte le variazioni giornaliere e stagionali. I risultati mostrano che diversi tipi di sorgente e la presenza di bacini idrici, insieme, promuovono un'elevata eterogeneità termica tra i corsi d'acqua appartenenti allo stesso bacino idrografico, con importanti implicazioni ecologiche. Inoltre, gli impianti idroelettrici ad acqua fluente possono influenzare il regime termico fluviale, ma il loro impatto non è stato ancora considerato, nonostante essi siano molto diffusi. Dunque, è stata monitorata la temperatura dell'acqua lungo una sequenza di tratti fluviali interessati da derivazioni idroelettriche. L'analisi del regime termico ha rivelato che nei tratti derivati il tasso di riscaldamento è doppio rispetto a quello naturale mentre nei canali di derivazione la temperatura dell'acqua rimane pressoché costante. La presenza di centrali idroelettriche in sequenza determina un cambiamento del profilo termico longitudinale del fiume che passa da continuo a "gradini".

Negli studi successivi è stata indagata la relazione tra il regime termico e il biota acquatico combinando una ricerca sistematica della letteratura riguardante gli effetti della temperatura sui macroinvertebrati d'acqua dolce con tre studi in campo condotti rispettivamente su biofilm, macroinvertebrati e pesci. Un'indagine di un anno con campionamenti mensili di benthos in corsi d'acqua con diversa variabilità termica annuale ha permesso di esaminare i pattern spazio-temporali delle comunità, disgiungendo l'effetto del regime termico fluviale da quelli di altri fattori ambientali. I risultati mostrano che la temperatura dell'acqua influisce sulla dominanza dei gruppi di perifiton e dei macroinvertebrati e sulla loro dinamica nell'arco dell'anno. Inoltre, la variabilità termica induce una desincronizzazione fenologica tra le popolazioni di alcuni taxa che vivono nei diversi corsi d'acqua. Poiché il cambiamento climatico è una delle prime minacce per i sistemi lotici montani, è stata infine valutata l'idoneità dell'habitat della trota fario in un fiume regolato, in diversi scenari climatici, evidenziando un deterioramento dovuto soprattutto all'aumento della temperatura. Complessivamente, la presente tesi ha contribuito al campo della ricerca termica, con particolare attenzione ai torrenti di media montagna, colmando lacune riguardanti la caratterizzazione del regime termico fluviale, i fattori che lo influenzano e gli effetti sugli organismi e sulle comunità acquatiche.

Parole chiave

Temperatura dell’acqua, invasi, centrali idroelettriche, alghe, macroinvertebrati, pesci, cambiamento climatico.


Thermal heterogeneity
Water temperature monitoring in 16 sites for ~5 years
Twater (°C)
Watercourses
Thermal sensitivity
Twater (°C)
Tair (°C)
ROR plants' thermal alterations
Upstream
Downstream
Mean
Max
Twater (°C)
Jan Feb Mar May Jun Jul Aug Oct Nov Dec
Monitoring of Twater in 4 by-passed stretches for ~4 years
with ROR plants
without ROR
Twater (°C)
Distance from the source
Temperature-macroinvertebrates
Systematic review
223 articles, 51 years
Experimental
Theoretical
N° Articles
Water temperature variability
Biofilm
Biofilm*1000
Chlorophyll a
Autotrophic index
Mass (mg/m²)
QUANTITY
Cyanobacteria
Diatoms
Green algae
Red algae
Percentage
COMPOSITION
Jun Jul Aug Sep Oct Nov Dec Jan Feb Mar Apr
Field survey:
12 months*5 sites
Biofilm +
Macroinvertebrates
Twater (°C)
5 streams
Macroinvertebrates
d = 2
TAmp
BBray
β-annual dissimilarity (BBray)
Tannual variability (TAmp)
Taxonomic factorial map
+ Environmental variables:
Disturbance
Physico-chemistry
Resources and Substrate
Climate change and fish habitat suitability
Assessed by:
• Fish density-flow curves
• PKD risk
Flow (m³/s)
Twater (°C)
2020
2100
Jan Mar May Jul Sep Nov Jan
Siliceous rocks
Limestone rocks
Serio watershed, Orobic Alps, Italy
Serio River
ROR plant

INTRODUCTION

INTRODUCTION

1. Energy, temperature, and biodiversity

1.1 Energy-species distribution

One of the main research goals of Ecology is to understand the patterns of biodiversity (the variety and abundance of species) and the processes and mechanisms involved. Naturalists have been particularly fascinated by the gradient of increasing biodiversity from the poles to the equator and from high to low altitudes (Darwin, 1959; Humboldt, 1808; Wallace, 1976). Latitudinal and elevation gradients regard terrestrial and aquatic organisms, both plant and animals, suggesting the existence of some general mechanisms controlling species diversity related to climatic conditions that reflect the energy availability in the environment. Moreover, the latitudinal gradient is valid for marine organisms too. First discussions about the effect of energy on the ecosystems go back to Hutchinson & MacArthur (1959); Lindeman (1942) and Odum (1962) that argued that the energy flow controls the partitioning of biomass along the food web, affecting the trophic structure of the ecosystems. Wright (1983) extended at larger scale the idea that the diversity of a trophic level is determined by the amount of energy from the level below and proposed that "the latitudinal biodiversity gradient has somehow been generated and maintained as a direct consequence of greater energy availability towards the equator" (*species-energy hypothesis*).

The overall energy of the ecosystems encompasses the radiation energy, the chemical energy, and the thermal energy. Radiation energy (and specifically photosynthetically active radiation, PAR) is used by plants to synthetize biomass by the photosynthesis. Such process requires water that, besides providing the electrons for the reaction, allows the absorption of nutrients. Therefore, water availability, more than light, limits the primary production and explains the global distribution of plants (Hawkins et al., 2003; Huang et al., 2021) as they use only a small fraction of the incident PAR (~1%) (Opik & Rolfe, 2005). Then, plant tissues feed herbivores and other heterotrophic organisms in the food web. These organisms, together with the autotrophic ones, constitute the chemical energy of the ecosystems. Higher productivity (the rate of biomass generation) corresponds to more individuals (*productivity hypothesis*, Wright (1983)) and more individuals lead to more species (*the more-individual hypothesis*, Srivastava & Lawton (1998)). In fact, a greater diversity of plants allows for the evolution of a wider range of specialist herbivores thanks to the increase of habitats availability (Hutchinson & MacArthur, 1959; Pielou, 1975), which, in turn, promote a wider range of consumers (predators, parasites and pathogens) (Gaston, 1996). In sum, radiation and chemical energies together affect the species diversity, increasing biomass and abundance through population dynamics and speciation processes (Evans et al., 2005).

The third form of energy of the ecosystem is the thermal one, quantified by the temperature. It cannot be used by organisms but influences the biodiversity in two main ways. First, temperature sets the limits to maximum diversity either as absolute value and as seasonal variability: organisms living at low and high temperatures and/or in high thermal variability environments need physiological adaptation strategies and have high energetic cost (*ambient energy hypothesis*, Turner (2004)). Thus, organisms have diversified over time within these limits till saturating the habitats (Clarke & Gaston, 2006). Second, temperature can affect diversity by influencing the rate at which organisms make use of radiative and chemical energy. Indeed, temperature controls the conversion of radiation into biomass (photosynthesis) and the transfer rate of energy along the food web. Temperature may affect biodiversity also by other ways, for instance affecting the rate of population speciation and extinction (*metabolic theory of biodiversity*, Allen et al., (2002) and Stegen et al., (2009)) but evidences for that are equivocal (Clarke, 2017).

Originally formulated to explain biodiversity pattern in terrestrial systems the species-energy theories have been extended to seas (Fraser & Currie, 1996; Rex et al., 2005).

The overall amount of energy in the ecosystems affects biodiversity. However, it is important to distinguish among the different forms of energy, as they act on plants and animals by very different processes as described above. Variables as temperature and light (PAR) and, for terrestrial ecosystems, water availability (precipitation) too, can be considered as proxies of the amount of the different forms of energy. Such climatic axes allow to describe the global patterns of biodiversity (Currie, 1991; Hawkins et al., 2003) and to distinguish the mechanisms by which energy influences diversity. Especially at large scale, temperature has often been used as a proxy of energy to describe biodiversity, but loosely, as it refers only to the thermal energy.

Characterizing biodiversity patterns in freshwater ecosystems is more challenging than in terrestrial ones as they constitute a small area of the Earth’s surface (0.8%) and are scattered across the planet. This is especially true in rivers, because of the dendritic nature of hydrographic networks. However, studies carried out at a global scale showed that freshwater species diversity typically decreases with increasing latitude (Gaston & Blackburn, 2000; Oberdoff et al., 1995; Rosenzweig, 2010) and altitude (Dodds et al., 2019; Vinson & Hawkins, 2003) following the gradient observed for terrestrial diversity. Indeed, lentic (lakes, ponds, and wetlands) and lotic (rivers, streams, and springs) waterbodies are open heterotrophic systems, connected and sustained by the terrestrial ones. Thus, environmental gradients on lands reflects also in waters, influencing for instance flow, water temperature, and resource availability. At the global scale freshwater biodiversity distribution is driven by the history (evolution and dispersal) and the climate (temperature and precipitation) while at smaller scales (from regional to microhabitat) aquatic biodiversity is determined by environmental variables (such as hydrological and thermal regimes, resources, hydrochemistry, morphology, and hydraulics) and biological mechanisms (species interactions and dispersal dynamics) acting as filters of species distribution (*landscapes filters hypothesis*, Poff, 1997; Tonn, 1990). The structure and the functioning of aquatic assemblages at each level depend on the species traits that allow to overcome the challenges presented by such filters. Water temperature constitutes an important environmental filter that contributes to set aquatic assemblages mostly at the valley/reach (waterbody) scale.

1.2 Temperature and biodiversity

The relationship between temperature and biodiversity in plants and animals (ectotherms and endotherms) is controlled by two independent factors: the mean temperature and/or its variability. Regarding the first, it is recognized that in cold (as polar regions or high altitudes) and warm (as deserts or hot springs) environments, specific physiological challenges set by extreme temperatures could be achieved only by certain organisms (Box 1). Moreover, such temperatures limit the primary production controlling nutrient availability and transpiration and thereby constrain the overall diversity (that depends on the total abundance/biomass as described by the *more-individuals hypothesis*). On the other hand, strong thermal variability limits biodiversity because it requires more generalist physiology that is more energetically expensive than a specialist physiology (Stevens, 1989). Thus, the low diversity at high latitudes and altitudes might mainly be driven by the large thermal variability (up to 60-90 °C and 15-25 °C for terrestrial and aquatic environments respectively) rather than by the low mean temperature (up to –(30-60) °C and ~0 °C for terrestrial and aquatic environments respectively). Nonetheless, the mechanisms underpinning the reduction of diversity in these habitats are not clear yet and the discussion is still opened (Clarke, 2014). The two factors (mean temperature and thermal variability) could act in parallel and synergistically or antagonistically so much that the critical factor could be the interaction between mean temperature and thermal variability (Estay et al., 2014; Gaston, 1999).

Ectotherms: animals for which habitat temperatures determine body temperatures. Ectotherms may have a variable body temperature or may maintain it stable by moving from one site to another. They are unable to produce and conserve adequate metabolic heat to maintain a body temperature above the external temperature. Antonym of **endotherms** (mammals and birds).

Freshwater ecology has largely investigated the relationship between water temperature and aquatic communities. To investigate biodiversity patterns along a gradient of temperature several surveys have been conducted in rivers, from mouth to source, and especially in geothermal and mountain streams. Such studies highlighted peaks of species richness around 20-30 °C for invertebrates, macrophytes, and microalgae (Brock, 1978; Jacobsen et al., 1997; Quenta-Herrera et al., 2021) and around 20-25 °C for fish (Griffiths et al., 2014; Oberdorff et al., 2011). At low temperatures (below ~10-15 °C) the aquatic invertebrate fauna is dominated by insects while at high temperatures (above ~25 °C) by crustaceans, nematodes, molluscs, and chironomids. Fish assemblages-temperature pattern strongly varies across biogeographical regions; however, salmonids dominated in cold waters (at least in the Northern hemisphere) (Griffiths et al., 2014; Oberdorff et al., 2011). Similarly, algae community composition is highly variable depending on biogeography and local environmental factors (Alahuhta et al., 2020; Morgan, 2016); anyway, in cold waters of mountain and glacier streams algae assemblages are dominated by diatoms and diatoms/cyanobacteria respectively (Hieber et al., 2001; Peszek et al., 2022; Rott et al., 2006; Tang et al., 1997).

The first research attempting to understand the effect of a temperature increase on aquatic biota dated back to the ’70s when scientists affiliated with the *Savannah River Ecology Laboratory* (Georgia, USA), led by Eugene Odum, started to investigate the effect of heated waters coming from nuclear and fossil-fuels power plants on river organisms (Smith et al., 2001). Thus, *Savannah River Ecology Laboratory* greatly contributed to the development of aquatic thermal ecology with numerous field studies focusing on the population dynamic of fish, turtles, invertebrates, and plants in thermally altered waterbodies (Elliott et al., 1975; Gibbons & Sharitz, 1974; Gibbonson & Sharitz, 1981). On the other hand, studies investigating aquatic communities facing cold conditions appeared later, in the ’90s, when researchers started to explore invertebrate assemblages of arctic and alpine glacier streams (Brittain & Milner, 2001; Castella et al., 2001; Milner & Petts, 1994; Milner et al., 2001; Petts & Bickerton, 1994).

Despite the remarkable advances in the temperature-biota relationship most of the studies carried out in freshwater systems focused on the effect of mean temperature while thermal variability responses have not been well addressed so far.

Box 1

1.1 Temperature constrains organism physiology

Temperature sets the limits (upper and lower) of life on Earth constraining the physiological processes of organisms. Increasing temperature corresponds to a greater molecular motion that, in turn, leads to the thermal denaturation of the macromolecules (especially proteins) and the disruption of the cellular structure. Some adaptations as the increase of weak interactions (i.e Van der Walls interactions) contribute to maintain the structural integrity. Nevertheless, it was found that Eukarya complete their life cycles at most at 45-60 °C while some Bacteria and Archaea can live above 100 °C thanks to their cellular membrane architecture (Clarke, 2014). On the other hand, lower thermal limits seem to be set by the freezing point (~0, -2 °C for fresh and salt water respectively). In fact, the life cycle of most terrestrial, freshwater, and marine ectotherms and plants occurs above that point. Some terrestrial species can survive also in colder environments (up to -70-80 °C for some angiosperms and lichens and -196 °C for some invertebrates such as tardigrades) by preventing the ice formation in the tissues (freeze avoidance or supercooling) or, by contrast, by allowing the freezing of extracellular water (freeze tolerance or hibernation) that leads to dehydration and/or vitrification. Endotherms (mammals and birds) can complete their life cycle at an environmental temperature below the water freezing point (-20 °C or below) since their body temperature is kept in the range 30-45 °C depending on the species (Clarke, 2014).

The ability of ectotherms, endotherms, and plants to tolerate low temperatures is highly variable across species, clades, and geographic locations, while tolerance to heat is strikingly invariant across latitudes, altitudes, and phylogeny (Addo-Bediako et al., 2000; Sunday et al., 2011). In fact, although thermal tolerance limits are strongly related to the adaptation to the current climate, the upper thermal limit is constrained by a physiological boundary that limits its evolution beyond certain temperatures whereas the lower limit is partially related to the ancestral climate of the origin and, thereby, more variable among clades (Bennett et al., 2021).

1.2 Freshwater organisms at thermal extremes

Geothermal springs and glacial streams are an optimal setup to discover the thermal limits of aquatic organisms. Research conducted in hot springs revealed that unicellular algae (such as *Cyanidium caldarium*) live at 45-55 °C (Doemel & Brock, 1970) as well as some fungi (Tansey & Brock, 1972) whereas plants (such as *Dichanthelium lanuginosum*) are found also at 65 °C. Yet, some invertebrates (such as crustaceans, nematodes, chironomids, and molluscs) tolerate temperatures around 42-53 °C (Hoeppli, 1926; Ocaña, 1991) while some species of fish belonging to the genus *Cyprinodon* live in springs at 38-46 °C (Minckley & Minckley, 1986; Montejano & Absalon, 2009). By contrast, the coldest aquatic environments are glacial streams and lakes where the temperature is around zero. In such habitats, the invertebrate community is dominated by Chironomidae (Diptera) (Maiolini & Lencioni, 2001) surviving in harsh conditions thanks to several strategies. Besides the supercooling and the hibernation that involved the synthesis of specific substances promoting or hampering the freezing of the haemolymph, physiological mechanisms include the accumulation of lipids and glycogen as food reserves. Moreover, adaptative strategies involve changes in morphology (smaller size and melanin protection), and in behaviour (habitat selection and cocoon building) that allow to keep a higher body temperature. Invertebrates of cold environments have developed phenological strategies including quiescence and dormancy and phenological plasticity to regulate their life cycle depending on environmental changes (Füreder, 1999; Lencioni, 2004).

2. Water temperature of running waters

2.1 Water thermal regime

In rivers, the water temperature varies in time and space giving place to a composite of patterns of absolute temperatures, diel and seasonal amplitudes, and rates of change, defined as “thermal regime”. The thermal regime can be described in terms of magnitude, variability, frequency, duration, and timing of events (Figure 1) (Arismendi et al., 2013) in the same way as the riverine flow regime (Olden & Poff, 2003; Poff, 1996).

2.1.1 Temporal variability

In temporal scale, the water temperature varies, following both a diel and an annual cycle. The daily minimum generally occurs in the early morning and the maximum in the late afternoon/early evening. The daily variability is lower in winter than in summer. Rivers also experience an annual temperature cycle, which follows a sinusoidal pattern with the annual maximum and minimum occurring in the late summer and the late winter respectively (Figure 1). Such patterns (daily and annual) are more pronounced in headwater streams and at high latitudes (Ward & Stanford, 1982; Webb & Walling, 1993). Close to the equator the seasonal variability of water temperature is very low but small streams can experience a marked daily thermal variability.

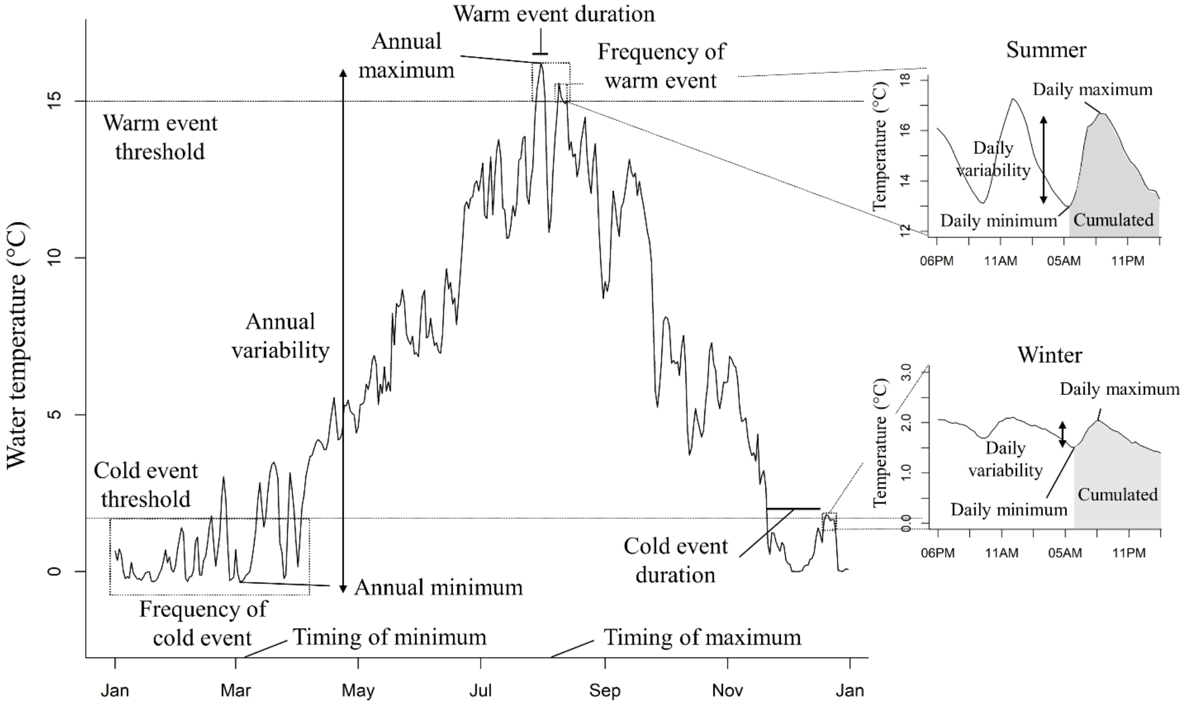


Figure 1. Annual thermal profile showing descriptors of thermal magnitude (annual maximum and minimum, daily maximum and minimum, cumulated), variability (annual and daily), duration (i.e: duration of warm and cold events), timing (day of maximum and day of minimum) and frequency (number of events exceeding the cold and warm threshold. Warm and cold event thresholds were chosen at 15 and 2 °C respectively. The annual profile is based on daily water temperatures while the daily profiles on hourly measures (Sanguigno stream, ~1400 m a.s.l, Orobic Alps, Italy, year 2020).

2.1.2 Spatial variability

Naturally, the mean daily water temperature varies in a downstream direction (as stream order increases) following different profiles identified as linear, asymptotic, parabolic, uniform, and complex, depending on several factors such as climate, altitude, flow, presence of tributaries and morphology (Figure 2) (Fullerton et al., 2015). Daily variations are generally smaller in headwater streams fed by groundwater and deep lowland rivers and greater in streams more exposed to meteorological conditions.

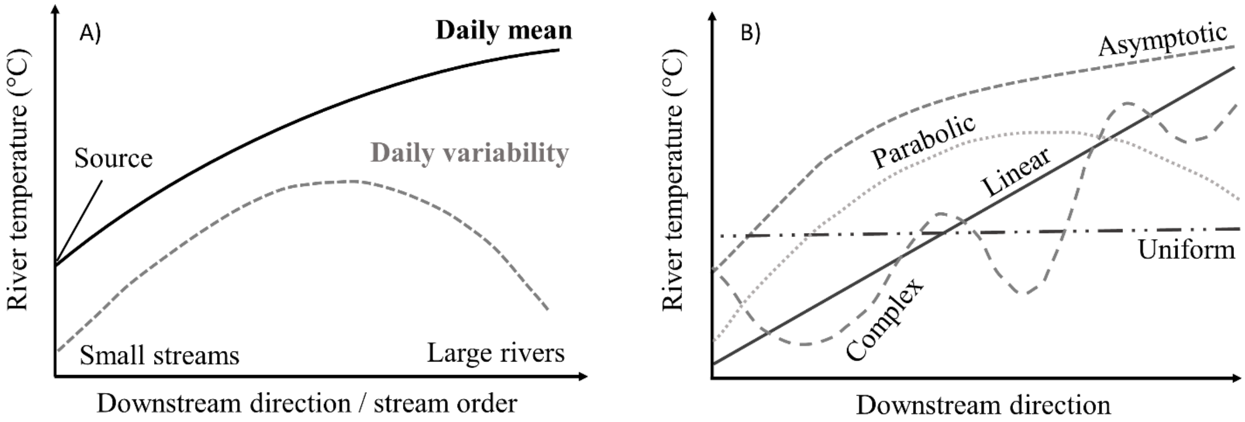


Figure 2. A) Mean daily and daily variability of water temperature as a function of downstream direction/ stream order (adapted from Caissie (2006)) in the case of an asymptotic profile and B) representations of five different longitudinal thermal profiles (adapted from Fullerton et al., (2015)).

2.2 Factors influencing river temperature

The natural thermal regime in rivers is mainly determined by the following factors:

- atmospheric conditions, related to the geographical location (latitude/longitude/altitude), including air temperature, precipitation, wind, humidity, solar radiation, and evapotranspiration/condensation;
- physical descriptors as river flow including the presence of inflows and outflows, volume and depth of water, slope, and turbulence;
- local topography, related to riparian vegetation, aspect, and lithology;
- morphology and streambed features related to sediments, hyporheic exchange, and groundwater inputs (Caissie, 2006).

Thus, for example, in shaded rivers having great flow, groundwater inputs, north exposition, and high slope, the water temperature keep low, while in low flow rivers, exposed to solar radiation, with low slope, and without groundwater or tributaries inflows, the temperature is higher.

Apart from these factors, the natural water temperature regime of rivers can be modified considerably by anthropogenic factors. Indeed, changes in the catchment land cover and, in particular, deforestation and removal of riparian vegetation cause an increase in water temperature (Johnson & Jones, 2000). Similarly, thermal effluents coming from nuclear and fossil-fuel power plants and factories and, to a minor extent, from wastewater treatment plants increase the riverine water temperature (Kinouchi, 2007; Madden et al., 2013; Raptis et al., 2016). The decrease in flow caused by water withdrawal for irrigation or water supply or hydroelectric power generation as well as the presence of dams, weirs, and reservoirs influence the riverine thermal regime.

In the case of dams, water temperature downstream depends on the level of the outflow: the effect is different if the discharge occurs as overflow from the surface layer of the basin (especially from weirs and small dams) or from the hypolimnion (especially in deep reservoirs) (Hester & Doyle, 2011; Mbaka & Mwaniki, 2015). Reservoirs affect the river thermal regime altering the seasonal and diel variability downstream (Casado et al., 2013; Horne et al., 2004) and modifying the timing of thermal events (Cowx et al., 1987; Preece & Jones, 2002). In this sense reservoir management, abstraction degrees (Olden & Naiman, 2010) and, dam features play an important role. Hypolimnetic-release dams decrease the riverine thermal fluctuations over time due to the thermal constancy of the hypolimnion, in particular in deep reservoirs (depth >15-20

m) where the water temperature is around 4 °C all year long (Figure 3A) (Deas & Lowney, 2000; Hester & Doyle, 2011; Olden & Naiman, 2010). By contrast, shallow and small impoundments with hypolimnetic-release decrease thermal fluctuations but increase water temperature downstream (Figure 3B) (Chandesris et al., 2019; Lessard & Hayes, 2003; Mbaka & Mwaniki, 2015). Yet, superficial-releases from reservoirs (as well as ponds or lakes outflows) increase both thermal variability and temperature value in downstream rivers (Figure 3C) (Seyedhashemi et al., 2021). Some studies have focused on the thermal impact of penstocks and diversion in the case of hydroelectric reservoirs (Dickson et al., 2012; Frutiger, 2004; Zolezzi et al., 2011) while much fewer investigations have been carried out on plants installed along the river although their number is higher and constantly increasing (Lange et al., 2018; Zarfl et al., 2015). According to some studies carried out in rivers subjected to run of river (ROR) hydropower plants, the diverted water cools down while the residual water in the by-passed stretch, having a lower flow, warms up faster than the natural rate (Figure 3D) (Gibeau & Palen, 2020). Moreover, to the best of the authors' knowledge, no studies investigated the cumulative impacts of run of river (ROR) power plants on the riverine thermal regime, despite their widespread distribution, especially in the Alps (Permanent Secretariat of the Alpine Convention, 2009).

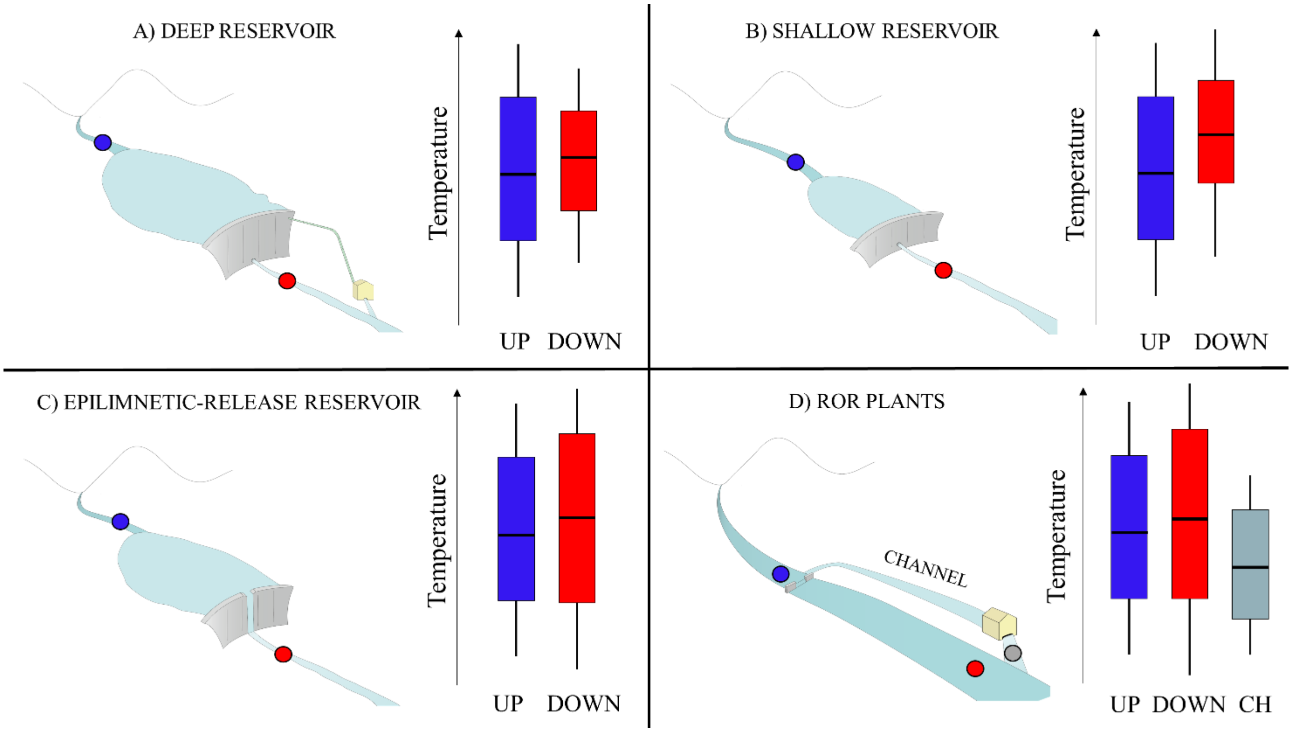


Figure 3. Examples of thermal alterations caused by A) deep reservoirs (depth>15-20 m), B) shallow reservoirs, C) reservoirs with epilimnetic release, and D) run of river power plants (draft edited by Luc Drochon)

Another anthropogenic factor affecting the water thermal regime is climate change, causing a global increase in air and water temperatures and an alteration of the thermal patterns (see section 4. Climate change).

2.3 Thermal sensitivity

Air temperature generally exerts a major influence on water temperature (Crisp & Howson, 1982; Smith & Lavis, 1975) so that a first, easy approach, to define how stream temperature responds to atmospheric conditions consists of the assessment of the thermal sensitivity. Indeed, it is possible to determine slope and intercept values of the linear regression between daily, weekly, or monthly values of air and water temperature. The slope of the regression indicates how thermally sensitive a given stream water is to changes in air temperature while the strength of the correlation (R^2) specifies how well water temperature can be predicted from air temperature. Thus, streams dominated by groundwater or meltwater sources, as well as watercourses fed by hypolimnetic release reservoirs have a low sensitivity which also results in a small daily and seasonal variability. By contrast, large rivers and/or small streams without riparian shading or significant groundwater inputs exhibit higher sensitivity approaching one (Kelleher et al., 2012).

2.4 Water temperature monitoring

Unlike air temperature which is monitored continuously and almost everywhere, often also in remote areas, the temperature of running waters is measured in an unsystematic way and the presence of recording networks varies from country to country. For example, in Europe over 10,200 stations measure atmospheric parameters, organized in networks and coordinated at a supra-national level by the World Meteorological Organization (WMO). By contrast, several countries lack a network of water temperature monitoring, and the recordings are limited to a few stations managed by local agencies or research centres. In North America, long-term recordings of water temperature have been carried out in several drainage systems across USA and Canada (Kaushal et al., 2010; Webb, 1996). In Europe, some countries as France (Beaufort et al., 2016), the UK (Hannah & Garner, 2015), and Switzerland (Michel et al., 2020) have a widespread network of riverine temperature stations while, to the best of the authors' knowledge, in Italy only 48 stations are in operation and all are located in the Alto Adige province.

Water temperature stations are usually located along hillslope and lowland rivers while mountain streams are generally neglected.

Besides the measurements in "official" monitoring stations, several data have been collected by portable dataloggers installed in the watercourses within ecological-environmental projects. Such type of studies, despite being scattered and covering very different time scales (from a few weeks to some years), allowed to assess the water thermal regime of small streams, also in mountain areas. Thus, glacial and headwater streams have been thermally characterized in detail in some areas (Brown & Hannah, 2008; Cadbury et al., 2008; Uehlinger et al., 2003) providing useful information about the drivers that control the water thermal regime and its influence on the aquatic biota in those contexts.

Several point measurements of water temperature are collected as background information during ecological site-specific studies or bioassessment programs. However, such sporadic measurements can lead to false estimations of the temperature regime as they cannot detect temporal fluctuations. Thus, they can only provide rough support for ecological studies.

Although the Water Frame Directive (WFD, CE, 2000) requires the assessment of physico-chemical parameters for the evaluation of the ecological quality of running waters (Annex V 1.1 and 1.2.), some issues hamper adequate surveys. First, the legislation (WFD and the national transpositions) requires the monitoring of water temperature through weekly (or monthly) point measurements which provide only a rough estimation of the riverine thermal regime, and the thermal regime is not incorporated into environmental flow assessment. Second, there are few indicators to assess modifications of the thermal regime (i.e the metrics of thermopeaking elaborated by Vanzo et al., (2016) and Zolezzi et al., (2011)) and are not systematized. Third, few methods assess the ecological consequences of thermal alterations and are not integrated into bioassessment programs yet.

Environmental flow (e-flow): amount of water required for the aquatic ecosystem to continue to thrive and provide the services we rely upon (Water Framework Directive).

3. Water temperature and lotic aquatic biota

Water temperature has been recognised as a key factor shaping both aquatic ecosystem structure and functioning (Coutant, 1999; Karr & Dudley, 1981; Odum, 1968). It influences the organisms both directly and indirectly; indeed, metabolic reactions and enzyme functions depend on temperature but also geophysical processes such as the degradation of organic matter and the solubility of chemical species (Cairns et al., 1975) ultimately affecting water quality and aquatic biota.

Stream aquatic biota is mainly composed of biofilm, macrophytes, macroinvertebrates, and fish.

3.1 Biofilm and macrophytes

Biofilm comprises the assemblage of organisms attached to substrates including microalgae, bacteria, and fungi, embedded in an extracellular matrix. In headwater streams, periphyton, the autotrophic component of biofilm, can contribute as much as 80% to the total primary production. Temperature affects the biomass of periphyton (Morin et al., 1999) controlling the rate of primary production through its effects on the biochemical processes of photosynthesis (Medlyn et al., 2002). Moreover, it can alter the composition of algal communities depending on the thermal preference of each taxon. For example, a high thermal variability can induce seasonal changes in the algal composition promoting green algae and cyanobacteria in summer and diatoms in winter (Allan & Castillo, 2007). However, other factors such as light and nutrient availability (especially phosphorus, nitrogen, and silica), water velocity, and disturbance are pivotal, especially in mountain streams (Biggs, 1988; Hill & Dimick, 2002). Specifically, light, and nutrients promote algal growth, unlike grazing and disturbance. Macrophytes encompass all the vegetal macroscopic organisms living in the rivers. They are generally confined to lowland rivers and lateral zones with a low current and respond to environmental conditions like periphyton. Thus, is important to understand the factors that control the growth and the composition of micro and macro algae assemblages, also because they constitute the basis of the food web (Bernhardt & Likens, 2004; Larned, 2010).

3.2 Macroinvertebrates

Aquatic macroinvertebrates are a heterogeneous group, consisting of aquatic invertebrates larger than 500 µm (Hauer & Resh, 2017) belonging to phyla such as Arthropoda (Crustacea and Insecta), Mollusca (Gastropoda and Bivalvia), Annelida, Nematoda, Platyhelminthes, Porifera, Cnidaria and Bryozoa (Astorga et al., 2011; Konrad et al., 2008; Resh, 2008). They constitute the major component of secondary production and play a key role in food webs, linking organic matter resources with upper trophic levels (Merritt et al., 2017). Macroinvertebrates exhibit a wide variety of reproductive, phenological, trophic, metabolic, physiological, and behavioural strategies adapted to their specific environments (Hauer & Resh, 2017). As macroinvertebrates are ubiquitarians, common, abundant, and highly diversified and exhibit different sensitivity to perturbations, they provide measurable responses to multiple environmental conditions and therefore, are widely used as bioindicators (Cañedo-Argüelles et al., 2020; Cummins, 1974; Hynes, 1970; Moore & Schindler, 2008). Among the environmental conditions that affect the taxonomic and functional diversity of macroinvertebrate communities, there are water quality, hydrological alterations, substrate type, resource (quality and quantity), and predation.

In headwater streams, insects dominate (in particular Plecoptera, Ephemeroptera, Trichoptera, Coleoptera, and Diptera) (Figure 4) and the macroinvertebrate community is composed mainly of shredders and collectors as the majority of the organic resource consists of the particulate coarse organic matter coming from terrestrial environments (Vannote et al., 1980). In mountain streams, the major stressors are the variations in flow and thermal regimes as well as the fluctuations in food resource availability.

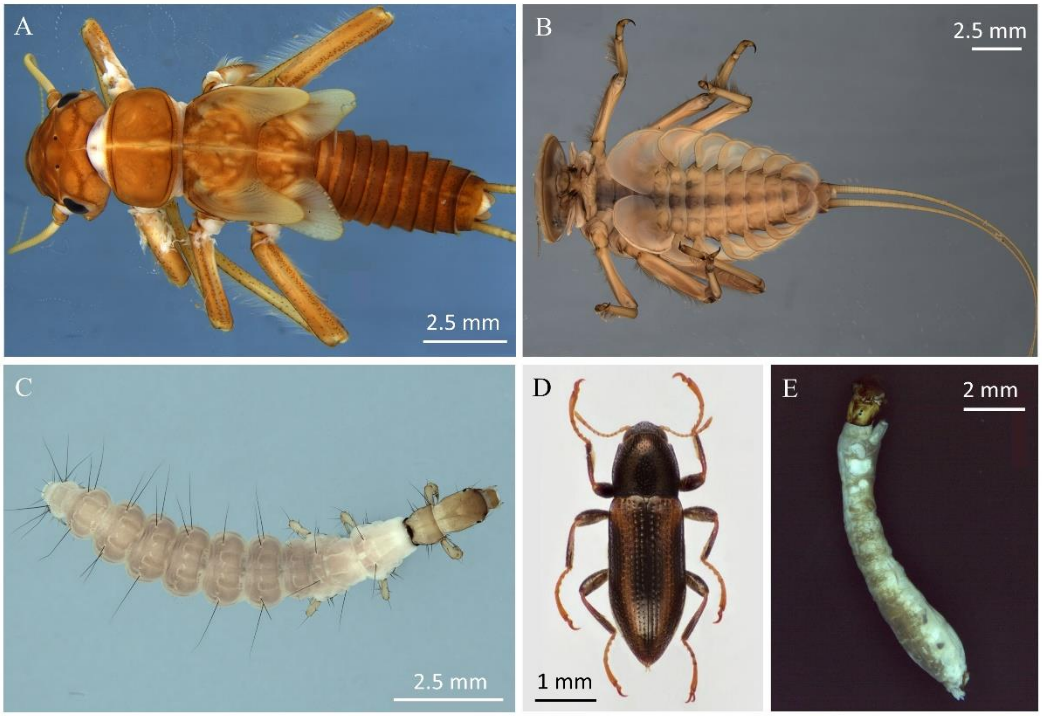


Figure 4. Examples of insects inhabiting mountain streams: A) *Perlodes intricatus* (Plecoptera), B) *Epeorus alpicola* (Ephemeroptera) C) Rhyacophilidae (Thrichoptera), D) Elmidae (Coleoptera) and E) Simulidae (Diptera) (Photos by Luca Bonacina and Maxance Forcellini).

Water temperature drives the distribution of the species, affecting macroinvertebrate community composition and abundance (Hawkins et al., 1997). Indeed, according to the thermal equilibrium hypothesis, the distribution of many lotic species depends on their thermal preference, since fecundity and adult size gradually decrease with increasingly cold or warm conditions (Sweeney & Vannote, 1978). Thus, both locally within the watershed, and over large geographic areas, the stability (the ability to recover after perturbations) of a subpopulation reflects a dynamic equilibrium among temperature, metabolism, and fitness of individuals. Macroinvertebrates respond to the entire water thermal regime including absolute temperatures, diel and seasonal amplitudes, and rates of change. Low temperatures induce dormancy mechanisms (Danks, 1987), allowing survival in harsh environmental conditions and, at the same time promoting temporal taxa segregation or, by contrast, synchronization among congeneric organisms (Harper & Pilon, 1970; Hildrew & Edington, 1979). For many organisms, temperature changes can trigger specific life-cycle phases such as migration, embryonic, and larval development, egg hatching and timing and duration of emergence (Figure 5) (Angilletta, 2009).

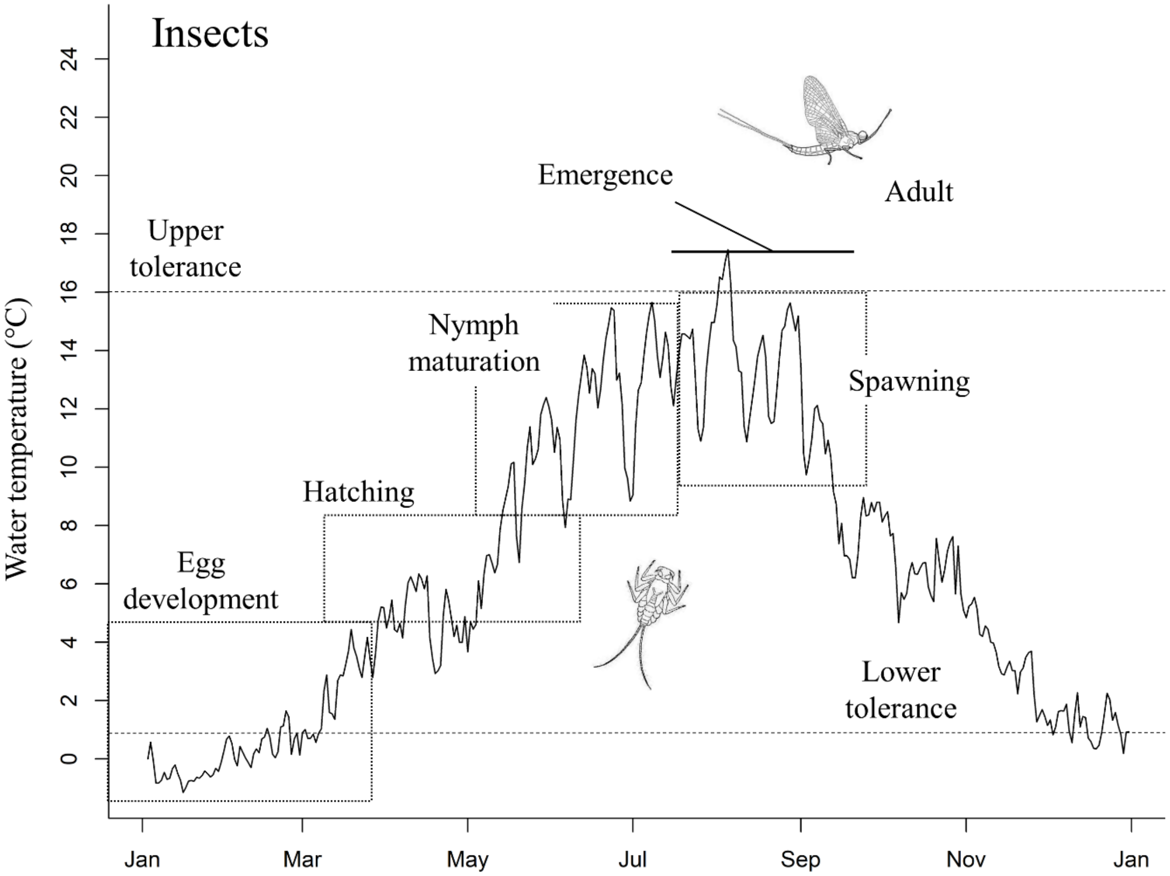


Figure 5. An example of the life-history of insects in relation to the thermal regime.

Each species requires a specific temperature range described by the performance-temperature relationship, an asymmetric bell curve where performance reaches the maximum at the optimal body temperature and then decreases approaching zero at the critical thermal limits (minimum and maximum) (Figure 6) (Angilletta et al., 2002).

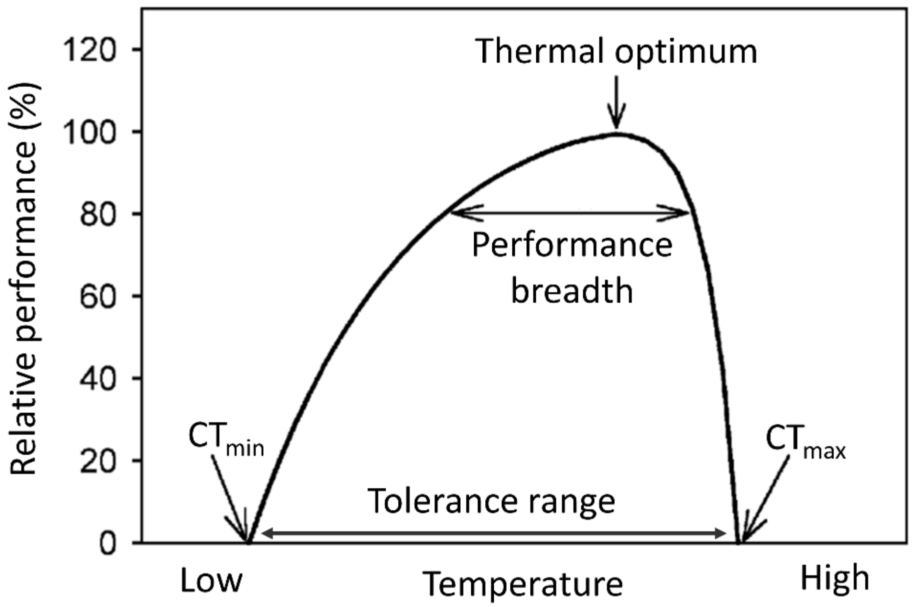


Figure 6. Typical thermal performance curve for ectotherms (adapted from Huey & Stevenson (1979)). CTmax, critical thermal maximum; CTmin, critical thermal minimum.

Stenothermal macroinvertebrate species occupy a restricted temperature range while eurythermal species can tolerate a wider one (Jones et al., 2017). When approaching their thermal limits, organisms show signs of stress, resulting in changes in behaviour (migration, locomotion, and feeding) (Bruno et al., 2012), physiology and metabolism (respiration, assimilation and excretion, growth rate and body size) (Sweeney, 1978; Zimmerman & Wissing, 1978), reproductive strategies (fecundity, hatching time and success) (Brittain & Mutch, 1984; Everall et al., 2015), and susceptibility to predators (Smolinský & Gvoždík, 2014; Śniegula et al., 2019), pathogens and parasites (Pritchard & Zloty, 1994).

Despite macroinvertebrates have been used for decades to assess the status of aquatic ecosystems as a result of environmental stresses, their responses to temperature are poorly documented and have not been systematically evaluated. Most studies investigating the effect of water temperature on macroinvertebrates focus on the average or the extreme values (i.e effects of high temperatures on the life cycle) while the variability is overlooked, especially at the community level.

3.3 Fish

Fish distribution and abundance depend on the thermal structure of the waterbodies, i.e the spatial distribution of temperatures (Coutant, 1987; Picard et al., 2022). Indeed, as macroinvertebrates, each fish species has its specific thermal limits (Elliott & Elliott, 2010). For riverine fish summer is the main feeding and growing season (Forseth et al., 2001) while winter involves energy saving and survival strategies including quiescence, sheltering, nocturnal behaviour, and starvation (Crozier & Hutchings, 2014; Heggenes et al., 2017). Temperature affects specific phases of the life cycle as hatching, and spawning which can be inhibited or activated in different conditions, as well as the ability to migrate (Jonsson & Jonsson, 2009) and the outbreak of diseases (Figure 7) (Carraro et al., 2017).

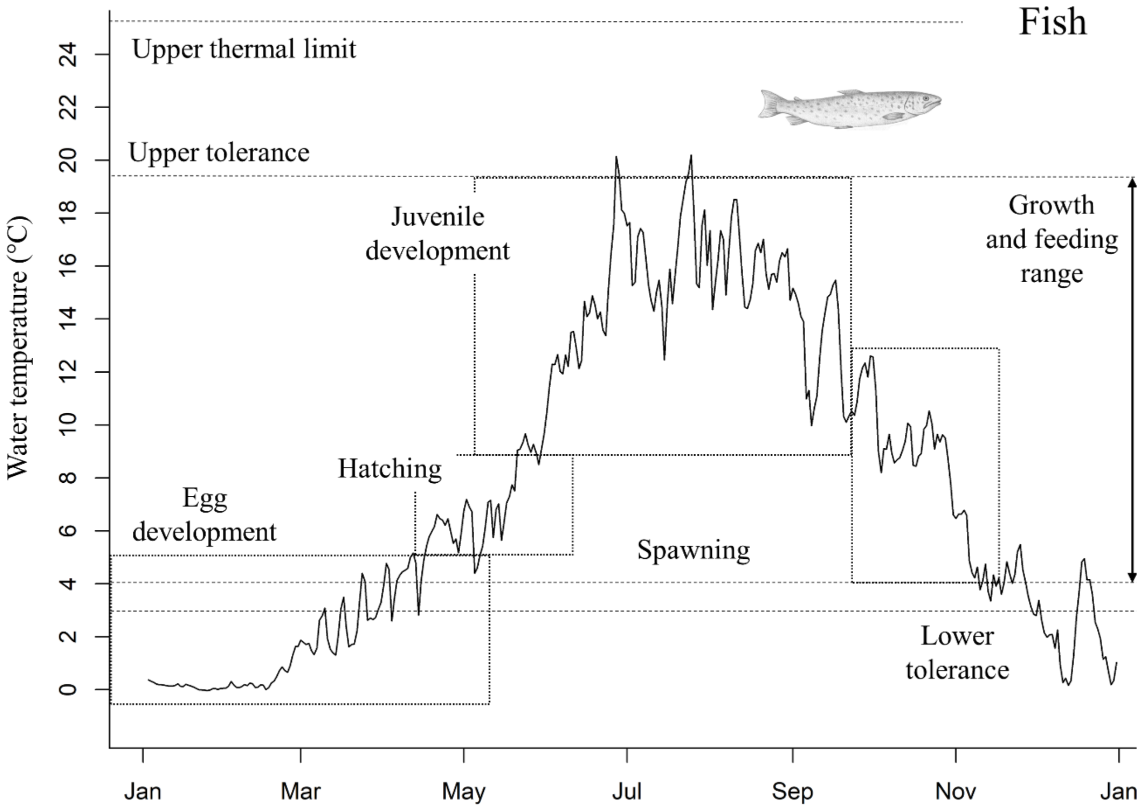


Figure 7. An example of the life-history of fish in relation to the thermal regime.

In mountain streams fish are absent or belong to few species, mostly salmonids, that require cold, clean, well oxygenated, and fast-flowing waters. Factors threatening freshwater salmonid population consist of glacier retreat, shift of precipitation regimes and increase of water temperature caused by climate change (Carlson et al., 2017; Pitman et al., 2020). Furthermore, in the last decades salmonid populations have encountered decline and local extinction due to the dissemination of the proliferative kidney disease (PKD), caused by the myxozoan parasite *Tetracapsuloides bryosalmonae.* The proliferative and inflammatory response to parasite stages is temperature dependent (Okamura et al., 2011) and causes the decline of fish populations especially during extremely warm summers (Burkhardt-Holm et al., 2005). Thus, in the next decades, due to the global warming, the decline of salmonids caused by the proliferative kidney disease is expected to worsen, especially in mountain streams where the temperature is increasing faster (Hari et al., 2006; Adrien Michel et al., 2020). The effect of temperature changes on fish populations should be evaluated considering also other factors like the habitat (water depth, current velocity, and substrate type) and the water quality.

4. Climate change

Recent climate change refers to the shift in temperatures and weather patterns observed worldwide since the industrial revolution due to human activities that, generating greenhouse gases from the burning of fossil fuels, have changed the atmospheric radiation balance. Indeed, from 1880 to 2022 the atmospheric concentration of carbon dioxide has shifted from ~280 to 420 ppm leading to an accumulation of energy in the atmosphere and an increase of global surface air temperature of about 1.2 °C. The rate of temperature change has increased reaching 0.2 °C/decade in the last 30 years, more than twice than at the beginning of the XX century but with large variations across the Earth being higher over lands than over oceans and at high altitudes and latitudes (Pepin et al., 2015; Rantanen et al., 2022; Sutton et al., 2007). For example, the rate of warming of Alpine climate has been 0.3 °C/decade and the increase in the last hundred years has been of 2 °C: twice the global average. Such warming led to a decline of the glaciers that have shrunk by more than half since the early 1900s with a higher melting in the last few years (Sommer et al., 2020; Zemp et al., 2019). Furthermore, temperature changes have shortened the snow accumulation season and anticipated the time of meltwater runoff (Barnett et al., 2005).

Climate change profoundly affects freshwater systems modifying the hydrological cycle and the thermal regime of water bodies. Water temperatures are rising globally (van Vliet et al., 2013; Wanders et al., 2019) and the rate of warming is higher in water than over land (Orr et al., 2015;

Seyedhashemi et al., 2022) and particularly sharp in small waterbodies of high altitudes and latitudes (Michel et al., 2021; Niedrist & Füreder, 2020). Especially in mountain streams, changes in the water thermal regime also occur due to the modification in the quantity, timing, and duration of snowmelt water supply associated with shorter and warmer winters (Confortola et al., 2013; Michel et al., 2022).

Climate change results in a global temperature increase (climate warming) and in a change of precipitation patterns that, influencing the ecosystem energy amount (through an effect on productivity too), affects the species distribution globally and locally. Freshwater ecosystems are highly vulnerable to climate change: several studies highlighted extinction rates of freshwater organisms matching or exceeding those suggested for better known terrestrial taxa (Xenopoulos et al., 2005). However, the extent of climatic change varies among regions and ecosystems (Pörtner & Peck, 2010; Wrona et al., 2006) affecting especially mountain waterbodies and its effect on species distribution depends on local-scale variables (Heino et al., 2009) as hydrothermal regimes, resources, hydrochemistry (*landscape filter hypothesis*).

5. Alpine streams as an optimal setup for thermal ecology studies

As exposed in the previous chapters, Alpine streams represent an optimal setup to study the influence of water thermal regimes on aquatic biota for several reasons. First, mountain hydrographic networks generally display a high thermal heterogeneity due to the variable sources of water inputs (Brown & Hannah, 2008) and anthropogenic alterations (Dickson et al., 2012) that lead to contrasting annual thermal patterns depending on the type of stream. Second, mountain water bodies host huge biodiversity (Rahbek et al., 2019) due to local endemism driven by habitat isolation and adaptation to specific conditions caused by steep environmental gradients (Muhlfeld et al., 2020). Indeed, mountain organisms are highly diversified to adapt to different environmental conditions, also exhibiting contrasted thermal preferences. Moreover, the Alps, as well as the other Southern-European Mountain systems host both cold-adapted arctic-alpine species (Hewitt, 1999; Schmitt, 2007) and warm-adapted Mediterranean species (Tierno de Figueroa et al., 2013) and this makes the study of organism thermal responses particularly interesting. Third, mountain streams, contrary to lowland rivers, are less exposed to multiple stressors such as pollution and habitat degradation that hamper to properly assess the effects of water thermal regime on aquatic organisms and communities. Lastly, climate change is proceeding faster in mountain environments and thus, investigating temperature-biota relationship in such streams provides useful elements to understand how biodiversity responds to changes in the water thermal regime.

This thesis includes a field part that was carried out in the Serio watershed (Orobic Alps) because, besides reflecting the points previously discussed, such catchment had already been surveyed by the University of Milano-Bicocca. Specifically, a project involving the hydroelectric power plants installed along the Serio River contributed to define the environmental flow of several by-passed stretches (Fornaroli et al., 2016, 2019) while other activities had been carried out in the Goglio Valley to assess the impacts of the reservoirs on the stream structure and functioning (Petruzziello et al., 2021). The Serio watershed has been affected by hydroelectric exploitation since the beginning of the XX century and several dams and run of river power plants were built along its watercourses (Figure 8). Consequently, its environment is strongly anthropized as is the case of most Alpine catchments (Comiti, 2012). The past investigations provided useful information about the taxa (fish and macroinvertebrates) living in the watercourses of the Serio catchment, the riverine environmental conditions (specifically for water quality and flow), and the management of reservoirs and run of river power plants.

All the surveys presented in this thesis have been carried out in stream sites ranging from ~500 to ~1500 m a.s.l since at such altitude: i) the thermal heterogeneity is supposed to be the maximum, ii) both cold alpine and warm Mediterranean macroinvertebrate species occur, providing a variety of thermal responses and, iii) snow and ice do not make the winter samplings impractical.

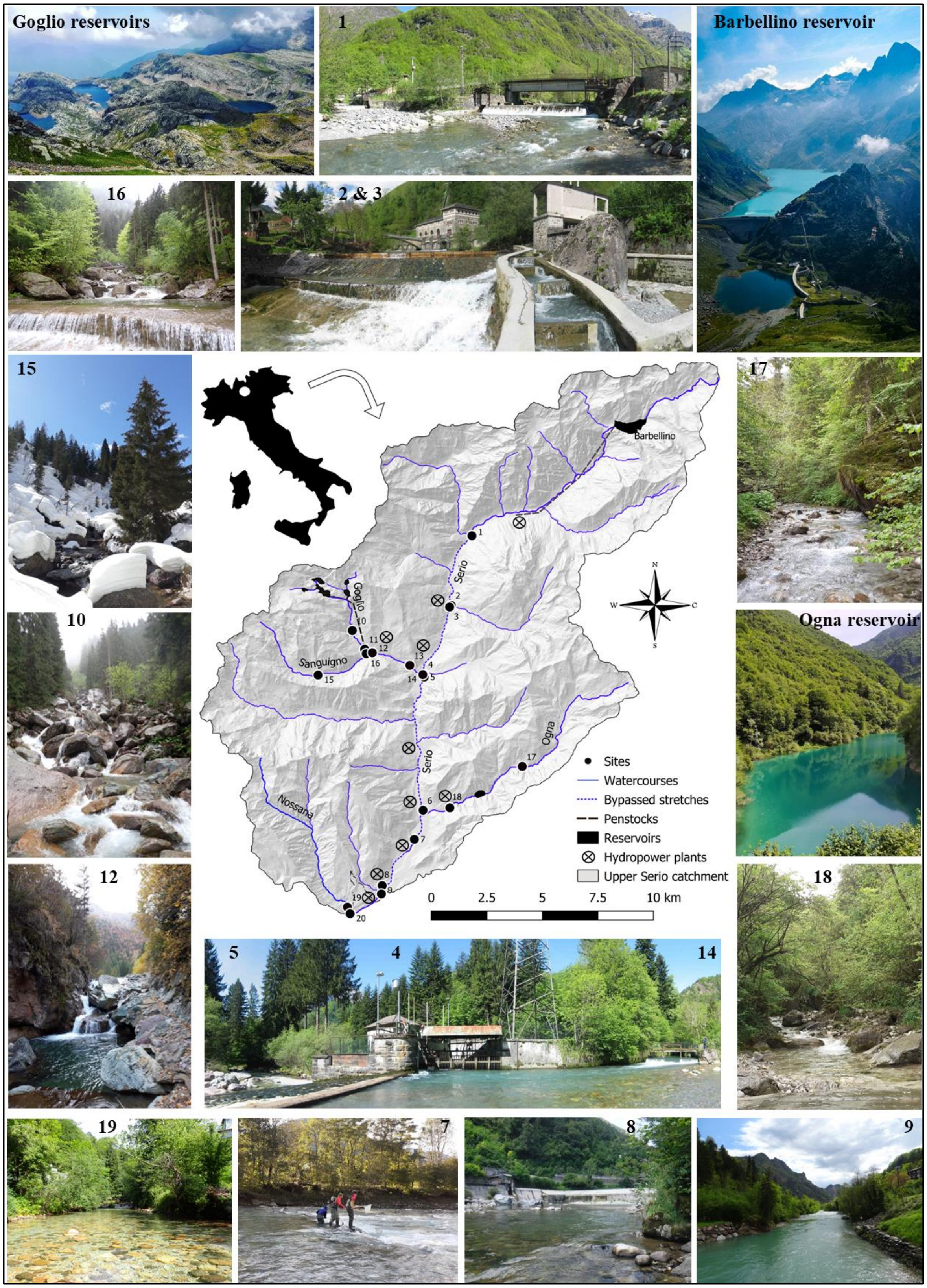


Figure 8. Study area (picture by Luca Bonacina, Riccardo Fornaroli, Sergio Canobbio, Manuela Rotasperti, Ramon Occioni and Aldo Sara)

6. Thesis outline

This thesis addresses the following topics:

I. Assessment of the water thermal heterogeneity across mid-altitude streams in relation to both natural and anthropogenic drivers and analysis of the thermal alterations induced by the run of river power plants.
II. Investigation of the relationship between water thermal regime and aquatic biota at different trophic levels with particular emphasis on the annual thermal variability

The content is organized into six chapters referring to six papers published or submitted. The first part is dedicated to the understanding of water thermal regimes of mountain watercourses through an analysis of the temporal (daily and seasonally) and spatial (along and among watercourses) patterns in relation to both natural and anthropogenic drivers. In **Chapter 1** the water thermal regime of 16 mid-altitude stream sites of the Serio watershed (Orobic Alps, Northern Italy) is examined. Such monitoring sites had been selected along five watercourses characterized by different sources (snowmelt/stormwater vs. groundwater) and anthropogenic pressures (presence of reservoirs). Water temperature was monitored for five years with high-frequency measurements (10-60 min) and the seasonal and daily variations were described along and among watercourses highlighting the ecological implications related to the spatial thermal heterogeneity. **Chapter 2** focuses on the thermal alterations caused by run of river power plants whose impacts have not yet been considered, neither in the scientific literature nor in bioassessment programs despite their widespread distribution. Thus, a survey was carried out along the upper Serio River which is characterized by a cascade system of run of river power plants. Specifically, the water temperature was measured continuously for more than 4 years at the extremes of 4 stretches subjected to water diversion. Thermal patterns were examined daily, and seasonally quantifying thermal alterations induced by flow diversion. The second part of the thesis is dedicated to the effects of the water thermal regime on the aquatic biota and includes a literature review and three field studies regarding different trophic levels: biofilm, macroinvertebrates, and fish, respectively. Macroinvertebrates were studied in detail as they represent the optimal target to investigate the temperature-lotic biota relationship. Nevertheless, also biofilm was taken into account for its bottom-up effect on macroinvertebrates while fish were considered to estimate long-term changes in river habitat under global warming.

Chapter 3 presents a systematic literature review that synthesizes the current state of knowledge about the water temperature-freshwater macroinvertebrates relationship based on 223 papers published from 1970 to 2020. Specifically, the main objectives are: (i) to collate and summarize responses of freshwater macroinvertebrates to different temperature conditions, comparing the results of experimental and theoretical studies; (ii) to understand how the focus of research on the effects of temperature on macroinvertebrates has changed during the last 51 years; and (iii) to identify research gaps regarding temperature responses, ecosystem types, organism groups, spatiotemporal scales, and geographical regions to suggest possible research directions. **Chapter 4** reports the study carried out on biofilm, involving one year of monthly samplings in five streams characterized by different thermal regimes, while **Chapter 5** focuses on macroinvertebrates collected at the same time as the biofilm. In both studies, the aim was also to disentangle the effect of the water thermal regime from other environmental variables related to water physico-chemistry, flood disturbance, resource availability, and substrate type.

In **Chapter 6** the habitat suitability of Serio River for *Salmo trutta* is estimated under different climatic scenarios by combining a hydraulic and thermal assessment based on fish density-flow curves and the proliferative kidney disease risk whose effect is enhanced by high temperatures. In the conclusion, besides providing a synthesis of the overall findings, possible future directions of research and management strategies are presented.

FIRST PART:
THERMAL REGIMES OF MID-ALTITUDE STREAMS AND NATURAL AND ANTROPOGENIC DRIVERS

CHAPTER 1

Spatial heterogeneity of water temperature across an alpine catchment

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CHAPTER 1. Spatial heterogeneity of water temperature across an alpine catchment

Abstract

Temperature is recognised as an important driver in aquatic ecosystems. Despite that, the understanding of thermal heterogeneity across river networks at different spatiotemporal scales is limited but necessary to assess the importance of site-specific vs. regional controls. In the present study, we investigated the water thermal regime in five mid-altitude watercourses (500-1500 m) of the Serio River watershed (Orobic Alps, Northern Italy) characterized by inputs from different sources (snowmelt/stormwater vs. groundwater) and by human alterations (presence of reservoirs). Water temperature was monitored in 16 sites in 2017-2022 using high-resolution (10-60 min) dataloggers and thermal patterns were examined in relation to meteorological conditions (air temperature) and stream features. The results show that the water thermal regime depends on the watercourse typology as well as on weather conditions and anthropogenic alterations. Siliceous and not regulated streams were more dependent on air temperature than groundwater-fed and reservoir-regulated streams. Overall, the study demonstrates a high thermal heterogeneity at the basin scale, similar to the one found in alpine catchments with glacier influence, and the same thermal patterns found at the regional scale with groundwater and reservoir water supplies flattening the seasonal and daily thermal variability. The high thermal heterogeneity suggests relevant ecological implications for the spatiotemporal dynamics of aquatic communities.

Keywords

River thermal regime, reservoirs, hydropower production, groundwater, lotic ecosystems, aquatic communities, climate warming.

1. Introduction

Temperature is a pivotal factor shaping aquatic ecosystem structure and functioning (Odum, 1973, Hester, 2011). Water temperature controls geophysical processes such as the degradation of organic matter and the solubility of chemical species ultimately affecting water quality (Cairns et al., 1975; Rajwa-Kuligiewicz et al., 2015). It influences primary production (Lamberti & Steinman, 1997; Morin et al., 1999) and affects organism physiology and metabolism, phenology, fitness, behaviour, and survival (Bonacina, et al., 2022; Coutant, 1999; Dallas & Ross-Gillespie, 2015). Moreover, temperature relates to the outbreak of diseases (Carraro et al., 2017) and to the ability to migrate (Brittain & Eikeland, 1988; Jonsson & Jonsson, 2009).

At a larger scale, water temperature drives the spatiotemporal patterns of aquatic communities affecting the distribution of the species and the richness and composition of communities (Hawkins et al., 1997; Picard et al., 2022; Potapova & Charles, 2002; Timoner et al., 2020). Despite that, an investigation of water thermal variability across water bodies at different spatiotemporal scales is difficult, especially in mountain areas, due to the need of continuous data. At the regional scale, the thermal regime has been deeply investigated in some river networks for example in UK (Hannah & Garner, 2015), France (Seyedhashemi et al., 2022), Canada (Webb, 1996) and United States (Mohseni, Stefan, & Eaton, 2003). At a smaller scale, several studies focused on specific riverine stretches have been carried out (Arscott et al., 2001; Castella et al., 2001; Finn et al., 2022; Haidekker & Hering, 2008) while at the catchment scale only few studies have been conducted, mainly in glaciated basins (Brown & Hannah, 2008; Cadbury et al., 2008; Dickson et al., 2012). Riverine water temperature depends on atmospheric conditions (air temperature, solar radiation, wind speed, precipitation, evaporation and snow melting), topography (upland shading, side inputs, riparian vegetation, bedrock, aspect, channel morphology (slope, water speed, turbulence, inflow/outflow) and riverbed features (hyporheic exchange and groundwater input) (Caissie, 2006). Furthermore, anthropogenic actions such as deforestation, input of high temperature effluents, flow diversion for hydroelectric power production and irrigation purposes as well as the presence of reservoirs and weirs impact riverine the thermal regime (Brown & Krygier, 1970; Casado et al., 2013; Dickson et al., 2012; Frutiger, 2004; Kinouchi, 2007). Finally, as a consequence of global warming water temperature is rising even faster than air temperature (Kaushal et al., 2010; Pekárová et al., 2011; Seyedhashemi et al., 2022), especially in mountain streams (Hari et al., 2006). For example, Niedrist & Füreder (2020) recorded a 2.5±0.6 °C increase in the mean water temperatures in the last decade in non-glacial Austrian streams while Michel et al., (2020) observed a 0.37±0.11 °C/decade increase in the Swiss rivers due both to the increase of air temperature and to the river flow reduction in the last 20 years.

In alpine rivers, water temperature affects the structure of aquatic communities (Fureder et al., 2002; Milner et al., 2009). For example, in several glacier-fed streams in Europe water temperature was found to be negatively related to the taxonomic richness and the diversity of macroinvertebrate assemblages (Castella et al., 2001; Milner et al., 2001). Other authors pointed out that the sharp daily and monthly thermal variability of mountain streams affected the composition of both macroinvertebrate and algae communities (Band et al., 2004; Von Fumetti et al., 2017; Gustafson, 2008). Strong differences in water temperature in small alpine basins were observed for the interaction of multiple factors such as different water sources (meltwater, groundwater, precipitation), channel geomorphology, basin characteristics (geology, aspect, and altitude) and human infrastructures (reservoirs, water abstractions) (Brown & Hannah, 2008; Dickson et al., 2012; Küry et al., 2017; Uehlinger et al., 2003). However, studies investigating the impact of both 'natural' and anthropogenic factors on the thermal heterogeneity of mid-altitude stream networks are still few, especially at fine temporal resolution and for multiple years. Thus, the appraisal of the thermal heterogeneity of stream networks at a local scale as well as the understanding of the processes driving the water temperature regime is fundamental for the assessment and prediction of the ecological patterns and processes in mountain streams.

The present study reports the results of an intensive study of water temperature in 16 sites across the Serio catchment (Northern Italy) which is fed from different sources (snowmelt/stormwater vs. groundwater) and undergoes hydrological impacts related to the presence of reservoirs. Specifically, the article aims (1) to characterize the spatiotemporal temperature dynamics of 5 watercourses of the Serio catchment; (2) to determine the key hydrometeorological and anthropogenic factors influencing the stream temperature; and (3) to compare the thermal patterns in the Serio catchment with the ones observed at different spatial scale. Furthermore, the ecological implications of thermal heterogeneity in the mountain river system are discussed.

2. Materials and Methods

2.1 Study Area

The Serio catchment is a not glaciated watershed situated in the Orobic Alps (Northern Italy); the upper part covers an area of 383 km^2 and lays between ~400 and 3050 m a.s.l (Figure 1). We selected a priori 5 watercourses representative of different water sources (snowmelt/stormwater and groundwater-fed) and human alterations (presence of reservoirs) supposing that they will exhibit different thermal patterns (Figure 1). Thus, we surveyed water temperature along Serio River, the main watercourse, and along 4 of its tributaries: Sanguigno, Goglio, Ogna and Nossana. Such streams are characterized by different sources depending on the lithology: streams with groundwater inputs in limestone rocks: Ogna and Nossana and snowmelt/stormwater streams in siliceous rocks: Sanguigno and Goglio. Serio River springs from the Barbellino reservoir (1,862 m a.s.l., 18.5 million m^3 of capacity, depth>60 m) and flows in Adda River after 124 km. Along its course, there are several run of river hydroelectric plants that divert the water for hydroelectric purposes (but the studied sites were not located within the bypassed reaches so they were not affected by ROR alterations). Goglio and Ogna are also affected by human regulation as reservoirs and hydroelectric plants were built since the beginning of the XX century. We monitored water temperature in 16 sites between 456 and 1,395 m a.s.l in the period 2017-2022 with fine time step frequency (10-60 min). Specifically, 5 sites (S1->S5) were placed along Serio River, two sites (SAN1, SAN2) along Sanguigno, five sites (G1->G5) along Goglio, two sites (O1, O2) along Ogna, and two sites (N1, N2) along Nossana (Table 1). Sanguigno stream is characterized by a snowmelt/stormwater source, and it is not affected by any human alterations while Goglio stream represents its regulated counterpart as it springs from reservoirs (5.4 million m^3 of capacity, depth>20 m). On the other side of the valley, Ogna stream has some groundwater inputs and is divided in two parts by a reservoir (15,000 m^3 of capacity, depth<12 m): the upper Ogna, upstream, and the lower Ogna downstream. Nossana is a karstic stream that runs underground for about 7 km and then springs to the surface 500 m before the confluence with Serio River. Thus, upper Ogna represents Sanguigno groundwater-fed counterpart while lower Ogna represents the upper Goglio groundwater-fed counterpart. The survey was designed for a research project aiming to investigate the effects of the water temperature on the aquatic biota thus the monitoring sites were concentrated on 5 watercourses.

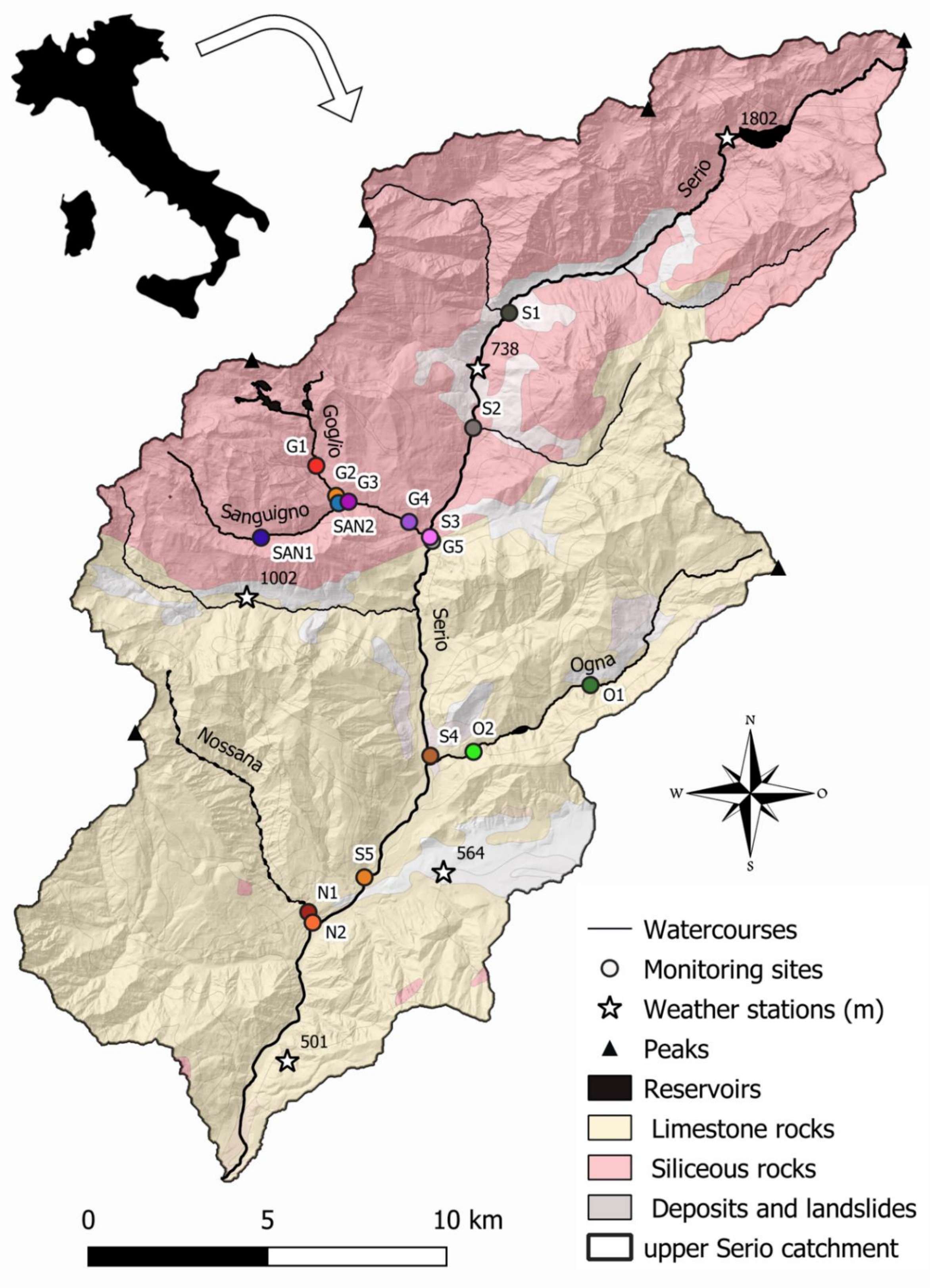

Figure 1. Map of the study area, Orobic Alps (Northern Italy).

Table 1. List of the monitoring sites with their features. *For regulated stream the source is considered the reservoir, for which is indicated the capacity (V) and the depth (d).

Watercourse	Site	Source	Regulation	Area catchment (km^2)	Altitude (m a.s.l.)	Distance from the source (km)
Sanguigno	SAN1	snowmelt/stormwater	/	7.7	1395	4,290
	SAN2	snowmelt/stormwater		11.5	975	6,970
upper Goglio	G1	snowmelt/stormwater	Reservoir (V=5.4 Mm^3; d>20 m)	8.1	1128	1,540
	G2	snowmelt/stormwater		13.6	971	2,620
lower Goglio	G3	snowmelt/stormwater	Reservoir (V=5.4 Mm^3; d>20 m)	25.4	932	3,140
	G4	snowmelt/stormwater		31	718	5,020
	G5	snowmelt/stormwater		32.2	633	5,850
upper Ogna	O1	snowmelt/stormwater-groundwater	/	18.1	970	7,441
lower Ogna	O2	snowmelt/stormwater-groundwater	Reservoir (V=0.15 Mm^3; d<12 m)	27.5	583	1,500
Nossana	N1	groundwater	/	0.08	468	0,133
	N2	groundwater	/	0.28	456	0,494
Serio	S1	snowmelt/stormwater	Reservoir (V=18.5 Mm^3; d>60 m)	88.5	784	9,196
	S2	snowmelt/stormwater		124.4	671	13,014
	S3	snowmelt/stormwater		173.5	623	16,466
	S4	snowmelt/stormwater-groundwater		230	511	22,959
	S5	snowmelt/stormwater-groundwater		272.6	474	27,365

2.2 Data collection

Water temperature was measured continuously (every 10-60 min depending on the datalogger) in the period July 2017-September 2022 using iButton devices (DS1925L and DS121Z sensors:

range -40-85 °C and -5-26 °C, accuracy: ±0.5°C and ±1.0°C resolution: ±0.0625 °C and ±0.125 °C respectively) fixed in the riverbed. The devices were calibrated, set using the 1-Wire® software, and placed in each site for at least two years in the period 2017-2022 (see Table 1SM for details). Based on these temperature time series, we calculated the daily mean, maximum and minimum temperatures at each site. Where water temperature data were lacking, due to sensor failure or loss (~26% of the data) the values were estimated from air temperature using Generalised Additive Models (GAM) relating daily water temperature (mean, maximum and minimum) to air temperature (mean) time series plus the week number as an extra smoothing parameter (see Krajenbrink et al., 2021 for details). In addition, the entire water temperature series of the quinquennium 2017-2022 (July to July) was reconstructed for all sites to allow comparison and increase the robustness of the analyses. GAMs were developed by "mgvc" (Wood, 2022) R package using a gaussian distribution and provided an excellent performance (Root Mean Square Error generally below 1 °C, see Table 2SM). Air temperatures (daily means) at the 16 sites were retrieved from the five meteorological stations of the upper Serio catchment (Figure 1, www.arpalombardia.it) using an interpolation based on altitude, considering the vertical gradient of each month calculated for the study area for the decade 2011-2021 (see Fiorenzo et al., 2008 for details).

2.3 Data analysis

To visualize the thermal regime of each stream site, we plotted the annual thermal profile based on daily mean values. The sites were grouped according to their watercourse. Kruskal-Wallis test and Dunn's multiple comparison test were performed to identify significant differences among mean daily water temperature and daily water temperature range (maximum-minimum) of watercourses in winter (December, January, and February) and summer (June, July and August), and over the whole year. Pairwise Wilcoxon rank sum tests were performed to compare thermal regimes among groups (stormwater vs groundwater and regulated vs not regulated). Furthermore, to assess the thermal sensitivity (Kelleher et al., 2012 sensu) of each watercourse we examined the correlation between daily air and water temperatures, and we identified similar patterns. The thermal regime includes the means, the absolute temperatures as well as the diel and seasonal amplitudes, so we calculated several temperature metrics related to the mean (annual, summer, and winter), the extremes (annual maximum and minimum), the seasonal fluctuation (maximum annual variability, maximum summer variability and maximum winter variability) and the daily range (annual mean, summer and winter maximum). We used these metrics as inputs to a principal components analysis (PCA) to describe the spatial thermal heterogeneity of the stream network. However, to compare our results with other studies we obtained an indication of the spatial thermal heterogeneity by calculating the maximum range of each thermal metric across the basin (considering all sites) as done by (Brown & Hannah, 2008). Thus, for example, the summer thermal heterogeneity was assessed as the maximum difference of summer means across all sites and likewise in winter or annually considering both the average and the variability. All the analyses were carried out using a representative year calculated from the average values of the quinquennium 2017-2022 (July-July) to remove the interannual variability and to focus on the spatial variability. Analyses were performed by R project software.

3. Results

3.1 Annual thermal profile

The water temperatures of 16 sites in the upper Serio catchment showed different patterns (Figure 2). All sites except for those belonging to Nossana stream (N1, N2) exhibited a sinusoidal curve reaching a minimum in winter (December-February) and a maximum in summer (at the end of July-beginning of August) following the air temperature pattern even if the maximum in water was slightly delayed with respect the air maximum, especially in upper Goglio, Ogna, and Serio. The sinusoidal pattern was more pronounced in some watercourses like Sanguigno and lower Goglio. Nossana showed a constant profile with a temperature around 8 °C all year long in both sites. In general, water temperature increased from upstream to downstream even if in the Sanguigno site SAN1 it was warmer than in SAN2 during January-May probably due to the snow isolation. Water temperature fluctuations at a fine scale (daily) followed air temperature fluctuations and were more marked in Sanguigno and Serio. For successive analyses, sites were grouped by watercourses since they exhibited similar profiles apart from the upper and the lower Ogna that were kept separate.

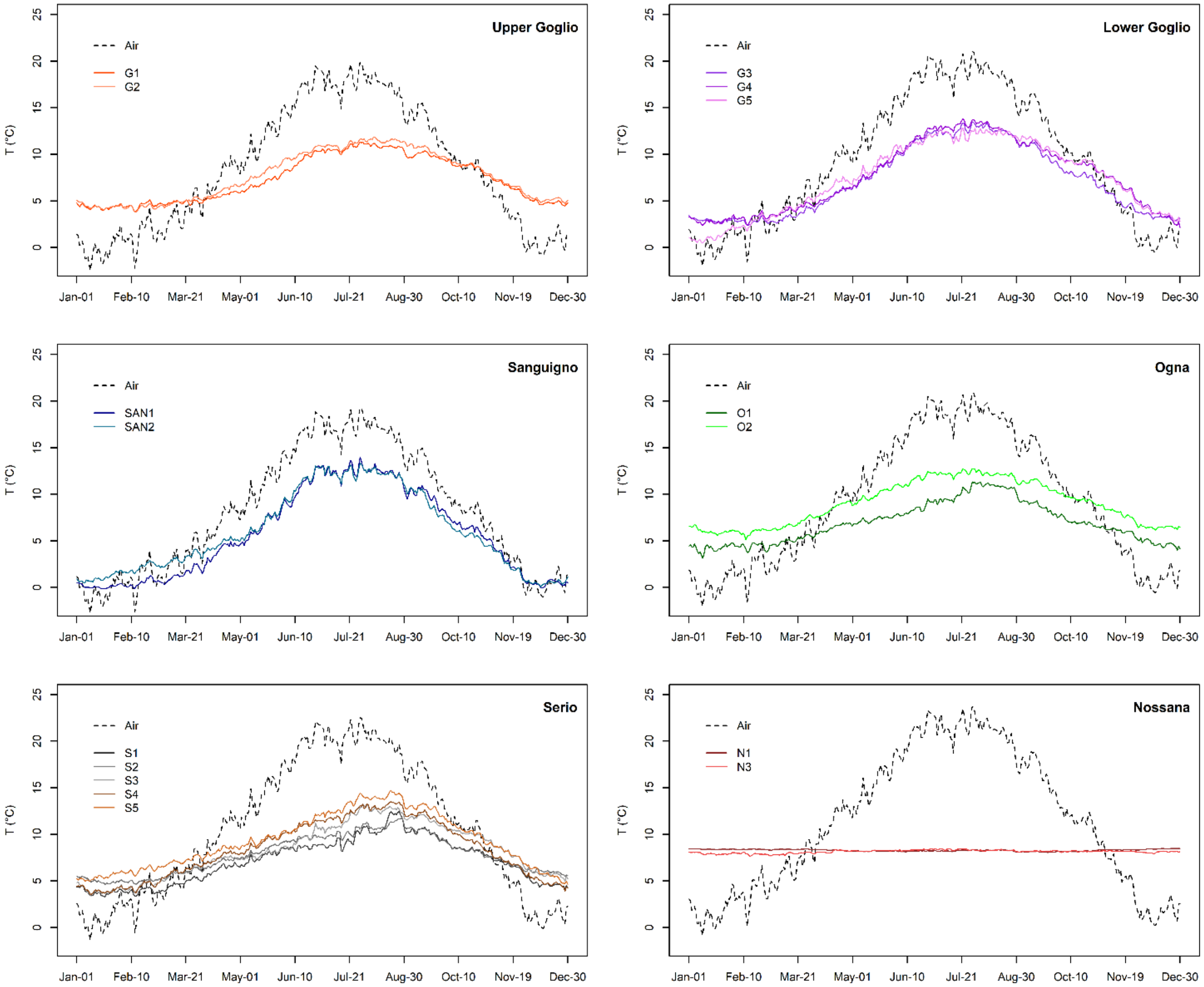

Figure 2. thermal profile of the monitoring stream sites grouped by watercourse.

3.2 Thermal regime

The studied watercourses displayed a gradient of annual thermal variability (ΔTYmax: maximum daily mean – minimum daily minimum, Table 2) (Figure 3A) with the highest variation in Sanguigno (15.0 °C) followed by lower Goglio (12.5 °C), Serio (10.1°C), upper Ogna (8.2 °C), upper Goglio and lower Ogna (7.8 and 8.0 °C), and Nossana (0.6 °C) (Table2). However, the annual averages were quite similar in all the watercourses ranging from ~6-6.9 °C (Sanguigno and upper Ogna) to 7.4 (upper and lower Goglio), ~8.15 °C (Serio and Nossana) and 9.0 (lower Ogna) (Table 2, Figure 3AYear). Regarding the daily range, Sanguigno and Serio displayed the larger annual daily variation (>2.0 °C in mean) followed by upper Ogna and lower Goglio (1.6 and 1.5 °C), upper Goglio and lower Ogna (1.1 °C) and Nossana (0.5 °C) (Figure 3B Year; Table 2). A similar pattern (but with a sharper slope) was observed in summer with Sanguigno and Serio reaching 6.0 and 4.6 °C of maximum daily variation, followed by lower Goglio and upper Ogna (3.7 and 2.9 °C), upper Goglio and lower Ogna (2.3-2.0 °C) and Nossana (1.0 °C) (Figure 3B Summer; Table 2). By contrast, in winter the maximum daily variability was lower (<2 °C) and more similar in the studied watercourses except for Serio River which exhibited a maximum daily variation of 2.7 °C (Figure 3B Winter; Table 2). The greater extremes were measured in Sanguigno for both warm and low temperatures (>16 °C and <0 °C; Table 2).

Table 2. Annual mean, maximum and minimum daily temperature (TYmean, TYmax, TYmin); summer and winter daily means (TSmean, TWmean); annual, summer and winter maximum variability (ΔTYmax, ΔTSmax, ΔTWmax) and annual, summer and winter means of daily temperature range (ΔTdYmean, ΔTdSmax, ΔTdWmax) in the 16 monitored sites.

Thermal metrics (°C)		Annual			Summer	Winter	Seasonal variability (maximum)			Daily range		
		mean	max	min	mean	mean	year	summer	winter	annual mean	summer maximum	winter maximum
Watercourse	SITE	TYmean	TYmax	TYmin	TSmean	TWmean	ΔTYmax	ΔTSmax	ΔTWmax	ΔTdYmean	ΔTdSmax	ΔTdWmax
upper Goglio	G1	7.24	12.29	3.40	10.51	4.53	7.53	1.68	1.34	1.02	1.97	1.30
	G2	7.61	12.69	3.46	11.07	4.51	8.07	1.78	1.57	1.01	2.28	1.18
lower Goglio	G3	7.11	14.63	2.06	12.10	2.94	11.11	3.76	1.17	1.43	2.79	1.29
	G4	7.59	14.89	1.93	12.43	3.14	11.67	3.45	2.20	1.31	2.91	1.48
	G5	7.43	14.73	0.21	11.98	2.38	12.49	2.71	4.00	1.73	3.69	1.96
Sanguigno	SAN1	5.61	16.81	-0.23	11.89	0.43	14.11	4.66	1.54	2.35	5.95	1.82
	SAN2	6.43	16.41	-0.31	12.92	0.66	14.99	5.30	2.73	1.82	4.73	2.07
upper Ogna	O1	6.91	13.07	2.86	9.91	4.43	8.21	3.14	2.11	1.57	2.92	1.96
lower Ogna	O2	9.00	13.89	4.76	11.99	6.16	7.67	1.90	1.75	1.10	1.99	1.25
Serio	S1	7.08	14.37	2.47	10.05	4.02	9.14	4.27	1.53	2.00	3.47	2.93
	S2	7.76	13.32	4.03	10.44	5.21	7.22	2.48	1.37	1.57	2.86	1.85
	S3	8.19	15.24	2.85	11.77	4.61	9.77	3.87	2.56	2.10	3.54	2.81
	S4	8.34	15.22	3.05	12.30	4.53	9.94	2.68	2.71	2.07	3.85	2.42
	S5	9.25	16.96	3.53	13.17	5.88	10.07	3.73	2.61	2.27	4.57	2.65
Nossana	N1	8.29	8.85	7.76	8.22	8.40	0.44	0.29	0.23	0.46	0.79	0.75
	N2	8.14	9.10	7.09	8.29	7.93	0.84	0.35	0.55	0.64	1.03	1.19
Thermal heterogeneity		3.64	8.11	8.07	4.95	7.97	14.55	5.01	3.76	1.89	5.16	2.18

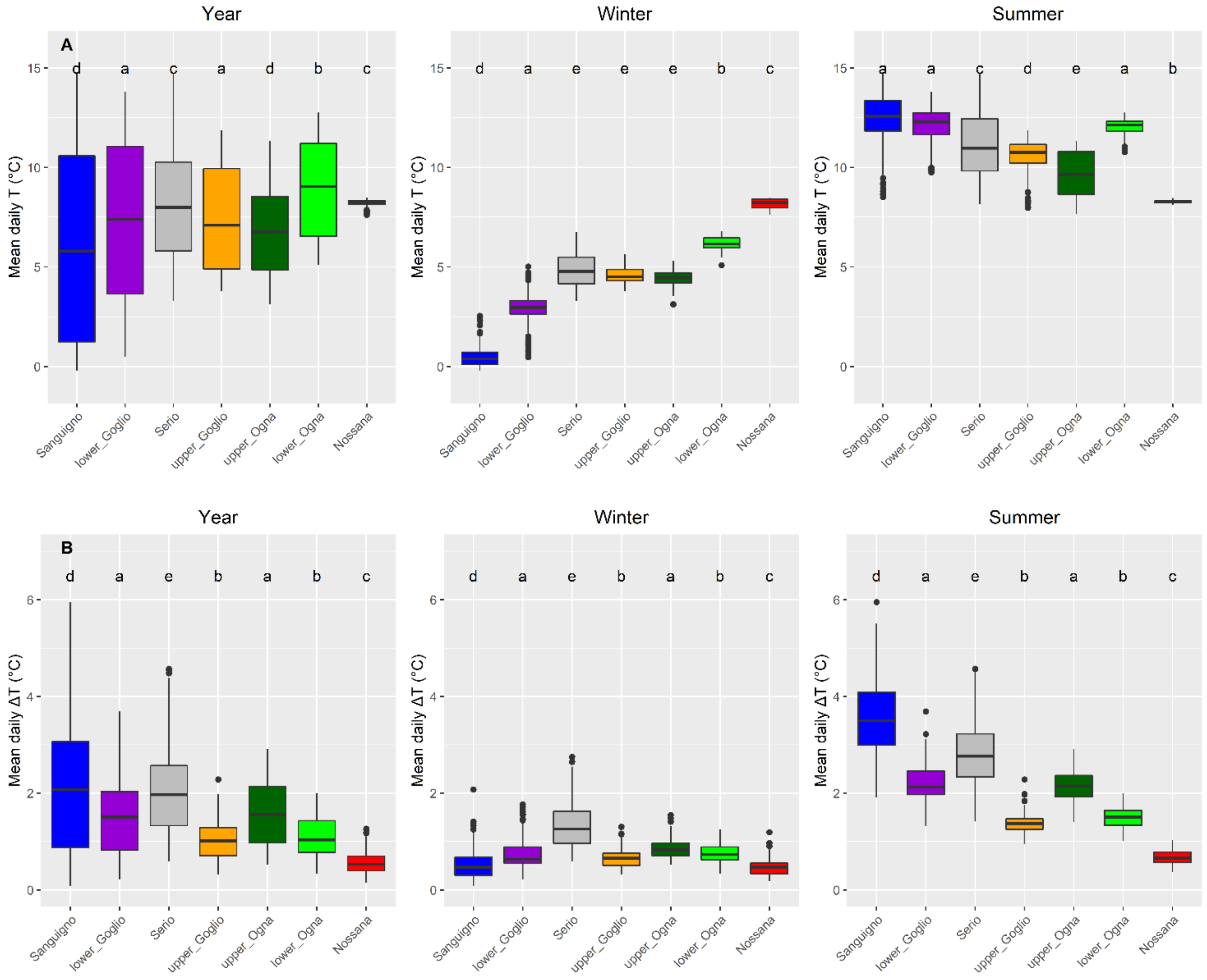

Figure 3. Boxplot representing the mean daily water temperature (A) and the mean daily temperature range (B) of each watercourse in the whole year, in winter and in summer. Different lowercase letters indicate significant differences among categories (Dunn's multiple-comparison test, $p<0.001$)

3.2.1 Source

In upper and lower Ogna, the annual water thermal variation was 8.2 and 7.7 °C, respectively, whereas in Sanguigno and upper Goglio it was 15.0 and 8.2 °C. Thus, limestone tributary streams characterized by groundwater inputs exhibited lower annual variability than streams belonging to silica watersheds (Wilcoxon test, W: 151,544, $p<0.001$ for upper Ogna vs Sanguigno and W: 182,454, $p<0.001$ for lower Ogna vs. upper Goglio). Nossana stream displayed an even lower annual water thermal variation (0.9 °C).

3.2.2 Upstream regulation

Watercourses regulated upstream by reservoirs exhibited lower variations. Indeed, the annual thermal variability was significantly lower in upper Goglio than in Sanguigno (8.2 vs. 15.0 °C, Wilcoxon test, W: 315,615, $p<0.001$) and the annual thermal variability in lower Ogna was lower than in upper Ogna even if the difference was less marked (7.7 vs. 8.2 °C, Wilcoxon test, W: 97,993, $p<0.001$). The variation in lower Goglio was between those in Sanguigno and in upper Goglio due to the flow contribution from both streams (annual variability about 15, 13.3, and 8.2 °C in Sanguigno, lower Goglio, and upper Goglio, respectively). Serio is regulated upstream by Barbellino reservoir, but its temperature annual variation is greater than in upper Goglio (11.4 vs 8.2 °C), even if, especially close to the source (S1), the thermal regime of Serio was not significantly different from the one of upper Goglio (Wilcoxon test, W: 57,132, $p<0.001$).

3.3 Thermal sensitivity

To identify the thermal sensitivity, we examined the correlation between daily air and water temperatures. Figure 4 clearly shows the existence of different thermal patterns with a ratio ($slope=\Delta Twater/\Delta Tair$) ranging from zero (Nossana) to 0.7 (Sanguigno). Indeed, Sanguigno ($s=0.69$) is the more thermally reactive watercourse, followed by lower Goglio ($s=0.51$), upper Goglio-Serio-Ogna ($s\cong0.30$-0.40), and Nossana ($s=0.0$).

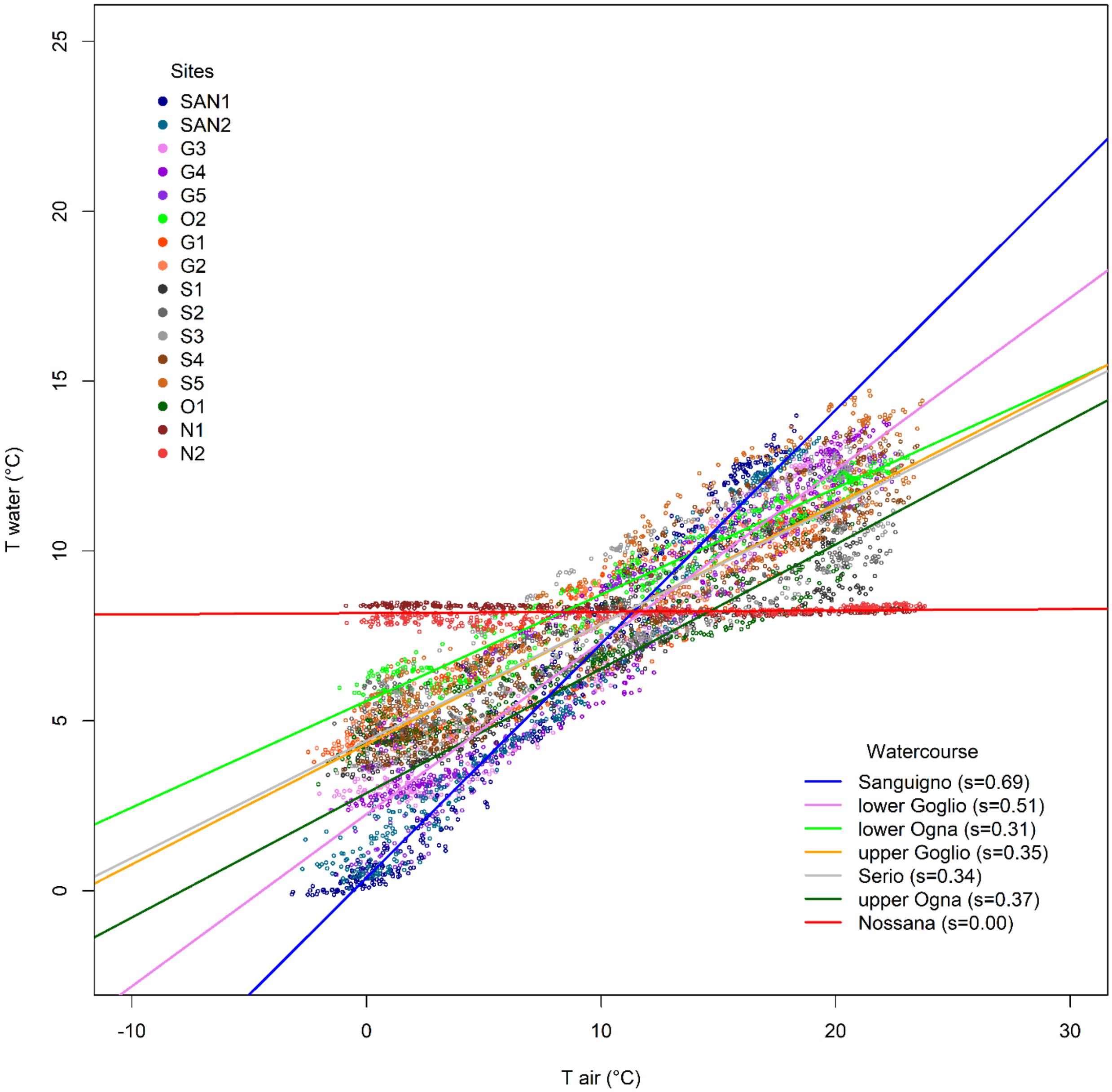

Figure 4. Correlation between daily air and water temperatures of the 16 monitored sites. Regression lines were elaborated on watercourses basis and the ratio between water and air temperatures (s=ΔTwater/ΔTair) is indicated in brackets.

3.4 Thermal heterogeneity

The different thermal regimes were described through 11 thermal metrics (Table 2) and were distinct in the multivariate space (Figure 5). The first and second principal components of the PCA accounted for about 72% and 15% of the variance, respectively, with the first axis (PC1) related both to the annual and summer thermal variability (ΔTYmax, ΔTSmax) and to the summer maximum daily range (ΔTdSmax) while the second (PC2) mainly related to the annual average (TYmean). The third component (PC3) was related to the annual daily range (ΔTdYmean) and the summer average (TSmean). Sites belonging to the same watercourse exhibited similar thermal regimes. Overall annual variability (PC1) discriminated watercourses, with the highest difference between Sanguigno and Nossana, while annual average (PC2) and/or annual daily range (PC3) discriminated sites within the same watercourse. Indeed, downstream sites displayed higher temperatures (TYmean, TWmean, TSmean) and higher annual daily range (ΔTdYmean). Nevertheless, the downstream site of Ogna (O2) was warmer (TWmean, TYmean, TYmin) than the upstream (O1) and with lower annual thermal variability (ΔTYmax).

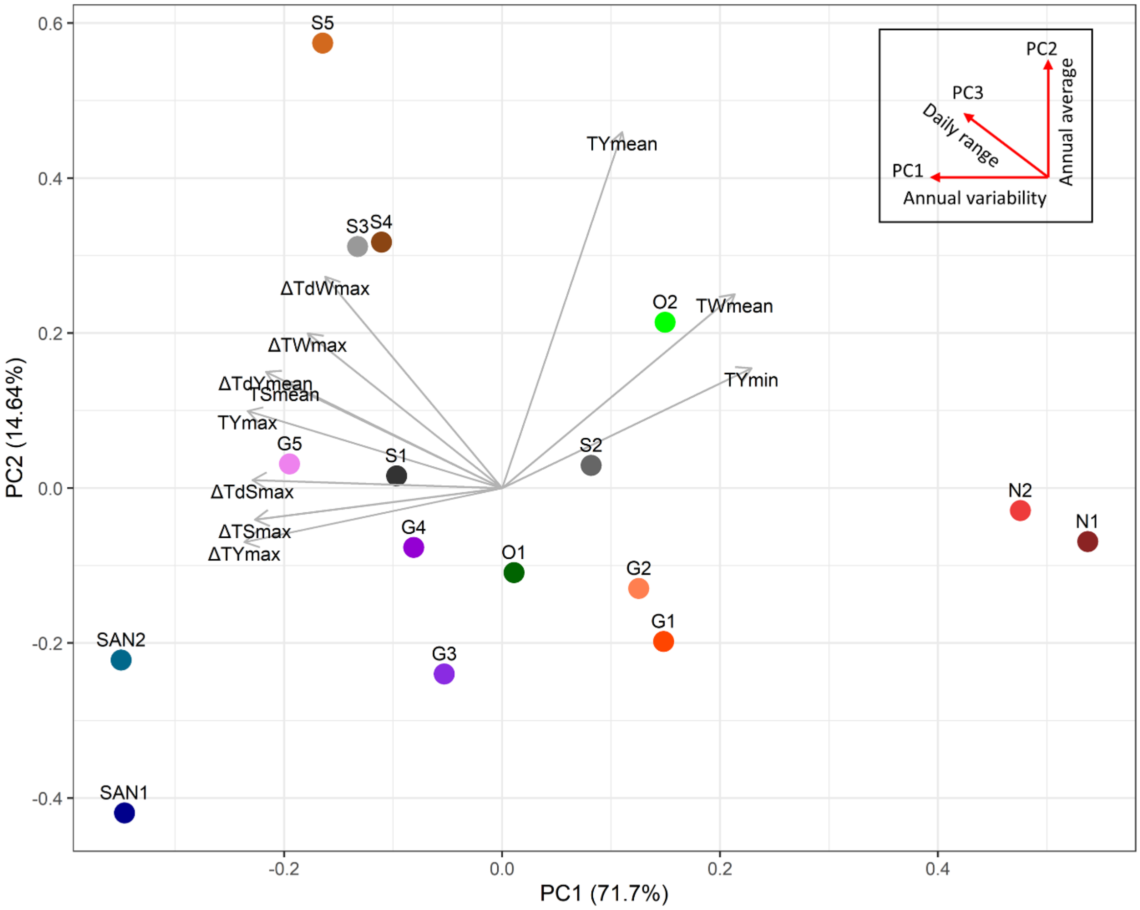

Figure 5. Principal components analysis (PCA) biplot showing the spatial heterogeneity of stream site thermal regimes (points) within the upper Serio catchment based on 11 eleven thermal metrics (arrows).

4. Discussion

4.1 Factors driving thermal patterns

Our results showed a significant difference between the thermal regime of streams flowing on silica and limestone substrate and between not regulated and regulated streams. Regarding the influence of lithology, we observed higher annual and daily water thermal variability with higher maxima and lower minima in siliceous watershed streams (Sanguigno and upper Goglio) than in limestone watershed ones (upper Ogna and lower Ogna respectively) which are fed also by groundwater with constant temperature all year long. These results are in line with the observation of Küry et al., (2017) who found that annual thermal variability was significantly higher in fissure streams than in karst springs. Similarly, Kamberovic et al., (2019), studying algal assemblages in ophiolitic and limestone springs (n=20) across the Konjuh mountains (Bosnia Herzegovina, 400-1000 m a.s.l) measured higher summer temperatures in the former rather than in the latter ones (10.4 vs 9.0 °C in average). Regarding the influence of reservoir regulation, we observed lower annual and daily variation in both regulated streams (upper Goglio and lower Ogna) than in the non-regulated ones (Sanguigno and upper Ogna) but with lower maxima in upper Goglio (~12.3 °C vs. ~16.6 °C, Table 2 TYmax) than in lower Ogna where temperatures were higher both in summer and winter (14.0 °C vs. 13.1 °C in summer and 4.8 °C vs 2.9 °C in winter, Table 2). Those differences were attributed to the type of reservoirs. Hypolimnetic-release dams decrease thermal fluctuations over time due to the thermal constancy of the hypolimnion, in particular in deep reservoirs (depth >15-20 m) where, due to thermocline, hypolimnetic water temperature is always around 4° C (Hester & Doyle, 2011; Lowney, 2000; Olden & Naiman, 2010). By contrast, shallow and small impoundments (such as Ogna reservoir, 15,000 m^3, depth<12 m) and/or epilimnetic-release dams show a contrasting pattern with increasing temperature downstream (Lessard & Hayes, 2003; Mbaka & Mwaniki, 2015). Thus, the temperature increase downstream the Ogna reservoir (~2 °C both in summer and winter) was consistent with the one measured in summer by Chandesris et al., (2019) in Ravel and Dompierre reservoirs (France) and by Casas et al., (2000) and Menéndez et al., (2012) downstream Spanish impoundments. Watercourses regulated by deep reservoirs (upper Goglio and Serio, depth>20 m) exhibited thermal patterns in line with other studies (Céréghino et al., 2002; Webb & Nobilis, 1995; White et al., 2016) with lower thermal variability (annual and daily) and winter temperatures around 4 °C, especially in the sites close to the hypolimnetic release (G1 and S1).

Finally, Nossana displayed a very constant temperature the whole year (~8.3 °C) due to the proximity to the groundwater source (~130-500 m) as found in other karstic streams (Beracko & Revajová, 2019; Bottová, Derka, & Svitok, 2013). Analysing the thermal sensitivity of the upper Serio watercourses we detected the same distinct thermal patterns of sensitivity identified by Piccolroaz et al., (2016) at the regional scale (38 Swiss rivers). Sanguigno can be defined as thermally reactive exhibiting a slope of water-air temperature correlation (s=0.69) typical of natural rivers and lake outlets (s=0.73). By contrast Ogna, Serio and Goglio can be defined as thermally resilient as they exhibited a ratio typical of regulated and snow-fed watercourses (0.30-0.36). Note that even the upper Ogna, which is not regulated upstream, displayed a thermal sensitivity (s=0.37) like the regulated streams, highlighting that groundwater inputs in this case exert the same action of a water storage (glaciers or impoundments) flattening the seasonal fluctuations. Conversely, the lower Goglio showed a thermal sensitivity intermediate to the Sanguigno and the upper Goglio (s=0.69>0.51>0.35), consistent with the two distinct water sources. Finally, Nossana can be defined as not thermally reactive as its thermal pattern was independent of the air dynamics like that of glacier streams close to the moraine and karstic streams (Uehlinger et al., 2003).

4.2 Catchment-scale thermal heterogeneity

Our survey revealed an extremely high thermal heterogeneity in the upper Serio watershed due to the interaction of different source types and management practices. The spatial heterogeneity accounted for both the annual variability and the annual averages that exhibited contrasted patterns as shown in Figure 5 (PC1 and PC2 respectively). The higher thermal difference among watercourses was observed both in summer and winter with almost 5-8 °C on average between Sanguigno (12.4° C in summer and 0.5 °C in winter) and Nossana (~8 °C all year long). The differences among summer and winter daily variations lead to the high heterogeneity of the annual thermal variability (14.9 °C Sanguigno vs 0.9 °C Nossana). By contrast, the difference in the daily range was marked only in summer with Sanguigno and the Serio exhibiting >2 °C of daily temperature variation (average, while the daily variation in Nossana was very little: ~0.5 °C). We compared our results with other studies addressing water thermal heterogeneity at the mountain catchment scale even if very little information is available for watercourses of mid-altitudes (500-1500 m). Brown & Hannah (2008), monitoring summer water temperature at 29 sites in the Taillon–Gabiétous basin (French Pyrénées, 7.7 km^2, 1780-2030 m a.s.l), observed a very high thermal heterogeneity (14.2 °C, daily mean temperature among sites) due to different conditions (glacier streams vs non-glacier south-facing hillslope streams) with a maximum difference of 17.1 °C. However, considering only streams not fed by glaciers (hillslope streams and groundwater streams) the thermal heterogeneity was comparable to the one found in our study (7-8 °C, summer daily means across sites). On the other hand, Cadbury et al., (2008), monitoring summer temperatures in 7 sites within the glacial Rob Roy basin (New Zealand, 16 km^2, 600-800 m a.s.l) found a lower thermal heterogeneity (~4.5 °C and ~8 °C summer means and maxima across sites), in particular for non-glacier streams (~3.5 °C summer means across sites). Also, Dickson et al., (2012) investigating water temperature at 7 sites in the glacial Ödenwinkelkees catchment (Central Austria, 9.2 km^2, ~2100 m a.s.l) observed a summer thermal heterogeneity of about 6 °C (in average) between glacier-fed and groundwater-fed streams. However, along the same glacier stream, a high temperature variation (~2 °C in summer) was found between sites located upstream and downstream of the inflow of a reservoir effluent. Especially during the overspill period, the water in the regulated site came from the surface of the reservoir and was 4 °C warmer than the water upstream of the diversion. At a larger spatial scale, (Küry et al., 2017b) investigating the thermal patterns of 41 high-altitude spring sites in the Swiss Central Alps (maximum distance ~300 km, altitude range ~1700-2500 m a.s.l), observed a high thermal heterogeneity depending especially on altitude and exposure. Indeed, sites annually differed at most for 4-5 °C (on average) with a gradient of 0.37 °C/100 m and 2-3 °C of difference between springs exposed North and South. Overall, the presence of both glacial and non-glacial watercourses increases the thermal heterogeneity at the catchment scale. Nevertheless, our results indicate that a similar or even higher heterogeneity can be found in mountain watercourses at mid-altitude due to different water sources and anthropogenic modification, both in summer and winter.

4.3 Ecological implications of thermal heterogeneity

The high water thermal heterogeneity over a range of time scales (daily to annual) within a relatively small area (15-20 km, as the crow flies) suggests relevant ecological implications for the aquatic biota. According to the thermal equilibrium hypothesis, hemimetabolous insect distribution depends on the species' thermal preference, since fecundity and adult size gradually diminish with increasingly cold or warm conditions (Sweeney & Vannote, 1978). Also, fish distribution and abundance depend on the thermal structure of the waterbodies, i.e. on the spatial distribution of temperatures (Coutant, 1987). A previous study carried out in the Goglio catchment pointed out significant differences among macroinvertebrates of the three stretches (Sanguigno, upper Goglio, and lower Goglio). The highest dissimilarity was found between the communities in upper Goglio and Sanguigno suggesting the possible influence of thermal alterations caused by the presence of reservoirs (Petruzziello et al., 2021). Similarly, several studies showed significant differences in diatoms (Krajenbrink et al., 2021), macrophytes (Abati et al., 2016), macroinvertebrates (Gibbins et al., 2001; Jackson et al., 2007; White et al., 2016) and fish (Edwards et al., 1979) communities downstream and upstream of a reservoir, partially driven by thermal modifications. Thus, we could expect a lower abundance of EPT taxa between O1 and O2 sites related to the temperature increase (+2 °C on average) (Lessard & Hayes, 2003) that brings ~20% of the year above 12 °C in O2 (Figure 6A).

However, the investigated watercourses displayed a thermal heterogeneity mainly related to the variability (annual and daily) rather than to average values suggesting the prevailing role of the former. Within a certain range, a high temperature variability can enhance species diversity providing a wider interval of thermal optima, even though suboptimal conditions occur over a portion of the year (Ward, 1976). For example, (Gustafson, 2008), investigating Ephemeroptera from 45 mountain streams of the Sawtooth Mountains (Idaho, USA), observed an increase in mayfly diversity (8->14 taxa) with increasing daily temperature variation range (4->12 °C). Consistently, preliminary macroinvertebrate samplings revealed a higher number of mayflies taxa (n=7) in Sanguigno, which is characterized by the highest maximum daily variation range (~5 °C), than in upper Ogna (n=6) and Nossana (n=5). Temperature changes trigger specific life-cycle phases such as migration, embryonic and larval development, egg deposition and hatching, and emergence (Brittain, 1990; Danks, 1978). So, for example, we can assume that *Serratella ignita* (Ephemeroptera), in which post-diapause development takes place above 5 °C (Bohle, 1972), hatch later in the coldest sites (Elliott, 1978) as Sanguigno and lower Goglio where water temperature keeps below that threshold for around half of the year (Figure 6A). Similarly, *Salmo trutta* hatching occurs at water temperatures above 5 °C (Elliott & Elliott, 2010) implying a sharp difference in available growth time across streams (>90% of the year in Nossana and lower Ogna; ~70-90% in Serio, upper Ogna and Goglio ~50% in Sanguigno; Figure 6A). On the other hand, egg deposition of *Cottus gobio* is optimal at a temperature around 8-10 °C (Dorts et al., 2012) making the reproduction especially suitable in Nossana stream where such temperature occurs all year long (Figure 6A). Indeed, previous studies showed well-structured populations of bullhead in Nossana (Bonacina, Canobbio, et al., 2022) and higher abundances in Nossana than in Serio (~0.15 ind/m^2 vs 0.009-0.03 ind/m^2 depending on the site Serio site, Bonacina personal observation). Water thermal regimes with contrasting annual variability can enhance shifts in the phenological cycles including desynchronization between populations (Cheney et al., 2019; Imholt et al., 2010) and changes in voltinism (Everall et al., 2015; Mackay, 1984). Thus, we can speculate distinct voltinism patterns among populations inhabiting the different watercourses and in particular in Nossana stream as the thermal constancy may induce asynchrony in the life cycle of some taxa (Bottová, Derka, & Svitok, 2013; Dobrin & Giberson, 2003). Yet, water temperature constitutes a physiologic threshold (lethal or sub-lethal) for the organism (Dallas & Rivers-Moore, 2012; Elliott & Elliott, 2010) constraining both in space and time the distribution of the species. For example, *Epeorus sylvicola* (Ephemeroptera) has an upper thermal limit of 15 °C and, consequently, we can expect its disappearance in SAN1, SAN2, and S5 when that threshold is exceeded (~5% of the year, Figure 6B) as observed by (Ouahsine et al., 1996) in the Tifferguine River (Atlas Mountains, Morocco). Overall, the effects of temperature on aquatic biota are numerous with implications at different levels, from life history attributes to the community (Bonacina et al., 2022). Thus, within a small area, distinct thermal responses linked to the high thermal heterogeneity could affect the spatiotemporal dynamics of aquatic communities (especially macroinvertebrates) including changes in the dominance and the incidence of the species within and among communities.

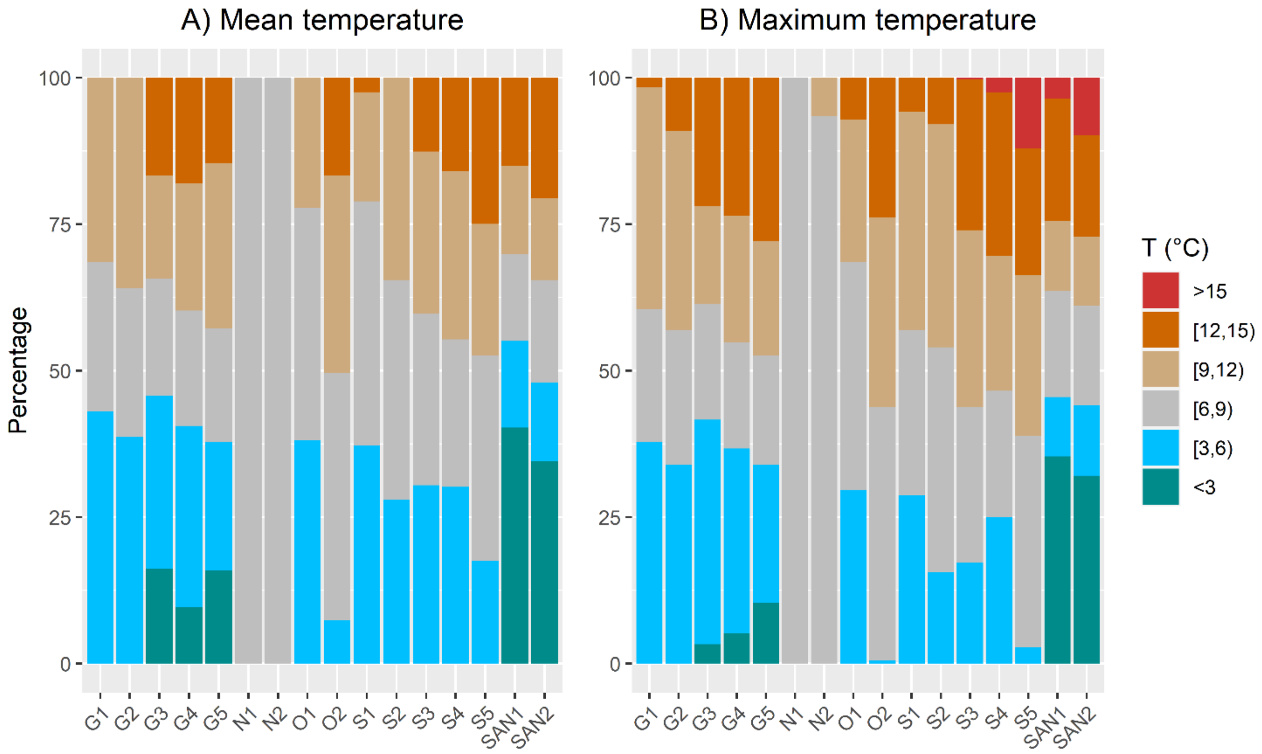

Figure 6. Percentage of days in one year with mean (A) and maximum (B) water temperature given in ranges of three-degree steps in each site.

5. Conclusion

Our survey, based on the water temperature monitoring in 5 streams of the upper Serio catchment provided new evidence of the extremely high thermal heterogeneity within the watershed due to the combined effect of the different water sources and the presence of reservoirs. Our study demonstrated (1) high thermal heterogeneity at the basin scale, similar, or greater than, the one found in alpine catchments for the interaction of glacial and non-glacial water sources and (2) the same thermal patterns found at the regional scale with groundwater and reservoir water supplies flattening the seasonal and daily thermal variability. Such thermal heterogeneity includes differences in averages (both in summer and winter) and annual and daily variations. The wide variability of water temperatures indicates the range of thermal habitats available for organisms over relatively small areas. However, other physical variables (such as hydrological conditions, resource availability and substrate types) and biotic processes (i.e. competition and predation) (Becquet et al., 2022; Hieber et al., 2005) influence aquatic communities in mountain streams and should be considered in addition to temperature when interpreting patterns of richness and abundance. Thermal regimes of mountain streams are likely to be altered by the ongoing climate warming and by the presence of water infrastructure (reservoirs, diversions), threatening aquatic ecosystems. We should expect higher temperatures, especially during summer heatwaves, also due to a reduction in discharge in non-glacial streams, associated with shorter and warmer winters (Confortola et al., 2013). Thus, we foresee higher thermal variability in non-regulated snowmelt/stormwater-fed streams (such as Sanguigno), due to their high thermal reactivity to air, than in groundwater-fed streams (such as Nossana and upper Ogna) which are less exposed to thermal changes, especially in sites close to the source. Likewise, mountain streams regulated by deep reservoirs (such as the upper Goglio and Serio) might be less exposed to increasing temperatures as the large volume of cold waters exerts a strong thermal buffer unlike watercourses fed by shallow reservoirs (such as lower Ogna). Possible changes in the aquatic communities include the extinction of cold-stenothermal taxa, the alteration of the habitat distribution (reduction/expansion), changes in abundance, phenology, and life history strategies as well as invasion of allochthonous species (Fenoglio et al., 2010). Nevertheless, high thermal heterogeneity may provide refugia for the different species increasing ecosystem-scale resilience.

Data

Data are available at: 10.6084/m9.figshare.21685229

Supplementary material

Table 1SM. water temperature monitoring period with the available data (not missing) expressed as percentage of days.

Site	Temperature monitoring		Available data (%)
	Start	End	
SAN1	14/07/2017	30/09/2022	78.52
SAN2	14/07/2017	30/09/2022	70.90
G1	14/07/2017	29/10/2021	70.28
G2	14/07/2017	30/09/2022	87.71
G3	14/07/2017	26/06/2019	96.91
G4	14/07/2017	26/06/2019	56.46
G5	14/07/2017	26/06/2019	55.48
O1	06/12/2019	30/09/2022	66.18
O2	20/12/2019	30/09/2022	91.53
S1	05/07/2018	30/09/2022	93.02
S2	05/07/2018	30/09/2022	84.75
S3	27/07/2018	30/09/2022	50.98
S4	05/07/2018	30/09/2022	59.04
S5	05/07/2018	30/11/2020	87.26
N1	05/07/2018	30/09/2022	56.98
N2	10/10/2018	30/09/2022	81.46
		Mean	74.34

Table 2SM. Performance of the GAM models used to predict daily water temperature (mean, maximum and minimum) of each monitoring site assessed with the Root Square Mean Error (RMSE) and the adjusted R^2.

Site	RSME (°C)			R^2_{adj}		
	mean	max	min	mean	max	min
SAN1	0.73	0.94	0.93	0.98	0.97	0.95
SAN2	0.93	1.03	1.09	0.97	0.97	0.95
G1	0.87	0.91	0.88	0.89	0.89	0.88
G2	0.57	0.64	0.60	0.96	0.95	0.95
G3	0.57	0.61	0.72	0.98	0.98	0.96
G4	0.48	0.50	0.59	0.98	0.98	0.97
G5	1.06	1.10	1.04	0.90	0.90	0.89
O1	0.89	0.96	0.93	0.87	0.88	0.85
O2	0.73	0.78	0.76	0.92	0.92	0.91
S1	1.11	1.45	1.06	0.85	0.80	0.85
S2	0.93	1.03	1.01	0.86	0.86	0.83
S3	0.82	0.92	0.85	0.94	0.93	0.93
S4	0.63	0.78	0.69	0.96	0.96	0.95
S5	0.66	0.79	0.75	0.95	0.95	0.93
N1	0.18	0.24	0.25	0.25	0.20	0.22
N2	0.38	0.43	0.52	0.17	0.25	0.19
Mean	0.72	0.82	0.79	0.84	0.84	0.82

CHAPTER 2

From a continuous thermal profile to a stepped one: the effect of run of river hydropower plants on the river thermal regime

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CHAPTER 2. Effects of run of river hydropower plants on the river thermal regime

Abstract

Both reservoirs and run of river power plants affect the thermal regime of rivers but despite the higher number of the latter few studies have focused on their effect. In this study, we investigated the water thermal regime of Serio River (Northern Italy), a subalpine river regulated by a reservoir and characterized by a cascade system of run of river power plants. Water temperature has been monitored continuously for more than 4 years at the extremes of 4 stretches subjected to water diversion and thermal alterations have been quantified. Our results show that hydroelectric power plants act locally causing a considerable thermal alteration that increases with the distance from the diversion weir. Indeed, within the by-passed stretch, the rate of warming doubles the natural gradient (0.47 °C/km vs 0.19 °C/km annually) with peaks in summer (0.73-0.90 °C/km on average). By contrast, the run of river power plants keep the water temperature almost constant in the diversion channels. Thus, a cascade system of run of river plants shifts the overall riverine thermal regime from a continuous to a “stepped” longitudinal profile. Results highlight that the thermal effects of run of rivers plants are not negligible and should be considered and monitored continuously. Since there are thousands of hydropower plants powered by flowing waters it’s time to consider their thermal impacts in environmental flow policies and bioassessment programs.

Keywords

Flow regulation, thermal alterations, renewable energy, e-flow, bioassessment, climate change

1. Introduction

Rivers are complex and dynamic ecological systems with a strong influence on the territory. The key drivers in the riverine processes are the flow and the thermal regimes (Chinnayakanahalli et al., 2011). The river flow controls habitat availability and suitability of fish, benthic production, trophic web relationships as well as spatiotemporal patterns of macroinvertebrate communities (Bowen et al., 2003; McIntosh et al., 2002). Furthermore, flow regulates the transport of solutes and sediments and the fate of organic matter, and shapes the riverbed morphology affecting the riparian zone and the connectivity with the terrestrial environment (Gintz et al., 1996; Mao et al., 2009). Temperature influences the ecosystem functioning (Odum, 1973; Cummins, 1974; Karr & Dudley, 1981; Coutant, 1999) controlling primary production, degradation of organic matter, and solubility of chemical species (Lamberti & Steinman, 1997; Morin et al., 1999; Robinson et al., 2001; Cairns et al., 1975; Jacobsen et al., 2003). Moreover, it shapes the spatiotemporal patterns of aquatic biota constraining the ecological niche of the species (Céréghino et al., 2002; Cox & Rutherford, 2010; Elliott & Elliott, 2010). Regarding macroinvertebrates, temperature is related to several life traits such as metabolism, life cycle, fitness, and behaviour (Bonacina et al., 2022). Water temperature is so important for biological pathways that, for instance, it has been used as the main criterion for the definition of the fish riverine zonation. In Italy the Salmonid area, the Cyprinid area with deposition on the rocky substratum, and the Cyprinid area with deposition on aquatic plants have been defined according to the following range: $T<16°C$, $17<T<20°C$ and $21<T<25°C$ respectively (Zerunian, 2002). However, an overall survey of the river network thermal regime at a regional or macroregional scale has never been done, so the zonation is approximate.

Despite the recognized biological importance of both flow and thermal regimes, research and environmental flow (e-flow) policies have been focused primarily on water quantity (Olden & Naiman, 2010; Webb et al., 2008).

Indeed, specific metrics have been developed to investigate the ecological effects of hydrological alteration (Lancaster & Downes, 2010; Poff & Zimmerman, 2010, Poff et al., 2017) and European countries have adopted various tools to manage water abstractions and maintain a flow consistent with a good ecological status (Water Framework Directive) without considering the associated thermal alteration.

The natural drivers that control the riverine water thermal regime are well known and include atmospheric conditions, hydrological factors, topography, and channel morphology (Caissie, 2006; Webb & Walling, 1997). However, anthropic activities such as thermal effluents, variations in the flow regime, reservoirs, and water diversions can play a crucial role (Caissie, 2006; Petts & Gurnell, 2005). Regarding hydroelectricity production, some studies have focused on the thermal impact caused by penstocks and diversion coming from reservoirs, while plants installed along the river are less documented although their number is higher and constantly increasing (Lange et al., 2018; Zarfl et al., 2015). Most of such plants are represented by the run of river (ROR) plants; they divert the water from the river and drive it to the turbines throughout channels or penstocks and then release it again into the river. The volume of the diverted water is generally higher than the volume left in the riverine channel (the e-flow) and runs into channel/penstocks long from a few hundred meters to some kilometres depending on the specific environmental context. In Northern Italy, the plants powered by reservoirs/basins are 225 while plants powered by flowing waters are 1,422. They provide 19,264 and 13,026 GWh, respectively, corresponding to 60.6 and 39.4% of the hydroelectric production (Permanent Secretariat of the Alpine Convention, 2009). Similarly, in Switzerland, where 55% of total electricity is produced by the hydroelectric sector, there are 100 hydroelectric plants powered by reservoirs and 566 hydroelectric plants powered by flowing waters. They supply 16,650 and 18,830 GWh respectively, i.e. 47% and 53% of the total hydroelectric production (Permanent Secretariat of the Alpine Convention, 2009). Other types of diversion include nuclear, and fossil fuelled bypass sections that bring water to cool the plants and then release it again into the river. Such plants are located mostly along lowland rivers. Often ROR plants are located sequentially and coupled with the presence of a reservoir upstream that permanently ensures water to the whole hydroelectric system. In such cases, multiple infrastructures affect the water temperature, and the overall riverine thermal regime depends on the interaction of their impacts, as in the study hereafter presented.

While several studies investigated the thermal impact induced by low river flow downstream of reservoirs and small dams at different scales (Casado et al., 2013; Chandesris et al., 2019; Maheu et al., 2016; Seyedhashemi et al., 2021; Xu et al., 2021) very few addressed the thermal impacts in by-passed stretches subjected to power plants. Among them, Wawrzyniak et al., (2012) investigated the longitudinal and temporal thermal pattern of the Rhone River (France) in relation to hydroelectric and nuclear power plant diversions and Gibeau & Palen (2020) surveyed the ROR thermal impact in by-passed reaches of Douglas and Fire creeks (British Columbia, Canada).

The present study reports the results of an intensive survey of water temperature undertaken along the Serio River (Northern Italy), a subalpine regulated river characterized by a cascade system of ROR plants. We addressed the following questions:

- Which is the impact of ROR plants on the riverine thermal regime at seasonal and daily scales in the by-passed stretches?

- Which are the main drivers that control the thermal regime of a subalpine river affected by ROR plants' impacts?
- Which is the overall effect of a cascade system of ROR plants on the riverine longitudinal thermal profile?

2. Materials and Methods

2.1 Study Area

This study was conducted in the upper part of Serio River in the Orobic Alps (Northern Italy). The upper Serio catchment covers 383 km^2 and lays between ~400 and 3,050 m a.s.l; the river is regulated upstream by a high-altitude reservoir located at 1,862 m a.s.l. and having a volume of 18.5*10^6 m^3. The water is channelled in penstocks and falls for about 1,000 meters on the turbines of the Dossi hydroelectric power plant (43 MW). Then, it is released in a compensating basin and from that to Serio River at 840 m a.s.l. (Figure 1A). 7 ROR plants are located in sequence along the upper Serio, so that the river flow is diverted through a weir in a lateral channel that conveys the water to the turbine and then returns it into the river, mixing it with the e-flow left in the main channel until the following hydroelectric intake structure withdrawing it again (Figure 1B). 4 ROR plants were considered in this study and the monitoring sites were located at the extremes of each stretch, i.e., upstream (just downstream the hydroelectric weir) and downstream (just upstream the release of water coming from the power plant) (Figure 1B). Regarding the effects of ROR plants, upstream sites were considered "not altered" while downstream sites were considered "altered" since the reduction of water flow due to ROR diversion was supposed to deviate the water temperature from the natural condition. Flows were typically diverted to run through the turbines day and night as long as the river flow was enough to generate power and to comply with the requirements for e-flow in the by-passed stretches. Such requirements for e-flows (Q_e) change across stretches, ranging between 0.47–1.36 m^3/s, and correspond approximately to 10% of the mean annual flow. Flow diversion occurred for almost all the year, except for occasional interruptions of a few days due to low flows or floods. ROR plants can swirl at most a flow corresponding to the diversion grant limit (Q_d) (Table 1). From July 2018 to January 2020 the first power plant was inactive, so the first riverine stretch (S1-2), in that period, represented the undisturbed condition, namely the absence of the ROR plants' impact (hereafter identified as S1-2*). An additional monitoring site (S5) was located downstream of the second hydropower release (downstream S4) to assess the overall effect of two consecutive ROR hydropower plants on the river thermal regime. Another site (S4C) was located at the same altitude as S4 but in the diversion channel, to assess the effect of ROR plants on the temperature of the diverted water for one complete year (September 2020-September 2021).

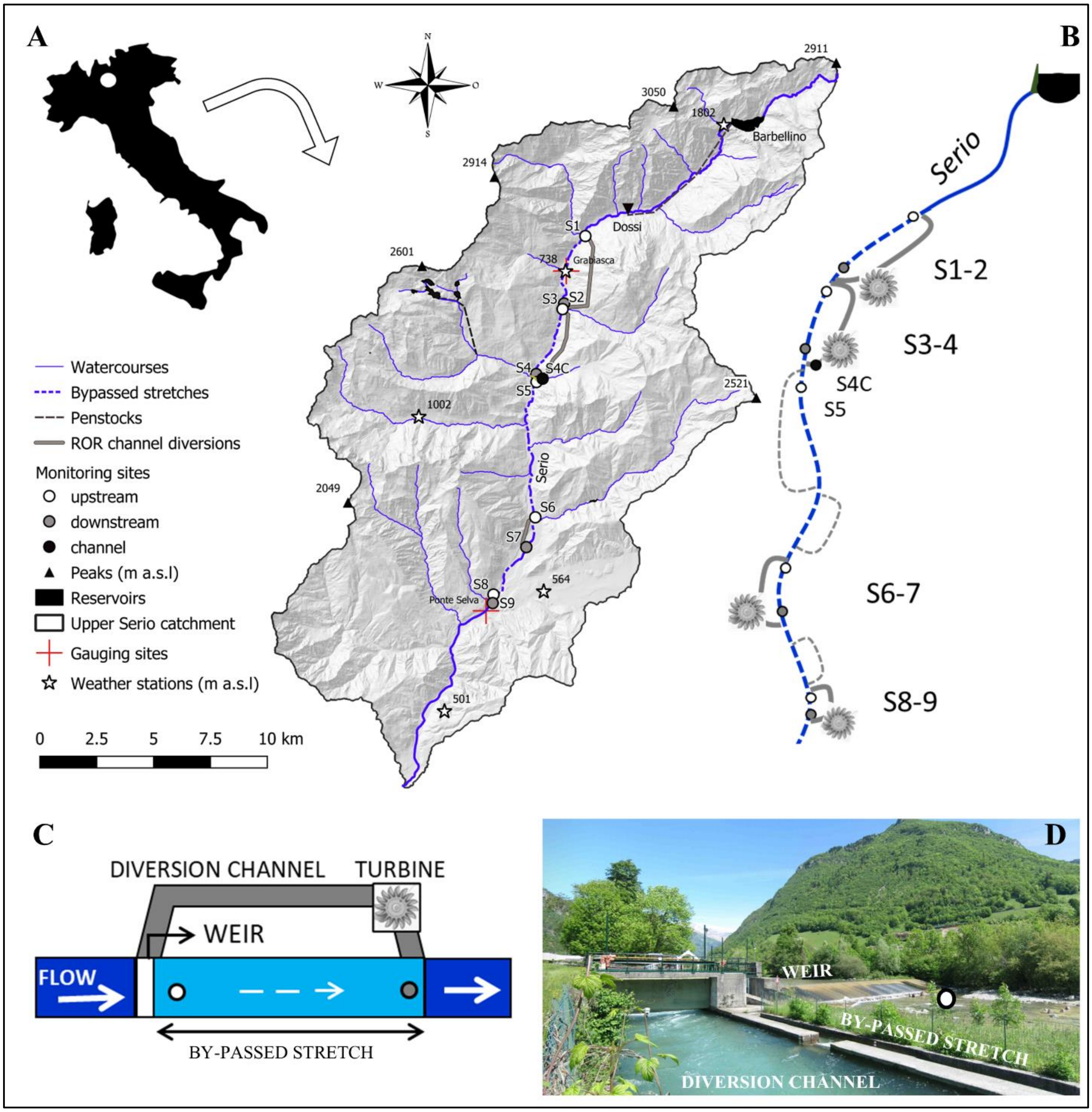

Figure 1. Map of the upper Serio catchment (A), schematic representation of the cascade system of the considered ROR plants with the monitoring sites (ROR plants not considered in the research are shown with grey dot lines) (B), schematic representation of a ROR plant (C) and picture of site S8 showing the weir, the diversion channel, and the beginning of the by-passed stretch (D).

Topographic data were elaborated through a Geographic Information System analysis (Qgis 3.4.14) and include the altitude of the monitoring sites, the distance from the reservoir, the length of the river stretches and their slope (Table 1).

Table 1. List of the monitoring sites in the Serio River. S4C site is located in the diversion channel of the S3-4 stretch.

Monitoring sites	Altitude (m a.s.l.)	Distance from reservoir (m)	Length of the stretch (m)	Slope %	Position in the diverted stretch	e-flow =Q_e (m^3/s)	Diversion grant limit (m^3/s) =Q_d
S1	784.03	9,196	3,703	2.905	upstream	0.47	6
S2	676.47	12,899			downstream		
S3	671.88	13,014	3,315	1.349	upstream	0.55	9.7
S4	627.17	16,329			downstream		
S4C	630	/	/	/	/	/	/
S5	623.84	16,466					
S6	511.09	22,959	1,528	0.648	upstream	1.133	12
S7	501.19	24,487			downstream		
S8	474.35	27,365	379	1.201	upstream	1.361	10.3
S9	469.8	27,744			downstream		

2.1 Water temperature

Water temperature was monitored in each site for more than 4 years (July 2018-September 2022) with two different types of data loggers (iButton-1921Z: range -5-26 °C, resolution: ±0.125°C, accuracy: ±1.0°C, measurement interval: 60 min and iButton-1925: range: -5-26 °C, resolution: ±0.0625°C, accuracy: ±0.5°C measurement interval: 10 min). The data loggers were cross-calibrated to ensure reliable comparisons, synchronised using the 1-Wire® software, and then fixed on the riverbed of each monitoring site. Water temperature data were downloaded and a linear interpolation between consecutive measurements was performed to obtain a continuous series of the water temperature (one value per minute) and lastly the daily mean, maximum and minimum values. When water temperature data were lacking due to sensor failure or loss (~30% of the data) the values were estimated separately for each site from air temperature by Generalised Additive Models (GAM) using daily water temperature (mean, maximum, and minimum) and air temperature (mean) time series plus the week number as an extra smoothing parameter (see Krajenbrink et al., (2021) for details) to have a continuous data set. GAMs were developed by “mgvc” (Wood, 2022) R package using a gaussian distribution and provided an excellent performance (Root Mean Square Error (RMSE) ~0.82 °C, see Table 1SM). For site S2 we performed two different models based on water data collected when the power plant was off (S2*) and on (S2). In S9 few data were collected and were not reliable since water temperature was locally influenced by a small intermittent spring coming from the river shore, so we did not consider them in the analyses.

2.3 Air temperature

Mean daily air temperatures of the 5 meteorological stations located in the upper Serio catchment were obtained from the Regional Environmental Protection Agency website (www.arpalombardia.it) and used to estimate air temperatures in the monitoring sites throughout an interpolation based on altitude as described in Fiorenzo et al., (2008). Thus, we calculated the mean monthly gradient (lapse-rate) of the 2011-2020 decade in the upper Serio catchment using a linear interpolation that correlates the mean monthly temperature of each meteorological station with the altitude as proposed by Garen & Marks (2005). Then, the daily air temperatures monitored by the meteorological stations were reported to the sea level using the calculated vertical gradient of the considered month and averaged. Finally, the air temperature was retransferred to the elevation of the monitoring site using the lapse-rate of the considered month (Waring & Running, 1998).

2.4 Flow data

Mean daily flows in each riverine stretch have been reconstructed using the daily flow data monitored by the gauging sites, the diversion rates, and the residual flow provided by the hydropower’s operator. The residual flow (Q_r) is the flow left by the plants in the by-passed stretches and usually correspond to the e-flow (Q_e). The gauging sites were located at the extremes of the study area: the first, Grabiasca, downstream of S1 while the second, Ponte Selva, about 500 m downstream of S9, as shown in Figure 1A. In addition, on several occasions, the riverine current speed was measured (collecting data every 0.5-1 m by the HACH-FH950 electromagnetic flowmeter) and data were used to calculate the discharge flow by both mid and mean section methods (averaged) (Gore & Banning 2017; Mirauda et al., 2011). These values were used to better calibrate the flow estimations. Indeed, the total flow in each stretch was estimated by scaling the gauging site flow measurements on the watershed area of each stretch. Thus, the flow in the stretches (Q_s) affected by ROR diversions consisted of the residual flow (Q_r) when the total flow estimation (Q_t) was smaller or equal than the hydroelectric grant limit; in the other case, it resulted from the difference between the estimated total flow and the hydroelectric grant limit (Q_d, see Table 1). The same procedure proved to be robust in a previous study where a high correlation between the instantaneous flow measured at each site (*n*=85) and the estimated mean daily flow was observed (r=0.75, p<0.001; Figure S1 Supplementary material of Fornaroli et al. (2019)).

$$Q_s=Q_r \text{ if } Q_t\leq Q_d$$
$$Q_s=Q_t-Q_d \text{ if } Q_t>Q_d$$

2.5 Data analysis

2.5.1 Serio water thermal regime

To describe the water thermal regime of each site, we plotted the annual thermal profile based on daily values (mean, maximum and minimum) averaged for the 4 years of the survey (July 2018-July 2022). One-way ANOVA followed by the multiple comparisons Tukey’s HSD test was performed to compare daily water thermal mean and range (maximum-minimum) of each monitoring site through seasons and point out possible significant differences. Similarly, the significance of the differences between water temperature downstream and upstream of each stretch (both daily means and maxima), normalized for the stretch length was tested. These analyses were conducted separately for each season, identified as winter (December–January–February), spring (March–April–May), summer (June–July–August), and autumn (September–October–November).

2.6 Drivers of water thermal regime

To identify the main drivers that control the water thermal regime of Serio River explanatory variables related to meteorology, topography, and flow were selected and their respective contribution was assessed to describe the water temperature using model selection and optimization. Stochastic models were preferred to deterministic ones as they require fewer input data and are relatively simple in implementation and application. Thus, daily water temperatures were analysed using the GAM model as previously described (2.1). However, in this case, other variables (see Table 2) that allow to better describe the water temperature along the whole upper Serio were included. The relevant variables were selected by a forward procedure starting with a model based only on daily air temperature (T_a) and adding one more variable step by step. At each step the performance of the model was assessed using the RMSE. The selection stopped when the addition of a new variable did not improve the accuracy of the result by at least 0.05 °C (Table 2SM). The optimal model was fitted using 70% of the data (homogenously distributed among seasons and sites) and validated with the remaining dataset (30% of the data) in each site using the RMSE and the adjusted R^2 parameter (R^2_{adj}). The thermal sensitivity (Kelleher et al., 2012) was assessed at each site correlating daily air and water temperatures and analysing the slope of the regression ($s=\Delta Twater/\Delta Tair$). All the analyses were performed in R project software.

Table 2. Variables identified as potential drivers for the upper Serio water thermal regime with mean, standard deviation, and range.

Variable	Type of variable	Acronym	Unit	mean	sd	range
Mean daily air temperature	Meteorology short term	Ta	°C	10.88	7.54	-6.59-28.68
Week number	Meteorology long term	Wn		26.59	15.06	1-53
Distance from the reservoir	Topography distance from the source	D	m	18,008.62	6,039.14	9,344.5-27,579.5
Length from the weir	Topography effect of ROR plant	L	m	888.74	1,387.48	0-3,703
Mean daily flow in the by-passed stretch	Hydrology	Q_s	l/s	5,421.29	5,958.41	313-101,747.18
Mean daily flow in the diverted channel	Hydrology	Q_d	l/s	1,346.90	2,541.15	0-11,955

3. Results

3.1 Thermal regime of Serio River

The annual water thermal profiles were plotted to compare the thermal patterns in not-altered (upstream) and altered (downstream) sites as shown in Figure 2.

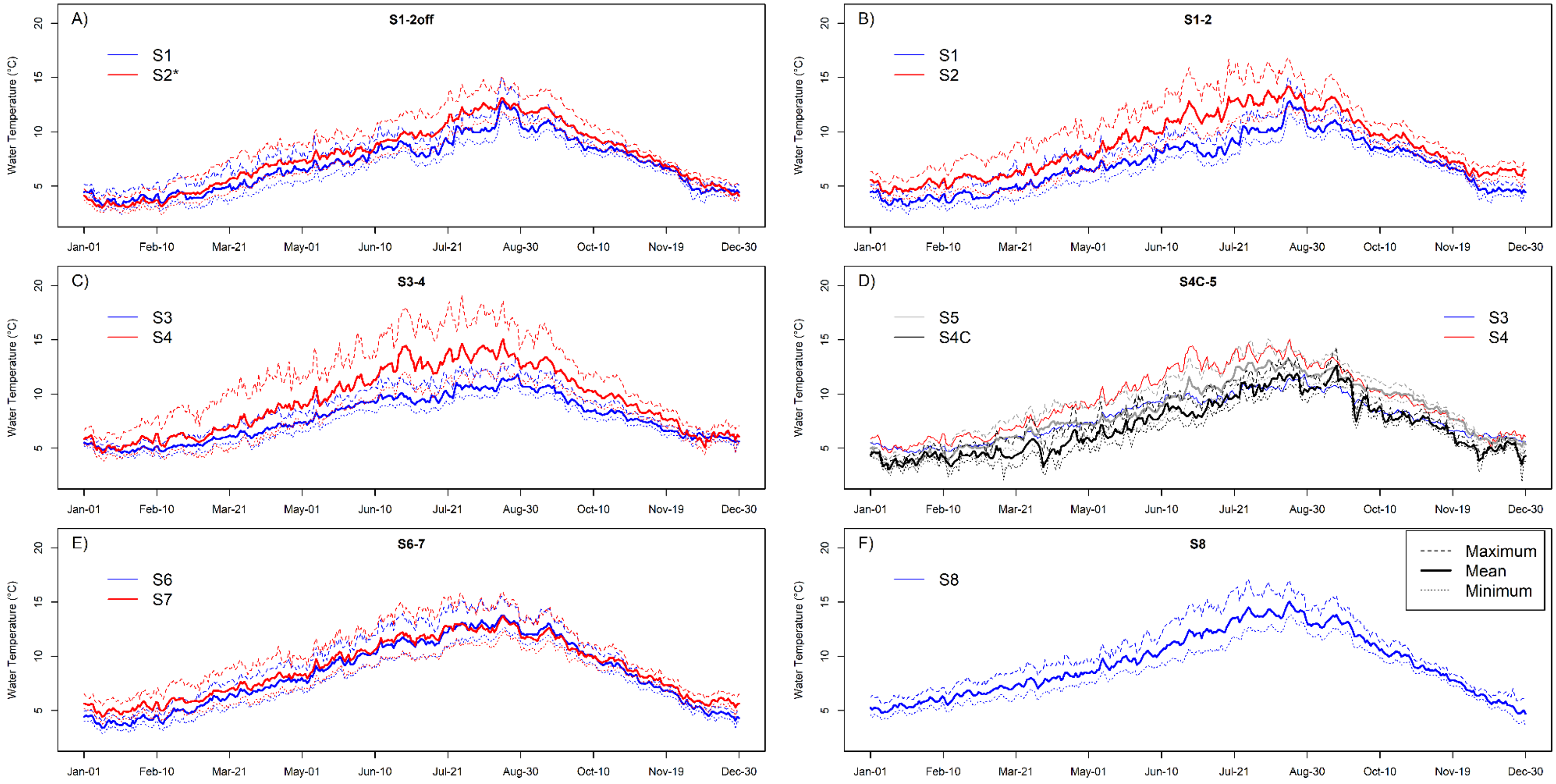

Figure 2. Water thermal regime in the monitoring sites of the upper Serio River averaged on 4 years (July 2018-July 2022). Upstream (blue lines) and downstream (red lines) water temperature (daily minimum, mean and maximum) are reported per each by-passed stretch (graphs A, B, C, E). For the last stretch (graph F) only the upstream temperatures are indicated. Graph D compares the thermal profiles of the diverted water (S4C), of the river water downstream the ROR release (S5), upstream and downstream the by-passed stretch (S3 and S4 respectively).

Annual thermal profiles exhibited a seasonal pattern ranging from 3-5 °C in December-February to 10-16 °C in July-August (on average) with water temperatures increasing with increasing distance from the headwater (from S1 to S9), especially in summer. Downstream sites (S2*, S2, S4, S7) were warmer than their upstream counterparts, especially S2 and S4 that showed sharp differences between the maximum and the mean (Figure 2 graphs B, C).

As shown in Figure 3A water temperature was significantly different between unaltered and altered sites both at annual and seasonal scale except for S6-S7 during summer and autumn. Site S4C (diverted water) was generally more similar to S1 site (both annually and seasonally) than to the adjacent sites (in particular S3, S5). The daily water temperature range presented marked seasonal patterns, with smaller variations in winter (generally below 2.5 °C) than in the rest of the year. All altered sites have a significantly higher daily variation compared to their unaltered counterparts, both annually and seasonally. Such variation reached a daily range up to 6-8 °C in sites S2 and S4 unlike S1 and S3 (<5 °C) (Figure 3B). The diverted water had the same temperature (or even lower) along its running way (from S3 to S4C) while the river water temperature increased from S3 to S4 and decreased after the input of the diverted water in S5 (Figure 3A). Site S4C had the smaller range of daily variation (<3 °C) and seasonal variation (Figure 3B).

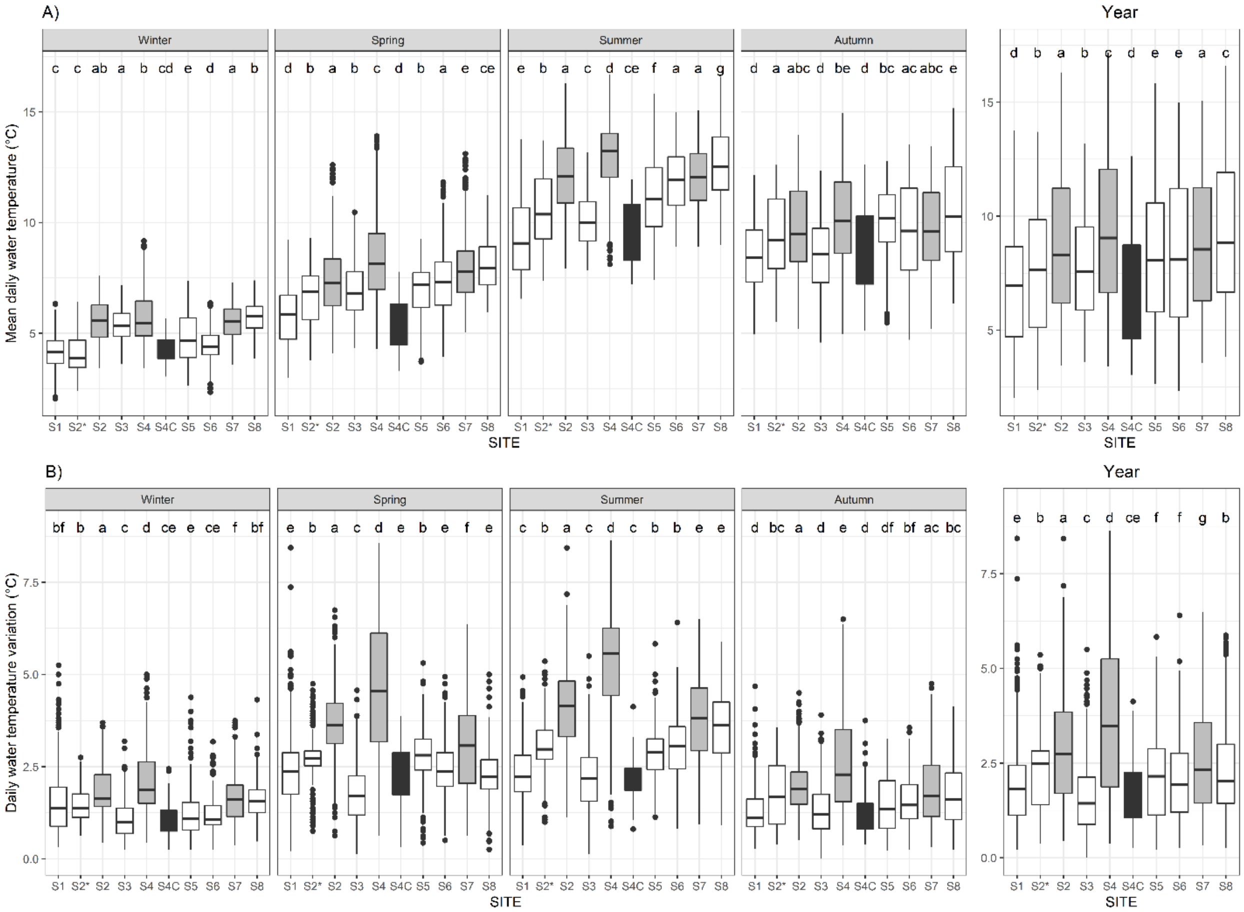

Figure 3. Mean daily water temperature and temperature range in the monitoring sites of Serio River in the different seasons. Different lowercase letters indicate significant differences among sites in the same season (Tukey's multiple-comparison test, p<0.001). White and grey colors indicate not altered and altered sites respectively, while black identifies diversion channel.

3.2 ROR plants thermal alteration in the diverted stretches

The first power plant was inactive in the period July 2018-January 2020 allowing the estimation of the longitudinal natural thermal gradient in the stretch S1-S2* (0.19 °C/km in average) that was significantly lower than the altered stretches at annual scale (0.47, 0.48 and 0.30 °C/km S1-2, S3-4 and S6-7 respectively, Figure 4A year). This is particularly clear in summer when temperature variation in the stretches S1-2 and S3-4 was greater (0.73, and 0.90 °C/km in S1-2, S3-4 vs 0.32 °C/km in S1-S2*, respectively) as shown in Figure 4A Summer. The differences in the thermal gradient assessed with maximum daily temperatures were even sharper, with gradients of 0.25, 0.63, 0.87 and 0.53 °C/km in S1-2*, S1-2, S3-4, S6-7 respectively (Figure 4B Year) and peaks of 2-3 °C/km in S1-2 and S3-4 (daily mean, Figure 4B Summer). The variation in S6-7 was smaller than in S1-2 and S3-4 (Figure 4A and 4B Year) with a marked seasonal pattern ranging from 0.69 °C/km in winter and 0.09 °C in summer and autumn (Figure 4A). However, it was still significantly different from the natural gradient measured in S1-2* both for means and for maxima (Figures 4A and 4B Year).

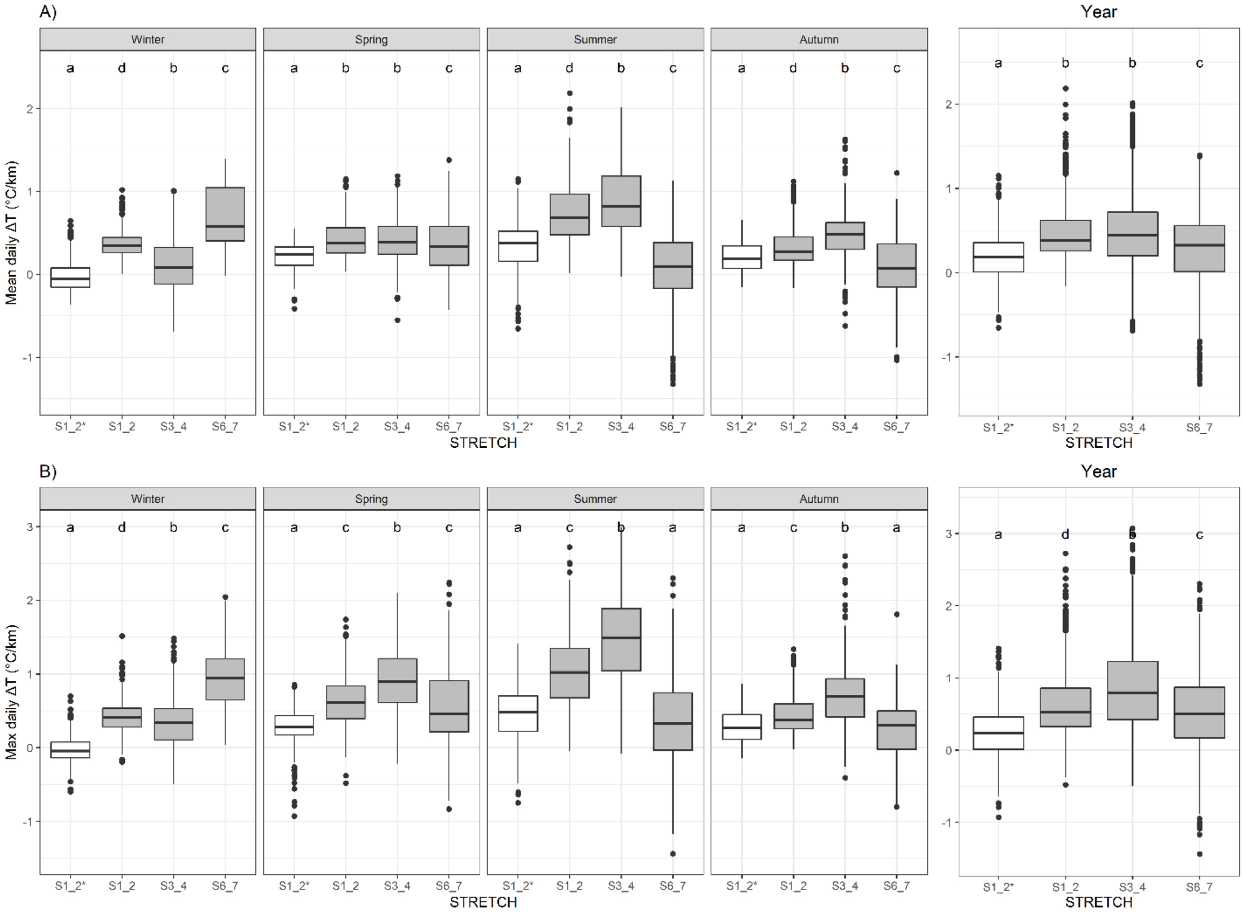

Figure 4. Mean (A) and maximum (B) daily water temperature variations between downstream-upstream sites. White color indicates the first stretch when the ROR plant was inactive. Different lowercase letters indicate significant differences among sites in the same season and in the whole period (Tukey’s multiple-comparison test, p<0.001).

3.3 Drivers of water thermal regime

Based on the stepwise regression it was possible to identify the main drivers that control the water thermal regime of the upper Serio River. Indeed, according to the forward selection the most explicative variables are air temperature (Ta), week number (Wn), distance from the headwater (D) and distance from the weir (L) (see Tables 2SM and 3SM):

$$Tw \sim s(Ta) + s(Wn) + poly(D, 3) + poly(L, 2)$$

The model provides an overall excellent performance (RMSE<0.8°C and $R^2_{adj}>0.92$) and can be successfully used to predict water temperature along the entire upper Serio River since the predictive capacity is high in all sites (RMSE<1°C and $R^2_{adj}>0.79$). Daily air temperature (Ta) was the most explicative variable of water temperature explaining the 77% of the total observed variance (Table 3). However, the correlation Tw~Ta alone varies among sites with higher values in downstream sites (0.37 and 0.39 in S2 and S4) than in the downstream ones (0.28 and 0.26 in S1 and S3) (Figure 5) pointing out the possible influence of ROR plants on the relationship between air and water temperature. Nevertheless, the thermal sensitivity (s=0.39) in the unaltered site S6 was similar to that one of the altered sites.

The other explicative variables were related to the period of the year (Wn) and the topography (D and L) while flows (Q_s and Q_d) were not retained as they did not improve significantly the model fit (Table 2SM). The effect of ROR plants can be disentangled by the L variable; indeed the sites whose thermal regime is not influenced by ROR plants have a distance from the weir equal to zero.

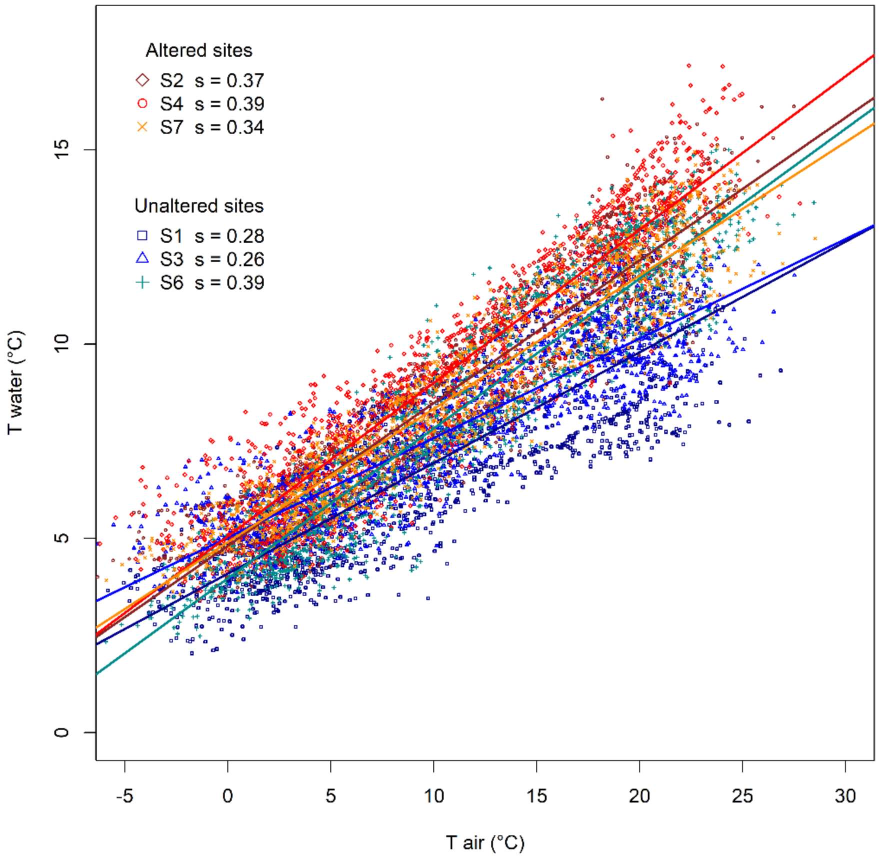

Figure 5. Correlation between daily air and water temperatures. Altered and unaltered sites were identified by red and blue colors respectively. The slope of the regression (s=ΔTwater/ΔTair) is indicated.

4. Discussion

4.1 Water thermal regime

The water thermal regime of Serio River is characterized by consistent seasonal (~8-12 °C) and daily variations (from 1-2 °C in winter to 6-7°C in summer in altered sites) as well as by site variations (Figure 2), in line with other similar rivers as the Noce River (Trentino, Italy, Zolezzi et al., 2011). According to Piccolroaz et al., (2016), Serio can be defined as a “resilient” river concerning thermal sensitivity because, due to the high-reservoir regulation, the dependence of water on the atmospheric conditions (ΔTwater/ΔTair=0.33, considering the whole upper Serio) is below 0.55, the threshold separating thermally resilient and thermally reactive rivers. In addition, its sensitivity is close to 0.30, the typical value of reservoir regulated rivers estimated at a regional scale. Similarly, the thermal gradient of the upper Serio is around 0.21 °C/km (from S1 to S8) which is a typical value for intermediate responsive rivers (Caissie, 2006) and is slightly below the natural rate of 0.25-0.27 °C/km, estimated in the Douglas Creek (British Columbia, Canada; Gibeau & Palen (2020)). The water thermal regime of the upper Serio depends mainly on meteorological conditions (daily mean air temperature and period of the year) but also on the presence of hydropower plants (both high-altitude reservoir and ROR plants) whose influence, according to our model, is related to the distance from the reservoir and the ROR weir (D and L respectively). The flow was not retained as an explicative variable of the water thermal regime as the topography was already sufficient to obtain reliable estimates. Thus, in this case, thermal alteration seems related to riverine structural features as stretch length and distance from the headwater rather than to flow management. This makes the water temperature prediction more feasible since data referring to the flow released by ROR plants are generally not available (at least not for all plants). It must be noted that within the by-passed stretches the flow is almost always (>300 days/year) the e-flow.

4.2 ROR plants’ thermal alterations

According to the results (Figures 2 and 4), ROR plants alter the thermal regime in the by-passed stretches, especially in S1-2 and S3-4. Indeed, the rate of warming double in the presence of water diversion than in “natural” conditions (~0.47 vs 0.19 °C/km in S1-2* annually) and even larger in summer and considering the daily maxima (~0.8 vs 0.3 °C/km summer mean; ~0.8 vs 0.25 °C/km annual maximum; ~1.5 vs 0.5 °C/km summer maximum) (Figure 4). ROR plants, reducing considerably the flow in the by-passed stretch (~1/10 of the diverted flow on average, Table 1), increase of water temperature from air temperature

(Figure 5 Tw/Ta in altered vs unaltered sites) causing a sharp thermal variation (mostly warming but also cooling) within each stretch. The maximum daily water thermal alterations occurred during the summer heat waves when the warm air and the prolonged drought exacerbated the thermal impact of the ROR plants. In these periods the daily variation reached about 0.73-0.90 °C/km (in S1-2 and S3-4 on average) with peaks over 2.5 °C/km. For example, site S4 was around 4 °C warmer than S3 (14 vs 10 °C Figure 2) on average with maxima differing more than 8 °C (in ~3 km). Such variations were in line with the one estimated by Gibeau & Palen (2020) for the by-passed stretches of Douglas and Fire creeks (0.46 and 0.33 °C/km the annual average up to 0.86-1.24 °C/km in summer). By contrast, no marked alterations were observed in the Rhone River (France) where the thermal gradient in the by-passed stretches and in the unaltered ones was comparable (~0.05 °C/km). In that case, the differences between the by-passed stretches and the diversion channels were +0.5-0.6 °C in summer and -0.6-(-0.2) °C in winter (in 12-14 km), considerably lower than in Serio River (2-3 °C in summer and 0-1.5 °C in winter in 3-4 km).

However, such sharp alterations were observed especially in S1-2 and S3-4 stretches while the thermal gradient in S6-7 differed significantly from the S1-S2* one only in winter and spring. Moreover, the thermal sensitivity in S6 was comparable to the one observed in the other downstream sites (~0.34-0.39 in S2, S4, and S7). This could be explained by i) the inflow of a tributary stream (Ogna) between S6 and S7 that, despite its low flow (<1 m^3/s) might contribute to cool the water, especially in summer, ii) the groundwater upwelling due to the change of the lithology from siliceous to limestone downstream of S5, and iii) the shorter length of the stretch (1.6 km vs 3-3.7 km). The inflow of Ogna could also explain the sharp winter thermal gradient since, in winter, the temperature is higher in Ogna than in Serio in S6 (Bonacina, personal observation). The observed effect of ROR plants (~2.7 °C in summer in S1-2 and S3-4) agreed with the one reported by Prats et al., (2010) for Ebro River (2.3°C). In that case the primary cause was the input of high temperature effluents from nuclear plants which, however, had a heating effect all year long while ROR plants cause both water heating and cooling.

4.3 From a continuous water thermal profile to a stepped one

ROR hydropower plants withdraw water to produce energy and then, discharge it again into the river. The temperature of the water released through the turbines is similar (or even colder) to the upstream water temperature (Figure 2 and Figure 3, S4C vs. S3 sites) because the diverted channels are often underground or shaded and the flow velocity is high (2-3 m/s).

As the ratio between the two flows (diverted and residual) is around 10:1, the mixing mitigates the thermal variation occurred within the by-passed stretch. In the case of a cascade system of ROR plants, the overall impact (both in the by-passed stretches and in the diverted channel) must be defined comparing the longitudinal thermal profile with the thermal profile of a reference river not affected by ROR plants. Thus, we used Eq4 to compare the water temperature longitudinal profile of Serio River with or without all 7 ROR plants. (Figure 6).

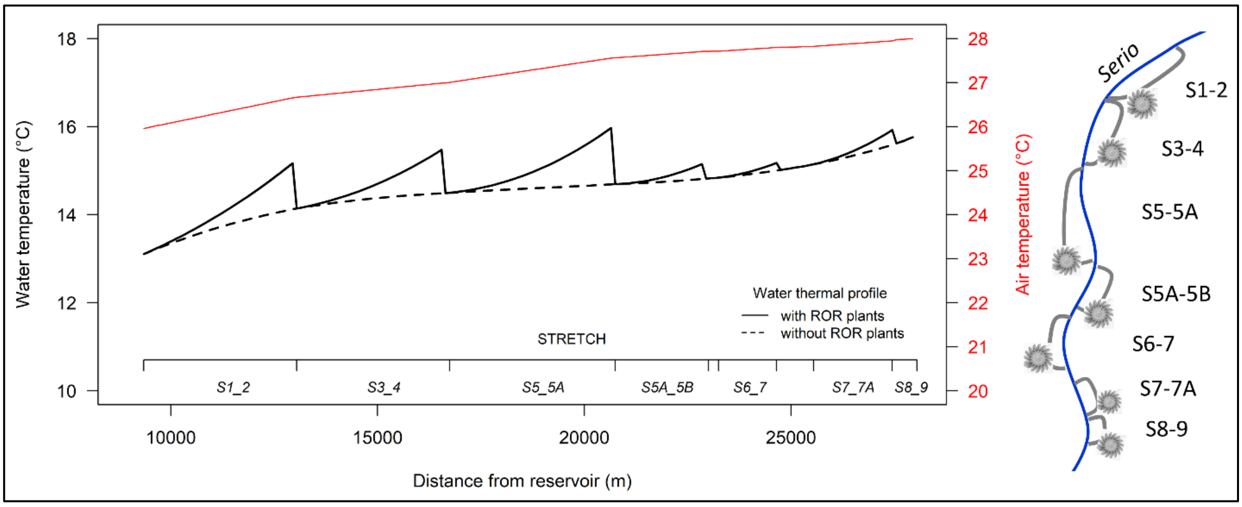

Figure 6. Longitudinal water thermal profile (daily mean) of the upper Serio River with or without ROR plants in the 35th week (Tair at Ponte Selva = 28 °C).

As shown in Figure 6, in the absence of ROR plants the longitudinal water thermal profile follows a continuous pattern typical of headwater streams (Fullerton et al., 2015) while with ROR plants it exhibits a “stepped” profile with sharp drops downstream the releases from ROR plants, especially for the longer stretches (S1-2, S3-4 and S5-5A).

Indeed, ROR plants act in two opposite ways: on one side they cause marked local heating due to the flow reduction in the river channel, on the other side they cause cooling in the diverted channel. Overall, a cascade system of ROR plants shifts the whole riverine thermal regime from a continuous to a “stepped” profile.

4.4 Ecological implications of ROR thermal alteration and e-flow policies

Thermal variation in the observed range (1-8°C) could affect the aquatic biota as shown by (Lessard & Hayes, 2003) studying the effect of thermal alteration caused by small dams with superficial discharge. Indeed, they observed that small dams warmed the water downstream causing shifts in macroinvertebrate community composition, an increase in fish species richness, and a reduction in the densities of brown trout, brook trout, and slimy sculpin populations. Thus, we can suppose differences in macroinvertebrate assemblage composition at the extremes of the stretches driven by an increase in water temperature and similarly between upstream and downstream of the ROR water release due to the sharp thermal drop. Similarly, the contrasting thermal conditions may affect the growth of fish (in our case *Salmo trutta* dominated) since the cumulated degree-day substantially differ (i.e: ~3161, 4211, and 3433 °C/year in S3, S4, and S5 respectively) as discussed by Gibeau & Palen (2020). Such possible changes should be investigated by disentangling the effect of water temperature from other factors such as hydrology and water quality, already integrated into the e-flow bioassessments.

In light of the presented results, the temperature monitoring laid down by Directive 2006/44 (Parliament, 2006) seems pretty inadequate to detect ROR thermal impacts because the thermal regime has daily and seasonal variations not detectable with a weekly sampling. The monthly sampling established by the Italian transposition (D.Lgs 152/2006) is obviously even more inadequate. Moreover, according to the Directive the thermal alteration must not exceed 1.5 °C with respect to the natural conditions (in salmonid waters). Probably ROR plant diversions cannot be identified as “thermal discharges”; however, their indirect impacts in the by-passed stretch can easily overcome the threshold of 1.5 °C.

Rising temperatures have been observed in rivers in the last years (Bonacci et al., 2008; Hari, 2006; Michel, 2020) and dry periods are expected to be more frequent and intense due to global warming, in particular in the Alps (Viganò et al., 2015), so the thermal alterations could have important ecological effects on lotic systems in the close future and should be investigated deeply (Fuso et al., 2023). To properly quantify possible impacts of ROR thermal alteration specific indicators should be elaborated as it has been done to assess thermopeaking caused by hydropeaking (Carolli et al., 2015; Vanzo et al., 2016).

To the author’s knowledge this is the first study highlighting the thermal effect of a cascade system of ROR plants on a subalpine river and only few studies (Gibeau & Palen, 2020; Wawrzyniak et al., 2012) investigated the effect of single ROR plants in different geographical contexts. As, especially in mountain regions, there are thousands of plants powered from flowing waters (Figure 7), further research, at a larger scale, should attempt a rigorous investigation of the thermal alterations induced by ROR plants. Indeed, local factors such as channel morphology, tree canopy, dam characteristics, and management practices could display different thermal patterns.

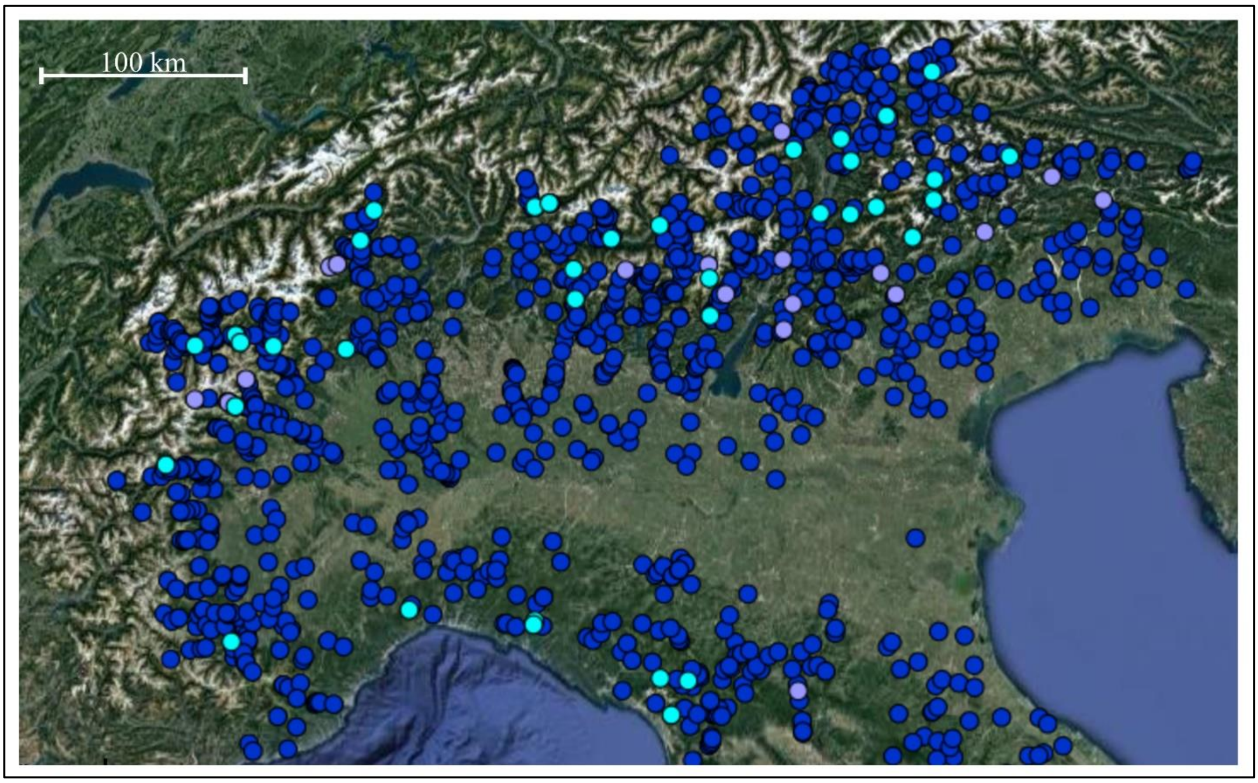

Figure 7. Hydropower plants powered by storage/reservoir (violet and light blue) and by flowing waters (blue) in Northern Italy (Italian Energy Services Manager, GSE S.p.A: www.gse.it).

5. Conclusion

This study showed that the thermal regime of Serio River depends firstly on the meteorological conditions and secondarily on the anthropogenic impact caused by hydropower plants. Two different impacts are acting on the upper Serio water thermal regime in opposite ways and at different spatial scales. In the by-passed stretches where the flow is reduced by water withdrawal for ROR plants, the dependence between air and water temperature is strengthened, especially at the maximum distance from the weir. Hence, locally, the rate of warming (cooling) is higher in the stretches subjected to ROR plants diversion than in the “natural” stretches. On the other hand, ROR plants reduce the dependence between air and water temperature in the diverted channels. Thus, altogether, a cascade system of ROR plants shifts the overall riverine thermal regime from a continuous to a “stepped” profile.

Similarly to the development of flow-ecology relationships that have been done in the last twenty years regarding e-flow policies, now emphasis must be placed on the temperature-ecology relationship. This information could allow to predict/describe thermal alterations and to assess their impacts on the aquatic biota. Indeed, possible interventions on the management of e-flow, on the length of the by-passed stretches, on the vegetation shading and on the channel morphology could mitigate such alterations also from a global warming mitigation perspective.

Supplementary material

Table 1SM. Performance of GAM models used to predict water temperature for the whole monitoring period (July 2018-July 2022) expressed with the root-mean-square error (RMSE) and the R^2_{adj} for each site.

SITE	RMSE (°C)			R^2_{adj}		
	T mean	T max	T min	T mean	T max	T min
S1	1.03	1.24	1.04	0.87	0.84	0.86
S2*	0.45	0.68	0.54	0.98	0.96	0.96
S2	0.95	1.22	0.93	0.92	0.90	0.91
S3	0.93	1.03	1.01	0.86	0.86	0.83
S4	1.24	1.44	1.26	0.88	0.89	0.84
S5	0.82	0.92	0.85	0.94	0.93	0.93
S6	0.63	0.78	0.69	0.96	0.96	0.95
S7	0.74	0.98	0.77	0.94	0.92	0.92
S8	0.66	0.79	0.75	0.95	0.95	0.93
Mean	0.82	1.00	0.86	0.92	0.91	0.91

Table 2SM. Selection of the variable through a forward approach. The optimal model is shown in bold.

GAM models	RMSE (°C)	R^2_{adj}
Tw~s(Ta)	1.369	0.778
Tw~s(Ta) + s(Wn)	1.009	0.879
Tw~s(Ta) + s(Wn) + poly(D, 3)	0.846	0.915
Tw~s(Ta) + s(Wn) + poly(D, 3) + poly(L, 2)	**0.775**	0.929
Tw~s(Ta) + s(Wn) + poly(D, 3) + poly(L, 2) + (s(Qr) + s(Qd))	0.764	0.931

Table 3SM. Water thermal regime model presented with the intercept, the average slope of each factor with the standard error and the p-value.

The equation is: Tw~s(Ta) + s(Wn) + poly(D, 3) + poly(L, 2)

Parametric coefficient	Estimation	Standard Error	p value
Intercept	8.484517	0.009195	<0.001
poly(L, 2)1	31.364518	0.849883	<0.001
poly(L, 2)2	6.44114	1.00246	<0.001
poly(D, 3)1	42.089232	0.9145	<0.001
poly(D, 3)2	-7.365209	0.838301	<0.001
poly(D, 3)3	16.193198	0.89854	<0.001
Smooth terms:			
Ta	7.82	8.661	<0.001
Wn	8.849	8.993	<0.001

Table 4SM. Performance of model expressed with the root-mean-square error (RMSE) and the R^2adj assessed in each site.

	RMSE (°C)	R^2_{adj}
S1	0.907	0.849
S2	0.718	0.933
S3	0.927	0.797
S4	0.966	0.888
S5	0.745	0.927
S6	0.638	0.955
S7	0.604	0.945
S8	0.695	0.946
Mean	0.775	0.905

SECOND PART:
EFFECTS OF WATER THERMAL REGIME ON THE AQUATIC BIOTA

CHAPTER 3

Effects of water temperature on freshwater macroinvertebrates: a systematic review

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CHAPTER 3. Effects of water temperature on freshwater macroinvertebrates: a review

Abstract

Water temperature is one of the main abiotic factors affecting the structure and functioning of aquatic ecosystems and its alteration can have important effects on biological communities. Macroinvertebrates are excellent bio-indicators and have been used for decades to assess the status of aquatic ecosystems as a result of environmental stresses; however, their responses to temperature are poorly documented and have not been systematically evaluated. The aims of this review are: (1) to collate and summarize responses of freshwater macroinvertebrates to different temperature conditions, comparing the results of experimental and theoretical studies; (2) to understand how the focus of research on the effects of temperature on macroinvertebrates has changed during the last 50 years; and (3) to identify research gaps regarding temperature responses, ecosystem types, organism groups, spatiotemporal scales, and geographical regions to suggest possible research directions. We performed a comparative assessment of 223 publications that specifically consider freshwater macroinvertebrates and address the effects of temperature. Short-term studies performed in the laboratory and focusing on insects exposed to a range of temperatures dominated. Field studies were carried out mainly in Europe, at catchment scale and almost exclusively in rivers; they mainly investigated responses to water thermal regime at the community scale. The most frequent biological responses tested were growth rate, fecundity and the time and length of emergence, whereas ecological responses mainly involved composition, richness, and distribution. Thermal research on freshwater macroinvertebrates has undergone a shift since the 2000s when studies involving extended spatiotemporal scales and investigating the effects of global warming first appeared. In addition, recent studies have considered the effects of temperature at genetic and evolutionary scales. Our review revealed that the effects of temperature on macroinvertebrates are manifold with implications at different levels, from genes to communities. However, community-level physiological, phenological and fitness responses tested on individuals or populations should be studied in more detail given their macroecological effects are likely to be enhanced by climate warming. In addition, most field studies at regional scales have used air temperature as a proxy for water temperature; obtaining accurate water temperature data in future studies will be important to allow proper consideration of the spatial thermal heterogeneity of water bodies and any effects on macroinvertebrate distribution patterns. Finally, we found an uneven number of studies across different ecosystems and geographic areas, with lentic bodies and regions outside the West underrepresented. It will also be crucial to include macroinvertebrates of high-altitude and tropical areas in future work because these groups are most vulnerable to climate warming for

multiple reasons. Further studies on temperature–macroinvertebrate relationships are needed to fill the current gaps and facilitate appropriate conservation strategies for freshwater ecosystems in an anthropogenic-driven era.

Keywords

Aquatic insects, thermal conditions, inland waters, biotic response, climate change, conservation.

Table 1. Glossary

Climate warming	Long-term increase of average air temperature near the surface of Earth also involving increased water temperature. This warming trend has been underway for a long time but has increased significantly in recent decades due to human activities.
Ectotherms	Organisms for which habitat temperatures determine body temperatures. Ectotherms may have a variable body temperature or may maintain a stable body temperature by moving from one site to another. Ectotherms are unable to produce and conserve adequate metabolic heat to maintain a body temperature above the external temperature. Antonym of endotherms.
Eurythermal species	Species tolerating a wide temperature range. Antonym of stenothermal species.
Hemimetabolous insects	Insects that undergo incomplete or partial metamorphosis (e.g. Plecoptera, Ephemeroptera, Odonata).
Holometabolous insects	Insects that undergo complete metamorphosis (e.g. Trichoptera, Diptera, Coleoptera).
Stenothermal species	Species that can only live in a narrow range of temperatures. Antonym of eurythermal species.
Temperature changes	Refers to a generic change in the water temperature conditions. *Temperature alteration*: temperature change of a water body caused by anthropogenic causes (such as thermal effluents of nuclear power plants). *Temperature gradient*: water temperature variation over a specified distance. In field studies, it includes lake temperature stratification and the altitudinal gradient of a mountain stream or a geothermal watercourse. In experimental studies, it can be set in tanks that reproduce or manipulate the natural gradient. *Temperature range*: defined as the different temperature levels set in experimental studies to which organisms are exposed to assess the temperature dependence of life-history traits. *Temperature variation*: defined as generic changes in experimental studies where water temperature is increased or decreased to simulate daily/seasonal fluctuations or temperature shocks. *Thermal shocks* are sudden and repeated changes in water temperature. *Thermopeaking* is thermal shock occurring in a watercourse impacted by hydropeaking. *Thermal stress*: organismal responses when the water temperature approaches species-specific critical thermal limits.
Temperature conditions	The thermal environment in which organisms/populations/communities live. Herein we classify temperature conditions for experimental studies as: high temperature, temperature variation, or temperature range; and in field studies as: climate warming, temperature regime, or constant temperature regime.
Thermal divergence	Refers to the presence of populations of the same species that show a different

	performance with respect to temperature due to their different evolutionary histories.
Temperature effects	Biological and ecological outcomes of temperature. They concern organism physiology, metabolism, phenology, fitness, behaviour, community ecology and evolution.
Temperature regime	Water temperature variability of a waterbody on both the temporal (e.g. daily, seasonal) and spatial scales. *Natural temperature regime*: spatial and temporal water temperature variability of a waterbody that is not affected by direct anthropogenic impacts. *Constant temperature regime*: the temperature regime of a waterbody characterized by constant temperature (typically karst streams and springs).
Thermal niche	The range of temperatures allowing population growth, or the temperature requirements of a species within its ecosystem. Depending on the methods used for its estimation the thermal niche is evaluated from organism traits (based on measurements of temperature dependence for life-history or other traits) and from biogeographical indications (based on the climatic region of the species distribution).
Thermal performance breadth	Range of body temperatures over which performance is greater than or equal to an arbitrary level of performance, usually expressed as a percentage of the maximal level. For example, an 80% performance breadth is the range of body temperatures over which performance is greater than or equal to 80% of the maximum (Figure 1). *Critical thermal maximum (CT_{max}) and minimum (CT_{min}):* maximum and minimum temperatures allowing normal performance. *Thermal optimum*: temperature corresponding to organismal maximum performance. *Thermal tolerance*: the difference between CT_{max} and CT_{min}.
Voltinism	The frequency or number of annual broods of an organism within a year.

1. Introduction

1.1 Macroinvertebrates

Aquatic macroinvertebrates are a heterogeneous group, consisting of aquatic invertebrates bigger than 500 µm (Hauer & Resh, 2017). They are found in marine and freshwater ecosystems, including seas, rivers, streams, springs, lakes, ponds, lagoons, wetlands, and transitional ecosystems. Macroinvertebrate communities are diverse and include thousands of species belonging to phyla such as Arthropoda (Crustacea (Amphipoda and Isopoda) and Insecta (Coleoptera, Diptera, Heteroptera, Odonata, Neuroptera, Ephemeroptera, Plecoptera and Trichoptera)), Mollusca (Gastropoda and Bivalvia), Annelida, Nematoda, Platyhelminthes, Porifera, Cnidaria and Bryozoa (Astorga et al., 2011; Demars et al., 2012; Konrad et al., 2008; Resh, 2008). This review focuses only on freshwater macroinvertebrates. Macroinvertebrates play important trophic roles in aquatic communities as a major component of secondary production; they have a key role in food webs, linking organic matter resources with upper trophic levels (Merritt et al., 2017). Macroinvertebrates are a highly diversified group of organisms adapted to live in wide-ranging hydrological and trophic conditions. This ubiquity reflects their evolutionary histories (Will K. W. & Resh V. H., 2008), including a wide variety of reproductive, phenological, trophic, metabolic, physiological and behavioural strategies adapted to their specific environments (Hauer & Resh, 2017). For example, some species utilize dormant eggs to survive dry conditions, or a diapause period when environmental conditions are harsh (Tougeron, 2019). Their life cycles range from multivoltine to semivoltine depending on the taxon. Populations of some species can switch to different life-cycle strategies depending on their geographical distribution and climatic conditions (Braune et al., 2008; Everall et al., 2015; Lamberti et al., 1987). Behavioural adaptations include differentiation of the ability to migrate and colonize new habitats to search for food sources or to avoid predators. According to the River Continuum Concept, in lotic ecosystems the trophic composition of the macroinvertebrate community changes along a watercourse due to gradually changing environmental conditions and resource availability. Allochthonous organic inputs decrease from upstream to downstream while autochthonous primary production increases. As a consequence, the partitioning of collectors/shredders/grazers and predators changes, as does the ratio of gross primary productivity and community respiration (Vannote et al., 1980). For all these reasons, the study of macroinvertebrates has been (Allan & Castillo, 2007; Cummins, 1974; Hynes, 1970) and will continue to be (Cañedo-Argüelles et al., 2020; Giersch et al., 2015; Moore & Schindler, 2008; Sundermann et al., 2011) a central part of aquatic ecology. Macroinvertebrates are widely used as bioindicators (Holt & Miller, 2010) because they are common and abundant, well studied and provide measurable responses to environmental stress. An unimpaired freshwater body commonly contains dozens of taxa, representing a wide range of habitat preferences and life-history strategies. This taxonomic and functional diversity can reflect responses to multiple environmental conditions, stressors, and disturbances, including the presence of fine sediment, metals, nutrients, invasive species, and hydrologic alterations. Accordingly, benthic invertebrates have been increasingly used as bioindicators since the 1950s (Beck, 1955), and many ecological indices based on macroinvertebrate assemblages have been developed. Such indices have been used to evaluate the effects of temperature on features of macroinvertebrate communities, for example, total taxa richness, relative proportion and/or richness of Ephemeroptera, Plecoptera and Trichoptera (EPT) (Fornaroli et al., 2020; Jourdan et al., 2018; Krajenbrink et al., 2021), Simpson and Shannon diversity indices (Arai et al., 2015) and Jaccard and Bray–Curtis indices of similarity (Burgmer et al., 2007).

1.2 The role of temperature

Water temperature is one of the primary factors affecting macroinvertebrates. Recording how benthic invertebrates respond to changes in water temperature is crucial to understanding the effects of climate change on freshwater ecosystems (Jourdan et al., 2018). Moreover, a deeper knowledge of temperature–biology relationships may allow researchers to disentangle the interacting effects of other aquatic ecosystem stressors like pollution, flow alteration and habitat reduction. Water temperature influences the solubility of gases (e.g. oxygen) and pollutants, toxicity of chemicals, pH, density, and electrical conductivity. Moreover, temperature controls nutrient cycles, organic matter degradation and primary production. Generally, higher temperatures promote microbial metabolic activity and photosynthesis and affect the development and performance of biotic communities. Each species requires a specific temperature range for optimal performance. The performance–temperature curve is an asymmetric bell curve where performance is maximized at an optimal body temperature and the extremes represent the critical thermal limits (minimum (CT_{min}) and maximum (CT_{max}); Figure 1; see Table 1 for glossary).

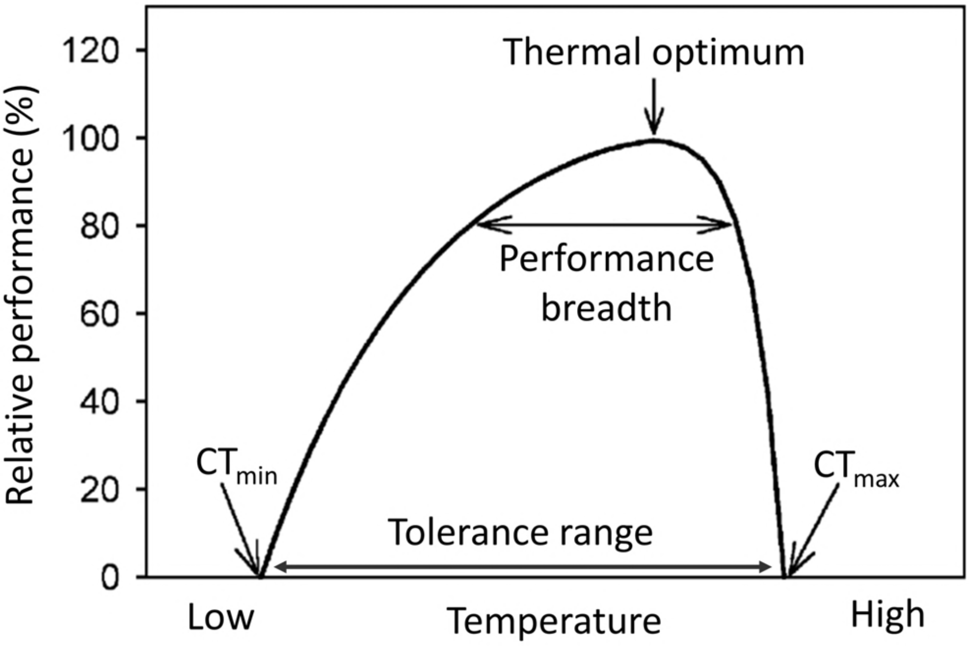

Figure 1. Typical thermal performance curve for ectotherms (adapted from Huey & Stevenson, 1979). CTmax, critical thermal maximum; CTmin, critical thermal minimum.

The range of body temperatures over which performance is equal to or greater than a specified level is called the thermal performance breadth and indicates the width of the individual thermal niche (Angilletta et al., 2002). Stenothermal macroinvertebrate species occupy a restricted temperature range while eurythermal species can tolerate a wider one

(Jones et al., 2017). For many organisms, temperature changes can trigger specific life-cycle phases such as migration, embryonic and larval development, egg hatching, and timing and duration of emergence (Angilletta, 2009b, 2009a). When approaching their thermal limits, organisms show signs of stress, resulting in changes in behaviour (migration, drift and locomotion) (Bruno et al., 2012; Sherberger et al., 1977a), physiology and metabolism (respiration, assimilation and excretion, growth rate and body size) (Sweeney, 1978; Zimmerman & Wissing, 1978), reproductive strategies (fecundity, hatching time and success) (Brittain & Mutch, 1984; Everall et al., 2015), and susceptibility to predators (Smolinský & Gvoždík, 2014; Śniegula et al., 2019), pathogens and parasites (Pritchard & Zloty, 1994). Other responses caused by temperature alterations can affect species distribution and macroinvertebrate community structure through invasions of alien species as well as extinction of vulnerable ones (Dallas & Rivers-Moore, 2014). The effects of temperature changes are often cumulative and also can vary depending on developmental stage (Dallas & Ross-Gillespie, 2015). Due to the strong link between temperature, life cycle and development of macroinvertebrates, several hypotheses have been proposed to explain how macroinvertebrates respond to different temperature conditions. The first attempt to establish a relationship between environmental temperature and biological mechanisms was the thermal equilibrium hypothesis (TEH) (Sweeney & Vannote, 1978). This hypothesis proposed that: (*i*) for each species, maximum adult body size reflects an equilibrium among developmental processes regulated by temperature, including larval growth rate and duration, maturation period of adult structures and rate of maturation processes, with maximum adult size and fecundity achieved at an optimum temperature within the thermal tolerance range; (*ii*) both locally and over large geographic areas, a species distribution is limited by fecundity and adult size, which gradually diminish with increasingly low or high temperature cycles (Sweeney, 1978). It follows that small adult size and reduced fecundity (leading to low levels of population recruitment and growth) are the basis by which temperature changes cause the extinction of aquatic populations (Sweeney et al., 2018). Other theories regarding the relationship between temperature, biological mechanisms and ecological patterns have been proposed (Atkinson, 1994; Kingsolver & Huey, 2008). During the last 20 years, researchers have begun to investigate the effects of global warming on aquatic communities. Due to the rapid development of this research and the increasing number of studies assessing the effects of temperature changes on freshwater communities, we carried out a review of the scientific literature published in the last 50 years to: (1) provide an updated, and comprehensive review of responses of freshwater macroinvertebrates to water temperature; (2) understand how the focus of research on the effects of temperature on macroinvertebrates has changed during the last 50 years; and (3) identify current research gaps regarding ecosystem types, taxa, spatial and temporal scales, and climatic regions to suggest future research directions.

2. Methodology

We performed a search for relevant publications in the ISI *Web of Science* (WoS) database using the search string: Title=((“temperature”) AND (“macroinvertebrates”) AND (“biotic response”) NOT (“other”)), where: “temperature” includes: temperature* OR thermal OR warm* OR heat OR climate change OR thermic; “macroinvertebrates” includes: invertebrat* OR macroinvertebrat* OR (aquatic AND insect*) OR benthos OR benthic OR Plecoptera OR Ephemeroptera OR Trichoptera OR (aquatic AND Coleoptera) OR (aquatic AND Diptera) OR mayfl* OR stonefl* OR caddisfl* OR (aquatic AND fly) OR (aquatic AND beetl*) OR chironomid* OR freshwater biota OR Odonata OR damselfl* OR neuropteran* OR Neuroptera OR Megaloptera OR megalopteran* OR dragonfl* OR (aquatic AND Heteroptera) OR (aquatic AND Hemiptera*) OR midg*; “biotic response” includes: stress* OR variation* OR dynamic* OR dietary OR food OR effect OR nich* OR phenology OR (life AND cycle) OR trait* OR growth OR reproduction OR mortality OR diseas* OR behaviour* OR performance OR dimension* OR size OR fitness OR success OR voltinism OR flexibility OR emergence OR (egg AND development) OR richness OR composition OR drift OR migration OR spatial OR pattern* OR gene* OR feeding OR predation; and “other” includes: fish* OR marine OR sea* OR ocean* OR coast* OR plankton OR brackish OR meiofauna OR oyster OR terrestrial OR soil OR coral OR foraminifer* OR alga OR diatom*. The literature search considered both original research and review papers published between January 1970 and December 2020 and generated 425 records. After examining the abstracts, only papers related to freshwater macroinvertebrates were retained while papers dealing with marine, lagoon or estuary ecosystems and vertebrates or micro-invertebrates were excluded. Ecotoxicological articles were also excluded when temperature was not the main focus so the number of publications dropped to 269. Finally, each paper was read in full to confirm its relevance to our review and 223 publications were retained (Figure 1SM). For each research article (N = 218) in our final database we recorded information including the ecological unit investigated (community, population, gene), focal taxon (recorded to order), temperature conditions, spatiotemporal scale of the study and sampling frequency (see Table 2 for full list of categories).

Table 2. Categories and sub-categories of information drawn from the selected publications.

Category	Description	Sub-categories
Ecosystem	Type of freshwater ecosystem considered	Lotic ecosystems: river, channel, spring Lentic ecosystems: lake, pond Laboratory*
Study	Type of study	Experimental, theoretical
Continent	Continent where the study was performed	Africa, Antarctica, Asia, Europe, Oceania, North America, Central America, South America
Climatic region	Climate according to the Köppen classification	Tropical, arid, temperate, cold, polar
Spatial scale	Environmental scale of the monitoring	Site-specific, catchment, regional, ecoregion, continental, global
Temporal scale	Period of the study	Decades (<100 years), years (<10 years), months (<1 year), days (<1 month), punctual
Survey frequency	Frequency of sampling/observations in the field or laboratory	Annual, seasonal, monthly, weekly, daily, hourly, subhourly, punctual
Level of investigation	Taxonomic level of the investigation	Order, family, genus, species
Ecological unit	Investigated level of biological organization	Community, population**, gene
Organism	Type of organism investigated	Taxonomic order
Temperature conditions	Category of temperature changes	Laboratory: high temperature, temperature variation, temperature range Field: climate warming, temperature regime, constant temperature regime
Other stress	Other stresses/factors investigated	Predation, pollution, photoperiod, oxygen availability, nutrient concentration, humidity, habitat, food availability, flow, other.

*Includes water-filled containers and baths, temperature-gradient tanks, flow-through systems, microcosms and mesocosms.

**Studies not referred to community or gene levels were attributed to population as individual responses were always investigated as representative of the population.

Biotic responses were collated into six categories of effect (physiological and metabolic, phenological, fitness, behavioural, ecological, evolutionary; Table 3).

Table 3. List of the biotic responses measured in relation to temperature in the selected publications.

Effects	**Biotic responses**
Physiological and metabolic	Gene expression, osmoregulation ability, respiration, body size and growth rate, size at emergence, assimilation/excretion, thermal limits
Phenological	Total time of development, time and length of hatching, time and length of emergence, voltinism, colour
Fitness	Fecundity and hatching success, larval recruitment
Behavioural	Drift, migration, predation, feeding
Ecological	Richness, taxonomic composition, density, distribution, food-chain length, community structure and trophic role, secondary production
Evolutionary	Genetic diversity

For each category listed in Tables 2 and 3, multiple selections were possible for a single paper, i.e. if different temperature conditions were investigated by a single publication, thus the total number of studies differs between categories and can exceed the number of publications (Table 1SM). To provide a comprehensive overview of the selected papers we carried out several analyses. (1) We performed a distribution analysis for each category, with the results presented in cumulative bar plots reporting the relative percentages of studies across ecosystem type, spatial and temporal scale, survey frequency, level of investigation and ecological unit as well as temperature conditions and other stresses investigated. We used pie-donuts charts to summarize the studied taxonomic groups and the types of effects and responses investigated. We performed principal components analyses (PCAs) to investigate the patterns of reported responses associated with ecosystem, temperature conditions, spatial scale, level of investigation, organism and continent (Stendera et al., 2012). (2) To assess how the focus of thermal research has changed during the last 50 years, we plotted bubble grid charts for each subcategory of temporal scale, spatial scale, ecological unit, and temperature conditions. (3) We used the above results and a global map showing the number of studies from each country/climatic region to identify areas where thermal studies on freshwater macroinvertebrates are still needed. All statistical analyses were performed using R project software (www.R-project.org) except for pie-donuts charts that were elaborated using Python (www.python.org) and the map that was drawn in Qgis (www.qgis.org).

3. Results

3.1 General overview

Our literature search identified 223 relevant publications (218 research articles and 5 reviews (Figure 2; Tables 4, S1). During the last decade, the number of publications reporting macroinvertebrate responses to temperature has increased, with a notable upturn in the number of theoretical studies.

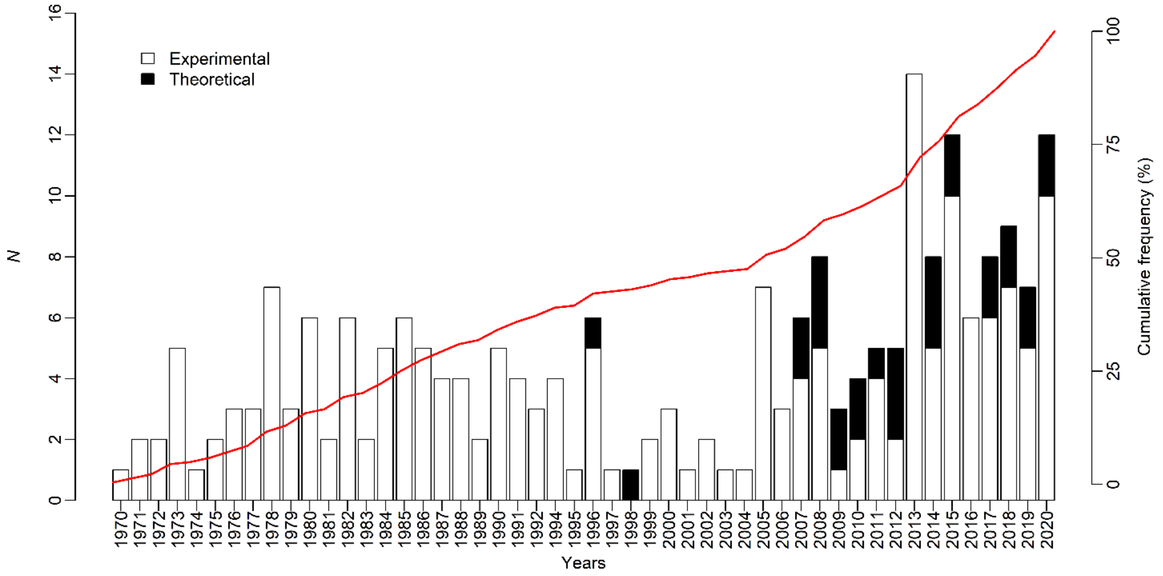

Figure 2. Number of publications (*N* = 223) on aquatic macroinvertebrate responses to temperature per year from 1970 to 2020.

Most studies were performed in the laboratory (*N* = 128), while among field studies lotic ecosystems were better represented (*N* = 91) compared to lentic ones (*N* = 16) (Figure 3A). Most studies were carried out at a site-specific (*N* = 109) or catchment scale (*N* = 45), followed by regional, ecoregional, continental and global scales (Figure 3B). The temporal scale covered ranged mostly from months (*N* = 103) to years (*N* = 59), with fewer studies employing shorter or longer periods (Figure 3C). Most studies used a daily or a monthly survey frequency (*N* = 57 and *N* = 52, respectively) followed by weekly or shorter intervals, although 41 studies did not provide the relevant information (Figure 3D). Investigations at the species level were most common (*N* = 191) (Figure 3E). Population (*N* = 151) and community (*N* = 59) studies were most prevalent, with gene-level studies relatively rare (*N* = 8) (Figure 3F). In laboratory studies were commonly exposed to different temperature ranges (*N* = 120) or to temperatures that approached their upper thermal limits (*N* = 16). Field studies tended to focus on the temperature regime (*N* = 74), with a small number investigating the constant-temperature regime of springs (*N* = 7), or climate warming (*N* = 20) (Figure 3G). Of other stresses associated with temperature by these studies (*N* = 66), the most common were food (both quality and quantity) (*N* = 19), photoperiod (*N* = 9), presence of predators (*N* = 7), flow regime (*N* = 6) and oxygen availability (*N* = 6) (Figure 3H).

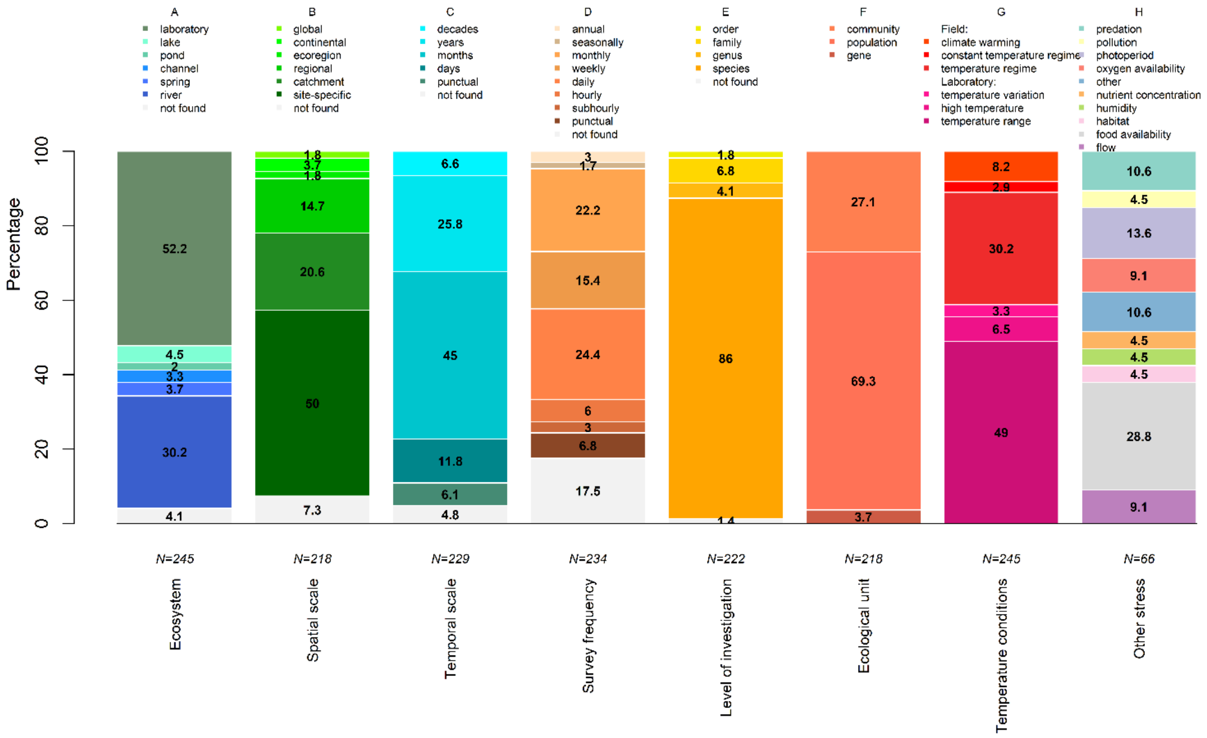

Figure 3. Distribution plots showing: the percentage of studies for each ecosystem type (A), spatial scale (B), temporal scale (C), survey frequency (D), level of investigation (E), ecological unit (F), temperature conditions (G) and other stresses (H).

Insects were the taxon studied most often (*N* = 338, followed by Malacostraca (*N* = 24) Clitellata (*N* = 10) and Gastropoda (*N* = 8) (Figure 4). Among insects, the majority of studies investigated Ephemeroptera (*N* = 80), Odonata (*N* = 61), Trichoptera, Diptera and Plecoptera (*N* = 57, 57, 55, respectively). Among other groups, the most popular orders were Amphipoda (*N* = 11), Isopoda (*N* = 8) and Littorinimorpha (*N* = 5) (Figure 4).

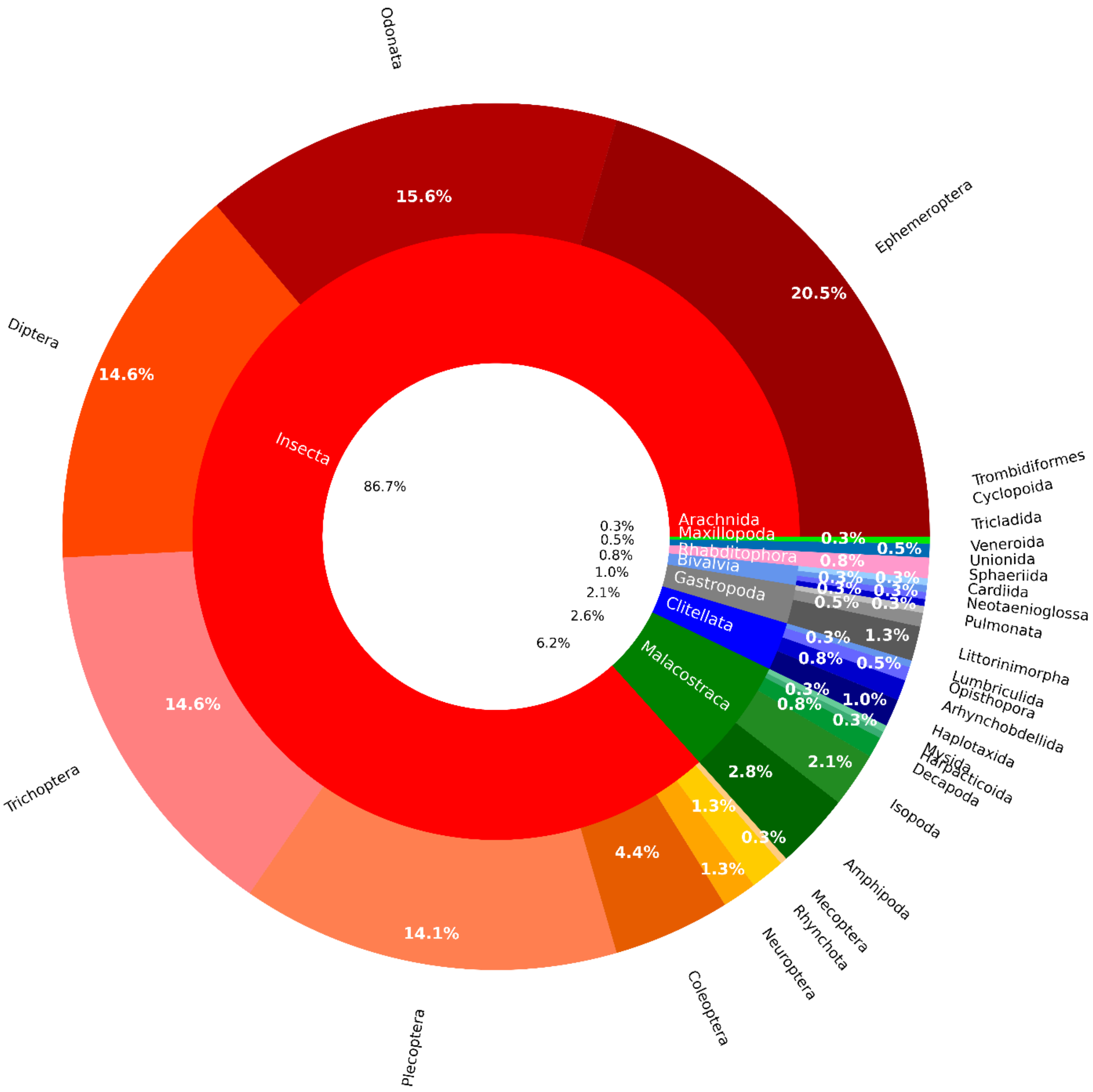

Figure 4. Pie-donut chart showing the relative proportions of specific organisms investigated (*N* = 390). The internal ring refers to classes, the external ring refers to orders.

Among the biotic responses measures with respect to water temperature (*N* = 525, Table 3), physiological and metabolic responses were studied most extensively (*N* = 163, followed by phenological and ecological (*N* = 132), fitness (*N* = 70), and behavioural responses (*N* = 24) (Figure 5). Among these categories, the most investigated responses were body size and growth rate (*N* = 85), time and length of emergence (*N* = 49), fecundity and hatching success (*N* = 47), time and length of hatching (*N* = 39), density, richness, and taxonomic composition (*N* = 34, 31, 31, respectively), the total time of development (*N* = 29) distribution and larval recruitment (*N* = 25, 23, respectively) (Figure 5).

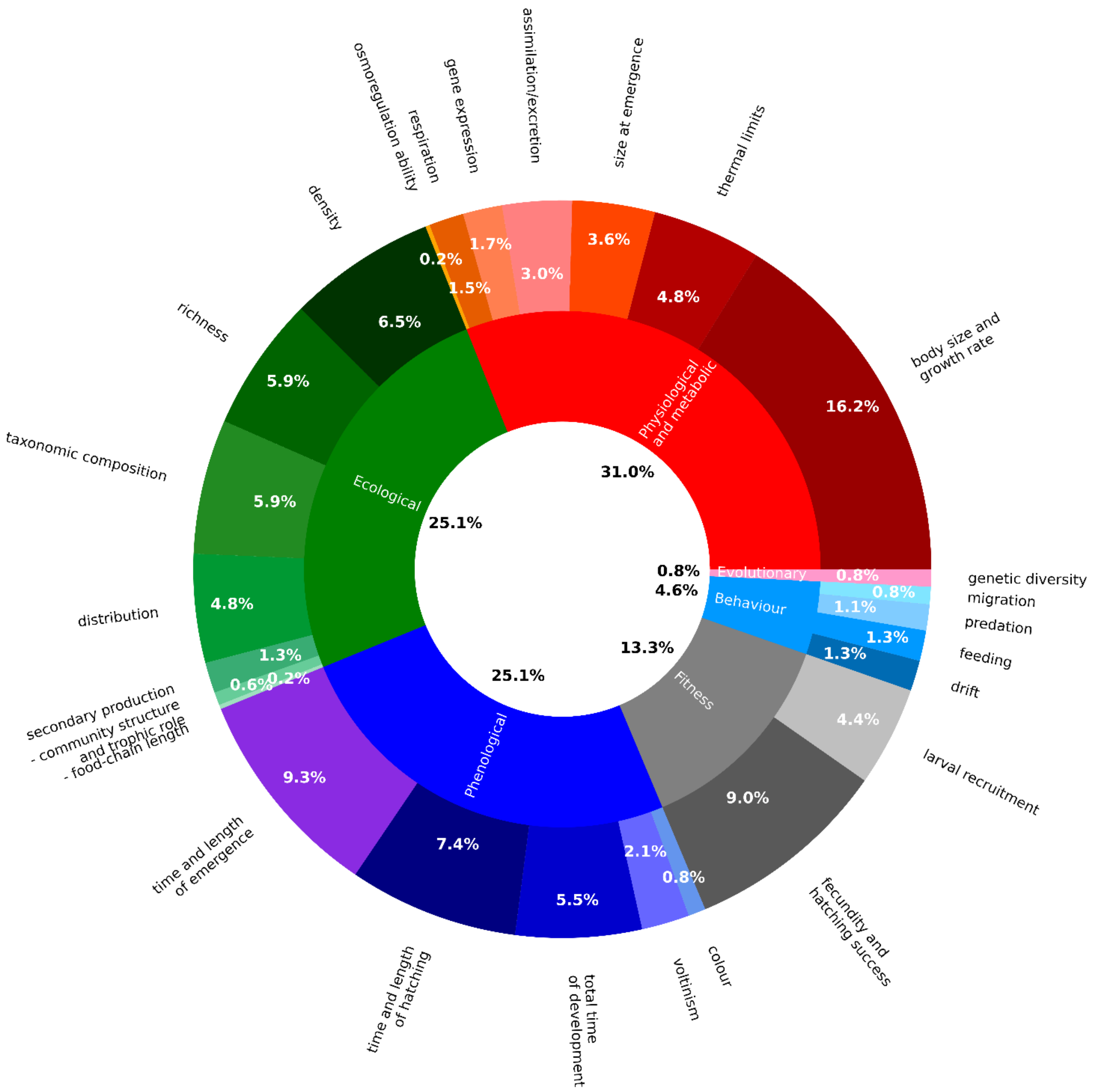

Figure 5. Pie-donut chart showing the relative proportions of responses investigated (*N* = 525) grouped by type of effect. The internal ring refers to effects; the external ring refers to responses.

PCA was useful to reduce the information provided by the multidimensional data set to investigate and interpret the clustering of temperature responses, examine patterns and identify potential research gaps. The results of PCA on the frequency of responses showed two main clusters, one related to biological responses (Dim1) and the other related to ecological responses (Dim2) (Figure 6).

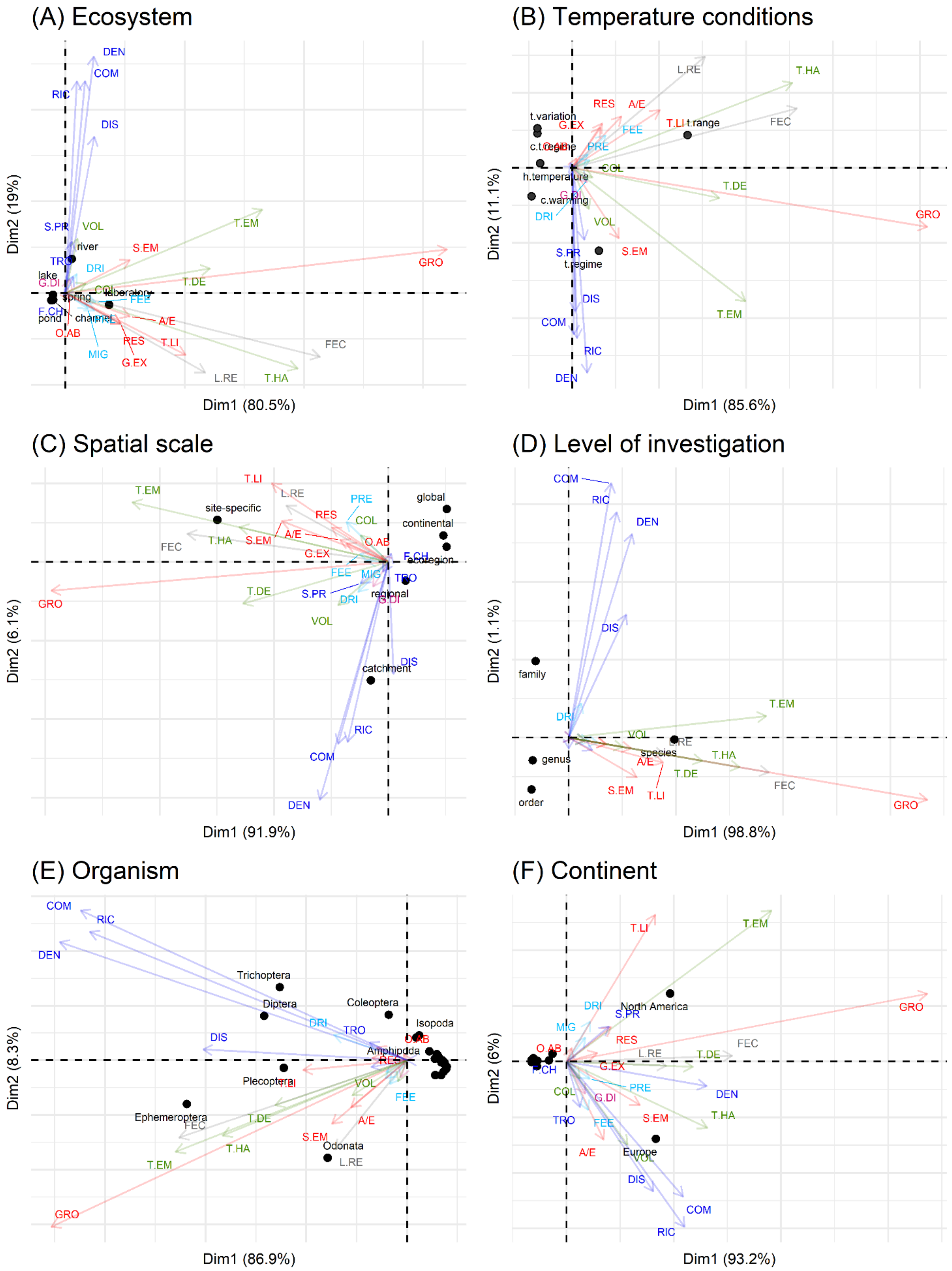

Figure 6. Results of principal components analysis (PCA) of recorded biotic responses of macroinvertebrates to temperature across ecosystem type (A), temperature conditions (B), spatial scale

(C), level of investigation (D), organism type (E), and continent (F). Variance explained (%) is shown in parentheses. Arrows represent the frequency of responses, grouped by colour depending on the type of effects (see Table 3 and Figure 5). Physiological and metabolic responses: gene expression (G.EX), osmoregulation ability (O.AB), respiration (RES), body size and growth rate (GRO), size at emergence (S.EM), assimilation/excretion (A/E), thermal limits (T.LI); phenological responses: total time of development (T.DE), time and length of hatching (T.HA), time and length of emergence (T.EM), voltinism (VOL), colour (COL); fitness responses: fecundity and hatching success (FEC), larval recruitment (L.RE); behavioural responses: drift (DRI), migration (MIG), predation (PRE), feeding (FEE); ecological responses: richness (RIC), taxonomic composition (COM), density (DEN), distribution (DIS), food-chain length (F.CH), community structure and trophic role (TRO), secondary production (S.PR); and evolutionary responses: genetic diversity (G.DI).

Taxonomic composition, richness, distribution, and density were often strongly associated with each other, as were physiological and metabolic, phenological and fitness responses although there were more variable patterns of association depending on the category considered. Biological responses were generally evaluated through laboratory experiments while ecological responses were most associated with field surveys (rivers). Also, voltinism was assessed in rivers (Figure 6A). The temperature conditions PCA exhibited the same pattern with biological responses mainly assessed exposing organisms to different temperature ranges (and to a lesser extent to temperature variation and constant temperature regime) (Dim1) while ecological responses were related to temperature regime and, secondly, climate warming (Dim2). Size at emergence, time and length of emergence, total time of development and body size and growth rate were shared between both axes (Figure 6B). Ecological responses were studied at catchment or regional scale while biological responses (time and length of emergence, fecundity, time and length of hatching, size at emergence, larval recruitment, and thermal limits) were investigated through site-specific surveys (Figure 6C). For biological responses, macroinvertebrates were identified at species level while most investigations were at family level for ecological studies (Figure 6D). Among the different orders, Ephemeroptera and Plecoptera were mainly associated with studies on growth, time and length of emergence, fecundity, time and length of hatching, total time of development and thermal limits while Odonata were related to studies on larval recruitment, size at emergence, assimilation/excretion and voltinism. Trichoptera and Diptera were mainly considered in ecological studies focusing on taxonomic composition, richness, and density (Figure 6E). Finally, ecological responses such as distribution, taxonomic composition, and richness but also responses in other categories, including voltinism, feeding and assimilation/excretion, were mainly investigated in Europe while thermal limits, time and length of emergence, secondary production, respiration and gene expression were more common in North America. Studies regarding growth, fecundity, larval recruitment, total time of development, predation and density were carried out in both continents (Figure 6F).

3.2 Trends in thermal research during the last 50 years

During recent years, the spatial scale of studies has increased, especially in the last 15 years (Figure 7A), although site-specific studies remain most common. Similarly, long-term investigations (decades) of the effects of temperature have appeared relatively recently (Figure 7B), likely due to the increasing availability of long-term biomonitoring data sets.

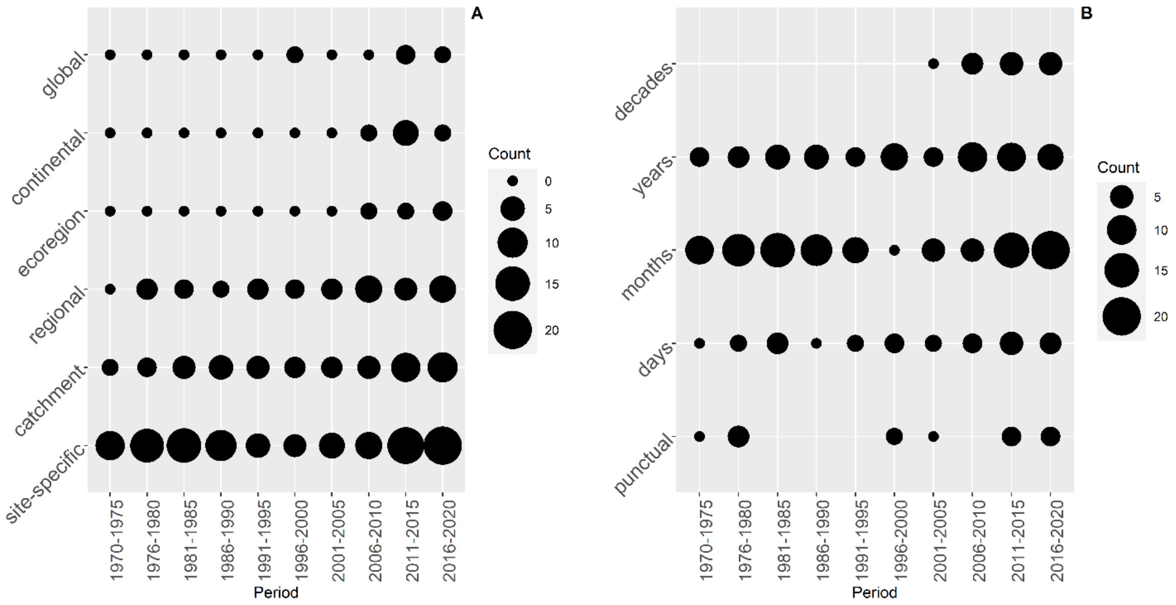

Figure 7. Bubble charts showing the number of studies from 1970 to 2020 that recorded responses of macroinvertebrates to temperature at specific temporal (A) (*N* = 229) and spatial (B) scales (*N* = 218).

Regarding the ecological unit of study, investigations of the genetic and evolutionary effects of temperature changes have appeared more recently than studies on the effects at population or community levels and remain less common (Figure 8A). Investigations of the effects of climate change also are relatively new but represent 17% of all publications in our database since 2006 (Figure 8B).

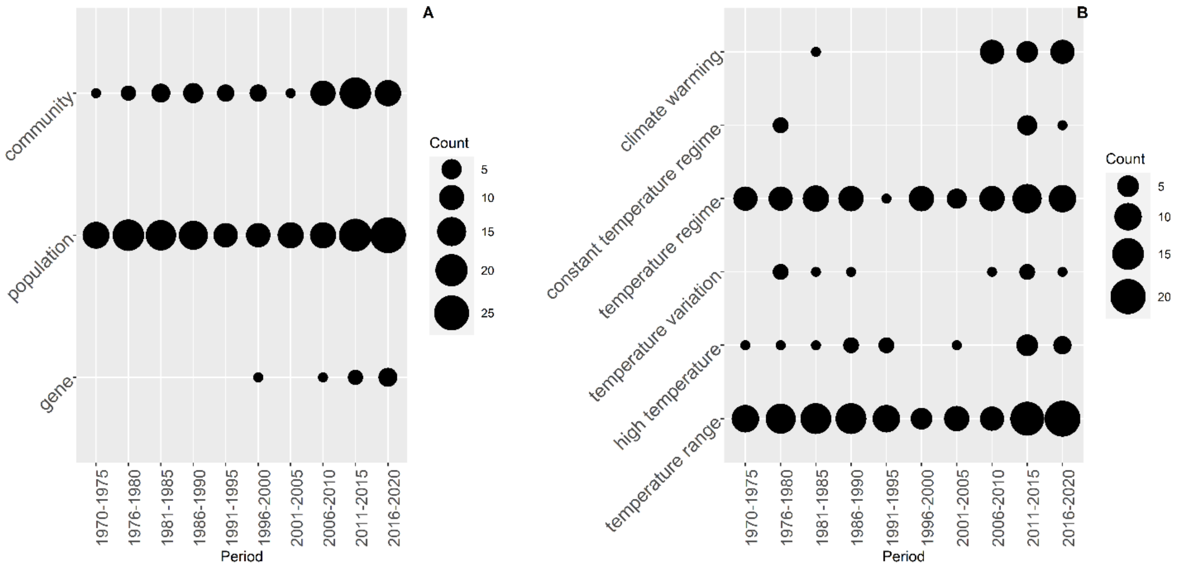

Figure 8. Bubble charts showing the number of studies from 1970 to 2020 that recorded responses of macroinvertebrates to temperature separated by ecological unit recorded (A) (*N* = 218) and temperature conditions (B) (*N* = 245).

There is an unequal distribution of study sites (*N* = 245) across the different climatic regions of the world, with temperate (~57%) and cold (~28%) regions best represented, followed by tropical, arid and polar (~5%) (Figure 9). Most studies (*N* = 192) have been carried out in Europe (~41%) and North America (~38%), with the rest of the world poorly represented (*N* = 53) (Figure 9).

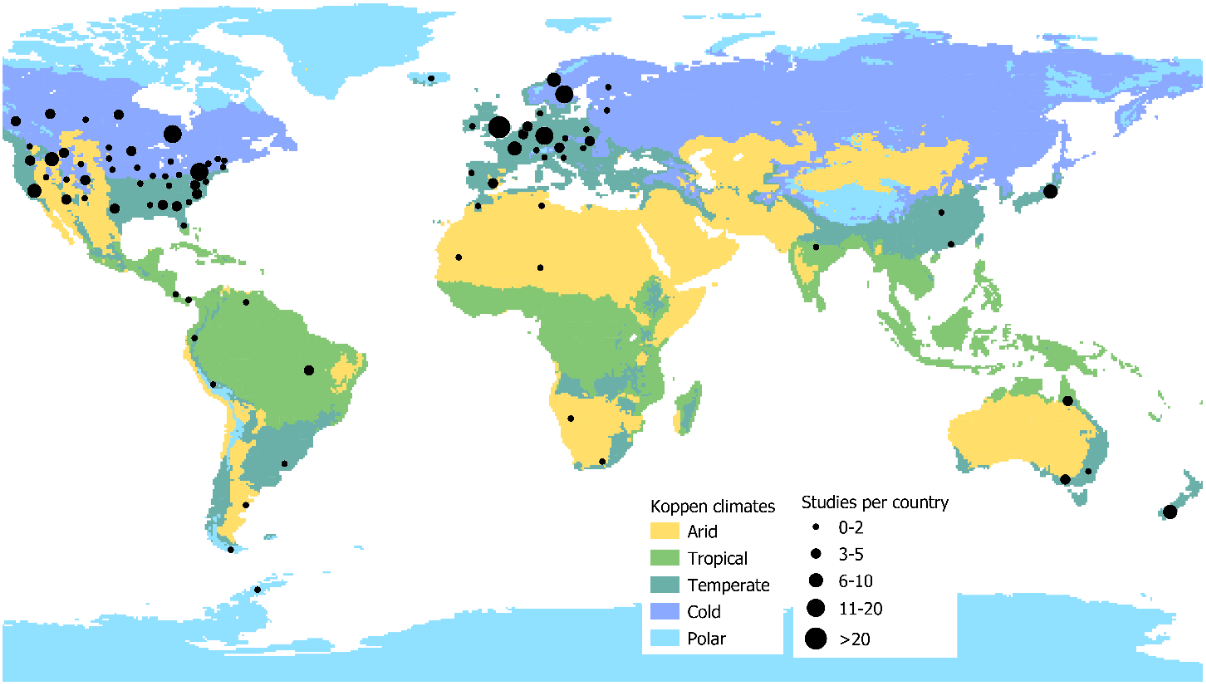

Figure 9. World map showing climatic regions and the number of studies per country/state (*N* = 245).

4. Discussion

4.1 Responses of macroinvertebrates to water temperature

Table 4 provides a summary of responses of macroinvertebrates to temperature.

Table 4. Responses of macroinvertebrates to temperature summarized from the studies included in our database. Additional references not included in the database are identified by an asterisk (*).

Effect	Biotic response	Overall patterns	References
Physiological and metabolic	Gene expression	Temperature influences the expression of genes involved in thermal regulation and their speed of replication.	Chou et al., (2018); *Ebner et al., (2019); Hotaling et al., (2020); Karouna-Renier & Zehr (1999); Kim et al., (2017); Lencioni et al., (2013); Lopez-Martinez et al., (2008); Martín-Folgar et al., (2015); *Schmeller et al., (2018); Swaegers et al., (2020); Teets et al., (2013)
	Osmoregulation ability	Higher temperatures imply higher osmotic concentration of haemolymph in aquatic arthropods.	Colburn (1983); *Orr & Buchwalter (2020)
	Respiration	Respiration rates increase with temperature.	*Bergström et al., (2010); Burton et al., (1976); Forster et al., (2012); Hamburger et al., (1994); Howell & Voshell (1982); Jones et al., (2018); Kim et al., (2017); Modlin & Jayne (1981); Rotvit & Jacobsen (2013); *Sinsabaugh (1997); Sweeney (1978)
	Body size and growth rate	Growth rate increases with warming until an optimum temperature, beyond which it declines. Females may invest resources into fecundity at the expense of the growth of somatic tissues, so females may be smaller than males in warm conditions.	Abbott (2013); *Atkinson (1994, 1995); *Bergmann (1847); Bottová et al., (2013a,b); Brittain (1983); Brittain et al., (1984); Brittain & Mutch (1984); Chadwick & Feminella (2001); Chavez et al., (2015); Cogo et al., (2020); Corkum & Hanes (1992); Culler et al., (2014); Elliott (1987); Fahy (1973); Fenoglio et al., (2005); Frouz et al., (2002); *Forster et al., (2012); Fuller & Fry (1991); Giberson & Rosenberg (1992a); Gresens (1997); Hamburger et al., (1994); Hassall, 2013); Hauer & Benke (1991); Hayashi (1988, 1996); Hines et al., (2016); *Horne et al., (2015, 2018); Howell & Voshell (1982); Humpesch (1981); Huryn (1996); Imholt et al., (2010); Ingram (1976); *Kingsolver & Huey (2008); Krishnaraj & Pritchard (1995); Leggott & Pritchard (1985); Li et al., (2009); Lillehammer (1985, 1986); Maier et al., (1990); Markarian (1980); Martins et al., (2016); McCafferty & Pereira (1984); McKie & Cranston (2005); McKie & Pearson (2006); McKie et al., (2004); Mochizuki et al., (2006); Moody et al., (2017); Muthukrishnan et al., (1988); Newell & Minshall (1978); Nilsson-Örtman et al., (2012,

			2014, 2013a,b); Ouahsine et al., (1996); Perry et al., (1987); Péry & Garric (2006); Pickup & Thompson (1990); Piggott et al., (2015); Pritchard & Pelchat (1977); Pritchard & Zloty (1994); Procter (1973); Rader & Ward (1990); Rempel & Carter (1987); Reynolds & Benke (2005); Rosillon (1988); Sarvala (1979); Scherr et al., (2010); Śniegula et al., (2019); Söderström (1988); Starr & McIntyre (2020); Stoks et al., (2012); Storey (1987); Suhling et al., (2015); Šupina et al., (2020); Sweeney (1978); Sweeney & Vannote (1978, 1984, 1986); Sweeney et al., (1986a,b); Turner & Williams (2005); Tüzün et al., (2017); Van Doorslaer & Stoks (2005a,b); *Verberk et al., (2021); Vogt et al., (2007); Wagner (1990, 2005); Wright et al., (1982); Zimmerman & Wissing (1978)
	Size at emergence	High temperatures lead to faster growth and smaller emergence size due to accelerated metabolism. Low temperatures slow down the growth rate potentially leading to larger emergence size. Temperature can promote sexual size dimorphism.	Abbott (2013); Brittain (1983); Chacón et al., (2016); Farkas et al., (2013); Giberson & Rosenberg (1992a); Hayashi (1988, 1996); Jonsson et al., (2015); Langford (1975); McCauley et al., (2015, 2018); Rosillon (1988); Śniegula et al., (2019); Söderström (1988); Sweeney & Vannote (1978, 1986); Sweeney et al., (1986b); Turner & Williams (2005); Wonglersak et al., (2020)
	Assimilation/ excretion	Higher temperatures enhance ingestion and excretion rates.	Anderson et al., (2017); Beracko & Revajová (2019); Bottová et al., (2013a,b); Culler et al., (2014); Martins et al., (2020); Moody et al., (2017); Muthukrishnan et al., (1988); Pandian et al., (1979); Péry & Garric (2006); Pickup & Thompson (1990); Stoks et al., (2012); Thompson (1978); Van Doorslaer & Stoks (2005a); Winterbourn et al., (2008); Zimmerman & Wissing (1978)
	Thermal limits	Stenothermal invertebrates occupy a small temperature range while eurytherms occupy wider ranges. Tropical species have narrower thermal tolerances compared to temperate ones.	*Brett (1952); Burton et al., (1976); Chadwick & Feminella (2001); Chou et al., (2018); Collier & Smith (2000); Cox & Rutherford (2000); *Dallas & Ketley (2011); *Dallas & Rivers-Moore (2012); Danks (1978); Dickson & Walker (2015); Elliott (1987); Giberson & Rosenberg (1992a); Hotaling et al., (2020); Martin et al., (1976); McKie & Pearson (2006); McKie et al., (2004); Mochizuki et al., (2006); *Niedrist & Füreder (2020); *Polato et al., (2018); Rogowski & Stewart (2016); Rosillon (1988); Sawchyn & Church (1973); *Shah et al., (2017); Sherberger et al., (1977); Shoup & Houghton (2013); *Stewart et al., (2013); Suhling et al., (2015); Sweeney & Vannote

			(1986); Sweeney et al., (1986a,b); Vogt et al., (2007); Wellborn & Robinson (1996)
Phenological	Total time of development	High temperatures shorten the development time, leading to more rapid emergence.	Abbott (2013); Abdullahi & Laybourn-Parry 1985); Bayoh & Lindsay (2003); Beracko & Revajová (2019); Elliott (1987); Fahy (1973); Frouz et al., (2002); Hauer & Benke (1991); Humpesch (1981); Huryn (1996); Imholt et al., (2010); Li et al., (2009); Mackay (1984); Maier et al., (1990); Marten (1990); McCafferty & Pereira (1984); McCauley et al., (2015); McKie & Pearson (2006); McKie et al., (2004); Pritchard & Pelchat (1977); Pritchard & Zloty (1994); Rosillon (1988); Śniegula et al., (2019); Söderström (1988); Sweeney & Vannote (1984); Sweeney et al., (1986b); Trottier (1971); Wagner (1990); Wright et al., (1982)
	Time and length of hatching	Hatching time decreases at higher temperatures. Low temperatures lengthen the hatching period and induce diapause.	Abdullahi & Laybourn-Parry (1985); Bohle (1972); Bouton et al., (2011); Brittain (1977, 1991); Brittain & Campbell (1991); Brittain & Mutch (1984); Brittain et al., (1984); Corkum & Hanes (1992); Elliott (1972, 1978, 1986, 1987); Friesen et al., (1979); Frouz et al., (2002); Giberson & Rosenberg (1992b); Gillooly & Dodson (2000a); Gong et al., (2002); Humpesch & Elliott (1980); Humpesch (1980a,b, 1982); Ichikawa et al., (2017); Leggott & Pritchard (1985); Lillehammer (1985,1986); Maier et al., (1990); Marten (1990); Mendonça et al., (2018); Muthukrishnan et al., (1988); Perry et al., (1987); Pritchard & Zloty (1994); Pritchard et al., (1996); Ross-Gillespie et al., (2018); Sarvala (1979); Sawchyn & Church (1973); Strange (1985); Sweeney & Vannote (1984); Zwick (1996)
	Time and length of emergence	Increasing temperatures lead to earlier emergence.	Abdullahi & Laybourn-Parry (1985); Chaćon et al., (2016); Cheney et al., (2019); Čmrlec et al., (2013); Coler & Kondratieff (1989); Danks (1978); Dickson & Walker (2015); Dingemanse & Kalkman (2008); Elliott (1987); Everall et al., (2015); Frouz et al., (2002); Hassall et al., (2007); Hayashi (1988, 1996); Huryn (1996); Imholt et al., (2010); Ingram (1976); Ivković et al., (2013); Jonsson et al., (2015); Killian & Lutz (1985); Langford (1975); Leggott & Pritchard (1985); Li et al., (2009); Lutz (1974); Maier et al., (1990); McCafferty & Pereira (1984); McCauley et al., (2015, 2018); McKie & Pearson (2006); Nebeker (1971); Perry et al., (1987); Péry & Garric (2006); Piggott et al., (2015); Pritchard & Zloty (1994); Procter (1973); Rempel & Carter (1987); Richter et al.,

			(2008); Starr & McIntyre (2020); Šupina et al., (2020); Sweeney (1978); Sweeney & Vannote (1986); Sweeney et al., (1986a,b); Trottier (1971, 1973a,b); Villalobos-Jiménez & Hassall (2017); Vogt et al., (2007); Watanabe et al., (1999); Wright et al., (1982)
	Voltinism	Higher temperatures favour a flexible life cycle and increase voltinism. Low temperatures cause longer developmental time and favour a univoltine cycle.	Beracko & Revajová (2019); Bottová et al., (2013a,b); Braune et al., (2008); Elliott (1987); Everall et al., (2015); Farkas et al., (2013); Mackay (1984); Newell & Minshall (1978); Pritchard & Zloty (1994); *Rivers-Moore et al., (2012); Söndgerath et al., (2012)
	Colour	Temperature may interfere with colour regulation.	Abbott (2013); Bouton et al., (2011); Hayashi (1988); McCafferty & Pereira (1984)
Fitness	Fecundity and hatching success	Fitness is maximized at the optimal temperature. Elevated temperatures imply lower fecundity and faster hatching accompanied by a lower hatching success. Low temperatures promote large broods and higher fecundity in females.	Bayoh & Lindsay (2003); Bovill et al., (2019); Brittain (1977, 1991); Brittain & Campbell (1991); Brittain et al., (1984); Corkum & Hanes (1992); Elliott (1972, 1987, 1986); Friesen et al., (1979); Giberson & Rosenberg (1992a,b); Gillooly & Dodson (2000a); Gong et al., (2002); Humpesch & Elliott (1980); Humpesch (1982, 1981, 1980a,b); Ichikawa et al., (2017); Imholt et al., (2010); Leggott & Pritchard (1985); Lillehammer (1985, 1986); Marten (1990); McKie & Pearson (2006); Newell & Minshall (1978); Péry & Garric (2006); Pritchard & Zloty (1994); Rader & Ward (1990); Rempel & Carter (1987); Rosillon (1988); Ross-Gillespie et al., (2018); Sarvala (1979); Sawchyn & Church (1973); Söderström (1988); Starr & McIntyre (2020); Strange (1985); Sweeney (1978); Sweeney & Vannote (1978, 1984); Sweeney et al., (1986b); Tennessen et al., (1982); Van Doorslaer & Stoks (2005b); Wright et al., (1982); Zwick (1996)
	Larval recruitment	Juvenile recruitment increases with temperature increase; at low temperatures hatching is inhibited.	Abbott (2013); Brittain (1991); Brittain et al., (1984); Chavez et al., (2015); Corkum & Hanes (1992); Danks (1978); Giberson & Rosenberg (1992b); Ingram (1976); Killian & Lutz (1985); Lencioni et al., (2013); Marten (1990); Martins et al., (2016); McCauley et al., (2015, 2018); Nilsson-Örtman et al., (2014); Pritchard & Pelchat (1977); Śniegula et al., (2019); Storey (1987); Šupina et al., (2020); Tüzün et al., (2017); Van Doorslaer & Stoks (2005b); Wright et al., (1982); Zwick (1996)
Behavioural	Migration	Macroinvertebrates migrate to locate their	Shah et al., (2020); Sherberger et al., (1977); Trottier (1973b); Van Doorslaer & Stoks

		preferred thermal environment	(2005a); *Waters (1965)
	Drift	Thermopeaking and high temperatures cause drift.	*Bruno et al., (2012); *Carolli et al., (2012); Coler & Kondratieff (1989); Dudgeon et al., (2020); Durrett & Pearson (1975); Piggott et al., (2015); Raddum (1985); Scherr et al., (2010); *Schülting et al., (2016); Wojtalik & Waters (1970)
	Predation	Predators may be more vulnerable to increasing temperature than their prey. Elevated temperatures compromise hunting capacity but also reduce avoidance ability in prey.	*Kishi et al., (2005); MacPhee et al., (2011); McKie & Pearson (2006); Quenta Herrera et al., (2018); *Rogowski & Stewart (2016); Sherberger et al., (1977); Smolinský & Gvoždík (2014); Śniegula et al., (2019)
	Feeding	At higher temperatures macroinvertebrates require more food/better food quality.	Bottová et al., (2013a); Gordon et al., (2018); Krishnaraj & Pritchard (1995); Navarro & Gonçalves Júnior (2017); Pandian et al., (1979); Pickup & Thompson (1990); Śniegula et al., (2019)
Ecological	Richness	The number of species generally increases with increasing annual temperature ranges. The highest temperatures lead to an impoverished community with better survival of eurythermal and generalist species. Global warming facilitates the extinction of stenothermal species.	Arai et al., (2015); Arthur et al., (1982); Barquín & Death (2011); Besacier Monbertrand et al., (2019); Burgmer et al., (2007); *Castella et al., (2001); Chinnayakanahalli et al., (2011); Čmrlec et al., (2013); Contador et al., (2014); Conti et al., (2014); Dudgeon et al., (2020); Durance & Ormerod (2007, 2009); Eversham & Cooper (1998); Feuchtmayr et al., (2007); Floury et al., (2013); Glazier (2012); Gordon et al., (2018); Gustafson (2008); Haidekker & Hering (2008); Jackson et al., (2007); Jourdan et al., (2018); Munari (2011); Nyquist et al., (2020); Poff et al., (2010); Rasmussen (1982); Saltveit et al., (1994); Sandin et al., (2014); Voelz et al., (1994); *Ward & Stanford (1982); Wellborn & Robinson (1996); Worthington et al., (2015); Živić et al., (2014)
	Taxonomic composition	The macroinvertebrate community is generally more diversified in ecosystems characterized by wide daily and seasonal temperature variation. Global warming leads to homogenization of macroinvertebrate communities.	Arai et al., (2015); Arthur et al., (1982); Barquín & Death (2011); Besacier Monbertrand et al., (2019); Burgmer et al., (2007); Cerini et al., (2020); Chinnayakanahalli et al., (2011); Čmrlec et al., (2013); Coler & Kondratieff (1989); Contador et al., (2014); Conti et al., (2014); Cooper (1980); Dudgeon et al., (2020); Durance & Ormerod (2007, 2009); Feuchtmayr et al., (2007); Floury et al., (2013); *Fornaroli et al., (2020); Gustafson (2008); Haidekker & Hering (2008); Jackson et al., (2007); Jourdan et al., (2018); Munari (2011); Nyquist et al., (2020); Piggott et al., (2015); Poff et al., (2010); Rasmussen (1982); Saltveit et al.,

			(1994); Sandin et al., (2014); Voelz et al., (1994); Worthington et al., (2015); Živić et al., (2014)
	Density	Temperature changes lead to alterations in species density depending on each species' thermal niche. Global warming increases the abundance of generalist species at the expenses of the stenothermal ones.	Arai et al., (2015); Arthur et al., (1982); Barquín & Death (2011); Besacier Monbertrand et al., (2019); Burgmer et al., (2007); Cheney et al., (2019); Čmrlec et al., (2013); Coler & Kondratieff (1989); Contador et al., (2014); Conti et al., (2014); Cooper (1980); Dudgeon et al., (2020); Durance & Ormerod (2007, 2009); Durrett & Pearson (1975); Feuchtmayr et al., (2007); Floury et al., (2013); Giberson & Rosenberg (1992a); Gustafson (2008); Haidekker & Hering (2008); Jackson et al., (2007); Jourdan et al., (2018); Nyquist et al., (2020); Poff et al., (2010); Raddum (1985); Rader & Ward (1990); Rasmussen (1982); Sandin et al., (2014); Voelz et al., (1994); Wagner (2005); Wellborn & Robinson (1996); Winterbourn et al., (2008); Worthington et al., (2015); Živić et al., (2014)
	Distribution	Distribution is influenced by a species' thermal optimum. Temperature changes affect the ecological niche occupied by the species promoting shifts in their distribution. Increasing temperatures cause the upstream spread of eurythermal species and reduce the habitat available for stenothermal species.	Arai et al., (2015); Baker & Feltmate (1989); Besacier Monbertrand et al., (2019); Cerini et al., (2020); Cheney et al., (2019); Chessman (2012); Chinnayakanahalli et al., (2011); Čmrlec et al., (2013); Conti et al., (2014); Cooper (1980); *Domish et al., (2011); Durance & Ormerod (2007); Eversham & Cooper (1998); Fenoglio et al., (2010); Haidekker & Hering (2008); Hering et al., (2009); *Mustonen et al., (2018); Nilsson-Örtman et al., (2012, 2013b); Nyquist et al., (2020); Pires et al., (2018); Poff et al., (2010); Saltveit et al., (1994); Sandin et al., (2014); Silva et al., (2019); Söndgerath et al., (2012); Timoner et al., (2020); Winterbourn et al., (2008)
	Food-chain length	Elevated temperatures cause an abrupt decline in food-chain length); below a critical threshold the relationship between food-chain length and temperature is not linear.	*Arim et al., (2007b); Glazier (2012)
	Community structure and trophic role	Temperature alterations may lead to changes in the composition of functional feeding groups. Grazers and scrapers appear especially vulnerable to warming.	Jonsson et al., (2015); Jourdan et al., (2018); *Pyne & Poff (2017); Sandin et al., (2014); Živić et al., (2014)
	Secondary	Secondary production	Bottová et al., (2013a); Ferreira et al., (2015);

	production	does not depend directly on temperature, although temperature can impact resource supply with effects on secondary production.	Humpesch (1981); *Junker et al., (2020); Newell & Minshall (1978); Patrick et al., (2019); Perry et al., (1987); Rader & Ward (1990); Sweeney & Vannote (1986)
Evolutionary	Genetic diversity	Temperature acts at an evolutionary scale causing thermal divergence in populations, promoting genetic divergence or causing fragmentation and temporal isolation leading to loss of genetic diversity.	*Bálint et al., (2011); *Chapman (2013); Herzog & Hadrys (2017); Johansson et al., (2016); Jordan et al., (2016); Stoks et al., (2014); Swaegers et al., (2020); Vogt et al., (2007)

4.1.1 Physiological and metabolic effects

4.1.1.1 Gene expression

Stressful environmental conditions such as heating induce the expression of several genes that control the activity of the heat-shock proteins (HSPs). The reviewed papers that reported genetic responses of macroinvertebrates to temperature changes all recorded upregulation or downregulation of different genes, including HSP genes (Karouna-Renier & Zehr, 1999; Lencioni et al., 2013). For example, when subjected to heat-induced stress, *Chironomus riparius* (Diptera) did not activate or repressed some HSP genes (e.g. HSP22) while others were activated (HSP23, HSP24, HSP34, HSP27 and HSP70) suggesting that the HSP subfamily possesses remarkable functional differentiation in response to stressful temperature conditions (Martín-Folgar et al., 2015). Similarly, Chou et al., (2018) observed that *Neocloeon triangulifer* (Ephemeroptera) larvae bred at a chronic threshold (30 °C) upregulated indicators of thermal stress (HSP90) but not genes sensitive to hypoxia (egg laying defective 9 (EGL-9) and lactate dehydrogenase (LDH)), indicating that the upper chronic thermal limit is not set by oxygen availability. Chronic thermal stress can lead to reductions in body size and fitness through reduced food intake, which results from the upregulation of genes producing histamine and dopamine (Chou et al., 2018). Upregulation of HSP70 has also been observed in stenotherm species (*Lednia* sp. (Plecoptera) and *Crunoecia irrorata* (Coleoptera)) in their natural temperature range, indicating that the thermal niche they occupy may not be optimal due to other limiting factors such as biotic interactions or resource availability (Ebner et al., 2019; Hotaling et al., 2020). This challenges the assumption that the distribution of insects in cold habitats reflects evolved preferences for those temperature conditions. (Teets et al., 2013) reported upregulation of genes involved in both glycogenolysis and gluconeogenesis in *Belgica antarctica* midges in response to heat and cold stress, suggesting that insects exposed to extreme environmental conditions mobilize carbohydrate energy stocks to allow rapid shifts in metabolism. Hotaling, et al., (2020), studying high-altitude stoneflies exposed to their CT_{max}, identified upregulation of genes involved in the developmental transition (ATP binding cassette subfamily A member 3 (ABCA3) and hexamerins (HEXA)). Studies on gene expression allow us to understand the physiological mechanisms underlying organismal responses to temperature changes and are imperative for correct interpretation of the causes driving biological responses at different levels, for example, to disentangle behavioural and evolutionary responses (Hotaling et al., 2020; Schmeller et al., 2018). As stated by Clarke (2003) we can identify the relationships between cellular thermal physiology and organismal physiology as well as between some macroecological patterns and temperatures, however, we are still unable to relate thermal physiology to ecology at the community scale, despite this link likely being a strong determinant of life-history traits, food-web dynamics, and biological diversity.

4.1.1.2 Osmoregulation ability

Temperature affects the regulation of haemolymph osmotic and ionic concentrations in invertebrates. In general, increasing temperatures increase ion transport rates (Orr & Buchwalter, 2020). We found only one study on macroinvertebrate osmoregulation in which (Colburn, 1983) observed that larvae of *Limnephilus assimilis* (Trichoptera) exposed to a wide salinity range (0–25%) could complete their development at low temperature because cellular Cl^- and Na^+ were maintained at low concentrations. On the contrary, at high temperatures (for example in hydrothermal water) they were unable to control Cl^- intake, leading to lower survival and decreased ability to complete development.

4.1.1.3 Respiration

As for all biological processes, respiration rate is positively correlated with temperature (Sinsabaugh, 1997), hence higher temperatures enhance the oxygen consumption of invertebrates, as shown by Bergström et al., (2010) for species in lake sediments. At higher temperatures, larger amounts of energy are required for metabolic maintenance, for both respiration and assimilation, compared to at the thermal optimum (Sweeney & Vannote, 1978; Vannote & Sweeney, 1980). However, due to the decrease in oxygen solubility with increasing temperature, oxygen availability is reduced simultaneously with this greater respiratory requirement (Forster et al., 2012). The sensitivity of species to this decrease in oxygen availability varies depending on the taxon. Some species such as *Leuctra hippopus* (Plecoptera) and *Asellus aquaticus* (Isopoda) can maintain a constant respiration rate independent of ambient oxygen levels (below a critical limit) (Kim et al., 2017; Rotvit & Jacobsen, 2013), whereas others, such as *Isoperla* spp. (Plecoptera) show a higher oxygen consumption with increasing temperature and a respiratory rate that is proportionally greater in larger species (Modlin & Jayne, 1981). Some chironomid species (e.g. *Chironomus anthracinus* (Diptera)) can shift from aerobic metabolism to partially anaerobic (Hamburger et al., 1994) as temperature increases (from 2 to 20 °C)

4.1.1.4 Body size, growth rates and size at emergence

Growth and adult body size depend on several processes regulated by temperature such as rates of ingestion, assimilation, metabolism, and excretion. Sweeney & Vannote (1978) conceptualized this temperature–growth–size relationship in their thermal equilibrium hypothesis (TEH) according to which maximum adult size is achieved at a thermal optimum while outside this optimal range body size is reduced. Several studies have demonstrated that higher temperatures can cause acceleration of metabolism and consequently lower investment in growth, leading to premature adult development. On the contrary, at low temperatures, metabolic activity is slowed down, allowing a greater proportion of adult tissue maturation (Brittain, 1983; Rempel & Carter, 1987; Sweeney et al., 1986a; Sweeney & Vannote, 1978; Vannote & Sweeney, 1980). The size–temperature relationship is generally assessed in laboratory studies, in which organisms are bred at a constant temperature and measured and weighed at frequent intervals (typically 1–3 days). Morphological traits considered include total length, head capsule width, thorax length, pronotal length, wing length, leg length, antennal length, and body mass, depending on the taxon and developmental stage. The observed temperature–body size relationship often follows an exponential curve (Brittain, 1983; Giberson & Rosenberg, 1992a; Rempel & Carter, 1987; Reynolds & Benke, 2005; Sweeney & Vannote, 1984). Growth rates are calculated from the change in body size (both length and mass) for specific intervals of the developmental period. The temperature–body size relationship can also be studied in relation to sex and or life-cycle phase. Some experiments have shown that at high temperatures females reach smaller adult sizes than males suggesting that somatic growth is traded off against reproductive capacity (McKie et al., 2004; Rempel & Carter, 1987) while in other studies sexual dimorphism appears unaffected by temperature, with other factors such as sexual selection or fertility playing an important role (Encalada et al., 2019; Lande, 1980). Although some evidence shows that higher temperatures lead to smaller adult body size (in agreement with the TEH), other studies on both terrestrial and aquatic ectotherms found a maximal adult size only at the coldest extreme of the species' thermal tolerance range and not at some intermediate temperature (conflicting with the TEH) (Atkinson, 1994; Atkinson, 1995; Sweeney et al., 2018). Such observations led to the development of the temperature size rule (TSR) (Atkinson, 1994), which was reformulated by (Kingsolver & Huey, 2008) as "hotter is smaller". It seems to represent a special case of Bergmann's (1847) rule according to which populations/species of larger size are found in colder environments. Subsequent studies (Forster et al., 2012; Horne et al., 2015), reviewing a large number of temperature–body size experiments involving freshwater, marine and terrestrial species have confirmed the TSR hypothesis and showed that warming-induced reductions in adult body size are larger for aquatic ectotherms than for terrestrial ones. Recently studies have begun to investigate the drivers that explain the TSR rule. Although temperature responses appear to be outcomes of phenotypic plasticity, latitudinal size gradients could depend also on genetic factors (Horne et al., 2015). Insect temperature–body size trends observed across latitudinal clines have not been replicated across altitudinal gradients (Horne et al., 2018). TSR explanations have focused on physiological processes (such as oxygen limitation and resource availability) and responses (shorter developmental times due to higher mortality at higher temperatures), and on ecological and evolutionary mechanisms (adaptation to temperature to maximize fitness). Many of these studies support oxygen as a significant factor (Forster et al., 2012; Verberk et al., 2021). The higher cost of oxygen uptake in warmer water and the greater demands on large bodies to maintain aerobic scope in warmer environments both play important roles in determining adult size (Woods, 1999) and could explain the different temperature–size responses between aquatic and terrestrial organisms (Forster et al., 2012) and across latitude and altitude (Horne et al., 2018).

4.1.1.5 Assimilation/excretion

High temperatures cause an increase in the fraction of energy needed for metabolism maintenance (Sweeney & Vannote, 1978), which requires greater food consumption and leads to faster gut clearance (Zimmerman & Wissing, 1978). At high temperatures, some organisms, such as *Hydropsiche betteni* (Trichoptera), seek better-quality food (animal material or algae instead of detritus) to cope with higher energy demands (Fuller & Fry, 1991), whereas *Chironomus riparius* (Diptera) and *Mesogomphus lineatus* (Odonata) do not show dietary changes depending on temperature (Pandian et al., 1979; Péry & Garric, 2006). Food uptake and assimilation rates increase with temperature up to the thermal optimum (Culler et al., 2014; Van Doorslaer & Stoks, 2005a; McCauley et al., 2018; Pandian et al., 1979; Péry & Garric, 2006; Stoks et al., 2012).

4.1.1.6 Thermal limits

Thermal limits are usually measured in laboratory studies (Figure 6A) by exposing organisms to temperatures increasingly distant from their optimal temperature range (Sherberger et al., 1977b). Organismal death occurs when the water temperature reaches the critical thermal limits (Chou et al., 2018; Rogowski & Stewart, 2016; Rosillon, 1988; Sherberger et al., 1977a; Sweeney et al., 1986a). The upper thermal tolerance can be determined by the LT_{50} test: this threshold represents the lethal upper temperature at which 50% of individuals die in a specified time. By contrast, the incipient lethal temperature (ILT) thermal limits are based on the most extreme temperatures at which 50% of the test organisms survive indefinitely after being transferred from an acclimation temperature directly into a constant-temperature tank where time to death is measured (Brett, 1952). A less time-consuming approach that requires smaller samples is the critical thermal method (CTM) which consists of assessing the behavioural stress response, defined as the “arithmetic mean of collected thermal points at which locomotor activity becomes disorganized to the point at which the organism loses its ability to escape conditions that will promptly lead to its death” (Lowe & Vance, 1955, p.2). For aquatic macroinvertebrates, the response includes the inability to remain attached to the substrate and hyposensitivity to stimuli. All these methods have been employed in studies of thermal biology and a review focused on terrestrial animals comparing these different approaches is available (Lutterschmidt & Hutchison, 1997). For aquatic insects, the upper thermal limit evaluated at 96 h (96-LT_{50}) and the CT_{max} are related by a significant positive linear relationship, establishing the CTM method for use (Dallas & Ketley, 2011). There have been various attempts to define the thermal threshold of different aquatic macroinvertebrate taxa based on laboratory experiments on individual species or using the relationship between the macroinvertebrate assemblage and the temperature regime of the water bodies where they are found. (Stewart et al., 2013) defined the upper thermal tolerance of 13 taxonomic groups (mainly at order level) of southwestern Australian macroinvertebrates by reviewing the existing literature and measuring LT_{50} for four key species. (Dallas & Rivers-Moore, 2012), using the CTM, determined the upper thermal limits for 27 families of South African macroinvertebrates. Polato et al., (2018) and Shah et al., (2017) quantified CT_{max} and CT_{min} of

62 EPT species from Colorado (USA) and the Andes, showing that the tropical (Andean) species had a narrower thermal tolerance than the temperate ones. Niedrist & Füreder (2020) redefined the temperature optima and thermal ranges for different species of EPT and chironomids (Diptera) using regression models for long series of water temperature data and showed that alpine benthic communities had moved to higher altitudes in the last decade due to glacial retreat.

4.1.2 Phenological effects

Phenological responses are related to the life cycle and the duration of developmental stages (Vannote & Sweeney, 1980; Ward & Stanford, 1982). Temperature influences the total development period as well as the number of annual cohorts, and the timing of hatching and emergence (Woods et al., 2021). Understanding how temperature regulates the life history of a taxon could allow us to predict its phenological responses to climate change (Dingemanse & Kalkman, 2008; McCauley et al., 2018). The available life-history studies involve both laboratory and field experiments (Figure 6A), with samples of macroinvertebrates observed regularly to assess the overall duration of development or that of specific stages. Moreover, the organisms are counted and/or measured (length and biomass) to understand the influence of temperature on each instar and the number of generations produced per year. In insects, phenological responses of aquatic stages are monitored by assessing embryonic time (from egg deposition to hatching), larval time (from hatching to emergence) or the entire aquatic period (from egg deposition to emergence) (Brittain, 1977; Giberson & Rosenberg, 1992b; Humpesch, 1980a). The developmental period of macroinvertebrates can vary from a few months up to 3 years. A species may be semivoltine, univoltine, bivoltine, trivoltine or polyvoltine where the number of broods in one year is <1, 1, 2, 3 or >3, respectively (Hynes, 1970). Some species can modify their developmental period in response to temperature (voltinism plasticity) (Braune et al., 2008).

4.1.2.1 Total time of development

Several studies have shown that increasing temperature leads to shorter developmental time. Sweeney et al., (1986a) showed that the larval development of *Leptophlebia intermedia* (Ephemeroptera) is shorter at higher temperatures and Sweeney & Vannote, (1984a) reported the same for *Cloeon triangulifer* (Ephemeroptera). Other studies confirmed that developmental time, within the tolerance range, decreases with increasing temperature for eurythermal species (Bayoh & Lindsay, 2003; Frouz et al., 2002; Imholt et al., 2010;

McCauley et al., 2015; Sarvala, 1979). By contrast, for stenothermal species like *Soyedina carolinensis* (Plecoptera), the shortest developmental time (~92 days) was observed at an optimal temperature (10 °C), increasing at both higher (15 °C) and lower temperatures (5 °C) (~109 and 141 days, respectively) (Sweeney et al., 1986b). The same pattern was observed for *Eukiefferiella ikleyensis* (Diptera), with the shortest larval stage at 14 °C compared to both higher (18 °C) and lower (9 °C) temperatures (~71, 74 and 110 days, respectively) (Storey, 1987). The relationship between temperature and developmental time for stenothermal species can be described by a parabolic curve (Elliott, 1987; Sweeney et al., 1986b) while for eurythermal species the trend typically follows a negative exponential model (Marten, 1990) or an inverse asymptotic correlation (Brendan G. McKie et al., 2004). (Frouz et al., 2002) reported that under increasing temperatures chironomid males developed faster than females.

4.1.2.2 Time and length of hatching

Temperature is a crucial determinant of invertebrate hatching time. In general, temperatures far from the optimal range induce diapause (Danks, 1987), an adaptation evolved by some organisms to extend the embryogenesis period until the environmental conditions are suitable (Pritchard et al., 1996). The relationship between hatching time and temperature follows a decreasing trend best described by a power function (Bohle, 1972; Brittain, 1977, 1982; Brittain & Campbell, 1991; Elliott, 1972, 1986; Giberson & Rosenberg, 1992b; Humpesch, 1980a; Mendonça et al., 2018), or a hyperbolic power function (Elliott, 1978; Friesen et al., 1979), at least within the temperature tolerance range. Hatching time decreases at higher temperatures, more sharply in warm-adapted species such as Odonata than in cold-adapted species such as Plecoptera (Bouton et al., 2011; Pritchard et al., 1996). Diapause is longer at high temperatures for stenothermal species; eurytherms can survive low temperatures by remaining dormant (Pritchard et al., 1996). Embryonic period is positively correlated with egg size and the relationship between these does not seem to change with temperature (in the range 10–25 °C) in both univoltine and multivoltine species of mayflies, stoneflies, caddisflies, Coleoptera, Hemiptera and dragonflies (Gillooly & Dodson, 2000b).

4.1.2.3 Time and length of emergence

Increasing temperatures typically lead to earlier emergence of insects (McCauley et al., 2018; Nebeker, 1971; Rempel & Carter, 1987; Vannote & Sweeney, 1980). In aquatic environments characterized by a variable temperature regime, the pivotal factor regulating emergence is temperature while in constant-temperature habitats photoperiod plays a major role (Ivković et al., 2013). Water temperature is the primary driver that determines the timing of emergence for holometabolous insects (where the pupae are submerged) while other variables (such as humidity and air temperature) are involved for hemimetabolous insects (Ivković et al., 2013; Trottier, 1973). In recent decades the emergence of Odonata adults takes place earlier in the year due to increased temperatures. According to Hassall & Thompson (2008), British Odonata have advanced their emergence by about 1.15 days per decade and 3 days per degree between 1960 and 2004, showing a phenological response to climate change similar to those observed for terrestrial taxa (Lepidoptera, amphibians, birds and plants) (Sparks et al., 2000). A similar pattern was reported for Dutch Odonata (Dingemanse & Kalkman, 2008) and the German population of *Gomphus vulgatissimus* (Odonata) (Richter et al., 2008). Although Odonata is the best-studied group in terms of temperature-related emergence, there are similar findings for EPT and Diptera (Chacón et al., 2016; Cheney et al., 2019; Čmrlec et al., 2013; Dickson & Walker, 2015; Nebeker, 1971; Nyquist et al., 2020).

4.1.2.4 Voltinism

In response to different temperature conditions, aquatic macroinvertebrates can show phenotypic plasticity that can speed up or slow down the development of adaptive strategies (Pritchard et al., 1996). For example, some stoneflies (e.g. *Nemoura cinerea*) are able to shift from a univoltine to a semivoltine life cycle when the eggs are exposed to a low temperature (10 °C) (Brittain, 1974). Under increasing temperature, some stoneflies (e.g. *Leuctra nigra*) and mayflies (e.g. *Ephemerella danica*) shift from semivoltine to univoltine, showing highly plastic phenology (Elliott, 1987; Everall et al., 2015). Many species have a synchronous life cycle coordinated by water temperature (Humpesch, 1980a; Sweeney & Vannote, 1984). For example, *Beatis alpinus* (Ephemeroptera) has a trivoltine/bivoltine or univoltine life cycle depending on altitude (Erba et al., 2003; Humpesch, 1979) although (Bottová, Derka, & Svitok, 2013) found asynchronous life cycles in specimens maintained at constant temperature conditions. By contrast, a recent study carried out in a karstic spring of the Western Carpathians (Beracko & Revajová, 2019) investigating more than 40 benthic species did not support the proposal that constant water temperature promotes asynchronous life cycles and reported different phenological responses. Some Plecoptera species (e.g. *Protonemura auberti* and *Leuctra albida*) had an additional winter cohort instead of entering diapause, other species from various orders (e.g. *Gammarus fossarum,* (Amphipodae) *Rhyacophila tristis* (Trichoptera) and *Protonemura austriaca* (Plecoptera)) showed an unchanged or even a longer nymphal development while others maintained fixed voltinism

(*Ephemerella mucronate* (Ephemeroptera), *Isoperla sudetica* (Plecoptera)). Odonata species tend to show a clear voltinism gradient along latitude and temperature clines: voltinism decreases from Southern to Northern Europe ranging from one generation every 1–2 years in the south to one generation every 5 years in the north (Söndgerath et al., 2012), indicating that higher temperatures correlated with increasing voltinism (Braune et al., 2008). Univoltine species are likely to be negatively impacted by increases in temperature extremes whereas multivoltine species are likely to be advantaged (Rivers-Moore et al., 2012).

4.1.2.5 Colour

McCafferty & Pereira (1984) noted that in larvae of *Hexagenia limbata* and *Stenacron interpunctatum* (Ephemeroptera) the colour of the body and wings, as well as the spotting pattern, depended on the temperature regime of the water in which larvae developed. The colour of the compound eyes and legs was independent of temperature. Abbott (2013) conducted experiments on female *Ischnura elegans* (Odonata), a three-colour polymorphic species, to investigate whether colour polymorphism was correlated with thermal performance. He found that life-history traits varied across colour morphs, suggesting that thermal performance was more associated with morphospecies rather than local thermal adaptation.

4.1.3 Fitness effects

4.1.3.1 Fecundity and hatching success

In most invertebrates, fecundity is directly proportional to female body size (Rempel & Carter, 1987). High temperatures reduce the capacity of organisms to exploit resources from the ecosystem (Marten, 1990), leading to a decrease in the energy available for egg production, and thus to lower fecundity (Dallas & Ross-Gillespie, 2015; Pritchard et al., 1996; Rempel & Carter, 1987; Rosillon, 1988; Sweeney & Vannote, 1978). Increasing temperature also leads to faster hatching and lower egg survival (Bouton et al., 2011), partly due to a greater risk of infection by fungi and bacteria (Harvell et al., 2002; Marcogliese, 2016). In response to stressful temperature conditions, aquatic insects face a trade-off between growth and reproduction. According to the TEH, fecundity varies with altitude and latitude, declining as temperatures move away from the optimum. For example, Van Doorslaer & Stoks (2005b), studying two congeneric damselflies *Coenagrion hastulatum* and *C. puella* (Odonata) widespread in northern and central Europe respectively, identified the evolution of latitudinal compensation to low temperature in line with predictions of the TEH, but only at the embryogenic stage and not at the larval stage. This observation stresses the importance of assessing thermal responses at different life-history stages. Each species has a specific thermal threshold for egg hatching and development, which will affect both population size and species distribution (Elliott, 1988; Lambret et al., 2017). Optimal temperatures promote the largest broods and eggs, higher hatching success and greater reproductive success (Bovill et al., 2015), while higher temperatures have significantly negative effects on egg survival and overall fitness (Starr & McIntyre, 2020). Low temperatures prolong dormancy and delay hatching (Danks, 2002; Lencioni, 2004).

4.1.3.2 Larval recruitment

With increasing temperature the nymph recruitment increases while growth rates increase exponentially (Chavez et al., 2015; Corkum & Hanes, 1992; Van Doorslaer & Stoks, 2005b; Humpesch, 1980b; Ingram, 1976; Lencioni et al., 2013; Marten, 1990; McCauley et al., 2018; Strange, 1985; L. L. Wright et al., 1982). Some studies show that survival rates differ between the sexes, suggesting an interaction between sex and temperature. Other factors may also play important roles in larval recruitment, such as the ability to reproduce parthenogenetically (Wright et al., 1982).

4.1.4 Behavioural effects

4.1.4.1 Migration and drift

Temperature varies seasonally and within a waterbody, especially in rivers and deep lakes. As ectotherms, aquatic macroinvertebrates must maintain their metabolic and physiological processes at levels high enough to survive and reproduce (Vannote & Sweeney, 1980). Aquatic species can track suitable thermal niches by dispersal through drift or active swimming, with drift being the most common dispersal type in rivers (Waters, 1965). There are two types of drift: catastrophic (mainly due to disruptive floods or hydropeaking as well as drought, high temperature and pollution) and behavioural, occurring when macroinvertebrates voluntarily leave their substrate in response to stress conditions that include temperature, predation or resource scarcity (Muller, 1954; Waters, 1965; Wiley & Kohler, 1980). A variety of studies have recorded distinct drift in benthic invertebrates exposed to thermal and discharge waves caused by sudden water release from hydropower plants, with catastrophic drift due to hydropeaking and behavioural drift caused by thermopeaking. Chironomidae, Simuliidae (Diptera) and Baetidae (Ephemeroptera) resulted the most abundant drifting taxa (Bruno et al., 2012; Carolli et al., 2012; Schülting et al., 2016). Temperature can influence drift, for example, Wojtalik & Waters (1970) observed that increased temperature resulted in nocturnal drift in Baetis vagans (Ephemeroptera) but not *Gammarus pseudolimnaeus* (Amphipoda), while at constant temperature conditions neither species drifted. Scherr et al., (2010) reported greater drift in the mayfly *E. alberta* at a high temperature (28 °C). High water temperatures can also promote emergence events as shown by Trottier (1973b) for the climbing speed of *Anax junius* (Odonata).

4.1.4.2 Predation

High temperatures may disproportionately influence organisms at higher trophic levels which are more strongly affected by alterations of energy fluxes across the food web (Gilman et al., 2010; Vasseur & McCann, 2005). Thus, theoretically predators may be more vulnerable to increasing temperatures than their prey. However, McKie & Pearson (2006) showed that predation of Australian chironomids by *Australopelopia prionoptera* (Diptera) was not influenced by different temperatures (12, 18 and 26 °C). This suggests that in macroinvertebrates characterized by broad physiological tolerances the predator–prey relationship may be unaffected by temperature. Thermal shocks did not alter predation of Ephemeroptera (Sherberger et al., 1977a), with mortality of individuals of *Isonychia* sp. at 33 °C for 30 min due to the presence of a predatory fish (*Cottus carolinae*) similar to that for the control group (14 °C). By contrast, Smolinský & Gvoždík (2014) found that during daily temperature extremes predation rates on newt larvae diminished, despite increased predator (dragonfly larvae) movement. Predation pressure may be lower at high seasonal temperatures or where fauna have a broad thermal tolerance range (Hildrew & Giller, 1994; Brendan G. McKie & Pearson, 2006; Reice, 1994).

In boreal freshwater systems, predator–prey interactions are particularly sensitive to thermal changes due to the simpler trophic web and to the presence of stenothermal species (M. K. Moore & Townsend, 1998; Thompson, 1978). For example, Kishi et al., (2005), studying the trophic chain of a boreal stream composed by a predatory fish (*Salvelinus malma*), an herbivorous caddisfly (*Glossosoma*) and periphyton, observed that thermal habitat alteration can change food-web structure *via* combinations of direct and indirect trophic interactions. Indeed, at high temperature (21 °C) *Glossosoma* larvae were promoted due to both the lower salmonid predation and the greater availability of periphyton. On the other hand, high temperature can reduce the ability to build cases in Trichoptera larvae due to the high energetic cost (Mondy et al., 2011) leaving them more exposed to predators. For example, Rogowski & Stewart (2016) observed decreased retreat building and higher mortality in *Leptonema* sp. (Hydropsichae, Trichoptera) at 22 °C.

4.1.4.3 Feeding

A variety of studies have shown that key consumers in freshwater ecosystems change their feeding behaviour depending on temperature conditions. Metabolism is enhanced by increased temperatures, and this generates the requirement for a greater energy intake (Vannote & Sweeney, 1980). Greater feeding efficiency can be achieved either by targeting resources that are more easily assimilated or by seeking higher quality food. For example, in a geothermal stream network characterized by a large temperature range (5–23 °C), at warmer temperatures (20 °C) the snail *Radix balthica* (Gastropoda) shifts to a more specialized diet while the black fly *Simulium aureoum* (Diptera) switches from active collection of sessile diatoms to passive filter-feeding on motile diatoms. On the contrary, the chironomid *Eukiefferiella minor* (Diptera) becomes more generalist at higher temperatures (Gordon et al., 2018). Diet and temperature may interact: food quality influences both growth rates and body size in shredders, scrapers and grazers of EPT and Diptera (Fuller & Fry, 1991; Giberson & Rosenberg, 1992a; Rosillon, 1988; Storey, 1987; Sweeney et al., 1986b, 1986a). The interactions among food, temperature, developmental time and fecundity suggest that the TEH should be adapted to include both food quality (Rosillon, 1988) and availability.

4.1.5 Ecological effects

Ecological responses to temperature involve the whole macroinvertebrate community and include relationships among the taxa and their trophic roles, as well as the structure of the community itself.

4.1.5.1 Community richness, taxonomic composition, and density

Macroinvertebrate community composition varies with temperature at both micro- and macro-geographic spatial scales; temperature affects the selection and maintenance of different species in water bodies (Vannote & Sweeney, 1980). A clear trend of increasing richness occurs with increasing temperature (along both altitudinal and latitudinal gradients); Castella et al., (2001) showed this pattern for glacier-fed streams across Europe. In the Po catchment (Italy), a clear altitudinal pattern in macroinvertebrate community composition was identified. Assemblages inhabiting high-altitude sites were characterized mostly by Plecoptera, Trichoptera, Coleoptera, and Diptera, whereas macroinvertebrate communities inhabiting lowland sites included mostly non-insect orders such as Clitellata, Gastropoda and Bivalvia. At the temporal scale, annual thermal variability promotes seasonal dissimilarity in macroinvertebrate assemblages (Arai et al., 2015; Vannote & Sweeney, 1980; Ward & Stanford, 1982) while inter-annual water temperature variations affect community composition. For example, Fornaroli et al., (2020) found that in Northern Italy inter-annual flow and temperature regime variations affected community richness with higher alpha diversity in warmer years but lower EPT taxa abundance. Extreme temperatures can cause decreases in both species numbers and density (Arai et al., 2015; Glazier, 2012; Vannote & Sweeney, 1980; Voelz et al., 1994) inducing shifts in community composition (Arim, Marquet, et al., 2007).

Climate warming may promote eurythermal and generalist species with a consequent expansion of these less-specialized macroinvertebrate communities (Domish et al., 2011). This is likely to affect springs and small streams more than large rivers (Haidekker & Hering, 2008). Increasing temperatures led to the upstream spread of eurythermal and rheophilic species from subalpine levels, causing homogenization of macroinvertebrate communities, especially for EPT (Timoner et al., 2020). Increasing temperatures thus result in movement of species upstream and an increase in invasive species (Jourdan et al., 2018).

4.1.5.2 Distribution

Temperature affects species distributions both positively and negatively: some can be expected to increase their distribution in response to climate warming (‘winning’ species as defined by Domish et al., 2011) while others become more restricted (‘loser’ species) (Arai et al., 2015; Besacier Monbertrand et al., 2019; Jacobsen et al., 2014; Sweeney & Vannote, 1978). Adaptation to a specific temperature range restricts species zonation to particular ecological niches along the temperature gradient (Arai et al., 2015; Sweeney & Vannote, 1978). In recent years, attempts have been made to predict the distribution of freshwater communities at national, continental, and global spatial scales by applying predicted air temperatures (sometimes together with precipitation predictions) to models using long-term aquatic monitoring data sets. Several indicators have been developed to assess the sensitivity and vulnerability of aquatic communities to climate change (Conti et al., 2014; Hering et al., 2009; Mustonen et al., 2018; Sandin et al., 2014). Among the environmental drivers that regulate taxa distribution, climatic drivers contribute substantially at a broad geographic scale but are insufficient to explain local community dynamics at catchment scale, where other variables such as habitat, geomorphology and land-use features play an important filtering role (Feld & Hering, 2007; Poff et al., 2010). Other factors influencing the macroinvertebrate community at the local scale include species thermal limits, adaptation capacity, drift propensity, resource use and interspecific interactions (Glazier, 2012).

4.1.5.3 Food-chain length

The amount of energy available in an ecosystem influences its food-web structure (Odum, 1968) and sets an upper limit to the length of the food chain (Hutchinson & MacArthur, 1959; Lindeman, 1942). Two theories regarding the relationship between temperature and food-chain length have been proposed. According to the metabolic theory (Arim, Marquet, et al., 2007), body size and food-chain length are inversely correlated with environmental temperature: at high temperatures, metabolic demand increases so that lower levels of the trophic web consume more energy and energy flow to upper trophic levels is reduced. According to the thermal tolerance hypothesis (Brock, 1985), biochemical similarity among the organisms that constitute a specific ecological community will lead to similarity in their thermal tolerance. Therefore, below the upper thermal limit, the food-chain length is independent of temperature while close to the limit it is considerably reduced (Brock, 1985). Glazier (2012) showed that in springs (characterized by constant temperature and flow regimes), food-chain length decreases with increasing temperature, but the decline is not linear, broadly in support of the thermal tolerance hypothesis.

4.1.5.4 Community structure and trophic role

Temperature changes in freshwater ecosystems potentially alter macroinvertebrate community structure, modifying trophic interactions within the aquatic food web. Taxon-specific trait information (www.freshwaterecology.info database) can be used to investigate the mechanisms through which temperature affects community structure. For example, Jourdan et al., (2018) used long-term data (10–30 years) on macroinvertebrates from several streams in the UK, Germany, Finland, and Latvia to show that the composition of functional feeding groups was strongly impacted by warming conditions and more intense precipitation events. In particular, grazers and scrapers appeared especially vulnerable at higher temperatures, as predicted by (Pyne & Poff, 2017) for the macroinvertebrate communities of the western USA. Trait information related to feeding, substrate and habitat specializations proved critical to understanding the responses of macroinvertebrates to temperature changes in Sweden (Sandin et al., 2014).

4.1.5.5 Secondary production

The metabolic theory asserts that secondary production will be relatively temperature invariant, recognizing resource supply as the sole driver, and this has been validated by studies carried out in Iceland's geothermal streams (Junker et al., 2020; Nelson et al., 2017). However, basal resource dynamics depend on many variables including light, nutrient availability and temperature so apparent relationships between temperature and production can be explained by the positive effects of temperature on resource supply (Junker et al., 2020). Inland waters are heterotrophic ecosystems in which secondary production is strongly supported by allochthonous organic matter rather than by internal primary production. Climate change-related mechanisms may increase the inputs of allochthonous dissolved organic carbon (Pagano et al., 2014; Porcal et al., 2009). In addition, primary production is strongly dependent on water temperature regime (Demars et al., 2011; Padfield et al., 2017) making a general trend of increased resource availability likely with global warming. However, in addition to an increased supply of both autotrophic and heterotrophic food resources at higher temperatures, decay rates of organic matter will also be accelerated, thus decreasing its availability to consumers (Rempel & Carter, 1986). In aquatic environments characterized by constant temperatures (springs), stonefly secondary production was found to be very high, possibly due to reliable resource supply due to stable temperature (Bottová, Derka, Beracko, et al., 2013) and flow regimes (Zimmerman & Wissing, 1978).

4.1.6 Evolutionary effects

4.1.6.1 Genetic diversity

Temperature can also have effects at an evolutionary scale, causing thermal divergence in populations of the same species, promoting genetic diversity, and leading to temporal segregation. For example, temperate and tropical populations of the chironomids *Echinoclaudius martini* and *Australopelopia pronioptera* (Diptera) have diverged in developmental time; moreover, different populations of *E. martini* have diverged in oocyte production (greater in the temperate population) as well as body size, suggesting that temperature could facilitate population differentiation (Brendan G. McKie et al., 2004). Indeed, tropical species often have higher thermal limits than congeneric temperate species (Chapman, 2013). For EPT species of Ecuadorian Andean and USA Rocky Mountains, Polato et al., (2018) showed that tropical and temperate mountain stream insects have diverged in thermal tolerance and dispersal capacity due to different seasonal temperature variations. Tropical species had narrower thermal breadths, less gene flow, higher population divergence, higher cryptic diversity, and higher speciation rates, rendering them especially vulnerable to rapid changes in thermal environments. Johansson et al., (2016) showed that the genetic population structure of the Icelandic freshwater gastropod *Radix balthica* living in contrasting geothermal habitats was influenced by both geographic distance and water temperature. Genetic variation decreased with increasing temperature, suggesting that natural selection had led to reduced genetic diversity in warm geothermal springs due to higher thermal specialization. Herzog & Hadrys (2017) used a 20-year data set on the genetic diversity of a population of *Orthetrum coerulescens* (Odonata) located in Crau (France) to identify a dramatic decline in genetic diversity caused by increased water temperatures mediated by the destruction of bank vegetation. At high altitudes, global warming is leading to the loss of glaciers, which promotes fragmentation, limits gene flow and leads to loss of genetic variation among populations of high-altitude freshwater invertebrates. For example, populations of *Lednia tumana* (Plecoptera) in the Glacier National Park (Montana, USA) showed reduced gene and nucleotide diversity and increased genetic isolation in response to glacier retreat during 1997–2010 (Jordan et al., 2016). Genetic loss has been predicted in some European meltwater species of stoneflies, caddisflies and mayflies from predictions of mitochondrial DNA variability under different climate change scenarios. Intraspecific (cryptic) genetic loss is a significant concern and should be included when estimating the effects of global warming on biodiversity loss (Bálint et al., 2011). Temperature and genetic variability may interact affecting mortality: dramatic effects of high temperature (20 °C) were observed in a population of *Chironomus riparius* (Diptera) with poor genetic variability (Vogt et al., 2007).

4.2 Future directions

As shown in Figure 7 there has been a shift in emphasis in research on the effects of temperature on aquatic macroinvertebrates from the 2000s, when studies at larger temporal (decades) and spatial (ecoregions, continents and global) scales began to be published. This increase is likely due to the availability of large databases and improved analytical tools. However, most studies on macroinvertebrate communities (now often related to rising water temperatures due to global warming) do not report measured water temperature, but instead use air temperature as a proxy (Besacier Monbertrand et al., 2019; Domish et al., 2011; Haase et al., 2019; Jourdan et al., 2018; Li et al., 2013). This approach may be limiting because it does not account for the high thermal heterogeneity of different water bodies nor their seasonal thermal variability. It is therefore essential to implement a monitoring network for water temperature, especially where there are few or no data. In recent years, several models have been developed that can effectively predict water temperature even at a regional scale and have proved useful both to reconstruct historical series and to enable temperature forecasts (Beaufort et al., 2016; Jackson et al., 2020; Toffolon & Piccolroaz, 2015). A deeper knowledge of the temperature conditions of aquatic ecosystems will allow evaluation of the effects of temperature alterations due to anthropogenic impacts, such as hydropower plants, deforestation, and thermal effluents. Detailed investigations of the temperature regime of freshwater bodies will provide the data necessary for a deep comprehension of aquatic processes related to temperature (Diamond et al., 2021; Ducharne, 2008) and thereby the effects of temperature on macroinvertebrates mediated by changes in oxygen availability, primary production, and organic matter availability (Verberk et al., 2021). While we found many studies analysing different kinds of responses by macroinvertebrates both in the laboratory and in the field (Figure 5), most of the literature regarding the effects of climate warming on macroinvertebrates concerns ecological responses related to community composition and taxa distribution (Figure 6B) (Arai et al., 2015; Besacier Monbertrand et al., 2019). In recent years, studies have begun to investigate the effects of temperature on food-web structure (e.g. trophic roles (Jonsson et al., 2015; Jourdan et al., 2018)) and trophic chain length (Glazier, 2012), but studies on the effects of climate warming on growth rates, phenology and fitness are relatively rare, despite a historical focus on these areas in laboratory studies (Figure 6B). As noted by some authors (Forster et al., 2012; Tan et al., 2021; Verberk et al., 2021), warming induces earlier emergence and body size reduction in aquatic species, thus, the latitudinal temperature–size responses will influence the impacts of climate warming on primary production, community structure and food-web dynamics. Temperature affects physiology, phenology, and fitness, but these effects have been investigated almost exclusively at the population level, on target species studied in laboratory experiments (Figure 6A, D). It will be important for future investigations to include these responses in field studies involving macroinvertebrate communities. Studying functional traits and ecosystem attributes (Cummins, 1974) can also include responses related to fitness, voltinism, trophic role and drift propensity that normally are not accounted for in structural taxonomy indices. Indeed, functional traits have already allowed a more comprehensive understanding of the effects of temperature changes on macroinvertebrate assemblages at large spatial and temporal scales (Besacier Monbertrand et al., 2019; Hering et al., 2009; Poff et al., 2010; Pyne & Poff, 2017). A trait-based approach aiming to extend our knowledge about the thermal and ecological preferences of each taxon could be a promising way to understand and predict macroinvertebrate assemblage changes both in structure and functioning.

A further point of concern is the unbalanced number of studies among different continents (Figures 6F and 9). We currently have very little information on the effects of water temperature on freshwater macroinvertebrates of 70% of our planet, with tropical, arid, and arctic climatic regions most unrepresented (Figure 9). The focus of research is restricted mostly to European and North American macroinvertebrate communities, often living in water bodies profoundly impacted by direct human intervention (Dodds et al., 2013), and studies investigating the ecological effects of temperature have been carried out almost exclusively in Europe (Figure 6F). This unbalanced distribution will inevitably lead to a somewhat distorted perception of macro-ecological patterns related to temperature. Future work should target water bodies in Asia, Africa, South America, and Antarctica to allow us to obtain a more global perspective.

Genetic investigations of tropical and temperate macroinvertebrates have shown that taxon thermal preference varies across latitudes due to evolved thermal adaptations. Comparative studies demonstrated that tropical species generally have a narrower thermal range compared to temperate ones, occupy narrower ecological niches, are more specialized and therefore more vulnerable (Polato et al., 2018; Shah et al., 2017). However, information on the temperature ranges of tropical macroinvertebrate species is currently available only for about 60 species. According to Van Vliet et al., (2013) and Wanders et al., (2019), the water bodies most vulnerable to global warming are likely to be small, especially in temperate and arctic regions. It is, therefore, crucial to include more lentic ecosystems in thermal research given that lakes and ponds have been poorly investigated (Figure 6A). They may be among the most vulnerable ecosystems to climate change because they are mainly in the boreal belt (Messager et al., 2016). Additionally, as reported by many authors (Bálint et al., 2011; Birrell et al., 2020; Brighenti et al., 2021; Jordan et al., 2016; Polato et al., 2018; Shah et al., 2017), mountain aquatic macroinvertebrates are likely to be the most threatened freshwater species due to their endemicity.

5. Conclusion

(1) Our review reveals that the effects of water temperature on macroinvertebrates are manifold with implications at different levels, from genes to communities, and involve multiple responses related to physiology, phenology, fitness, behaviour, community ecology and evolution. Despite substantial advances in thermal research in recent years, understanding how macroinvertebrate taxa and communities respond to different temperature conditions is far from complete.

(2) Temperature responses historically tested in laboratory studies, such as effects on body size, have not been assessed more widely at the community level. This will be necessary given their important macroecological implications.

(3) Studies involving gene expression have begun relatively recently. This promising avenue will provide an understanding of the physiological mechanisms underlying responses to temperature and allow us to disentangle behavioural and evolutionary adaptation.

(4) Increasing temperatures driven by climate change strongly threaten stenothermal macroinvertebrates, especially in mountain waterbodies, but these are poorly investigated. When estimating biodiversity loss driven by higher temperatures, both genetic and species loss should be considered.

(5) Tropical macroinvertebrates generally have a narrower thermal range and are more vulnerable to temperature changes; how they respond to changes in temperature should be examined in more detail.

(6) Our knowledge of macroinvertebrate–temperature relationships is based almost exclusively on studies carried out in the West, and in waterbodies greatly impacted by human activity; widening our perspective to include other regions will be important to enable a deeper understanding of the effects of climate change.

(7) Lakes and ponds are underrepresented in the published work and should be a focus of future studies because many are in the boreal belt that is warming faster that the global average.

(8) Extended spatiotemporal data sets often use air temperature as a proxy for water temperature and are derived almost exclusively for European rivers. Measuring water temperature data accurately will greatly improve our understanding of the effects of thermal heterogeneity on macroinvertebrate assemblage structure and the effects of temperature changes on aquatic ecosystem structure and functioning.

Data

Data are available at: https://doi.org/10.6084/m9.figshare.20584311.v1

Supplementary material

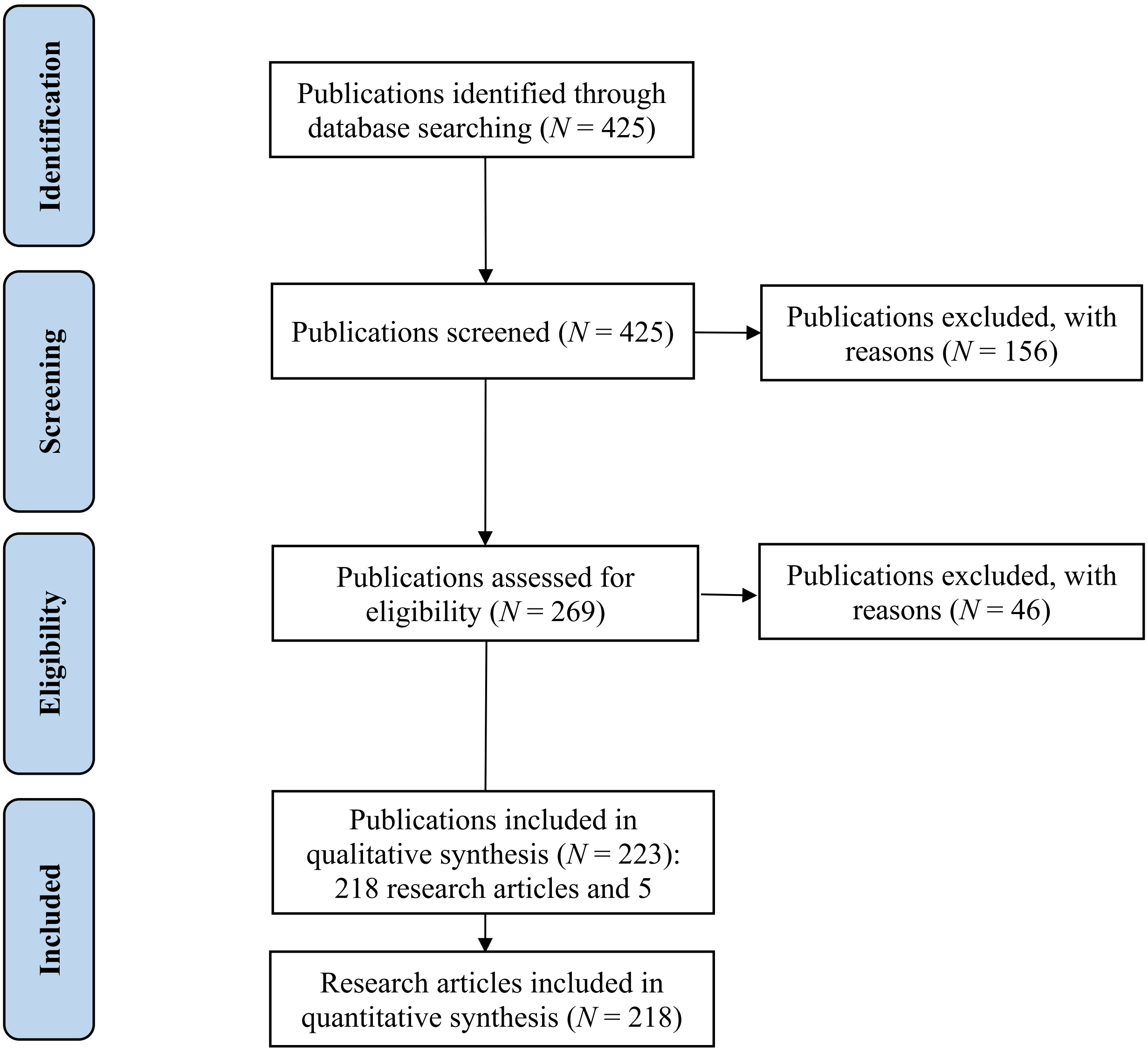

Figure 1SM. PRISMA flow diagram showing the different phases of article selection for the systematic review.

Table 1SM. Numbers of studies for each category of information extracted from the research publications (N = 218) included in the final database.

Category:	Ecosystem		Study		Continent		Climatic region		Spatial scale		Temporal scale		Sampling frequency		Level of investigation	
	channel	8	experimental	194	Africa	5	arid	11	catchment	45	days	27	annual	7	family	15
	laboratory	128	theoretical	24	Antarctica	2	cold	68	continental	8	decades	15	daily	57	genus	9
	lake	11			Asia	10	polar	6	ecoregion	4	months	103	hourly	14	order	4
	pond	5			Central America	2	temperate	139	global	4	punctual	14	monthly	52	species	191
	river	74			Europe	100	tropical	13	regional	32	years	59	punctual	16		
	spring	9			North America	92			site-specific	109			seasonal	4		
					Oceania	16							subhourly	7		
					South America	11							weekly	36		
Sum		235		218		238		237		202		218		193		219
	not found	10	not found	0	not found	7	not found	8	not found	16	not found	11	not found	41	not found	3
Total		245		218		245		245		218		229		234		222

Category:	Ecological unit		Organism			Temperature conditions		Other stress		Effects		Responses	
	community	59	Arachnida	Trombidiformes	1	climate warming	20	flow	6	behaviour	24	drift	7
	gene	8	Bivalvia	Cardiida	1	constant thermal regime	7	food availability	19			feeding	7
	population	151		Sphaeriida	1	high temperature	16	habitat	3			migration	4
				Unionida	1	natural thermal regime	74	humidity	3			predation	6
				Veneroida	1	temperature range	120	nutrient concentration	3	ecological	132	community structure and trophic role	3
			Clitellata	Arhynchobdellida	3	temperature variation	8	other	7			density	34
				Haplotaxida	4			oxygen availability	6			distribution	25
				Lumbriculida	1			photoperiod	9			food-chain length	1
				Opisthopora	2			pollution	3			richness	31
			Gastropoda	Littorinimorpha	5			predation	7			secondary production	7
				Neotaenioglossa	1							taxonomic composition	31
				Pulmonata	2					evolutionary	4	genetic diversity	4
			Insecta	Coleoptera	17					fitness	70	fecundity and hatching success	47
				Diptera	57							larval recruitment	23
				Ephemeroptera	80					phenological	132	colour	4
				Mecoptera	1							time and length of emergence	49
				Neuroptera	5							time and length of hatching	39
				Odonata	61							total time of development	29
				Plecoptera	55							voltinism	11
				Rhynchota	5					physiological and metabolic	163	assimilation/excretion	16
				Trichoptera	57							body size and growth rate	85
			Malacostraca	Amphipoda	11							gene expression	9
				Decapoda	3							osmoregulation ability	1
				Harpacticoida	1							respiration	8
				Isopoda	8							size at emergence	19
				Mysida	1							thermal limits	25
			Maxillopoda	Cyclopoida	2								
			Rhabditophora	Tricladida	3								
Sum		218			390		245		66		525		525
	not found	0		not found	3	not found	0	not found	0	not found	0	not found	0
Total		218			393		245		66		525		525

CHAPTER 4

Temporal patterns of stream biofilm in a mountain catchment

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CHAPTER 4. Temporal patterns of stream biofilm in a mountain catchment

Abstract

Biofilm is the dominant primary producer in mountain streams and sustains the higher trophic levels. Among the different algae groups, some, especially diatoms, have been studied deeply while an overall characterization of the community remains quite overlooked. The present study aimed to investigate the biofilm temporal pattern in mountain streams characterized by different water thermal regimes. A one-year quantitative campaign, with monthly samplings, was carried out in five subalpine streams in the Orobic Alps (Northern Italy) collecting biofilm from a large surface. The total biomass was quantified and the periphyton was analyzed both for composition (diatoms, green algae, cyanobacteria, and red algae) and for pigments. Disturbance, water temperature, physico-chemistry, substrate diversity, nutrients and light availability were evaluated at the same time of the biofilm samplings. Results show sharp biofilm variations over months. The disturbance was the primary factor affecting biomass and pigment content while the relative abundances of algae groups were mainly related to the light and to the water temperature. Overall, the study indicates that a quantitative and frequent investigation of the biofilm allows to understand the temporal changes and to detect the main drivers. Such information is useful to understand the ecosystem processes and the food web dynamics.

Keyword

Microalgae, dam, water temperature, light, substrate, PAM fluorimetry, bioassessment.

1. Introduction

Biofilm is the assemblage of both autotrophic and heterotrophic organisms attached to the substrata of aquatic systems (Whitton, 2012). The autotrophic component, called periphyton, comprises very different organisms from the taxonomic point of view but all performing photosynthesis. Bacillariophyta (diatoms), Chlorophyta (green algae), Cyanophyta (cyanobacteria), Rhodophyta (red algae) and Chrysophyta (gold algae) are the main groups. In mountain lotic systems, due to the perennial instability caused by running water, the primary producers are a minoritarian component. Nevertheless, they play a pivotal role sustaining the upper trophic levels and providing habitat for other organisms as invertebrates, protists, and bacteria (Rott et al., 2006). In headwater stream the periphyton can contribute as much as 80% to the autochthonous primary production (Hansson, 1992), and constitute an important source of energy for the higher trophic levels (Hauer & Lamberti, 2017). The ecological niche of biofilm is characterized by a long list of environmental variables including hydrology, substrate, light, nutrient availability, and temperature, showing stream type specific variation ranges (Allan & Castillo, 2007). In mountain streams the main factor that controls the biofilm growth is the flow; indeed, the current exerts a shear stress on benthic algae causing cell sloughing (Biggs, 1988; Power & Stewart, 1987). Extreme flows can have a strong negative impact on benthic biota that, due to high velocity, overturning of stones and tumbling abrasion, flows away (Power & Stewart, 1987; Robinson & Rushforth, 1987). The negative effects of floods on biofilm consist mainly in the decrease abundance and taxa richness. However, the size and type of substrate (rough or smooth) as well as the riverbed typology (armored or not) can play a pivotal role (Biggs & Smith, 2002; McAuliffe, 1984). The pattern of recolonization depends on the species of algae, the hydrology and the substrate type and is generally faster especially just after the flood and in streams where the disturbance is frequent (Biggs & Smith, 2002). Besides hydrology and substrate, light and nutrients are chief factors for the algal growth. Indeed, various studies suggested that in shaded streams the light availability is the limiting factor while nutrients exert that role especially in unshaded streams (Hill et al., 1995; Mosisch et al., 1999; Rosemond, 1993). The nutrient availability is controlled by inputs coming from riparian and terrestrial environments (Bernal et al., 2015; Hedin et al., 1998); phosphorus (PO_4^{3-}), nitrogen (NH_4^+, NO_3^-) and silica (SiO_2) are considered the most critical for the algal production, even if silica is often above the minimum request in lotic systems (Robinson et al., 2000). Overall, mountain running waters not subjected to pasture are very poor of phosphate, while nitrogen, available generally on the form of nitrate (NO_3^-) comes from the atmospheric deposition. Finally, the water temperature affects the biomass of periphyton (Morin et al., 1999) controlling the rate of primary production through its effects on photosynthetic physiology (Medlyn et al., 2002). Moreover, the composition of the algal communities depends on the thermal preference of each taxon, and temperature variations promote changes in the dominance of the main groups (green algae, cyanobacteria, diatoms, and red algae) throughout the seasons (Allan & Castillo, 2007). Multiple factors influence the biofilm growth and composition. However, few studies focused on the fine temporal patterns of biofilm in streams through an overall characterization of the community and they were mainly carried out in New Zealand (Biggs, 1995; Quinn & Hickey, 1990) and South America (Branco & Necchi, 1996; Branco & Necchi, 1998; Necchi et al., 1995; Pizarro & Alemanni, 2005). Instead, studies carried out in the Alps concerned mainly diatoms and cyanobacteria of Trentino springs (Italy) (Cantonati et al., 2005; Cantonati, Rott, et al., 2012; Gerecke et al., 2011) algae assemblages of Swiss glacier streams (Hieber et al., 2005; Uehlinger, 1991, 2006) and of Austrian watercourses (Rott et al., 2006; Rott & Wehr, 2016).

Traditionally, periphyton biomass has been estimated by the spectrophotometric determination of the chlorophyll a concentration. However, such method does not provide any information about the community composition. Microscopy is commonly used to identify and enumerate microalgae distinguishing genera or species from their morphological features. This approach has been mainly applied to diatoms which are considered good bioindicators to assess the ecological status of freshwater systems: several indicators based either on the presence/absence or on the relative proportions of these taxa have been developed (Poikane et al., 2016). However, microscopic analysis is laborious, time-consuming, and requires specific expertise (Echenique-Subiabre et al., 2016). Over the last two decades, new “real-time” tools have been developed to monitor periphyton communities. Such methods are based on fluorometry and can distinguish the main photosynthetic groups (i.e. cryptophytes, cyanobacteria, diatoms/dinoflagellates and green algae) in a mixed assemblage. For example, the fluorometer BenthoTorch allows the *in situ* monitoring of periphyton providing both quantitative estimation of biomass (expressed as Chl a content) and a characterization of the different algal groups. Thus, BenthoTorch has been applied to monitor water quality (Kahlert & McKie, 2014) and to detect potentially toxic benthic cyanobacteria both in rivers (Echenique-Subiabre et al., 2016) and in water supplies systems (Rosero-López et al., 2021). However, the signal concerns very small areas (1 cm^2) and this can lead to unreliable estimates of the total periphyton biomass (Harris & Graham, 2015) and to underestimates in thick biofilm, as the fluorescence response reflects only surface signals (0.1 mm thick layer) (Echenique-Subiabre et al., 2016).

Giving the importance of biofilm investigation to understand ecosystem processes and food web dynamics the present study aims to study the pattern of biofilm in mountains streams. Specifically, the biofilm temporal changes as related to environmental variables were monitored monthly among subalpine streams characterized by different water thermal regimes by an overall characterization accounting both for quantity (biomass and pigments) and composition (main groups). Different approaches were combined to overcome the methodological limitations described previously and explore changes in periphyton through a fast assessment (without a taxonomic identification). We supposed the total biomass would be mainly driven by the occurrence of floods contrary to the periphyton composition that would change over the months promoted by variations in water temperature and light availability. Concerning spatial variations, we expected that site specific features as substrate, water quality and light availability would explain differences in biofilm. On the other hand, we supposed that the annual water thermal variability would affect the overall (annual) periphyton assemblage, especially for what concerns the composition.

2. Materials and Methods

2.1 Monitoring plan and sites

One-year campaign (June 2020-May 2021) with monthly samplings was carried out in five stream sites in the upper Serio catchment (Orobic Alps, Northern Italy). Streams were characterized by different water sources (snowmelt/stormwater and groundwater-fed streams) and anthropogenic pressures (presence of reservoirs) leading to a different annual water thermal variability (annual daily maximum-annual daily minimum) ranging from ~1 to 16 °C. Sites GU and GD were situated in the Goglio catchment: GU at 975 m a.s.l., on a tributary stream not subjected to flow regulation and GD at 1128 m a.s.l., on the main channel, around 2 km downstream of a reservoir. Both streams are fed by snowmelt/storm waters. Due to flow regulation, GD displays a water thermal variability lower than GU (~16 vs ~9 °C). Sites OU and OD were located respectively upstream (970 m a.s.l.) and downstream (583 m a.s.l.) of a small reservoir in the Ogna catchment, along a stream fed by snowmelt/storm and groundwaters. Also in this case, the downstream site exhibited a lower variability compared to the upstream one (~7 °C vs ~8 °C). The NN site was situated in the Nossana catchment at 468 m a.s.l. on a groundwater-fed stream characterized by constant temperature (~8 °C), about 200 m from the spring. All the monitored streams had similar morphology and substrates, whose size ranged from gravel (0.2-2 cm) to big pebbles (>40 cm). The territory, at an altitude of 500-1200 m a.s.l is covered by woods composed mostly of beeches and firs while the riverbanks are characterized by the presence of willows, alders, birches, hazels, maples, and shrubs.

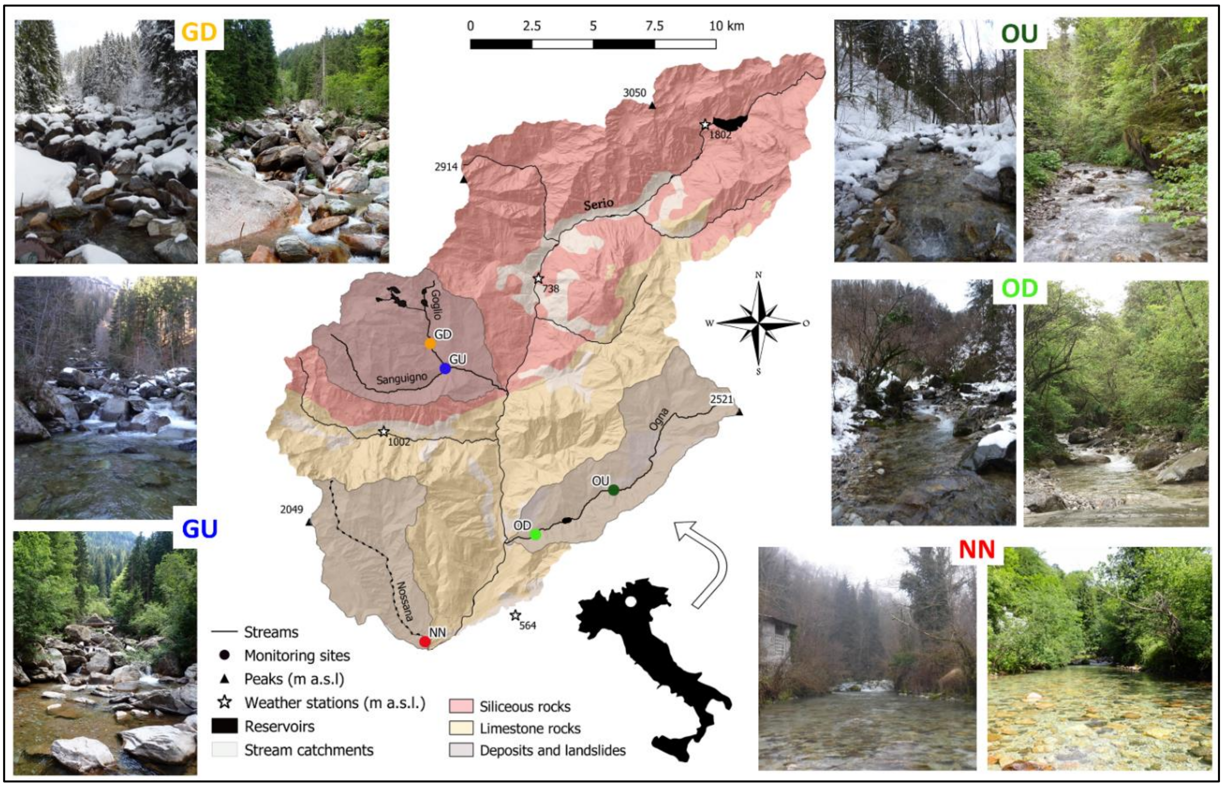

Figure 1. Study area with pictures of the stream sites in winter and summer.

2.2 Biofilm sampling

Biofilm was sampled according to the European and Italian methodology (APAT, 2007; CEN EN 14407, 2014), but monitoring a larger surface (0.5 vs 0.01 m^2). A dozen stones, representative of the different microhabitats (akal/microlithal/mesolithal/macrolithal/megalithal) (Hering et al., 2004) where chosen randomly in the riverbed. All stones from a given site were scrubbed in 500 ml of stream water, giving a single composite biofilm sample for each sampling (site*date). To calculate the sampling surface, we took a picture of the collected stones arranged on a squared sheet and measured the total area in QGIS. On the same day of the sampling, 10 ml of biofilm solution were frozen (-20 °C) for the pigment extraction while the rest was chilled to 4 °C and brought to the laboratory to be processed within 24 h. 100 ml of algal suspension were analyzed for dry weight (24 h at 105 °C) and ashes (4 h at 550 °C). The total mass of biofilm was calculated as the ash free dray mass (AFDM) normalized by the sampled surface (g/m^2).

2.3 Periphyton deconvolution

The composition of the periphyton component of biofilm was determined by the deconvolution function of Phyto-PAM II instrument (Heinz Walz GmbH, Effeltrich, Germany) that distinguishes the fluorescence signals emitted by four different groups of photosynthetic organisms: cyanobacteria, green algae, diatoms (and dinoflagellates), and red algae (organisms with phycoerythrin). The operating principle of PAM instrument is the same as BenthoTorch, commonly used for rapid assessment of phototrophic communities on river bottom substrates (Kahlert & McKie, 2014). As some studies indicate a mismatch between the estimates by microscopic observations and BenthoTorch results, especially in thick biofilms (Echenique-Subiabre et al., 2016) a larger sampling area was chosen (0.05 m^2 instead of 0.0001 m^2 of surface for replicate), the periphyton was removed from the stones and the resulting algal suspension was analyzed in the lab. Phyto-PAM II can distinguish also red algae (Kahlert & McKie, 2014), providing a more reliable description of the community, especially in streams, than BenthoTorch. The percentage of each algal group was calculated, and the composition diversity was estimated using the Shannon index. To assess the overall annual temporal dissimilarity (Legendre, 2019) within a site, we used the multi-date β-diversity indices (i.e., also known as multisite β-diversity indices (Baselga et al., 2022)) considering the Sorensen dissimilarity (BSor) and its components (turnover and nestedness).

2.4 Pigment determination

Pigment content was determined as follows: 10 ml of biofilm suspension were centrifuged at 10,000×g for 5 min; the supernatant was discarded, and 10 ml of 99.9% methanol was added to the concentrated pellet, well mixed, and incubated at 45 °C for 24 h in dark. Pigment concentration was calculated according to the following equations as the mean of three replicates per sample (Lichtenthaler, 1987):

$$\text{Chlorophyll a (mg/l)} = 16.72\ \text{Abs665} - 9.16\ \text{Abs652}$$

$$\text{Chlorophyll b(mg/l)} = 34.09\ \text{Abs652} - 15.28\ \text{Abs665}$$

$$\text{Carotenoids (mg/l)} = (1000{*}\ \text{Abs470} - 1.63{*}\ (\text{Chl a}) - 104.9{*}\ (\text{Chl b}))/221$$

Where Abs665, Abs652, and Abs470 are the absorbances measured by a spectrophotometer (DR600TM UV VIS Spectrophotometer Hach Lange) at a wavelength of 665, 652, and 470 nm, respectively. The concentration of each pigment was then reported to the sampled surface and expressed as mg/m^2.

Finally, the chlorophyll a concentration was used to estimate the proportion between autotrophic and heterotrophic organisms of the biofilm calculating the autotrophic index (Weber, 1973):

$$Autotrophic\ index = \frac{\text{AFDM biomass } \left(\frac{\text{mg}}{m^2}\right)}{Chlorophyll\ a\ \left(\frac{\text{mg}}{m^2}\right)}$$

Values between 50 and 100 indicate that the biofilm is composed only of autotrophic organisms unlike values greater than 100 (Weber, 1973).

2.4 Environmental variables

Stream microhabitat availability (HABITAT) was assessed using the standardized multi-habitat methodology used for macroinvertebrate sampling (Hering et al., 2004). When sampling periphyton the relative proportion of each microhabitat covering more than 10% of the stream sampling site was measured and the Simpson index was calculated for each habitat. The light exposure (EXPOSURE) was estimated as a percentage of the open sky, based on photographic pictures of the surrounding trees (0% = full canopy, 100% = no canopy) (see Cantonati and Pipp, 2000). Each water sample was characterized for electric conductivity (CE), dissolved oxygen (DO), and oxygen saturation (O2) using a probe HACH-HQ40d (Loveland, USA). In addition, 0.5 liters of water were collected and brought to the laboratory where pH was measured using a HANNA pH meter 211 (Woonsocket, USA), and nitrate nitrogen NO_3-N (NNO3) and Chemical Oxygen Demand (COD) were determined by using spectrophotometric test kits (Hach-Lange, Düsseldorf, Germany, LCK 340, and LCK1414, respectively). Total phosphorus (Ptot), and ammoniacal nitrogen NH_4-N (NNH4) concentrations were determined in the laboratory according to standard methods (APHA/AWWA/WEF, 2012). The water temperature was measured continuously (every 10 min) from Autumn 2019 to Autumn 2021 using iButton devices (DS1925L sensors: range -40-80 °C, accuracy: ±0.5°C, resolution: ±0.0625°C) fixed in the riverbed of the five stream sites. The average water temperature (TMean) of each sampling day was calculated as the mean of the 30 days before each sampling. Substrate movement associated with flood disturbance was measured using painted pebbles placed in the streambed according to Townsend et al., (1997). 15 locally sourced painted pebbles belonging to three size classes (50th, 75th, and 95th percentiles of the substrate size distribution) were placed in riffles, in random order in triplets (small, medium, and large), across the main flow of the stream at marked points on the stream bank. On each sampling day, the distance travelled by each stone was recorded and stones were placed back at their initial position (Death & Zimmermann, 2005). Flood disturbance (DISTURBANCE) was quantified for each sampling combining the displacement of the substrate with the moved mass by the following equation:

$$\text{Disturbance} = \frac{\sum_{i=1}^{n} m_i * d_i}{\sum_{i=1}^{n} m_i} \%$$

Where *m* is the pebble mass and *d* is the displacement (1 in displacement and 0 in no displacement case). Pebbles that could not be recovered were not considered since they could have been washed away or buried by sediments. In most cases (75%), all the pebbles were found. As several floods could occur within one month, the metric DISTURBANCE can be used as a proxy of the overall sediment movement between two consecutive sampling dates but cannot be directly linked to the flow. Light availability (HLIGHT) in each site was calculated by the GRASS software. The “r.sun” function was used to obtain the hours of light at each site as a function of the day of the year and the topography (location and mountain shadowing). Each site was represented by an area of 250 m^2 described by a digital terrain model with a resolution of 5 m. The light availability at each sampling day was measured as the mean of the daily light in the 30 days before. This indicator, coupled with the exposure, was considered more representative than the photosynthetically active radiation (PAR) that could have been measured monthly at each site: indeed, punctual PAR measures are very sensitive to weather conditions and the specific riverbed position (Melbourne & Daniel, 2003) and, thus, are not representative of monthly changes.

2.5 Statistical analysis

First, separate principal component analyses (PCAs) were performed to investigate the patterns of environmental variables and biofilm. In the biofilm biplot, the percentage of each algal group, the Shannon, and the autotrophic indexes were added as supplementary variables, thereby not contributing to the definition of multivariate axes. PCAs were performed using the function *prcomp* from the “factoextra” package (Kassambara & Mundt, 2020). Environmental variables and biofilm metrics among sites were compared by boxplots and Wilcoxon rank sum tests (paired by date) were performed. The Bonferroni-Holm method was used to adjust p-values for multiple comparisons. Then, the temporal changes of the most relevant environmental variables (according to the PCA) were described by plotting the monthly values in each site. Similarly, the temporal variations of periphyton were represented by considering biomass/pigments and composition separately. First, the time series of biofilm biomass, periphyton pigments, and autotrophic index were plotted for each site. Then, the temporal change in community composition was represented by cumulative bar plots with the relative abundance of each algal group (cyanobacteria, green algae, diatoms, and red algae) for each site. To identify differences among temporal patterns of biomass/pigments in each site Spearman correlations were used. The p-values were corrected for multiple inferences using Holm's method using the *rcorr.adjust* function from the “RcmdrMisc” package (Fox et al., 2022).

To assess how environmental factors were associated with the biofilm structure linear mixed-effect models (LMM) between biofilm metrics and environmental variables were developed and the relative contribution was determined. The *lmer* function in the “lme4” package (Bates et al., 2015) was used. Biomass, chlorophyll a, chlorophyll b, carotenoids, Shannon, and autotrophic indices were log+1 transformed while the relative abundance of each group was logit transformed (*logit* function from the “car” package (Fox et al., 2022) to normalize residuals and equalize variances. As predictors the more explicative variables according to the PCAs (Figure 2A) were used; DO and pH were excluded as they were highly correlated with TMean (r Pearson > 0.7) and exhibited always optimal values as well as O2. HABITAT, COD, and NNH4 were also excluded as they did not show any temporal pattern and poorly contributed to the variance explained by the PCA. Thus, DISTURBANCE, CE, NNO3, TMean, and the interaction term between EXPOSURE and HLIGHT were included as fixed effects while sites were included as random effects on the intercept. To account for temporal changes, the SEASON was included as a fixed effect, identified as winter (December–January–February), spring (March–April–May), summer (June–July–August), and autumn (September–October–November). The dredge function within the “MuMIn” package (Bartoń, 2019) was used to derive the optimal set of fixed effects tested within each LMM. This function fits different models comprising all the combinations of fixed effects and ranks them by the Akaike Information Criterion corrected for small sample size (AICc). The most parsimonious model within 2 AICc units of the best (the model exhibiting the lowest AICc value) was selected as the “optimal” model. The explanatory power of the statistical models was derived from marginal and conditional pseudo r-squared values ($R^2_{marginal}$ and $R^2_{conditional}$ respectively, see Nakagawa & Schielzeth, 2013), which quantify the variance explained by the fixed effects and by the entire model respectively. The values were obtained using the *r.squaredGLMM* function in “MuMIn”. The significance of each optimal model was obtained via likelihood ratio tests (see White et al., 2018); if SEASON was included in the optimal model, it was also included in the “null” model to test the joint effect of the other variables. Finally, to establish if differences in the water thermal regime could partially explain differences in periphyton composition among sites the annual water thermal variability was correlated with the annual temporal dissimilarity (BSor). All the analyses were performed in R project software (R Core Team, 2020).

3. Results

3.1 Patterns of environmental variables and biofilm

The total variance explained for environmental variables by the first two axes of the PCA was 44.3%: 24.6% by the first principal component and 19.7% by the second one (Figure 2A). The biplot shows high orthogonality between the variance associated with months and with sites, discriminating samplings both in time and space. Indeed, variations in time were described mainly by TMean, pH, DO, COD (and partially HLIGHT, DISTURBANCE and EXPOSURE) while variations among sites were described by NNO3, CE, NNH4, O2, HABITAT (and partially by EXPOSURE, and DISTURBANCE). The total variance explained for biofilm by the first two axes of the PCA was 78.5%: 55.2% by the first component and 23.3% by the second one (Figure 2B). PC1 was positively correlated with Chlorophyll a, Chlorophyll b, Carotenoids, Biomass, and diatoms and negatively with the Autorophic_index while PC2 was positively correlated with cyanobacteria and red algae and negatively with green algae. The biplot shows high orthogonality between the variance associated with biofilm quantity (biomass, pigments’ content, and autotrophic index) (PC1) and with periphyton composition (percentage of the main groups and Shannon index) (PC2) without displaying any specific pattern (in space and/or time).

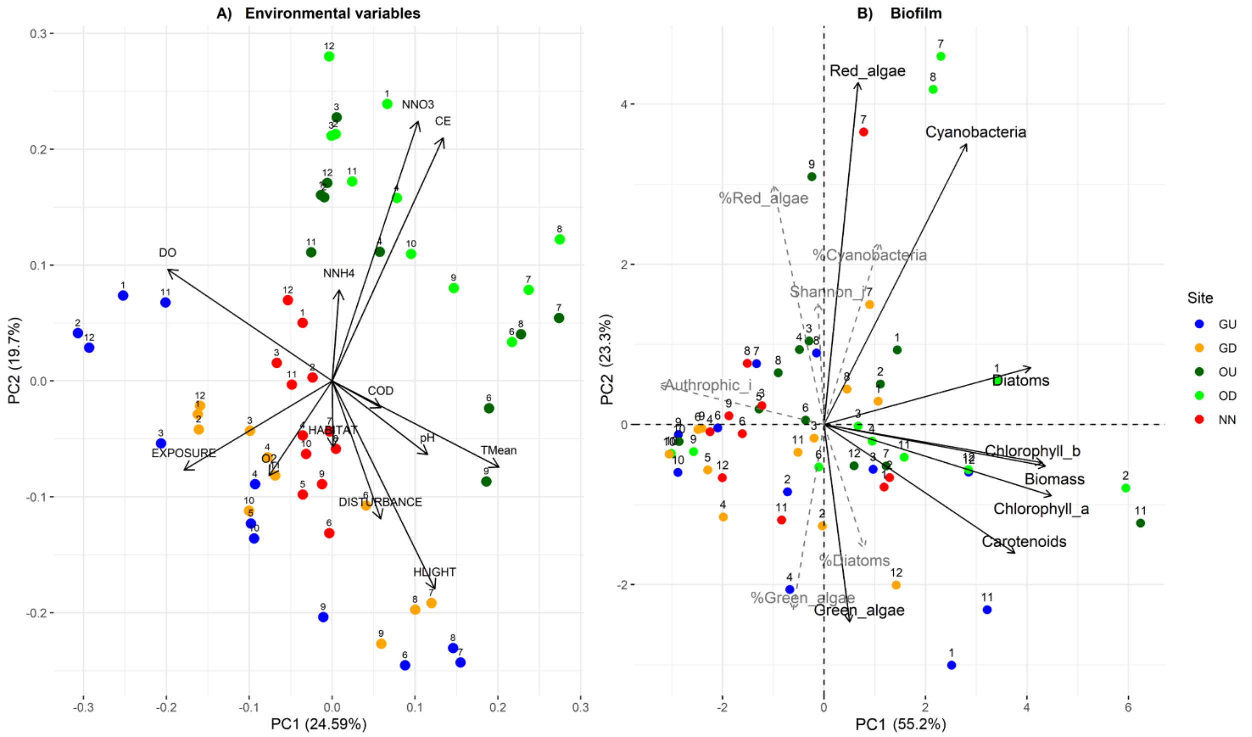

Figure 2. PCA on environmental variables (A) and biofilm (B). Biofilm metrics regarding the relative abundance of the main periphyton groups, the Shannon index, and the autotrophic index were added as supplementary variables (grey dot lines) only for visual purposes.

3.2 Spatial patterns

According to the environmental PCA, CE, NNO3, EXPOSURE, O2, NNH4, and HABITAT variables exhibited spatial differences (Figure 2A). Indeed, in sites influenced by groundwater inflows (OU, OD, NN) CE was higher (>200 µS/cm) than in sites dominated by snowmelt/stormwater (<85 µS/cm for GU and GD). Electric conductivity was also slightly higher in regulated sites (OU & GD) than in the unregulated ones (OD & GU) leading to significant differences among sites (Wilcoxon test, $p<0.05$). NNO3 was higher (>1 mg/l) in Ogna sites (OU and OD) than in the others and in GD was significantly lower than in NN (0.37 vs. 0.93 mg/l). GU and GD exhibited higher EXPOSURE (~70%) than OD and OU (<40%) but lower than NN (~95%). In all sites, O2 was always above 90% and HABITAT diversity was high (>0.74). The other variables did not vary significantly among sites. DO was always above 9 mg/l, and pH was neutral-weakly alkaline with slightly higher values in sites with groundwater inflows. COD was below 10 mg/l, indicating a low concentration of oxidable compounds, including ammoniacal nitrogen (NNH4<0.005 mg/l), and the concentration of total phosphorus (Ptot) was always below the methodological sensitivity (0.001 mg/l). DISTURBANCE varied between 0 and 100% in almost all sites and no significant difference was observed between regulated and unregulated sites. HLIGHT was around 4-6.5 h (on average) depending on the site, while TMean was 5-8.8 °C (Table 1; Figure 3).

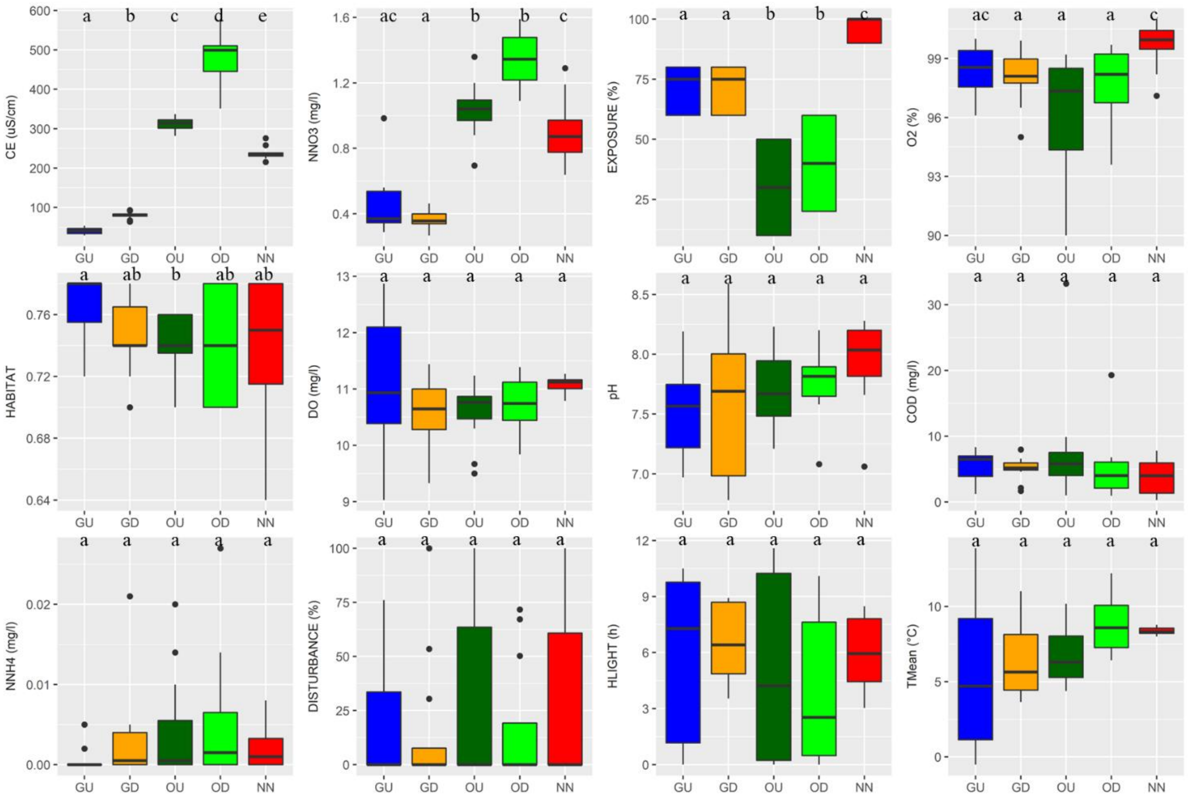

Figure 3. Boxplots comparing the annual variability of each environmental variable in the five stream sites. Different lowercase letters indicate significant differences among categories (Wilcoxon rank sum tests paired by month, using the Bonferroni-Holm method, $p<0.05$).

Table 1. Environmental variables of the five stream-sites expressed as annual average ± standard deviation and minimum and maximum values based on the monthly values.

Environmental variables	Acronynm		GU	GD	OU	OD	NN
Mean monthly temperatures (°C)	Tmean	mean±sd	5.5 ± 4.9	6.5 ± 2.6	6.6 ± 1.8	8.9 ± 1.8	8.4 ± 0.2
		min-max	-0.5 - 13.9	3.7 - 11.0	4.4 - 10.2	6.4 - 12.2	8.2 - 8.8
Electrical conductivity (µS/cm)	CE	mean±sd	40.7 ± 7.9	80.1 ± 8.6	311.1 ± 18.0	480.1 ± 61.2	239.4 ± 14.8
		min-max	29.1 - 53.7	64.1 - 93.4	282.0 - 337.0	351.0 - 578.0	224.0 - 276.0
Oxygen saturation (%)	O2	mean±sd	98.4 ± 1.3	98.1 ± 1.4	96.4 ± 3.0	97.7 ± 1.8	99.7 ± 1.2
		min-max	96.1 - 100.0	95.0 - 99.9	90.0 - 99.2	93.6 - 99.7	97.1 - 101.0
Dissolved oxygen (mg/l)	DO	mean±sd	11.12 ± 1.30	10.55 ± 0.65	10.56 ± 0.54	10.74 ± 0.48	11.07 ± 0.13
		min-max	9.03 - 12.87	9.33 - 11.44	9.50 - 11.24	9.84 - 11.39	10.79 - 11.22
pH	pH	mean±sd	7.54 ± 0.37	7.58 ± 0.63	7.66 ± 0.32	7.75 ± 0.27	7.94 ± 0.36
		min-max	6.97 - 8.19	6.78 - 8.59	7.21 - 8.23	7.08 - 8.20	7.06 - 8.28
Nitric nitrogen concentration (NO_3-N) (mg/l)	NN03	mean±sd	0.450 ± 0.190	0.365 ± 0.060	1.022 ± 0.173	1.343 ± 0.168	0.927 ± 0.182
		min-max	0.290 - 0.980	0.267 - 0.462	0.695 - 1.360	1.090 - 1.590	0.681 - 1.290
Ammonium nitrogen concentration (NH_4-N) (mg/l)	NNH4	mean±sd	0.001 ± 0.002	0.003 ± 0.006	0.004 ± 0.007	0.005 ± 0.008	0.002 ± 0.003
		min-max	0.000 - 0.005	0.000 - 0.021	0.000 - 0.020	0.000 - 0.027	0.000 - 0.008
Total phosporous (mg/l)	Ptot	mean±sd	<0.001	<0.001	<0.001	<0.001	<0.001
		min-max					
Chemical Oxygen Demand (mg/l)	COD	mean±sd	5.46 ± 2.43	5.09 ± 1.74	8.33 ± 8.56	5.03 ± 4.95	4.13 ± 2.68
		min-max	1.21 - 8.34	1.68 - 7.96	1.86 - 33.20	0.95 - 19.30	0.29 - 7.78
Microhabitat equitability	HABITAT	mean±sd	0.77 ± 0.02	0.75 ± 0.02	0.74 ± 0.02	0.74 ± 0.04	0.73 ± 0.05
		min-max	0.72 - 0.78	0.70 - 0.78	0.70 - 0.76	0.70 - 0.78	0.64 - 0.78
Disturbance (%)	DISTURBANCE	mean±sd	19.73 ± 30.89	15.32 ± 31.58	28.16 ± 40.18	16.50 ± 28.59	22.81 ± 39.73
		min-max	0.00 - 76.10	0.00 - 100.00	0.00 - 100.00	0.00 - 71.67	0.00 - 100.00
Percentage of the sky not covered by tree canopy (%)	EXPOSURE	mean±sd	71.67 ± 9.37	71.67 ± 9.37	30.83 ± 18.32	40.00 ± 19.07	95.83 ± 5.15
		min-max	60.00 - 80.00	60.00 - 80.00	10.00 - 50.00	20.00 - 60.00	90.00 - 100.00
Mean monthly hours of light (h)	HLIGHT	mean±sd	5.73 ± 4.46	6.51 ± 2.04	5.16 ± 5.02	3.94 ± 4.00	5.93 ± 2.05
		min-max	0.00 - 10.50	3.54 - 8.92	0.00 - 11.58	0.00 - 10.10	3.03 - 8.48

The overall biofilm biomass was 9.4±12.7 g/m^2 on average; the OU site had the lowest value (4.4±2.5 g/m^2), which was significantly different from those of OD, GU, and NN, where the highest value (15.0±24.9 g/m^2) was found (Figure 4B). OU had the lowest amount of pigment (2.9±3.2, 1.0±1.4, and 1.3±1.3 mg/m^2 of chlorophyll a, carotenoids, and chlorophyll b respectively) while OD the highest (11.1±14.5, 2.6±4.7, and 8.7±12.6 mg/m^2 of chlorophyll a, carotenoids, and chlorophyll b) but the spatial differences were not significant (Figure 4A). Diatoms were the most represented group (58.6%), followed by cyanobacteria (18.6%), red algae (17.1%), and green algae (14.1%) but with high inter and intra sites variability. For example, green algae were particularly abundant in GD and GU (15.7% and 11.4% respectively) and absent in NN where cyanobacteria were abundant (36%). Red algae represented 22.7% of the community in NN and OU. However, such differences were not significant (Figure 4C). The Shannon index was significantly lower only in OU (0.91 vs 0.97-1) (Figure 4D) while the average value of the autotrophic index was similar in all sites (~2800-3700) (Figure 4E) (Table 2).

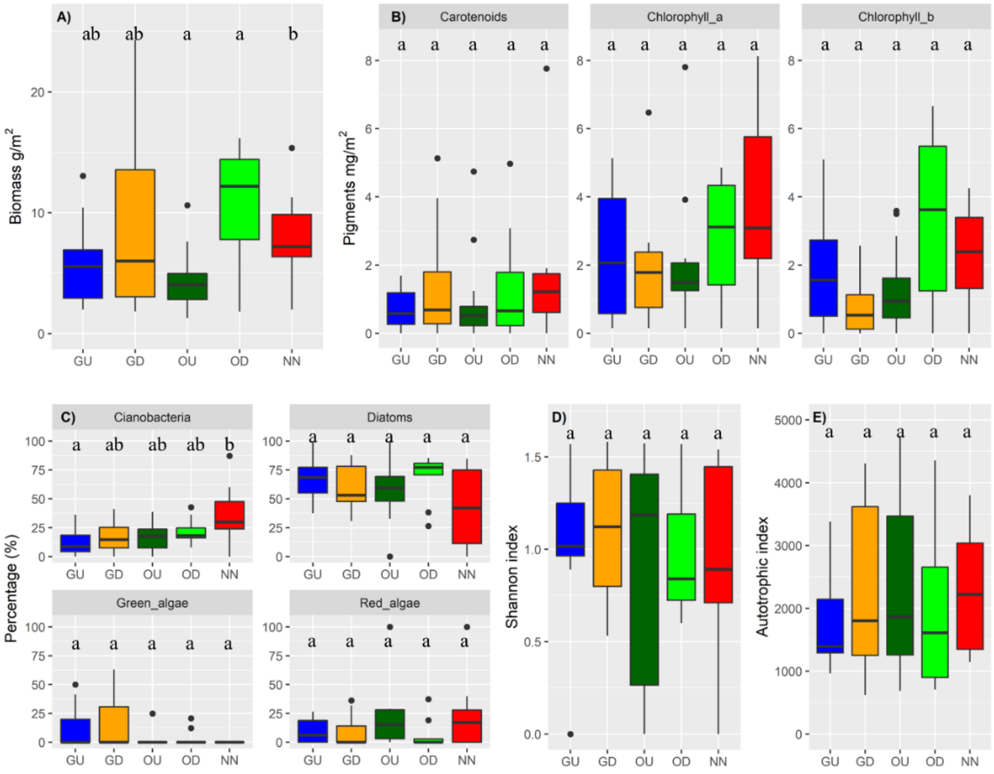

Figure 4. Boxplots comparing the annual variability of A) biofilm biomass B) pigment's component, C) the percentage of the main groups, D) Shannon index, and E) Autotrophic index in the five stream sites. Different lowercase letters indicate significant differences among categories (paired Wilcoxon rank sum tests (paired by sampling event), using the Bonferroni-Holm method, p<0.05). Outliers were excluded for a better visualization.

Table 2. Biofilm metrics of the five stream sites expressed as the annual average ± standard deviation and minimum and maximum values based on the monthly samples.

Biofilm Metrics		GU			GD			OU			OD			NN		
Biomass (g/m^2)	mean±sd	5.68	±	3.47	9.00	±	7.62	4.42	±	2.55	12.93	±	8.94	15.03	±	24.86
	min-max	1.99	-	13.05	1.83	-	24.30	1.29	-	10.63	1.82	-	36.78	1.99	-	93.20
Chlorophyll a (mg/m^2)	mean±sd	3.63	±	3.51	6.56	±	8.57	2.91	±	3.25	11.17	±	14.50	10.27	±	22.47
	min-max	0.15	-	10.78	0.15	-	23.96	0.15	-	11.05	0.15	-	51.82	0.15	-	81.22
Carotenoids (mg/m^2)	mean±sd	0.75	±	0.59	1.37	±	1.63	0.98	±	1.40	2.58	±	4.72	1.61	±	2.06
	min-max	0.00	-	1.69	0.00	-	5.13	0.00	-	4.74	0.00	-	16.76	0.00	-	7.76
Chlorophyll b (mg/m^2)	mean±sd	1.87	±	1.77	3.95	±	5.78	1.29	±	1.29	8.66	±	12.62	8.21	±	20.73
	min-max	0.00	-	5.09	0.00	-	16.14	0.00	-	3.59	0.00	-	36.16	0.00	-	73.88
% Cyanobacteria	mean±sd	12.28	±	11.98	16.50	±	13.74	17.01	±	12.99	22.00	±	10.04	36.15	±	23.04
	min-max	0.00	-	36.06	0.00	-	41.07	0.00	-	38.65	7.93	-	42.68	0.00	-	87.31
% Green algae	mean±sd	11.45	±	18.53	15.75	±	24.03	2.48	±	7.86	3.00	±	6.93	0.00	±	0.00
	min-max	0.00	-	50.00	0.00	-	63.12	0.00	-	24.84	0.00	-	20.68	0.00	-	0.00
% Diatoms	mean±sd	66.57	±	17.46	59.00	±	20.71	57.77	±	28.09	69.36	±	19.07	41.06	±	32.98
	min-max	37.47	-	100.00	30.61	-	87.90	0.00	-	100.00	26.40	-	85.35	0.00	-	84.79
% Red algae	mean±sd	9.70	±	10.44	8.76	±	13.72	22.74	±	29.48	5.65	±	11.93	22.79	±	28.17
	min-max	0.00	-	26.47	0.00	-	36.15	0.00	-	100.00	0.00	-	37.34	0.00	-	100.00
Shannon index	mean±sd	1.05	±	0.40	1.08	±	0.38	0.92	±	0.65	0.97	±	0.34	0.99	±	0.49
	min-max	0.00	-	1.57	0.53	-	1.58	0.00	-	1.57	0.60	-	1.57	0.00	-	1.54
Authrophic index	mean±sd	3,755.39	±	4161.18	3,383.92	±	3,164.60	2,825.20	±	2,217.80	3,358.95	±	3,631.99	3,188.27	±	3,314.58
	min-max	966.16	-	14,308.85	621.13	-	12,194.36	687.92	-	8594.51	709.89	-	12,137.93	1,147.44	-	13,250.06

3.3 Temporal patterns

According to the environmental PCA, TMean, pH, DISTURBANCE, HLIGHT, DO and EXPOSURE variables were associated with a temporal pattern (Figure 2B). GU was characterized by the highest thermal annual variability, as the daily mean temperatures ranged from -1 to 15.9 °C. In GD they were between 2.8 and 11.7 °C; in OU between 2.9 and 11.1 °C; in OD between 5.6 and 12.8 °C and in NN between 7.8 and 9 °C (daily mean). The water thermal variability was smaller in the sites fed by both snowmelt/stormwater and groundwater (OU and OD) than in the others (GU and GD) while the stream fed exclusively by groundwater (NN) had a stable thermal profile. The temporal pattern of DO was opposite to the one of water temperature in all sites except for NN where it was almost constant; pH and temperature showed parallel patterns. By contrast, DISTURBANCE exhibited strong temporal fluctuations with abrupt peaks in June, September, October, and May and maximum values (70-100%) in autumn. HLIGHT strongly varied through the year reaching 8-12 h in summer and 0-3 h in winter, of course, EXPOSURE had higher values in winter, in the absence of leaves on the trees, especially in Ogna sites (Figure 5).

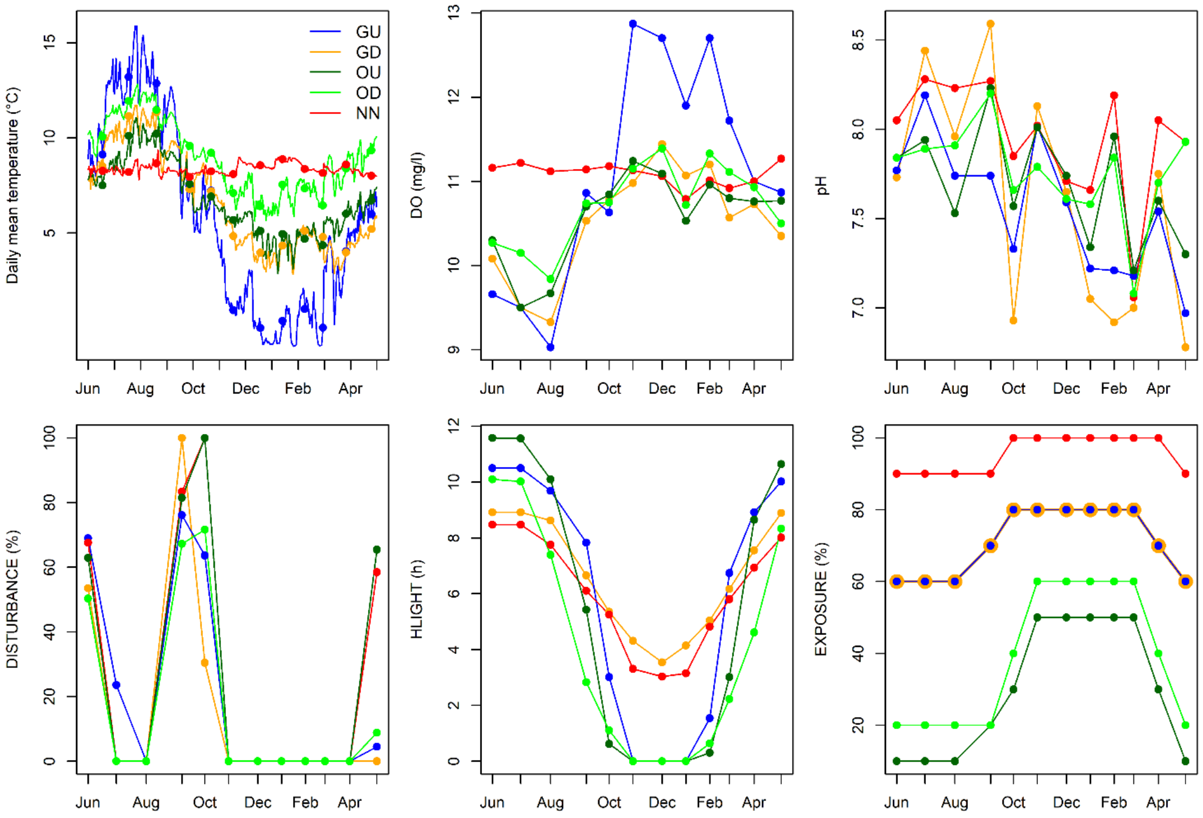

Figure 5. Temporal pattern of water temperature, dissolved oxygen, pH, disturbance, hours of light, and exposure in each site. For water temperature we plotted the annual thermal regime based on daily values.

Photosynthetic pigments and total biomass showed similar temporal patterns in each site, as confirmed by their positive correlation (Table 1SM). The highest values were observed in winter while lower values occurred in summer and after the floods (Figure 6A). By contrast, the autotrophic index was negatively correlated with biomass and photosynthetic pigments in all sites (Table 1SM) and had the highest values in summer and autumn (Figure 6A). Winter promoted green algae while summer cyanobacteria and red algae; diatoms were the dominant group in all sites (Figure 6B). In NN an exceptional algal bloom occurred in November when the total biomass and the Chlorophyll a and b reached 90 g/m^2, 81 mg/m^2, and 73 mg/m^2, respectively. Annually, the sites exhibited similar changes in periphyton composition as the temporal dissimilarity was 0.63, 0.61, 0.57, 0.49, and 0.58 in GU, GD, OU, OD, and NN respectively. The total β-diversity (BSor) corresponded to the turnover component (ratio between turnover and Sorensen indices =0.97) outlining that the temporal changes in community composition were driven almost only by the replacement and not by the loss/gain of groups.

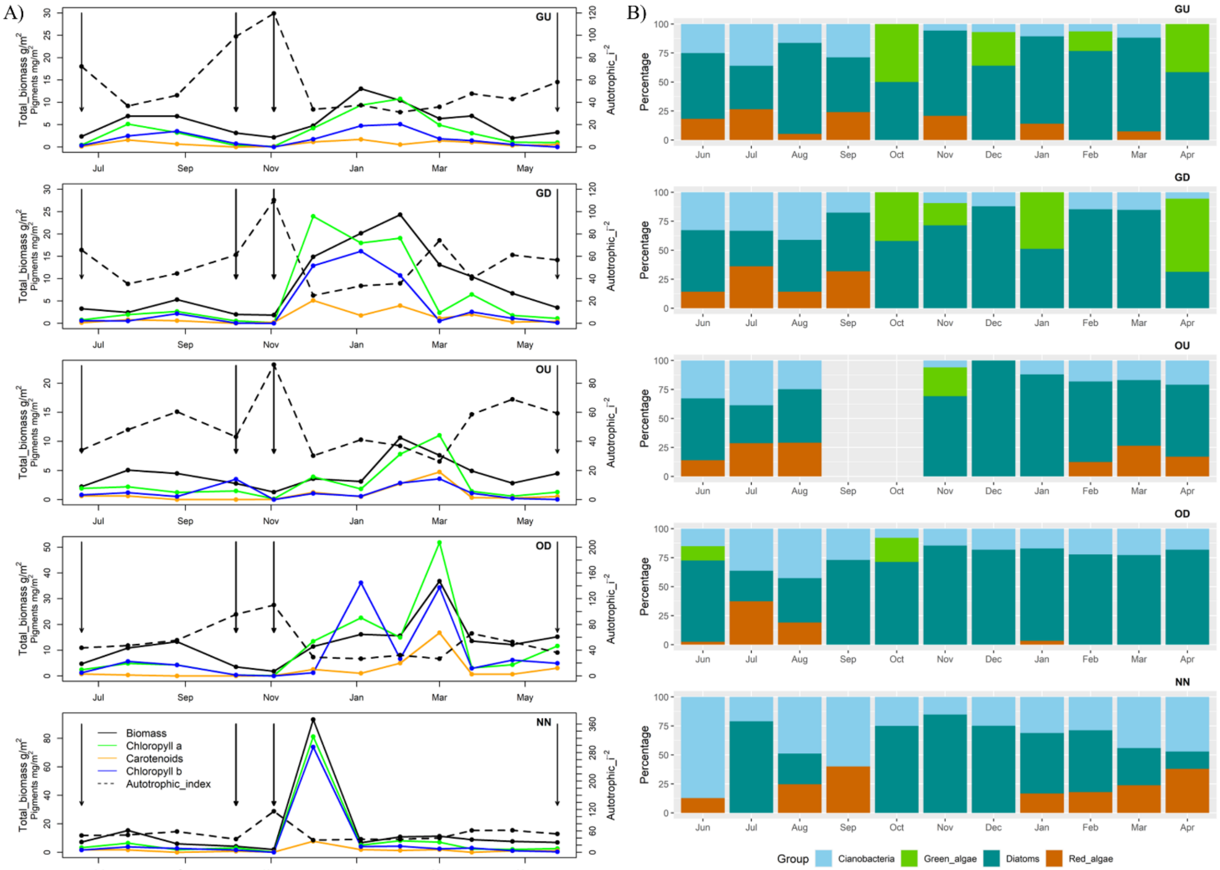

Figure 6. Temporal pattern of A) biofilm biomass, periphyton pigments, and autotrophic index and B) periphyton community composition. Black arrows represent the sampling dates following a flood (with the highest occurring in September and October). Missing data in community composition were due to Phyto-PAM malfunction or loss of samples**.**

3.4 Environmental factors and biofilm

In general, the selected environmental variables explained more than half of the generalized linear mixed models' variation, especially for Biomass, and Chlorophyll a ($R^2_{marginal} \geq 0.3$), while Shannon diversity remained unexplained. Biomass, Chlorophyll a, Chlorophyll b, Diatoms, and Carotenoids were negatively affected by DISTURBANCE (Table 4) contrary to the Autotrophic index. The time (SEASON) was pivotal to explain the amount of Chlorophyll a and carotenoids displaying different behaviour between winter and the other months (Table 2SM). The light availability expressed as the interaction between EXPOSURE and HLIGHT was negatively correlated to the relative abundance of diatoms and cyanobacteria that, conversely, were positively related to NNO3. TMean was the only variable explaining the relative abundance of green algae and red algae.

Table 4. Results of the most parsimonious linear mixed-effect models relating the different biofilm metrics to the main environmental variables. All the models include the sites as a random effect. The bold fixed terms indicate negative regressions.

Response	Fixed terms	$R^2_{marginal}$	$R^2_{conditional}$
Biomass	**DISTURBANCE**	0.30	0.48
Chlorophyll a	**DISTURBANCE** + SEASON	0.44	0.48
Chlorophyll b	**DISTURBANCE**	0.20	0.27
Carotenoids	**DISTURBANCE** + SEASON	0.34	0.34
Shannon index		0.00	0.00
Autotrophic index	DISTURBANCE	0.24	0.24
% Cyanobacteria	NNO3 + EXPOSURE: HLIGHT	0.25	0.25
% Diatoms	**DISTURBANCE + EXPOSURE: HLIGHT**	0.25	0.31
% Green algae	TMean	0.10	0.14
% Red algae	TMean	0.12	0.24

Annual water thermal variability and annual temporal diversity (BSor) were poorly correlated (R^2=0.18, *p*=0.48).

4. Discussion

4.1 Spatial pattern

The annual biofilm biomass ranged between 4.4 and 15.0 g/m^2 on average, depending on the site. Such values are in line with other studies carried out in various contexts as glacial streams (Joos, 2003; Peszek et al., 2022; Robinson et al., 2016), meadows streams (Elsaholi, 2011) and forested streams (Biggs, 1988; Fernandes & Esteves, 2003). However, huge variations (both in space and time) seemed to characterize the biofilm almost everywhere, as confirmed by the present study too. Sites regulated by reservoirs (GD and OD) exhibited higher biomass (9.0 and 12.9 g/m^2) than their unregulated counterparts (GU and OU, with 5.7 and 4.4 g/m^2 respectively). This suggests a positive effect of upstream regulation on the biofilm, possibly due to the higher flow stability, as shown also by (Smolar-Žvanut & Mikoš, 2014) along the Soca River (Slovenia). However, small flow variations could not be assessed due to the lack of gauging sites while the disturbance estimated by the pebbles' movement showed similar annual magnitude across sites (Figure 3) with floods occurring in synchrony. Chlorophyll a content ranged between 3 and 7 mg/m^2 on average, depending on the site, in line with other studies carried out in forest streams (Francoeur et al., 1999; Lehner et al., 2006; Pizarro & Alemanni, 2005; Rier & Stevenson, 2002). By contrast, such values are lower than those measured in unshaded streams where chlorophyll a reached 20-80 mg/m^2 (Biggs, 1988; Cattaneo et al., 1997; Quinn et al., 1996; Robinson et al., 2016). We ascribed the low primary production to the interaction of disturbance and canopy, both very high in mountain shaded streams. Moreover, the autotrophic index was about 3,000 (on average) in all sites, indicating a strong heterotrophy of the biofilm, also related to the low chlorophyll a content. Those values were generally higher than the ones reported in studies carried out in mountain streams, even if high temporal variations are common according to the literature (Biggs, 1988; Joos, 2003). Nutrient availability (nitrate and phosphate) did not play a pivotal role in the biofilm growth as their concentration were always very low (<1.4 mg/l and <0.001 mg/l respectively). Indeed, as already pointed out, in mountain streams nutrients can limit algal growth only in favorable conditions (high light availability and low disturbance) (Bernhardt & Likens, 2004).

Due to the low number of investigated sites and to the lack of taxonomic identification, it is difficult to relate the spatial dissimilarity in the community composition to specific environmental conditions. However, according to our models, periphyton groups were not associated with SEASON but with environmental variables such as nitrate concentration, water temperature, disturbance, and light availability highlighting also slight differences among sites (Table 4). NN site was characterized by a marked percentage of cyanobacteria in summer (>50%) and red algae in late winter-spring (20%) as observed in other groundwater streams (Hieber et al., 2001; Uehlinger, 2006). On the other hand, the absence of green algae probably depended on the short distance from the source (~200 m), limiting the colonization by green algae from terrestrial environments. By contrast, the high abundance of green algae in GD (15%) could be promoted by the colonization of Chlorophyceae and Conjugatophyceae coming from the high-altitude reservoirs. Indeed, such lakes host several species of green algae belonging, among the others, to the genera *Staurastrum, Staurodesmus, Crucigeniella, Planctosphaeria, Sphaerocystis* (Gentili et al., 2001). Cyanobacteria were especially abundant in NN (36%) and positively linked to nitrate concentration (and light availability) unlike reported by other studies showing no increase in cyanobacteria density with nitrate enrichment, due to their ability to fix atmospheric nitrogen (Allan & Castillo, 2007). The investigated sites displayed similar annual turnover, poorly related to the annual water thermal variability. By the fast assessment of the periphyton composition (based on the relative abundance of the 4 main groups), only great differences among sites could be detected. Nevertheless, several studies highlighted differences in community composition (occurrence and abundance of algal taxa) among waterbodies related to different lithology (limestone vs silica), hydrology, and shading (Cantonati, Angeli, et al., 2012; Gesierich & Kofler, 2010; Kamberovic et al., 2019; Larned, 2010).

4.2 Temporal patterns

One-year monthly sampling of biofilm revealed a strong seasonal pattern both in the total biomass and in the pigment concentration, along with a sharp variation of the autotrophic index. Indeed, especially in autumn, strong floods occurred in all streams causing a drastic reduction of the biofilm (Table 4). Floods also caused a change in the proportion of autotrophic and heterotrophic organisms and in November, when the periphyton dropped, the autotrophic index reached the maximum. In winter the biofilm recovered in all sites and the pigment content increased until spring. The obtained results indicate that the biofilm biomass negatively responded to the disturbance (Table 4), as also shown by other studies concerning mountain streams. For example, Power & Stewart (1987) surveying algal coverage before and after a strong flood in Oklahoma stream (New Zealand) observed a drop in the covered surface (-55%) while Biggs (1995) monitoring biofilm across several New Zealand streams, found a linear negative relationship between chlorophyll a and flood disturbance frequency. According to our field observations, the abrasion was the primary mechanism of biofilm removal because of the substrate overturning and tumbling while in glacier streams the scouring is mostly provoked by the suspended sediments (high turbidity) (Uehlinger, 1991). Although the pebble displacement method had already proven to be valid for the assessment of the ecological effect of floods (Biggs, 1995; Power & Stewart, 1987) flow data, unfortunately unavailable here, would have contributed to explain biomass variations during free flood periods. Indeed, biofilm biomass responds also to changes in current velocity (Biggs, 1996; Horner & Welch, 1981; Horner et al., 1990). In winter the low canopy can promote the growth of biofilm. Indeed, light is limited in small streams under dense tree cover (DeNicola, 1996; Larned & Santos, 2000; McConnell & Singler, 1999) and thereby, benthic algae populations tend to reach the maximum coverage just before the canopy development and then decline through the summer as observed in our surveyed streams (especially GU, GD, OU, OD that experienced the lower exposure) (Hill & Dimick, 2002). However, in this case, the time (SEASON) explained the temporal variations of Chlorophyll a better than the light availability (EXPOSURE: LIGHT) (Table 4), suggesting only small differences among sites. The autotrophic index followed a pattern opposite to the pigment concentration suggesting that the proportion between autotrophic and heterotrophic organisms changes over time. Moreover, floods shifted the benthic metabolism toward higher heterotrophy because the primary production was particularly affected, as also highlighted by Uehlinger et al., (1998). After the autumn floods, an exceptional algal bloom occurred in NN site and brownish algae probably ascribable to *Hydrurus foetidus* covered the whole riverbed. Such fast colonization was observed in glacier streams and karstic springs too (Cantonati et al., 2006; Hieber et al., 2001; Rott et al., 2006; Uehlinger et al., 1998).

Cyanobacteria were more abundant in summer, promoted by low light availability (Table 4) and similarly, red algae dominated in spring and summer thanks to higher temperatures (Table 4) as reported by Hieber et al., (2001) and Allan & Castillo (2007). By contrast, diatoms remained the dominant group for almost all months, with higher abundances in winter, when the light availability and the disturbance were low (Table 4). Surprisingly, green algae were found especially in winter, (Figure 6, Table 4) while the literature reports that this group responds positively to higher temperatures (Allan & Castillo, 2007). However, according to Hill et al., (1995) green algae also require high light intensity, not available in summer due to the canopy. Thus, we supposed that in the surveyed streams, the light was more limiting than the temperature. However, since the assessment of algal composition through conventional (biovolume-based counts on the microscope) and fluorimetric methods (in particular BenthoTorch that does not distinguish red algae) have been proven to differ Kahlert & McKie (2014), we recommend caution in the interpretation of community composition responses.

5. Conclusion

The survey, based on one-year monthly samplings, highlighted the extremely high temporal variability of biofilm, mostly driven by the disturbance and the seasonality. Indeed, floods dropped the biomass also shifting the benthic metabolism toward higher heterotrophy. All the environmental factors influence the periphyton community; however, water temperature and light availability were the most important factors related to the community composition. A succession of the main groups was encountered through the seasons; green algae dominated in autumn while cyanobacteria and red algae in spring-summer and summer-autumn, respectively. Spatially, higher values of biofilm biomass were measured in regulated sites and no green algae were found in the groundwater stream. Although sites were characterized by different annual thermal variability, they exhibited similar annual composition turnover. Overall, the study indicates that a quantitative and frequent (monthly) investigation of biofilm is needed to properly understand the temporal changes and that Phyto-PAM deconvolution is an effective method for bioassessments. Nevertheless, a deeper investigation would be useful for a thorough characterization of the community and for understanding the main drivers affecting it.

Supplementary material

Table 1SM. Correlation matrix between all the possible pairs of biofilm metrics in each site, reporting Spearman coefficient (ρ) and significance (p-value).

GD	ρ Sperman *p*-value	Biomass	Chlorophyll a	Carotenoids	Chlorophyll b	Autotrophic index
	Biomass		0.895	0.832	0.832	-0.573
	Chlorophyll a	0.0008		0.944	0.895	-0.804
	Carotenoids	0.0055	0.0001		0.755	-0.741
	Chlorophyll b	0.0055	0.0008	0.0135		-0.790
	Autotrophic index	0.0513	0.0081	0.0135	0.0089	

GU	ρ Sperman *p*-value	Biomass	Chlorophyll a	Carotenoids	Chlorophyll b	Authrophic index
	Biomass		0.825	0.713	0.837	-0.573
	Chlorophyll a	0.0067		0.776	0.900	-0.909
	Carotenoids	0.0368	0.0180		0.609	-0.657
	Chlorophyll b	0.0055	0.0006	0.0708		-0.753
	Autotrophic index	0.0708	0.0004	0.0606	0.0235	

OU	ρ Sperman *p*-value	Biomass	Chlorophyll a	Carotenoids	Chlorophyll b	Autotrophic index
	Biomass		0.573	0.522	0.545	-0.322
	Chlorophyll a	0.2563		0.851	0.797	-0.930
	Carotenoids	0.2664	0.0040		0.452	-0.778
	Chlorophyll b	0.2664	0.0152	0.2806		-0.713
	Autotrophic index	0.3079	0.0001	0.0204	0.0552	

OD	ρ Sperman *p*-value	Biomass	Chlorophyll a	Carotenoids	Chlorophyll b	Autotrophic index
	Biomass		0.839	0.711	0.839	-0.713
	Chlorophyll a	0.0051		0.788	0.818	-0.923
	Carotenoids	0.0368	0.0116		0.546	-0.855
	Chlorophyll b	0.0051	0.0069	0.0660		-0.685
	Autotrophic index	0.0368	0.0002	0.0036	0.0368	

NN	ρ Sperman *p*-value	Biomass	Chlorophyll a	Carotenoids	Chlorophyll b	Autotrophic index
	Biomass		0.741	0.531	0.601	-0.371
	Chlorophyll a	0.0406		0.818	0.720	-0.867
	Carotenoids	0.2261	0.0103		0.448	-0.762
	Chlorophyll b	0.1544	0.0494	0.2892		-0.706
	Autotrophic index	0.2892	0.0026	0.0316	0.0512	

Table 2SM. Results of the most parsimonious generalized linear mixed-effect models relating the different biofilm metrics to the main environmental variables. Values correspond to regression slopes ± standard error of the slope. Negative regressions are indicated in bold

Response		Intercept	DISTURBANCE	EXPOSURE : HLIGHT	Tmean	NNO3	SEASON			X^2	p-value	$R^2_{marginal}$	$R^2_{conditional}$
							spring	summer	autumn				
Biomass (g/m^2)	value	2.289	**-0.013**							24.85	<0.001	0.3	0.48
	se	0.162	**0.002**										
Chlorophyll a (mg/m^2)	value	2.363	**-0.016**				**-0.936**	**-0.921**	**-0.379**	15.59	<0.001	0.44	0.48
	se	0.205	**0.004**				**0.265**	**0.291**	**0.321**				
Chlorophyll b (mg/m^2)	value	1.417	**-0.013**							13.06	<0.001	0.2	0.27
	se	0.171	**0.003**										
Carotenoids (mg/m^2)	value	1.164	**-0.008**				**-0.528**	**-0.720**	**-0.235**	8.36	0.004	0.34	0.34
	se	0.130	**0.003**				**0.187**	**0.206**	**0.226**				
Shannon index	value	0.676								0	1	0	0
	se	0.033											
Autotrophic index	value	7.500	0.012							15.69	<0.001	0.24	0.24
	se	0.109	0.003										
% Cyanobacteria	value	**-3.649**		0.003		1.586				13.54	0.001	0.25	0.25
	se	**0.515**		0.001		0.417							
% Diatoms	value	1.200	**-0.016**	**-0.002**						15.64	<0.001	0.25	0.31
	se	0.354	**0.005**	**0.001**									
% Green algae	value	**-2.157**			**-0.129**					6.01	0.014	0.1	0.14
	se	**0.424**			**0.053**								
% Red algae	value	**-3.678**			0.197					6.76	0.009	0.12	0.24
	se	**0.622**			0.072								

CHAPTER 5

Spatiotemporal patterns of macroinvertebrate assemblages across mountain streams with contrasted thermal regime

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Abstract

Water temperature is recognized as one of the most important drivers shaping both aquatic ecosystem structure and functioning and is under increasing scrutiny due to global warming affecting not only thermal average but also regime variability. However, to date, no studies have disentangled the contribution of the annual thermal regime variability from annual thermal average and other environmental variables on the spatiotemporal pattern of macroinvertebrate assemblages in streams. In the present study we selected five subalpine stream sites of Serio watershed (Orobic Alps, Northern Italy) along a gradient of annual water thermal variability (with an annual range between ~1 to 17 °C) but with similar means. At each site, over a year, we sampled monthly macroinvertebrates and monitored environmental variables describing physico-chemistry, flood disturbance, and resource availability while water temperature was measured continuously (10 min). We described spatiotemporal relationships between macroinvertebrate assemblages and environmental conditions using co-inertia analysis and tested the contribution of the water thermal regime compared to the other environmental variables in driving the community structure. A strong co-inertia between environment and macroinvertebrates was observed with primarily floods and secondarily mean monthly temperature driving the temporal pattern (49% inertia) with two contrasted mechanisms related to loss/gain of taxa and substitution of individuals among taxa respectively. Spatial differences (51% inertia) were linked to annual thermal variability that promoted higher temporal dissimilarity in taxonomic composition. In addition, we observed significant macroinvertebrate responses to environment variables, with especially Plecoptera influenced by water temperature. Finally, we found a phenological desynchronization in *Amphinemurae sp.,* and *Serratella ignita* populations inhabiting contrasted thermal regimes. Even accounting for the overall environmental setting, the thermal regime remains the most important driver of the macroinvertebrate spatiotemporal pattern and controlling life cycles. As mountain streams are particularly exposed to thermal changes, we expect marked modifications in freshwater macroinvertebrate communities. Higher mean temperature and thermal variability will significantly affect community composition, especially cold stenothermal taxa. Nevertheless, phenological desynchronization occurring within a catchment characterized by a high water temperature heterogeneity could increase the chance of survival of the meta-populations at the catchment scale. Large-scale research across the Alps is however essential to identify the pool of threatened species and detect candidate streams as potential refuges.

Keyword

Aquatic insects, beta-diversity, thermal alterations, reservoirs, bioassessment, climate change, conservation.

1. Introduction

Temperature has been recognised as a pivotal factor shaping both aquatic ecosystem structure and functioning (Coutant, 1999; Karr & Dudley, 1981; E. P. Odum, 1968). Water thermal regime regulates primary production, metabolic processes, growth rates, and life cycle duration for all organisms (Angilletta et al., 2004; Dallas & Ross-Gillespie, 2015; Lamberti & Steinman, 1997; Morin et al., 1999; Robinson et al., 2001). It also controls geophysical processes such as the degradation of organic matter and the solubility of chemical species ultimately affecting water quality (Cairns et al., 1975; Jacobsen et al., 2003). Moreover, temperature relates to the outbreaks of diseases (Carraro et al., 2017), to the ability of fish to migrate (Jonsson & Jonsson, 2009), and constitutes a physiologic threshold (lethal or sub-lethal) for the species (Cox & Rutherford, 2010; Dallas & Rivers-Moore, 2012; Elliott & Elliott, 2010). In particular, water temperature influences behavioural and life history attributes of macroinvertebrates (Bonacina et al., 2022) inducing dormancy mechanisms (Danks, 1987) and modifying hatching and emergence timing (Braune et al., 2008; Čmrlec et al., 2013; Everall et al., 2015; Fenoglio et al., 2005; Finn et al., 2022; McCarty et al., 2022). Thus, thermal regime should affect the spatiotemporal dynamics of macroinvertebrate assemblages (Ward & Stanford, 1982; Ward, 1976). Despite the pivotal role of temperature, few studies addressed the effects of water thermal regimes (e.i daily and seasonal thermal variations) on macroinvertebrate assemblages. Some studies dealt with water thermal regimes and macroinvertebrates but were mostly carried out, either in hydro systems with constant water temperature (such as in karstic streams; (Beracko & Revajová, 2019; Bottová, Derka, & Svitok, 2013)) or with progressive water temperature gradient such as in geothermal streams (Kreiling et al., 2022; Quenta-Herrera et al., 2021; Woodward et al., 2010; Živić et al., 2014). Even studies investigating the water temperature-macroinvertebrate relationship in watercourses characterized by marked seasonal thermal variability neglected the influence of intra-annual changes (Von Fumetti et al., 2017; Haidekker & Hering, 2008; Krajenbrink et al., 2021; Küry et al., 2017a; Niedrist & Füreder, 2020; Polášková et al., 2022; White et al., 2016). Indeed, investigating fine temporal patterns with high temporal resolution requires heavy monitoring that hampered addressing properly the contribution of the thermal regime so far (Eady et al., 2013; Pedreros et al., 2020), especially in mountain streams while the thermal variability is high (Jacobsen & Dangles, 2017) but continuous monitoring complex.

River temperature depends on regional climatic conditions, topography, stream discharge, and groundwater exchanges (Caissie, 2006), as well as anthropic perturbations such as thermal effluents, reductions in river flow (due to irrigation or hydroelectric withdrawals), or water release from dams, can also play a crucial role. In addition, water temperatures are rising globally as a consequence of climate change, especially in mountain streams (van Vliet et al., 2013; Wanders et al., 2019). For example, Niedrist & Füreder (2020) observed an increase of mean water temperatures between 0.19 and 0.32 °C per decade in Austrian mountain streams, with summer mean rates reaching 2.5±0.6 °C/decade in non-glacial streams. Also, during the 1998–2018 period, Michel et al., (2021) observed an increase in mean water temperatures of 0.37±0.11 °C/decade in the Swiss rivers resulting from the joint effects of air temperature increase and discharge reduction. Additionally, the presence of reservoirs affects the thermal regime altering seasonal and diurnal variability (Casado et al., 2013; Horne et al., 2004), and modifies the timing of thermal events (Cowx et al., 1987; Preece & Jones, 2002) depending on reservoir management and abstraction degrees (Olden & Naiman, 2010; Zolezzi et al., 2011). Hypolimnetic releases generally decrease both seasonal and daily water temperature variation downstream of the dam due to the thermal constancy of the hypolimnion. Thermal changes driven by both global warming and reservoirs lead to considerable alteration of the structure (Krajenbrink et al., 2021; Petruzziello et al., 2021; White et al., 2016), and functioning (Olden & Naiman, 2010; Ward & Stanford, 1979) of mountain stream communities, especially during summer heatwaves (Christidis et al., 2015). However, basic knowledge about the influence of contrasted water thermal regimes on macroinvertebrate spatiotemporal dynamics are currently missing, especially in mountain streams where a large diversity of taxa with different thermal niche occurs over short spatial distance.

Mountain water bodies host huge biodiversity (Rahbek et al., 2019) due to local endemism driven by habitat isolation and adaptation to specific conditions caused by steep environmental gradients (Muhlfeld et al., 2020). Freshwater bodies of southern European mountain systems (such as the Alps, Apennines, Dinaric Alps, Pyrenees, Betic mountains, and the Carpathians) constitute hotspots of biodiversity, especially in the subalpine streams (mid elevation) with the presence in the upper slopes of the cold-adapted arctic-alpine species withdrawn in the periglacial areas after the rapid post-glaciation (Hewitt, 1999; Schmitt, 2007), but also of the warm-adapted Mediterranean species in the lower slopes (Tierno de Figueroa et al., 2013). Thus, for example, Italian freshwater endemics exceed 10% of the total Italian fauna with Plecoptera, Trichoptera, and Ephemeroptera orders exhibiting 30%, 25% and, 20% of endemisms respectively, mainly occurring in mountain lotic habitats at low elevations (Fochetti, 2012; Fochetti, 2020).

The present study aims to investigate the effects of contrasted water thermal regimes on the temporal pattern of macroinvertebrate assemblages in subalpine streams. Indeed, mountain streams represent an optimal setup to study specifically the influence of contrasted water thermal regimes as mountain hydrographic network generally displays a high thermal heterogeneity due to the variable sources of water inputs (Brown & Hannah, 2008) and is less exposed to multiple stressors such as pollution and habitat degradation. We thus selected various mountain streams characterized by different annual water thermal variability but similar means to disentangle the role of water temperature variability from mean temperature and limit other environmental drivers. Investigating fine (monthly) temporal patterns of communities through different thermal regimes required a difficult trade-off between sampling effort and the number of sites; here we selected five close stream sites expected to have comparable temperature means and environmental setting but different annual variability. We measured water temperature continuously in these sites and sampled macroinvertebrates monthly over one year. To better disentangle the effects of temperature variations, from other environmental covariables, we also included in our analyses monthly measures of variables characterising flood disturbance, physico-chemical conditions, resources availability, and substrate composition. First, we described the temporal variability of the different environmental variables including temperature, as well as several alpha and beta diversity indices quantifying the temporal changes of the communities within the different sites. Second, we used multivariate analyses to separate within-site monthly variations (our main focus) and between-site spatial differences. Concerning temporal variations, we expected that increased annual water thermal variability would generate temporal changes in macroinvertebrate assemblage structure, with important temporal variations in the abundance of stenothermal taxa such as Plecoptera. Concerning differences between sites, consistently, we expected a higher seasonal dissimilarity in macroinvertebrate composition in sites with higher annual thermal variability. Third, we used generalized linear mixed models to assess the relative importance of the temperature and other environmental variables on the temporal changes of the different alpha diversity indices. Finally, we assessed the temporal pattern of the size of several cold and warm-adapted species to compare their life cycle across stream sites and expected a mismatch for the different thermal regimes for species with high levels of temperature sensitivity.

2. Materials and Methods

2.1 Study sites

Our study was conducted from June 2020 to May 2021 in five stream sites of the upper Serio catchment in the Orobic Alps (Northern Italy) (Figure 1). Sites were selected in order to obtain a gradient of annual water thermal variability (from little to highly variable) but with similar means and similar environmental settings to properly focus on the role of the water thermal regime. For this objective, we choose stream sites located at similar altitudes (~500-1100 m a.s.l., to reduce variations in average annual air temperature), close to each other (Euclidean distance less than ~12 km), and in sub-catchments of similar size (23-27 km^2) but characterized by different water sources (snowmelt/stormwater and groundwater-fed streams) and human alterations (presence of reservoirs). Sites GU and GD were situated in the Goglio catchment: GU at 975 m a.s.l., on a tributary stream not subjected to flow regulation; GD at 1128 m a.s.l., on the main channel, around 2 km downstream of a reservoir. Both streams were fed by snowmelt/storm waters. Sites OU and OD were located respectively upstream (970 m a.s.l) and downstream (583 m a.s.l.) of a small reservoir in the Ogna catchment, along a stream fed by snowmelt/storm and groundwater. The NN site was situated in the Nossana catchment at 468 m a.s.l., on a groundwater-fed stream, at ~200 meters to the source. The GU site was supposed to show the largest annual thermal variability due to the exclusively snowmelt/stormwater inputs, NN the lower due to the exclusive groundwater inputs while the others were supposed to have an intermediate annual water thermal variability due to both snowmelt/storm and groundwater inputs or/and hypolimnetic releases from reservoirs.

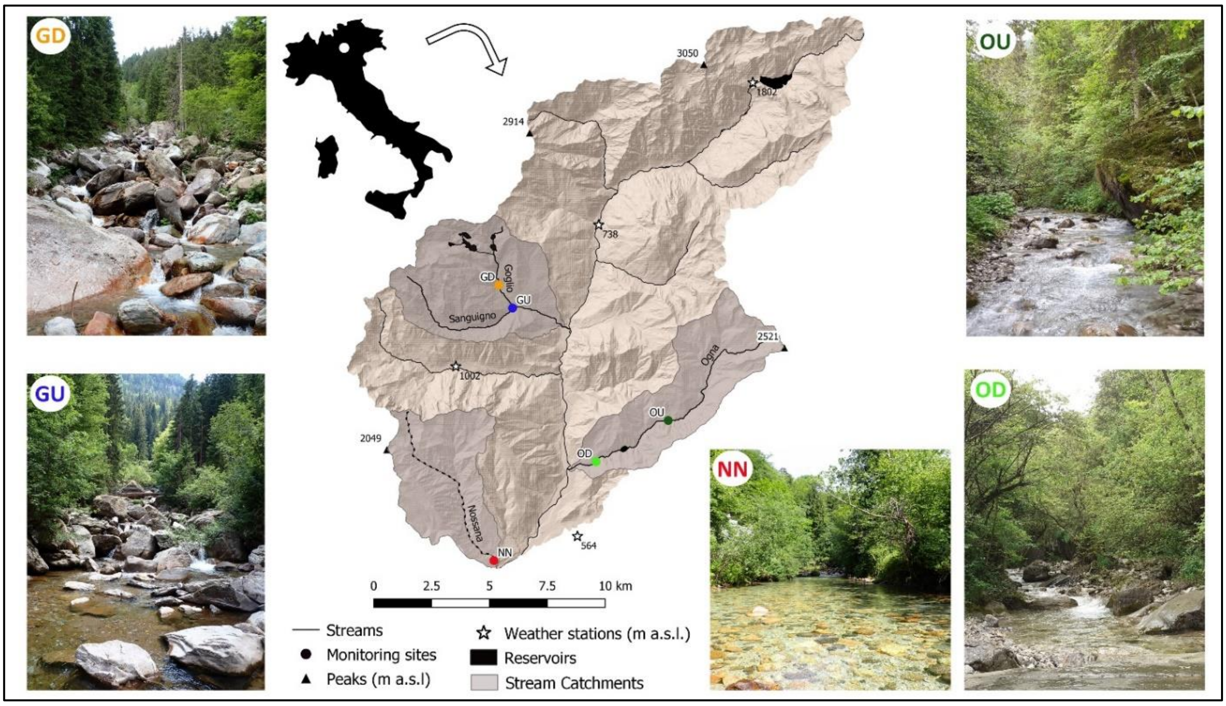

Figure 1. Map of the study area, in Italy. Study sites are represented by circles, with GU (blue) and GD (orange) in the Goglio catchment, OU (dark green) and OD (light green) in the Ogna catchment, and NN (red) in the Nossana catchment.

2.2 Macroinvertebrate sampling

At each stream site, a monthly sampling was carried out during a one-year campaign, from June 2020 to May 2021, providing 58 samples (12 months*5 sites with two missing samples in NN May and OU February). Macroinvertebrates were sampled with a Surber net (0.10 m^2, 500 µm mesh) following a standardised multi-habitat sampling procedure (Barbour et al., 1999; Hering et al., 2004). On each sampling occasion, we monitored the relative proportion of each substrate type (akal/microlithal/mesolithal/macrolithal/megalithal) taking into account only those with more than 10% coverage of stream site and collected ten Surber samples in proportion to the relative coverage of each substrate type. Surber samples were pooled and preserved with 96% ethanol. In the laboratory, taxa were identified according to standard keys (Campaioli et al., 1994; Tachet et al., 2010; Waringer & Graf, 2013). Ephemeroptera and Plecoptera were identified at the lowest taxonomic level possible (genus or species level), while the other taxa were identified mainly at the family level. Each specimen was also assigned to a size class based on its body length (following Tachet et al., 2010).

For each sampling, the following α-diversity indices were calculated: total abundance (Abundance), Shannon index (Shannon), total taxa richness (Richness), Ephemeroptera, Plecoptera, Trichoptera taxa richness (EPT), and the relative proportion of the main taxonomic groups: Plecoptera (%Plecoptera), Ephemeroptera (%Ephemeroptera), Trichoptera (%Trichoptera), Coleoptera (%Coleoptera) and Diptera (%Diptera).

2.3 Water thermal regimes

Water temperature was measured continuously (every 10 min) from Autumn 2019 to Autumn 2021 using iButton devices (DS1925L sensors: range -40-80 °C, accuracy: ±0.5°C, resolution: ±0.0625°C) fixed in the riverbed of the five stream sites. Based on these temperature time series, we calculated the daily mean at each site. Missing water temperature values due to sensor failure or loss (~20% of the data) were estimated from air temperature using Generalised Additive Models (GAM) relating daily mean water temperature to air temperature time series plus the week number as an extra smoothing parameter (see Krajenbrink et al., 2021 for details). GAMs were performed using “mgvc” R package (Wood, 2022) using a gaussian distribution and provided an excellent performance (Root Mean Square Error around 0.25 °C for NN, 0.50 °C for OU and OG, and 0.85 °C for GU and GD). Air temperatures in the five stream sites were retrieved from air temperatures monitored by the meteorological stations of the upper Serio catchment (www.arpalombardia.it) using interpolation based on altitude, considering the monthly vertical gradient calculated in the study area (see Fiorenzo, Mancino, Borghetti, & Ferrara, 2008 for details). To describe the thermal regime of each stream site, we plotted the thermal profile based on daily mean data and we assessed the annual water thermal variability (TAmp=amplitude between the minimum and maximum daily mean recorded during the year of sampling). Finally, to characterize the monthly thermal magnitude, we calculated the mean water temperature (TMean) of the 30 antecedent days of each sampling.

2.4 Environmental setting on each sampling date

Along with water temperature, we monitored other proximate environmental variables related to water quality, habitat, hydrology, and resource availability that have been recognised as important drivers of macroinvertebrate assemblages (Becquet et al., 2022; Hieber et al., 2005; Li et al., 2012). Regarding water quality, on each sampling, we measured electric conductivity (CE), dissolved oxygen (DO), and oxygen saturation (O2) using a probe HACH-HQ40d (Loveland, USA). In addition, 0.5 liters of water were collected in the field and brought to the laboratory where pH was measured using a HANNA pH meter 211 (Woonsocket, USA), and nitrate nitrogen (NNO3) and Chemical Oxygen Demand (COD) were determined using spectrophotometric test kits (Hach-Lange, Düsseldorf, Germany, LCK 340, and LCK1414, respectively). Stream habitat availability (HABITAT) was calculated by applying the Simpson index on the relative percentage of substrate types monitored on each macroinvertebrate sampling. To assess the impact of high flows on macroinvertebrates, we monitored the streambed displacement each month (i.e. at each sampling date). This method provides a relevant proxy of the impacts of floods in the absence of discharge data. Substrate movement associated with flood disturbance was measured using tracer particles placed on the streambed following Townsend, Scarsbrook, & Dolédec (1997). Fifteen locally sourced painted stones from three size classes were placed in riffles along three transects (five stones of the three size classes per transect at marked points on the stream bank). The three size classes correspond to the 50th, 75th, and 95th percentiles of the substrate size distribution. On each sampling event (site*date), the distance travelled by each stone was recorded and the stones were placed back at their initial position (Death & Zimmermann, 2005). Flood disturbance (DISTURBANCE) was quantified at each sampling event by combining the displacement of the substrate with the moved mass by the following metric:

$$DISTURBANCE = \frac{\sum_{i=1}^{n} m_i * d_i}{\sum_{i=1}^{n} m_i} \%$$

Where *m* is the tracer mass and *d* is the displacement (0 for “not moved” and 1 for “moved”). Lost stones (n=2-7 during flood events) were excluded since they could either be washed away or buried in sediments. As several flood events could occur within a month, the metric DISTURBANCE can be used as a proxy of the overall sediment movement between two consecutive sampling dates but cannot be directly linked to flow discharge. Resource availability includes both autochthonous and allochthonous organic matter and represents a good proxy of the trophic resources available for the food web (Marcarelli et al., 2011). Autochthonous organic matter was quantified by monitoring the benthic algae. At each sampling, we randomly collected a dozen of riverbed stones, and scrubbed the upper face in 500 ml of water, giving a single composite algae sample according to the diatom sampling methodology (APAT, 2007). To calculate the sampling surface, we took a picture of the collected stones arranged on a squared sheet and measured the total area in QGIS 3.4. In the lab, 100 ml of algae solution was dried in the furnace for 24 h at 105 °C, weighed (dry weight), and then burnt for 1 h at 550 °C and weighed for the loss on ignition (LOI) determination. Autochthonous biomass (ALGAE, expressed as g/m^2) was thus calculated as

LOI normalized by the sampled surface. Allochthonous organic matter was quantified based on coarse particulate organic matter (CPOM) sampled with macroinvertebrates and preserved in ethanol. Leaves, branches, and seeds were separated from moss and algae (autochthonous) and dried in the furnace for 24 h at 105 °C. Allochthonous organic matter was thereby expressed as density (g dry weight/m^2).

2.5 Data analysis

2.5.1 Description of the temporal changes in environmental conditions and community composition

To compare the annual average of the different environmental variables across sites, we performed Kruskal–Wallis and paired Wilcoxon rank sum tests, using the Bonferroni-Holm method to adjust p values for multiple comparisons. We then described the temporal patterns of the environmental variables by plotting the monthly value.

To examine the temporal pattern of macroinvertebrate assemblages, we plotted each monthly α-diversity index for each site. To characterise the monthly variation in community composition (temporal β-diversity) in each site we calculated both Sorensen and Bray-Curtis indices between two consecutive dates (n=10-11 depending on the site); providing the contribution of presence/absence and abundance in macroinvertebrate temporal dissimilarity, respectively. Sorensen index was partitioned to estimate the relative contribution of both the species turnover and nestedness components, referring to the replacement of taxa between sampling events, and the loss/gain of taxa, respectively. Similarly, Bray-Curtis β-diversity was decomposed into the balanced variation in abundance and the abundance gradient components (Baselga, 2013b), quantifying the dissimilarities caused by the substitution of the individuals of some taxa by the same number of individuals of different taxa, and the loss or gain of individuals, respectively.

2.5.2 Annual changes in community composition

To estimate the overall annual temporal dissimilarity (Legendre, 2019; Magurran et al., 2019) within a site, we used the multi-date β-diversity indices (i.e., classically known as multisite β-diversity index (Baselga, 2013a)) considering the Bray-Curtis dissimilarity (BBray_year) and its component, the balanced variation in abundance (BBal_year) and the abundance gradient (BGrad_year) across the 10 months sampled in common among the five sites. To assess how much of the annual temporal dissimilarity was due to each component in each site we calculated the multidate index βratio (Baselga, 2017), with a βratio >0.5 indicating that the Bray-Curtis dissimilarity is mostly driven by the balanced variation in abundance while the abundance gradient dominates for a βratio <0.5. β-diversity indices were computed with the "betapart" R package (Baselga et al., 2022).

2.5.3 Macroinvertebrate-environment co-structure: separating temporal and spatial effects

To characterise the link between monthly macroinvertebrate assemblage and monthly environmental conditions, we used Co-inertia Analyses (CoA; Dolédec & Chessel (1994)) which compute successive pairs of environmental and macroinvertebrate multivariate axes being as covariant as possible. To separate temporal effects (within-sites) from spatial effects (between-sites), we performed two different Co-inertia analyses (CoAs) of the environmental and macroinvertebrate datasets: a "within-sites" CoA and a "between-sites" CoA (Franquet et al., 1995). Prior analyses, macroinvertebrate abundances were log(x+1)-transformed to approach normality, while environmental variables were log(x+1)-transformed when necessary and normalized.

For the within-site CoA, removing differences among sites, we reported the correlation between scores of samples, by site, on the first two within-sites CoA axes (environmental and macroinvertebrate axes) to describe the temporal relationship between the environment and the community structure shared among sites. For the between-site CoA, removing differences among months, we also included the annual thermal variability (TAmp) and the annual β-diversity indices (BBray_year, BBal_year, BGrad_year) as "supplementary variables" (thereby not contributing to the definition of multivariate axes) to investigate if the difference in temporal variability among sites could explain part of the spatial differences among sites.

For both CoA analyses, the taxonomic-environmental correlation was assessed using the multivariate RV co-structure coefficient (Robert & Escoufier, 1976), calculated as the total co-inertia (sum of eigenvalues of a CoA) divided by the square root of the product of the squared total inertias (sum of the eigenvalues) from the separate analyses of each matrix. RV-coefficient ranges from 0 to 1, with a high RV-coefficient indicating a high degree of co-structure. We did not report the significance of the tests due to the lack of statistical power caused by the limited sample size. Analyses were performed using "ade4" R package (Dray & Dufour, 2007).

2.5.4 Detailing the environmental drivers of temporal dissimilarities in community composition

To strengthen our understanding of the effects of the main environmental drivers shaping the temporal variation of macroinvertebrate communities in the different sites we performed, in each site, multiple regressions on distance matrices (MRM) between matrices of assemblage dissimilarity (pairwise Bray-Curtis index and its component among all sampling dates) and environmental distance (pairwise environmental difference among all sampling dates) for main environmental variables contributing to the within-site Co-inertia. The coefficient r-squared (estimates the proportion of variance explained by the model) was calculated with 999 permutations. MRMs were performed using the “ecodist” R package (Goslee & Urban, 2007).

2.5.5 Detailing the effect of water temperature on temporal changes in macroinvertebrate community structure

As a complementary analysis to the within-site co-inertia, we developed regression models to assess how environmental factors contribute to community structure over time, specifically disentangling the effect of each environmental variable and pinpointing the taxonomic groups most affected by the water temperature variations. For this, we performed generalized linear mixed models (glmm) between widely used α-diversity indices (Abundance, Shannon, Richness, EPT, %Plecoptera, %Ephemeroptera, %Trichoptera, %Coleoptera, %Diptera) and environmental variables to assess their relative contribution over time. Mean monthly environmental variables were used as fixed effects, while the site was considered as a random effect. We used a gaussian error distribution with an identity link for Abundance, Shannon, and the percentage of each order indices while a poisson error model with a log link for Richness and EPT indices. We excluded NNO3 and DO from the models as they were highly correlated with CE (p=0.89) and TMean (p=-0.72) respectively (Figure 1SM) (Pearson, r>0.7, Dormann et al., 2012). Oxygen saturation was also excluded as it could never be a limiting factor (O2 > 90%) (Hicks, 2002) as well as HABITAT and COD as they showed similar values among samplings and poorly participated in the variance explained (eigenvalues lower than 0.20 on both the first two axes of the PCA, Figure 1SM). In the models, we thus only included monthly values for DISTURBANCE, CPOM, ALGAE, CE, and pH together with temperature (TMean). Environmental variables were log(x+1)-transformed whenever necessary and all were normalized prior modelling while for the biodiversity indices, only abundance was log-transformed. To pinpoint the most relevant environmental variables, we applied a multimodel inference approach based on information theory (Grueber et al., 2011) which identifies the most parsimonious model using the dredge function from the ‘‘MuMIn’’ (Barton, 2022) R package. This function fits the models including all the combinations of fixed effects and ranks them by the Akaike Information Criterion corrected for small sample size (AICc). The model selection of the fixed effects was performed using the maximum likelihood (ML) estimation. We selected the most parsimonious model with an AICc decrease not exceeding 2 units from the best (lowest value). The most parsimonious model was then fitted using a restricted maximum likelihood (REML) estimation to extract parameter values (Zuur et al., 2009). The proportion of variation explained by fixed and random effects was assessed with the Marginal R^2 and ICC_{adj} respectively (Nakagawa et al., 2017).

2.5.6 Taxa life cycle

To assess potential temporal mismatch in taxa life cycle among populations living in contrasted water thermal regimes, we examined the monthly evolution of the taxa size class distribution together with the cumulative water temperature profile of each stream site for EPT taxa present in all sites (n=15). Indeed, size class distribution has been recognised as an important biological trait to investigate life cycle patterns (Beracko & Revajová, 2019; Humpesch, 1981). We assigned to each specimen a length class as defined by Tachet et al., (2010), we calculated the relative abundance for each taxon and elaborated size-frequency bar plots reporting the monthly length class distribution in each site to describe the taxa life cycle. The cumulative water temperature profile of each stream site was calculated based on the degree-day from the 1st of January. Since body length was defined using size classes and the identification to species level was not always possible, caution has been taken in the interpretation of these results.

3. Results

3.1 Water thermal regimes and environmental setting

As targeted, the five stream sites displayed very different annual variations in water temperature around comparable means (Figure 2). GU was characterized by the highest annual variability going from -1 to 15.9 °C; GD from 2.8 to 11.7; OU from 2.9 to 11.1 °C; OD from 5.6 to 12.8 °C and NN from 7.8 to 9 °C (daily mean as shown in Figure 2). Nevertheless, even with distinct annual thermal variability, all sites were characterized by a similar annual thermal average (Kruskal Wallis test, p=0.16) with 5.8, 6.7, 6.8, 9.0 and 8.3 °C in GU, GD, OU, OD, and NN, respectively. Sites fed by both snowmelt/stormwater and groundwater (OU and OD) had a lower annual thermal variability compared to snowmelt/stormwater streams (GU and GD) while the stream fed exclusively by groundwater (NN) exhibited a stable thermal profile. Moreover, stream sites regulated by a reservoir (GD and OD) presented lower annual thermal variability (~9 and 7 °C) compared to their corresponding non-regulated sites (~17 and ~8 °C in GU and OD). Similarly, GD and OD had a higher minimum temperature (2.8 and 5.6 °C in GD and OD) compared to their corresponding non-regulated sites (-1 and 2.9 °C in GU and OU) (Figure 2B).

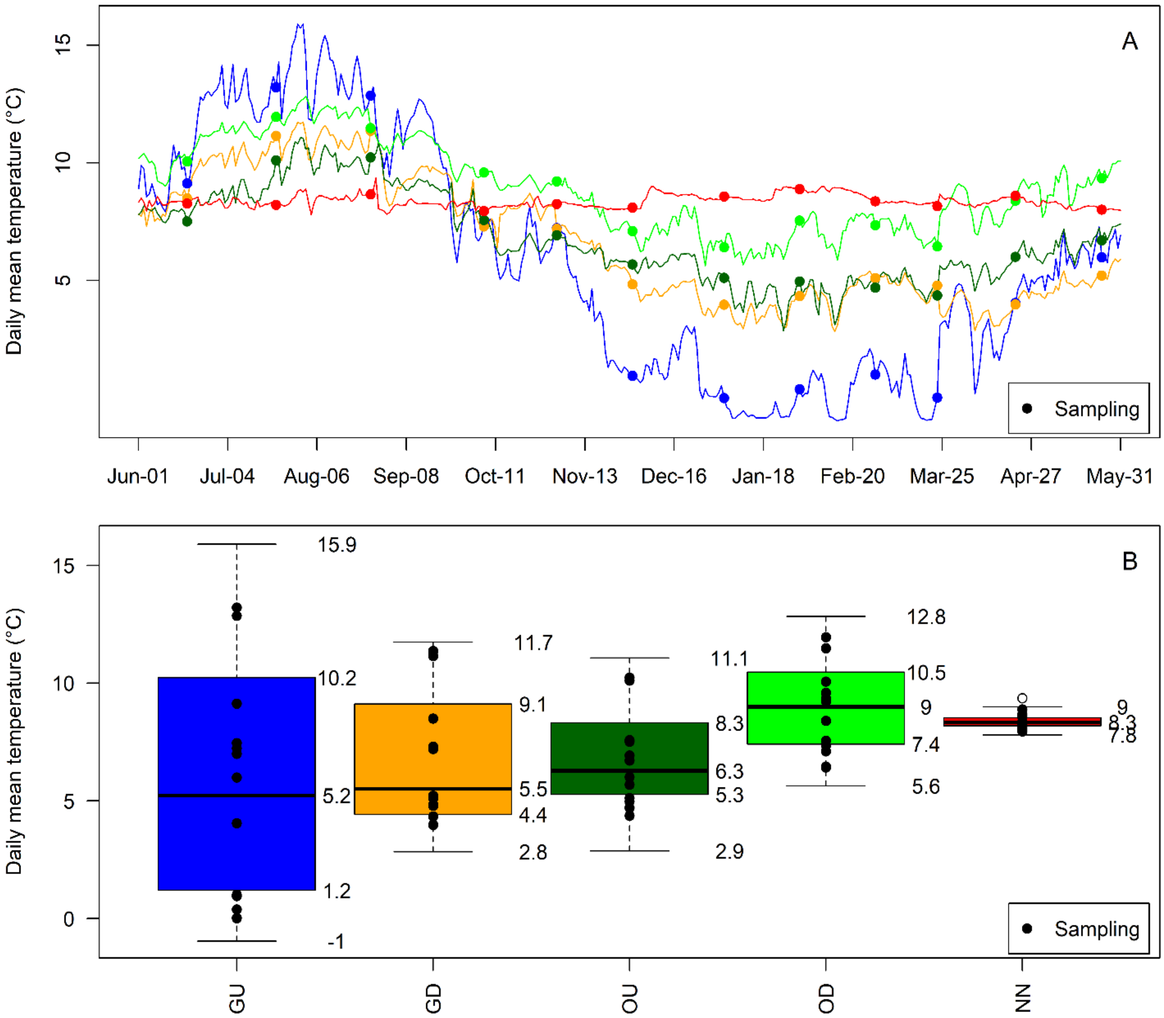

Figure 2. Annual thermal profile (A) and annual thermal variability (B) of the 5 stream sites: GU (blue), GD (orange), OU (dark green), OD (light green), and NN (red), based on daily mean values. Sampling dates are represented in panel.

Even with a drastic selection process of similar sites (except for water thermal variability) some variables exhibited spatial differences (Table 1). First, in sites influenced by groundwater inflows (OU, OD, NN) CE was higher (>200 µS/cm) than for sites dominated by snowmelt/stormwater (<85 µS/cm for GU and GD) (Wilcoxon test, W=0, $p<0.001$). Conductivity was also slightly higher in regulated sites (OU & GD) compared to their non-regulated counterpart (OD & GU) (Wilcoxon test, W=144, $p<0.001$ in GU-GD and W=0, $p<0.001$ in OU-OD). pH was neutral-weakly alkaline with slightly higher values in sites with groundwater inflows (pH>7.6 in OD, OU, NN) (Wilcoxon test, W=282.5, $p=0.048$). COD was very low (<10 mg/l) indicating a low concentration of oxidable compounds, while NNO3 was higher in OD (1.4 mg/l) compared to OU and NN (~1 mg/l) (pairwise Wilcoxon test, p<0.002 for both) and GD and GU (~0.4 mg/l) (pairwise Wilcoxon test, p<0.001 for both). In all sites, O2 was always above 90% and DO above 9 mg/l. Resources varied among sites with higher densities of CPOM in OU and OD (~14 and 19 g/m^2 respectively) and lower in NN (2.2 g/m^2) while ALGAE were more abundant in NN and OD (~3.2 and 2.6 g/m^2 respectively) and particularly low in OU (0.83 g/m^2) but with no significant differences (pairwise Wilcoxon test, $p>0.05$ unless NN-OU for ALGAE and pairwise Wilcoxon test, $p>0.05$ unless NN-GD, NN-OD, NN-OU for CPOM). Mean DISTURBANCE was similar in all sites (15-28%). There was no significant difference in DISTURBANCE between regulated and unregulated sites (Wilcoxon test, W=61.5, $p=0.491$ in GU-GD and W=72, $p=0.691$ in OU-OD). In addition, CE, O2, NNO3, COD, and HABITAT were almost constant in time, DO exhibited a temporal pattern opposed to water temperature (TMean) in all sites except NN where it was almost constant, and pH showed a synchronous pattern across sites. By contrast, DISTURBANCE, showed strong temporal fluctuations with abrupt peaks, especially in June, September, and October, and similarly CPOM, and ALGAE displayed monthly fluctuations, especially in OD, OU, and NN. Floods occurred in synchrony at all sites with maximum DISTURBANCEs (70-100%) in September and October when ALGAE and CPOM reached the lowest values (Figure 2SM).

Table 1. Environmental variables of five stream-sites expressed as annual average ± standard deviation and minimum and maximum values based on the monthly measurements.

Environmental Variables		Acronynm		GU	GD	OU	OD	NN
Water quality	Mean monthly temperatures (°C)	Tmean	mean±sd	5.49 ± 4.93	6.52 ± 2.60	6.81 ± 1.81	8.86 ± 1.82	8.40 ± 0.21
			min-max	-0.52 - 13.88	3.65 - 11.02	4.38 - 10.19	6.42 - 12.21	8.15 - 8.78
	Electrical conductivity (µS/cm)	CE	mean±sd	40.65 ± 7.88	80.07 ± 8.59	311.09 ± 17.97	480.08 ± 61.20	239.36 ± 14.82
			min-max	29.10 - 53.70	64.10 - 93.40	282.00 - 337.00	351.00 - 578.00	224.00 - 276.00
	Oxygen saturation (%)	O2	mean±sd	98.40 ± 1.25	98.12 ± 1.40	96.36 ± 3.01	97.74 ± 1.81	99.72 ± 1.18
			min-max	96.10 - 100.00	95.00 - 99.90	90.00 - 99.20	93.60 - 99.70	97.10 - 101.00
	Dissolved oxygen (mg/l)	DO	mean±sd	11.12 ± 1.30	10.55 ± 0.65	10.56 ± 0.54	10.74 ± 0.48	11.07 ± 0.13
			min-max	9.03 - 12.87	9.33 - 11.44	9.50 - 11.24	9.84 - 11.39	10.79 - 11.22
	pH	pH	mean±sd	7.54 ± 0.37	7.58 ± 0.63	7.66 ± 0.32	7.75 ± 0.27	7.94 ± 0.36
			min-max	6.97 - 8.19	6.78 - 8.59	7.21 - 8.23	7.08 - 8.20	7.06 - 8.28
	Nitrate nitrogen concentration (NO_3-N) (mg/l)	NNO3	mean±sd	0.45 ± 0.19	0.37 ± 0.06	1.02 ± 0.17	1.34 ± 0.17	0.93 ± 0.18
			min-max	0.29 - 0.98	0.27 - 0.46	0.69 - 1.36	1.09 - 1.59	0.68 - 1.29
	Chemical Oxygen Demand (mg/l)	COD	mean±sd	5.46 ± 2.43	5.09 ± 1.74	8.33 ± 8.56	5.03 ± 4.95	4.13 ± 2.68
			min-max	1.21 - 8.34	1.68 - 7.96	1.86 - 33.20	0.95 - 19.30	0.29 - 7.78
Substrate	Microhabitat equitability	HABITAT	mean±sd	0.77 ± 0.02	0.75 ± 0.02	0.74 ± 0.02	0.74 ± 0.04	0.73 ± 0.05
			min-max	0.72 - 0.78	0.70 - 0.78	0.70 - 0.76	0.70 - 0.78	0.64 - 0.78
Hydrology	Disturbance (%)	DISTURBANCE	mean±sd	19.73 ± 30.89	15.32 ± 31.58	28.16 ± 40.18	16.50 ± 28.59	22.81 ± 39.73
			min-max	0.00 - 76.10	0.00 - 100.00	0.00 - 100.00	0.00 - 71.67	0.00 - 100.00
Resources	Algae (g/m^2)	ALGAE	mean±sd	5.68 ± 3.47	9.00 ± 7.62	4.13 ± 2.46	12.93 ± 8.94	15.76 ± 25.94
			min-max	1.99 - 13.05	1.83 - 24.30	1.29 - 10.63	1.82 - 36.78	1.99 - 93.20
	Coarse particulate organic matter (g/m^2)	CPOM	mean±sd	9.66 ± 7.68	7.88 ± 4.02	14.41 ± 12.08	18.97 ± 16.23	2.22 ± 1.59
			min-max	0.28 - 23.69	1.45 - 13.49	1.78 - 38.81	3.25 - 53.80	0.61 - 5.72

3.2 Macroinvertebrate communities

In total, we collected 114,013 individuals belonging to 58 taxa. The mean taxonomic richness among samples was 21.4±4.4 ranging from 9 to 29 taxa. The mean density was 1964.7±1312.6 ind/m^2; GU was the site with the lowest density (1,538±963 ind/m^2) while OD with the highest one (2295±1223 ind/m^2). In total, in terms of relative abundance, Ephemeroptera was the most represented order (40.2%), followed by Plecoptera (18.6%), Coleoptera (17.1%), Diptera (14.1%) and Trichoptera (8.2%) but with high inter and intra sites variability. For example, Plecoptera were particularly dominant in GU and GD (~30% and 23% respectively) while Ephemeroptera in GD, OU and NN (>40%). Coleoptera represented ~27%-28% of the community in NN and OU while Diptera represented almost 25% in OD. The relative abundance of Trichoptera was particularly low in OU (<2%) (Table 2). Abundance, Richness, and EPT exhibited a strong temporal trend with minimum values (85-145 ind/m^2, 9-15 and 6-10 taxa respectively) in autumn when floods occurred and maximum values (2,927-4,806 ind/m^2, 24-28 and 12-18 taxa respectively) at the end of the winter. Plecoptera dominated in winter especially in GU and GD (60% and 30%) while Trichoptera abounded in late summer-autumn in OD and GU (40 and 20%) (Figure 3SM).

Table 2. Macroinvertebrate indices of five stream sites expressed as annual average ± standard deviation and minimum and maximum values based on the monthly samples.

Biodiversity Metric		GU	GD	OU	OD	NN
Abundance (ind/m^2)	mean±sd	1538.42 ± 962.96	2254.30 ± 1654.98	1919.73 ± 1522.63	2295.00 ± 1223.61	1804.00 ± 1158.48
	min-max	85.00 - 2927.00	145.00 - 4806.00	113.00 - 4635.00	108.00 - 4031.00	120.00 - 3696.00
Shannon	mean±sd	3.11 ± 0.41	2.89 ± 0.44	3.02 ± 0.57	2.92 ± 0.26	3.03 ± 0.31
	min-max	2.57 - 3.92	1.87 - 3.52	1.57 - 3.58	2.49 - 3.32	2.60 - 3.62
Richness	mean±sd	22.75 ± 4.25	22.67 ± 4.50	21.64 ± 6.10	19.33 ± 2.19	20.64 ± 3.96
	min-max	15.00 - 28.00	12.00 - 29.00	9.00 - 29.00	16.00 - 24.00	15.00 - 26.00
EPT	mean±sd	14.58 ± 2.71	14.42 ± 2.31	12.00 ± 3.13	10.75 ± 1.48	10.64 ± 2.54
	min-max	10.00 - 19.00	9.00 - 18.00	6.00 - 16.00	8.00 - 12.00	7.00 - 15.00
% Plecoptera	mean±sd	29.92 ± 23.75	22.87 ± 7.11	12.40 ± 7.78	16.73 ± 8.39	9.70 ± 5.12
	min-max	4.82 - 61.35	12.66 - 33.93	4.29 - 28.16	1.85 - 29.64	4.89 - 22.30
% Ephemeroptera	mean±sd	34.14 ± 16.60	47.54 ± 14.70	42.17 ± 21.42	33.61 ± 11.37	44.01 ± 16.26
	min-max	19.27 - 71.08	20.56 - 75.29	16.38 - 81.82	15.02 - 59.23	14.84 - 67.16
% Trichoptera	mean±sd	10.77 ± 9.74	8.47 ± 7.72	1.89 ± 1.16	12.28 ± 13.69	7.13 ± 3.86
	min-max	1.32 - 34.27	2.28 - 25.93	0.72 - 4.42	1.02 - 39.81	1.94 - 13.39
% Coleoptera	mean±sd	12.79 ± 7.25	6.92 ± 5.31	28.41 ± 20.00	11.89 ± 3.50	27.22 ± 17.85
	min-max	7.17 - 28.26	0.00 - 16.49	5.30 - 61.05	7.60 - 17.54	4.66 - 64.84
% Diptera	mean±sd	11.91 ± 14.35	12.43 ± 11.16	13.73 ± 9.54	24.76 ± 17.21	7.07 ± 4.69
	min-max	0.00 - 51.71	0.69 - 41.45	1.77 - 27.87	1.85 - 57.67	0.56 - 17.64

3.3 Temporal changes in community composition.

Annually, abundance-based dissimilarity (Bray-Curtis) was higher than the incidence (presence/absence) index (Sorensen) (Sorenson always below 0.5 unlike Bray-Curtis dissimilarity, Figure 3). Bray-Curtis dissimilarity was mainly controlled by the balanced variation in abundance compared to the abundance gradient (βratio=0.63-0.79 in the 5 sites), except for months sampled after floods in which the gradient in abundance (Gradient) overcame the balanced variation in abundance (Balanced) (Figure 3). During highly disturbed months (September-October) the total taxa abundance dropped by 95% (~80-150 ind/m^2 compared to a mean total abundance ranging between 1600-2200 ind/m^2 across sites).

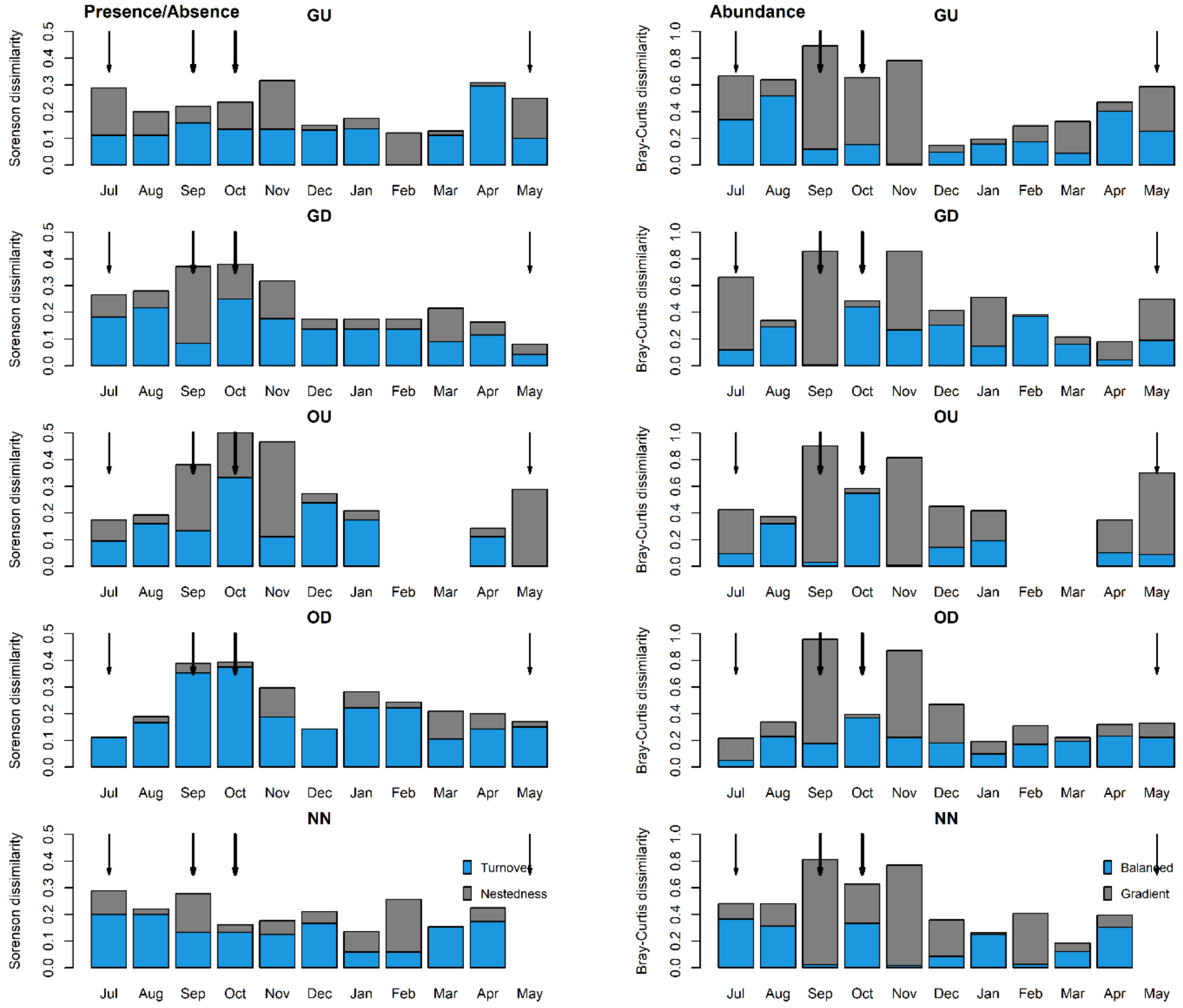

Figure 3. Temporal changes between two consecutive dates in community composition assessed using the Sorensen (on the left) and Bray-Curtis (on the right) dissimilarity indices additively decomposed in turnover/nestedness and balanced variation in abundance (Balanced)/abundance gradient (Gradient)

respectively. Black arrows represent the sampling date following a flood (with the highest occurring in September and October).

3.4 Temporal co-structure (within-site)

Forty-nine percent of the total inertia was related to temporal differences with the first and second axes of the within-sites CoA (Figure 4) explaining 74.3% and 18.8% of the inertia, respectively. Pearson correlation between the environment and the community composition datasets was 0.87 and 0.85 for the first and second axes respectively and the two datasets were highly related (RV=0.59). The first axis of the within-sites CoA showed that DISTURBANCE was mainly related to the common macroinvertebrate temporal pattern among sites with a negative effect of high disturbances on most taxa and resource availability (ALGAE and CPOM). The second axis indicated that temperature was also an important factor explaining the macroinvertebrate temporal pattern, with low temperatures (and a higher concentration of dissolved oxygen) associated with higher abundances of *Leuctra* sp., *Brachyptera* sp. and *Amphinemurae* sp. and lower abundances of *Serratella ignita* and Blephariceridae. According to the taxonomic factorial map, the abundance of all taxa was specifically negatively affected by DISTURBANCE, in particular in September and October (Figure 2SM). Moreover, the relationship between the biological and environmental first two axes (Figure 4SM) indicated a similar effect of DISTURBANCE on community structure across the 5 sites (Axis 1) contrary to TMean (Axis 2, Figure 4SM). We observed higher temporal dissimilarity in taxa assemblage for sites with higher temporal thermal variability, with sample dates of GU spread along the temperature axis unlike NN (see the taxonomic factorial map with the size of the ellipses decreasing from the site with the strongest thermal regime (GU) to the site with the lowest (NN), Figure 4B, Figure 4SM).

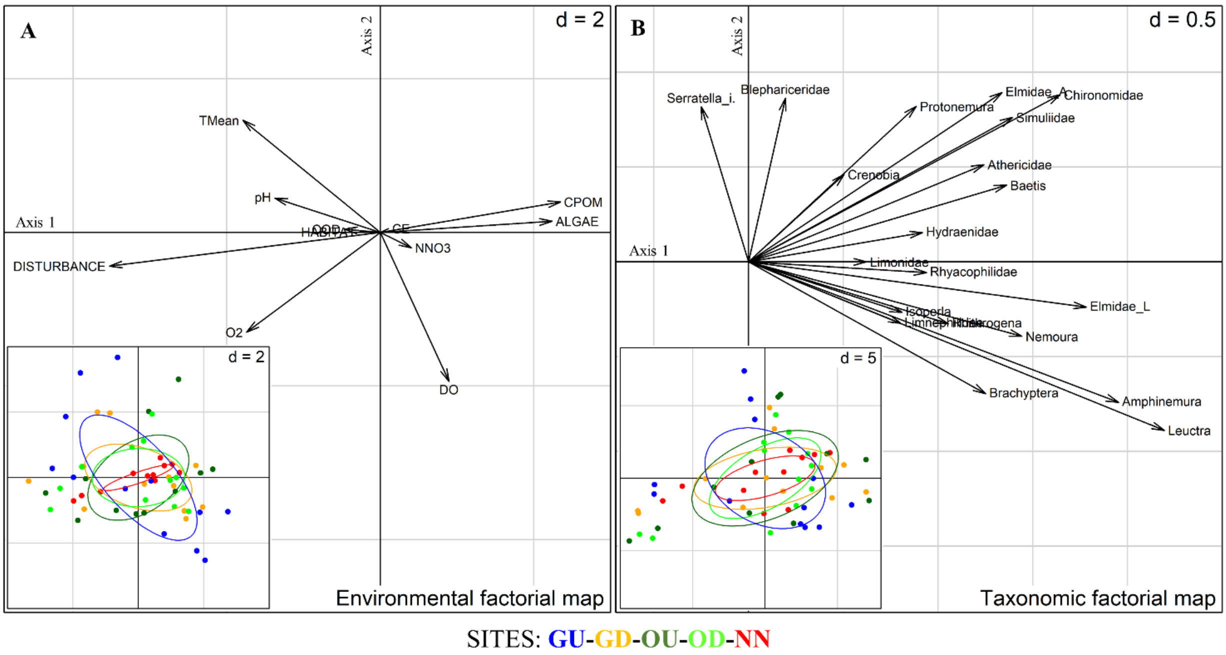

Figure 4. Factorial maps of the within-sites CoA representing the relative temporal (monthly) co-structure between the environmental conditions (A) and the community composition (B). For a better visualization only taxa with eigenvalues higher than 0.4 were plotted.

3.5 Spatial co-structure (between-sites)

Fifty-one percent of the total inertia was related to spatial differences among sites with the first and second axes of the between-sites CoA (Figure 5) explaining 58.1% and 30.6% of the inertia, respectively and the two datasets were highly related (RV=0.53). Both taxa and environment factorial maps of the between sites CoA showed that the three sub-catchments (Goglio-Ogna-Nossana) are well separated. Ogna sites (OU and OD) differed from Goglio sites (GD, GU) for CE and NNO3 while NN differed mainly due to higher pH and lower HABITAT compared to the other sites (Figure 5A). Higher abundances of *Isoperla* sp., *Ecdyonurus* sp., *Epeorus alpicola*, *Perla* sp. and Hydropsichidae characterised GU and GD sites while higher abundances of Hydraenidae, Philopotamidae, Athericidae, *Serratella ignita*, and Simuliidae were observed in OU and OD. *Ancylus* sp., Limnephilidae, and *Rhitrogena* sp. dominated in NN (Figure 5B). In addition, we observed that sites were ordered along the same axis in both factorial maps, corresponding to the annual water thermal variability (TAmp) in the environmental factorial map (Figure 5A) and the temporal dissimilarity in community composition (BBray_year and BBal_year) (Figure 5B).

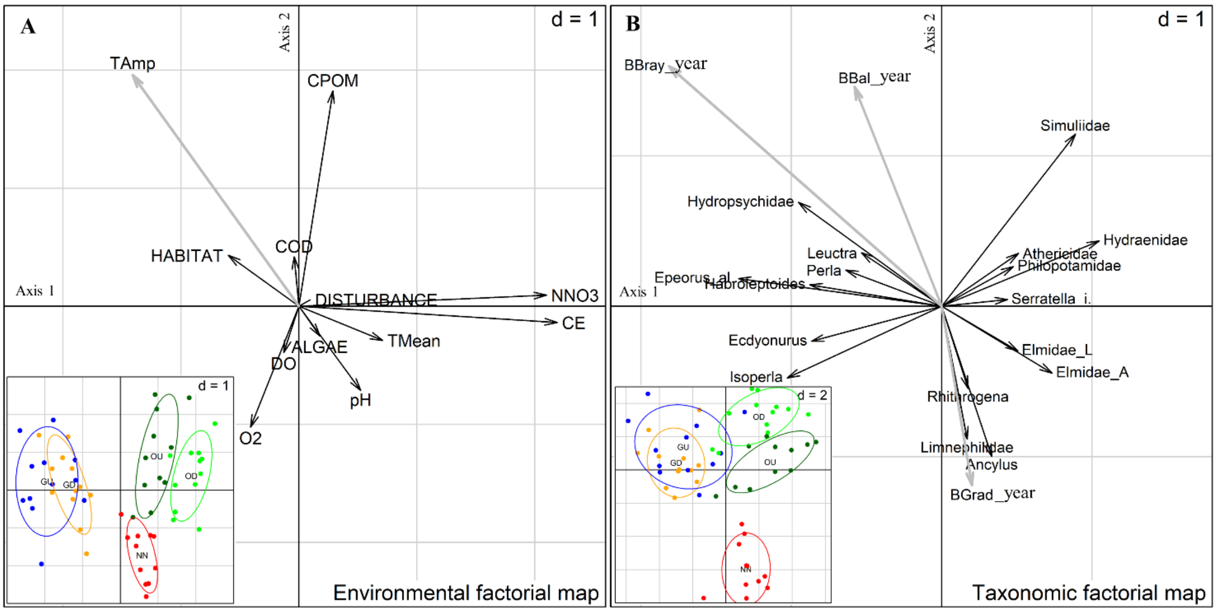

Figure 5. Factorial maps of the between-sites CoA representing the relative spatial co-structure between the environmental conditions (A) and the community composition (B). Annual thermal variability (TAmp), Bray-Curtis dissimilarity (BBray_year), balance variation in abundance (BBal_year), and abundance gradient (BGrad_year) (grey arrows) were plotted as supplementary variables only for visualization purposes. For a better visualization, only taxa with eigenvalues higher than 0.4 were plotted.

The components of Bray-Curtis dissimilarity showed a contrasted pattern with BBal_year positively correlated with TAmp unlike BGrad_year (Figure 5) as confirmed also by MRM based on pairwise comparisons (Table 1SM).

3.6 Disentangling the effect of water temperature on temporal macroinvertebrate structure

In general, the selected environmental variables explained more than half of the generalized linear mixed models' variation of the macroinvertebrate assemblages, especially for total abundance, EPT, and %Plecoptera ($R^2_{marginal} \geq 0.5$) while Shannon diversity and %Coleoptera remained unexplained by the environmental variables included in the models. The monthly mean temperature was negatively related with %Plecoptera, (slope=-8.5) and positively with %Trichoptera and %Diptera (slope=3.2 and 4.3 respectively; Table 3). The disturbance had a significant negative effect on Abundance, Richness, and EPT richness (slope=-0.8, -2.7 and -1.5, respectively) while resources (CPOM and ALGAE) are positively related to the relative abundance of Plecoptera (slope=3.5 for CPOM) and Diptera (slope=6.9 for CPOM and slope=4.0 for ALGAE) and negatively with the relative abundance of Ephemeroptera (slope=-

10.5 for CPOM) and Trichoptera (slope=-2.7 for ALGAE). CE was negatively related to EPT (slope=-1.7) while pH was never retained by the model selection procedure regardless of the biodiversity index. The random effect of the site for %Plecoptera, %Ephemeroptera, %Trichoptera %Coleoptera and %Diptera explained 27%, 17%, 25%, 34%, and 0% of the model variation (ICC_{adj}), respectively (Table 3).

Table 3. Results of the most parsimonious generalized linear mixed-effect models relating the different biodiversity indices to the main environmental variables. Values correspond to regression slopes ± standard error. Negative regressions are in bold.

GLM model		Inter	DIST	CPOM	ALGAE	CE	Tmean	R^2_{marginal}	ICC_{adj}
log(Abundance)	value	7.170	**-0.802**	0.288				0.71	0.00
	se	0.082	**0.091**	0.091					
Shannon	value	2.993						0.00	0.00
	se	0.053							
Richness	value	21.411	**-2.672**					0.36	0.11
	se	0.683	**0.449**						
EPT	value	12.514	**-1.454**			**-1.699**		0.52	0.11
	se	0.407	**0.267**			**0.409**			
% Plecoptera	value	18.436		3.548			**-8.456**	0.50	0.27
	se	2.587		1.489			**1.327**		
% Ephemeroptera	value	40.176		**-10.524**				0.34	0.17
	se	3.241		**2.094**					
% Trichoptera	value	8.114			**-2.702**		3.266	0.21	0.25
	se	2.120			**1.104**		1.092		
% Coleoptera	value	17.392						0.00	0.34
	se	4.344							
% Diptera	value	14.103		6.694	3.943		4.303	0.40	0.00
	se	1.381		1.479	1.427		1.451		

3.7 Taxa life cycle

We observed no clear trend on the 15 EPT taxa temporal variability in body length class distribution except for *Amphinemura* sp. (Plecoptera) and *Serratella ignita* (Ephemeroptera). Potential *Amphinemurae* species inhabiting Orobic Alps below 1000 m are *A. sullicicollis,* and *A. triangularis,* not identifiable at the larval stage for the lack of distinctive traits. *Amphinemura* sp. were mainly observed from January to May but in OD and NN specimens reached the maximum length (>10 mm) in March-April, while it occurred one month later in GD and GU. Small *Serratella ignita* larvae (≤5 mm) were observed from late spring (May-June) in NN and OD sites while only in summer (July-August) in OU, GD, and GU stream sites (Figure 6).

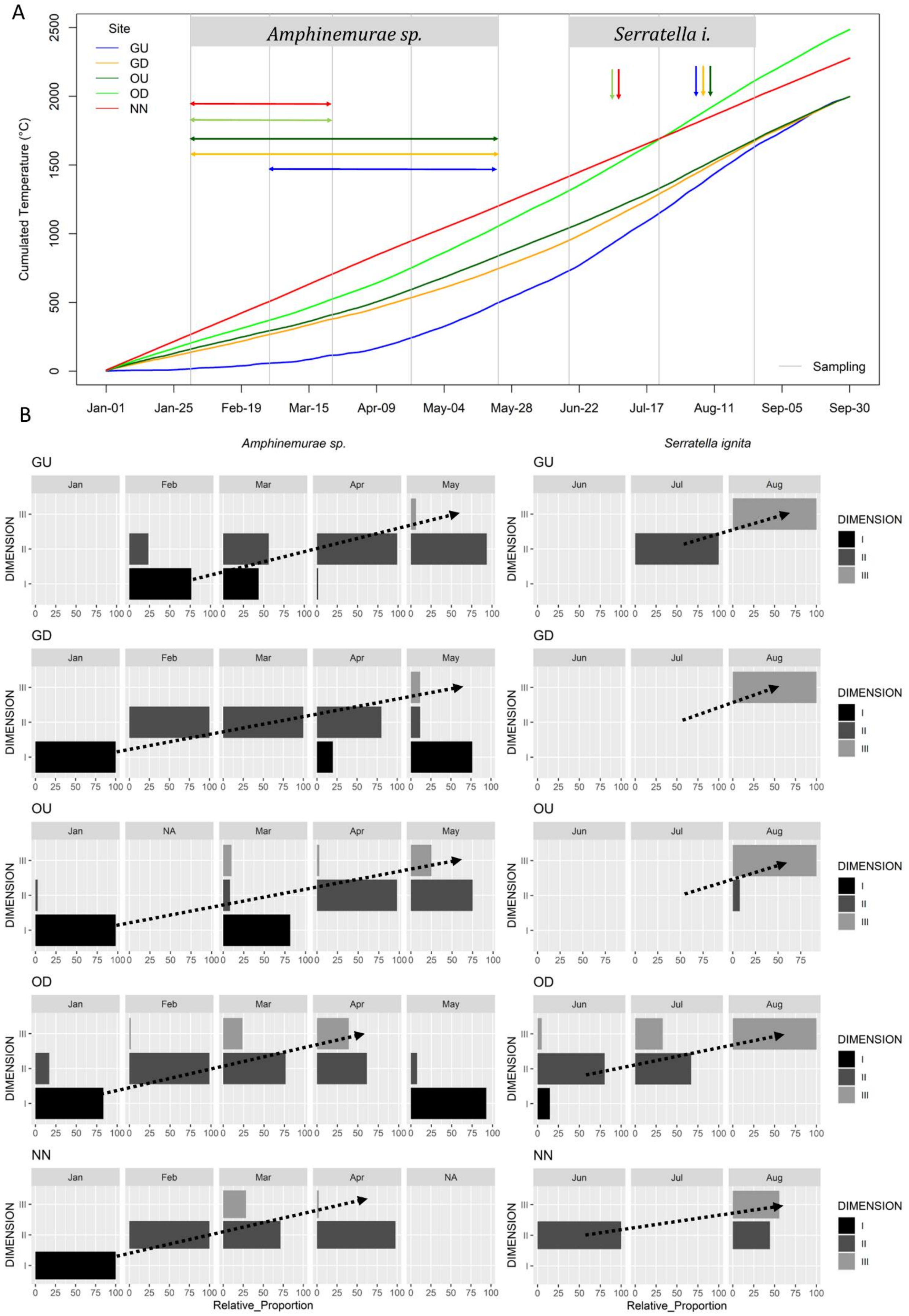
A
Site
GU
GD
OU
OD
NN
Amphinemurae sp.
Serratella i.
Cumulated Temperature (°C)
0
500
1000
1500
2000
2500
Sampling
Jan-01
Jan-25
Feb-19
Mar-15
Apr-09
May-04
May-28
Jun-22
Jul-17
Aug-11
Sep-05
Sep-30
B
Amphinemurae sp.
Serratella ignita
GU
GD
OU
OD
NN
Jan
Feb
Mar
Apr
May
NA
Jun
Jul
Aug
DIMENSION
I
II
III
0
25
50
75
100
Relative_Proportion

Figure 6. (A) Cumulative water temperature profile of each stream site (the thermal regime of 2021 was used for both taxa) and (B) body length class-frequency distribution of *Amphinemura* sp. and *Serratella ignita*. In panel A, horizontal-colored bars represent the time of development of *Amphinemurae* sp. specimens (from the occurrence of the smallest class size to the largest one) and coloured arrows represent the occurrence of the earlier specimens of *Serratella ignita*. On panel B, dimension refers to the three body length classes from the smallest (I), to the largest (III) sizes. Dimension: I≤2.5 mm, 2.5 mm<II≤5 mm, 5 mm<III≤10 mm. Dotted arrows were plotted only for qualitative comparison across sites.

4. Discussion

4.1 Water thermal variability and macroinvertebrate assemblages

In alpine catchments, even within a small geographic area and with similar annual mean temperatures, the thermal regime heterogeneity of running waters can be very high. Within our study catchment, the upper Serio catchment, continuous water temperature monitoring showed a marked intra-annual variation of water temperatures in different types of subalpine streams linked to both source type and water management practices (Figure 2). Similarly, (L. E. Brown et al., 2006) found a marked heterogeneity in water temperature patterns driven by dynamic water source contributions, proximity to the source, and hydro-climatological conditions in an alpine stream network in the French Pyrenees. Specifically, we measured higher annual thermal variability in the snowmelt/stormwater stream (~17° in GU), compared to groundwater stream (only ~1 °C in NN). In addition, water supply reservoirs substantially modified the downstream thermal regime, especially increasing the temperatures during winter (December-March). Below reservoirs (in GD and OD) winter temperatures were between 3 and 3.5 °C higher than upstream (GU and OU, respectively) as observed by Zolezzi et al., (2011) in the Noce River basin (Italy) and by Dickson, Carrivick, & Brown (2012) in the Eisböden catchment (Austria). In addition, contrary to our expectations, we measured higher summer (June-September) water temperature downstream to the reservoir in the Ogna catchment, probably due to the shallow reservoir (depth ~12 m) heating the whole water column in summer as found by Casas et al., (2000) and Menéndez et., (2012) in the Pyrenees.

As hypothesized, our results showed that water thermal variability generated temporal changes in macroinvertebrate assemblage structure, with the highest multi-date β-diversity obtained at the site with the highest thermal variability (~17 °C), and conversely (Figures 4 and 4SM). However, in our specific case study, flood disturbance was the first variable controlling the temporal pattern among sites, affecting simultaneously all sites (cf. DISTURBANCE, Figures 4 and 4SM), even in regulated streams. This might be due to the magnitude of the rain events that occurred during our study period within the whole upper Serio catchment causing synchronous floods across all stream sites, only slightly buffered by the reservoirs. Although the sediment displacement method has already proven to be valid for assessing the ecological effect of floods (Death & Zimmermann, 2005; Townsend et al., 1997), discharge data, unfortunately unavailable here, would have provided a more accurate understanding of the hydrological patterns across sites (Gibbins et al., 2001; White et al., 2016). While extreme flow events are known to induce drastic impacts on macroinvertebrate assemblages (Death, 2010), our results showed that taxa abundance and richness dropped simultaneously in all sites following each flood (Figure 3SM). This synchronous temporal change in community composition linked to flood events across sites was characterised by considerable loss of individuals of dominant taxa (Figure 3). Conversely, the thermal regime rather impacted the relative proportion of dominant taxa, with higher annual temperature variability promoting substitution of individuals among taxa (Figure 5, Table 1SM). Thus, our results suggest that the difference in the annual water thermal variability may partly drive the spatial macroinvertebrate dissimilarities among sites (Figure 5). Consistently, (Von Fumetti et al., 2017) found significant differences between high and lower altitude mountain macroinvertebrate assemblages mainly related to temperature amplitude and snow cover even if, in their study, temperature amplitude was also highly correlated to mean temperature contrary to our study (Table 1, Figure 2B). Indeed, several studies showed that the difference in mean annual temperatures explained a large proportion of spatial macroinvertebrate patterns in both alpine streams (Füreder & Niedrist, 2020; Milner et al., 2010) and foothill rivers (Haidekker & Hering, 2008) while thermal amplitude effect is rarely evaluated as it represents a confounding factor. In our study, we found that water thermal variability affected the structure of macroinvertebrate community influencing especially the relative abundance of Plecoptera that exhibited a marked annual fluctuation with the highest densities in winter, especially in GU and GD (Table 3, Figure 3SM, Plecoptera). Similarly, Arai et al., (2015) observed a sharp decrease in Plecoptera density from May to October related to the increase in water temperature in the Natori River basin (Japan). Also, Haidekker & Hering (2008) pointed out that Plecoptera abundance was negatively related to temperature, with a higher abundance (+15%) in colder German foothills rivers and, in line with our results, they found a positive relationship between temperature and the majority of Trichoptera taxa (Table 3). Note, however, that resource availability and some physico-chemical parameters also explained part of the community variation (Figure 5, Table 3), with positive link between both CPOM and ALGAE and Diptera, and negative link between CPOM and Ephemeroptera and ALGAE and Trichoptera. Our studies revealed that the investigation of the macroinvertebrate-temperature relationship should be carried out by monitoring water temperature continuously but also considering the whole environmental setting to avoid misleading results as already pointed out by (Jackson et al., 2007).

4.2 Possible consequences of stream thermal change

Mountain biota is threatened by environmental changes linked to both human pressures (e.g., water use, tourism activities (Taylor & Figgis, 2007) and the ongoing climate warming, proceeding 2–3 times faster than the global average (Hock et al., 2019) imperilling especially cold-adapted species. In mountain streams, we thus expect higher temperatures (in average and maximum), especially during summer heat waves. However, increasing temperature will also occur due to the modification in the quantity, timing, and duration of snowmelt water supply in non-glacial streams, associated with shorter and warmer winters (Confortola et al., 2013). Specifically, we foresee higher thermal variability (and higher temperature averages) in non-regulated snowmelt/stormwater-fed streams (as GU) due to their high thermal reactivity to air (Piccolroaz et al., 2016), while groundwater-fed streams (as NN and OU) might be less exposed to thermal changes, especially in sites close to the source (Piccolroaz et al., 2016). *Leuctrae* sp., *Amphinemurae* sp. and *Brachyptera* sp., strongly related to cold conditions (Figure 4), might be negatively affected by rising temperatures; while *Serratella ignita* associated with higher temperatures might benefit from these changes in the future as also pointed out by Fenoglio et al., (2010) and López-Rodríguez et al., (2009). Among the collected species: *Perla grandis*, *Dictyogenus fontium*, *Chloroperla susmicheli*, *Leuctra leptogaster*, *Leuctra braueri*, *Leuctra dolasilla*, *Protonemura lateralis*, *Nemura minima*, *Nemura mortoni*, *Brachyptera risi*, (Plecoptera), *Epeourus alpicola*, *Epeorus assimilis* (Ephemeroptera) and *Consorophylax consors* (Trichoptera), all, cold stenothermal, might be particularly negatively affected in the next decades (Knispel & Lubini, 2015), in particular in stormwater streams (as GU). Indeed, we found specimens of *Chloroperla susmicheli*, *Dictyogenus fontium*, *Consorophylax consors and Drusus discolor* in OU and GD (sites characterized by colder water: maximum mean daily temperature below 12 °C) but not in GU and OD maybe due to their more restricted thermal preferences (Küry et al., 2017a). On the other hand, mountain streams regulated by deep reservoirs (such as GD) might be less exposed to increasing temperatures as the large volume of cold waters exerts a strong thermal buffer (Piccolroaz et al., 2016). Thus, unless extremely low below-dam outflows warming rapidly, downstream reaches could constitute a refuge, especially for stenotherm taxa as suggested by the difference in the occurrence of the stenotherm species between GD and GU. Conversely, shallow reservoirs and/or superficial water releases, promoting higher temperatures downstream, are expected to strengthen the negative heating effects on the stenotherm aquatic fauna of mountain streams. Indeed, as Haidekker & Hering (2008) and Lessard & Hayes (2003) we observed low richness in particular of EPT taxa downstream of the shallow reservoir in OD (Table 2, Figure 3SM). Finally, we detected a mismatched life cycle for populations of *Amphinemura* sp. (Plecoptera) and *Serratella ignita* (Ephemeroptera) across stream sites linked to their thermal preference (Figure 6), with *Amphinemurae* species (*A. sullicicollis,* and/or *A. triangularis*) classified as cold stenothermal taxa (<10°C), while *Serratella ignita* as a eurytherm (Schmidt-Kloiber & Hering, 2015). Univoltine taxa, *Amphinemura* sp. emerges in spring, while *Serratella i.* in summer. We observed earlier hatching of *Serratella ignita* in warmer stream sites (OD, NN) explained by egg development of mayflies temperature dependent (Brittain, 1990). The hatching threshold observed (>5 °C) was consistent with the limit pointed out by (Bohle, 1972) and (Elliott, 1978). For *Amphinemurae* sp., the development was enhanced by higher temperatures (OD and NN sites) in line with the studies of (Langford, 1975) and Saltveit & Brittain, (2016). Note that in May a high percentage of small specimens (≤2.5 mm) was found in GD and OD sites, probably belonging to a cohort of a different species of *Amphinemurae* sp. as they are univoltine. Thus, with climate change, we will expect a strengthening of the mismatched life cycle patterns in these taxa across streams characterized by different water thermal regimes. The phenological desynchronization as a biological response to water temperature allows populations to overcome sublethal conditions (Li et al., 2011; Newbold et al., 1994). Moreover, a high phenological plasticity might confer adaptation to relatively rapid environmental change promoting population survival (Poff et al., 2006). Along with global warming, we expect changes in population interactions both within and among communities with possible implications for species competition and reproduction. For example, within a small catchment, the temperature increase may temporally segregate populations inhabiting streams with contrasted thermal conditions promoting their divergence due to reduced possibility for reproduction (Harper & Pilon, 1970; Hildrew & Edington, 1979). However, a clear mismatched life cycle was found only in two taxa suggesting that the phenological desynchronization may not be the only mechanism involved with water thermal heterogeneity. Indeed, other mechanisms such as adult longevity and/or dispersal ability together contribute to ecosystem-scale resilience in the face of ongoing climate change (Finn et al., 2022). However, to clearly assess species-specific phenological responses to temperature; specific studies collecting emergent adults are needed, associating phenological traits and community responses to contrasted water thermal conditions.

5. Conclusion

As far as we know the present study is the first examining the spatiotemporal pattern of stream macroinvertebrate assemblages across a gradient of annual water thermal variability but similar averages, disentangling the drivers and the mechanisms related to these patterns. According to our assumption, the spatial heterogeneity in water temperature regimes is an important driver of the spatial dissimilarity in macroinvertebrate assemblages even though further studies including more sites and with higher taxonomic resolution would improve our understanding of the role of the thermal regime. Nevertheless, even considering the effects of other environmental variables, water temperature remained a pivotal driver of the temporal pattern affecting density, and life cycles, especially for cold stenothermal species. As mountain streams are particularly exposed to thermal changes due to global warming and flow management, we expect marked modifications in freshwater macroinvertebrate communities. Although our results showed that water thermal variability enhanced temporal β-diversity, and in particular the changes in the dominance among taxa over the months we also conclude that cold stenothermal and endemic taxa will be threatened by the overall warming, especially in streams characterized by warmer peaks (snowmelt/stormwater streams). On the other hand, streams with low thermal variability, but low temperatures, potentially below deep reservoirs could constitute a refuge for cold stenothermal species. Overall, a higher thermal heterogeneity of the mountain streamscape may allow flexibility of community responses and contribute to ecosystem-scale resilience with climate change. Further research, at a larger scale, should attempt a rigorous investigation of the thermal preference of mountain taxa and investigate the dispersal abilities of the more vulnerable species to assess the role of more stable thermal environments as potential refuges and population sources for recolonisation as well as the reservoirs' management implications for conservation.

Supplementary material

Macroinvertebrate specimens are stored in the collection of the Museum of Natural Science "Enrico Caffi" of Bergamo (Italy).

Table 1SM. Results of the multiple regressions on distance matrices (MRM) between matrices of temporal macroinvertebrate assemblage dissimilarity considering Bray-Curtis index and its two components (balanced variation in abundance and the abundance gradient and the environmental variables controlling the temporal pattern (TMean and DISTURBANCE). For environmental variables we considered the pairwise difference among sampling dates within each site. Significative regressions are in bold.

SITE	MRM	Bray-Curtis			Balanced variation			abundance Gradient		
		Intercept	*p*	R^2	Intercept	*p*	R^2	Intercept	*p*	R^2
GU	Intercept	0.435	0.965	0.45	0.203	0.801	0.48	0.233	0.761	0.40
	TMean	**0.061**	0.003		**0.096**	0.001	0.48	-0.035	0.169	
	Disturbance	**0.101**	0.004		**-0.086**	0.020	0.48	**0.187**	0.008	
GD	Intercept	0.478	0.279	0.49	0.216	0.102	0.31	0.262	0.657	0.60
	TMean	0.032	0.275		0.041	0.052	0.31	-0.010	0.762	
	Disturbance	**0.132**	0.008		**-0.064**	0.004	0.31	**0.196**	0.001	
OU	Intercept	0.447	0.065	0.65	0.220	0.095	0.40	0.227	0.865	0.63
	TMean	0.075	0.053		**0.116**	0.019	0.40	-0.041	0.522	
	Disturbance	**0.128**	0.001		**-0.078**	0.003	0.40	**0.206**	0.002	
OD	Intercept	0.416	0.615	0.52	0.308	0.150	0.12	0.108	0.928	0.59
	TMean	0.016	0.815		0.032	0.399	0.12	-0.016	0.814	
	Disturbance	**0.200**	0.013		**-0.055**	0.027	0.12	**0.255**	0.002	
NN	Intercept	0.420	0.058	0.62	0.287	0.025	0.15	0.133	0.998	0.54
	TMean	0.319	0.413		-0.467	0.280	0.15	0.786	0.161	
	Disturbance	**0.122**	0.005		-0.042	0.073	0.15	**0.164**	0.004	

Pairwise Bray–Curtis dissimilarity of benthic macroinvertebrates was significantly correlated with TMean differences among dates only in GU (MRM test: p=0.003, Figure 5A). However, dissimilarity was significantly correlated with DISTURBANCE in all sites (MRM test: p=0.004 for GU, p=0.008 for GD, p=0.001 for OU, p=0.013 for OD and p=0.005 for NN). Similar results were obtained with the balanced variation in abundance but not for the abundance gradient that was not significantly and negatively related to monthly water temperature (unless in NN where the relation is positive) but significantly related to disturbance.

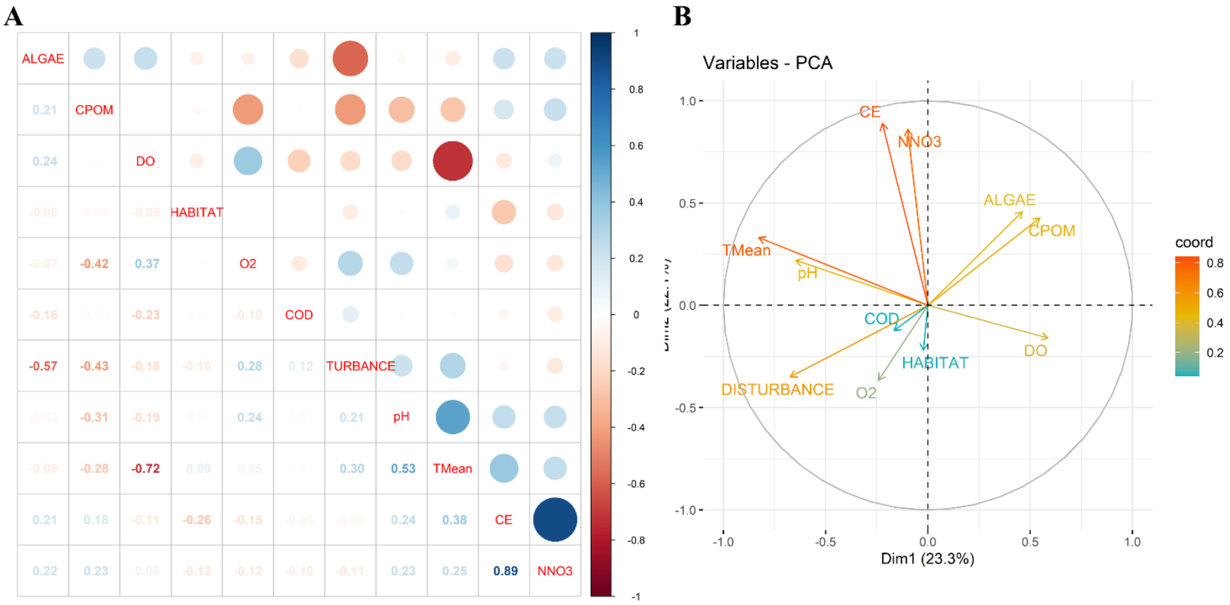

Figure 1SM. Pairwise Pearson correlation coefficient among pairs of environmental variables (A) and the scatter plot showing the first two PCA axes (B) showing the relationships among environmental variables.

Figure 2SM. Temporal pattern of environmental variables in each stream site (At NN site ALGAE reached 93.20 g/m^2 in November).

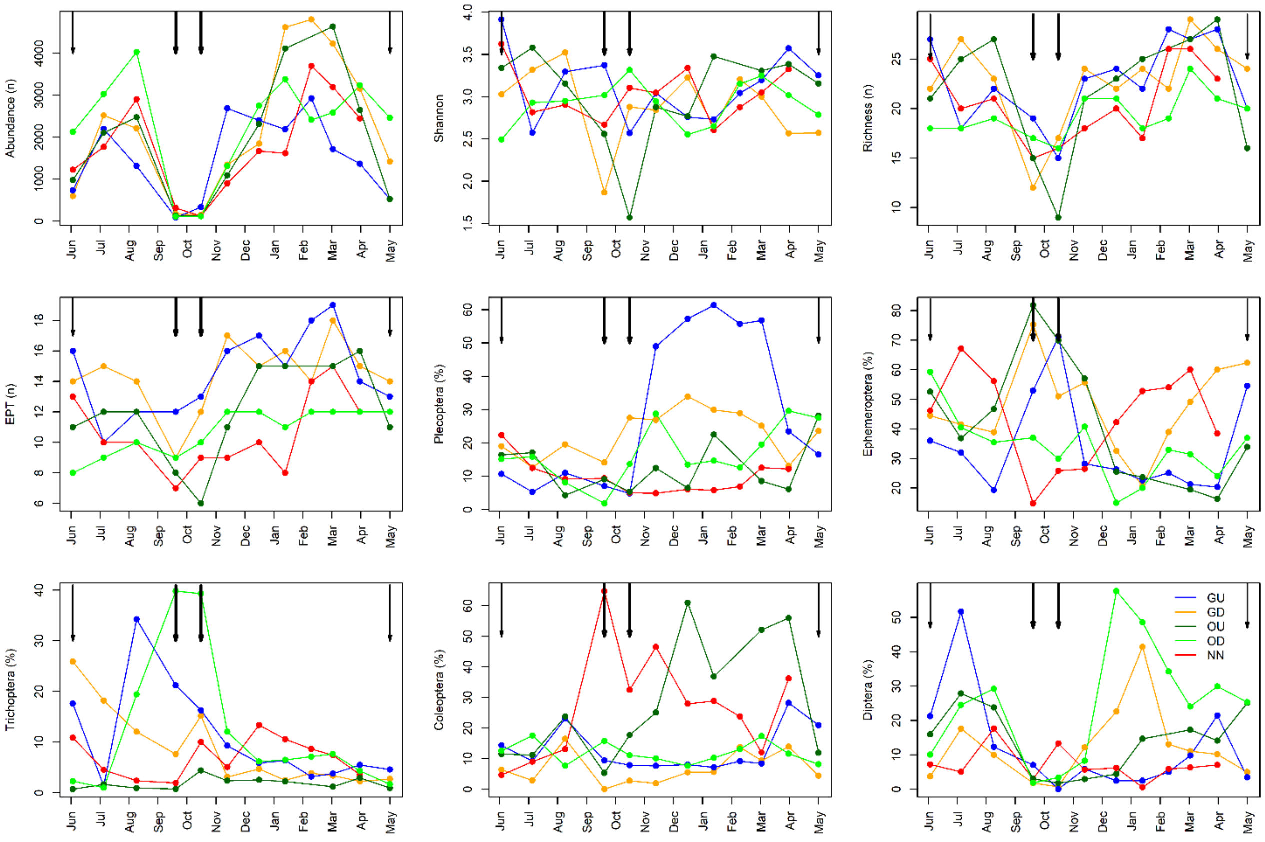

Figure 3SM. Temporal pattern of biodiversity indices in each stream site. Black arrows represent the sampling date following a flood (with the highest occurring in September and October).

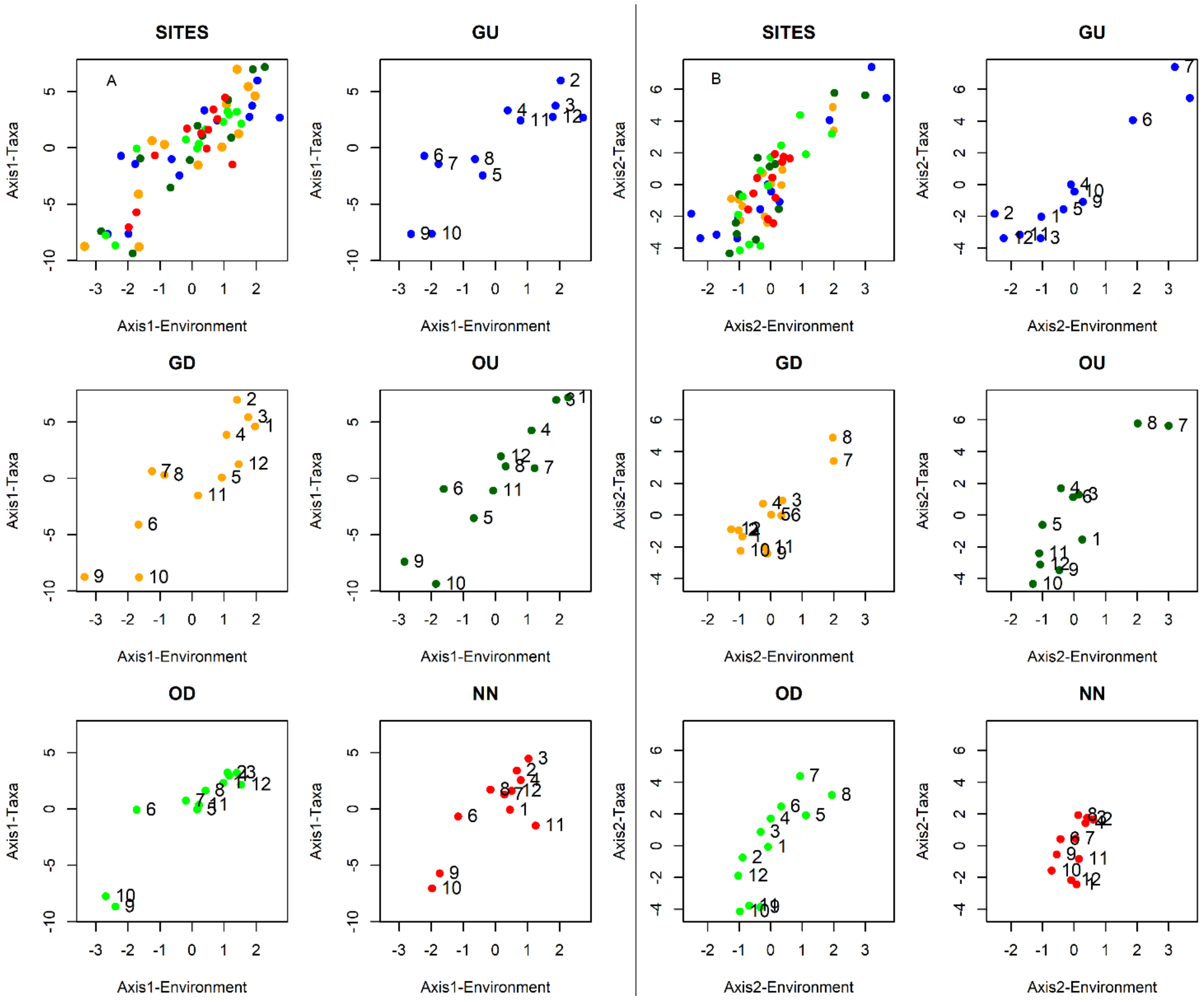

Figure 4SM. Correlation between Environment and taxa of the first (A) and the second (B) axes of the within-site Co-inertia analysis. Numbers refer to months.

CHAPTER 6

Evaluation of water temperature under changing climate and its effect on river habitat in a regulated Alpine catchment

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Abstract

Habitat quality of alpine rivers is largely affected by human activity. The exploitation of hydropower, combined with anthropogenic climate change, can alter mountain riverine ecosystems, leading to less suitable hydro-thermal regimes for the fish. Here, we present a new methodology to assess water temperature within a river featuring water exploitation for hydropower purposes, usable to assess the future potential deterioration of riverine habit suitability in response to (increasing) water temperature. We then propose an application focusing upon the case study of the Serio River, in Northern Italy, largely exploited by hydropower productions and highly populated by a very sensitive species, brown trout (*Salmo trutta*). The methodology proposed involves a set of tools, i.e. i) the hydrological model *Poli-Hydro*, to evaluate the natural hydrological regime, ii) a hydropower plants scheme to assess river water withdrawal, iii) fish density-environment curves to evaluate the hydraulic suitability in terms of trout potential density for adult, young, and fry as a function of hydraulic features, i.e. depth and velocity, and iv) a new, physically based model, *Poli-Wat.Temp*, to assess changes in river water temperature, and possible outbreaks of temperature dependant lethal conditions, such as proliferative kidney disease, and others. To provide an assessment of river suitability, possibly complementing (improving?) models based upon solely hydraulic indexes, we propose a new synthetic River Stress index, combining i) potential fish density as driven by hydraulic variables, and ii) thermal suitability. Given that utmost unsuitable conditions (thermally, and likely hydrologically) are expected under future climate conditions pending global warming, we then projected water temperature, and stream flows until the end of the century, in response to socio-economic scenarios of AR6 of the IPCC, to explore the potential for a future decrease of river quality. Water temperature would be largely susceptible to climate change with an increase up to +6.5 °C in the worst scenarios, while no clear trend is observed for fish density. Overall, potential density would decrease in winter for adults, and in summer for juveniles and fry in downstream sections. Therefore, by coupling hydraulic, and thermal suitability, one finds that i) Alpine rivers would likely face longer critical periods, with respect to those predicted based upon a solely hydraulic habitat-based assessment, and ii) continuous temperature increase as projected until the end of the century would result into worse conditions in summer months, seriously endangering fish guilds.

Keywords

Water temperature modelling; physical habitat modelling; river stress indicator; climate change

1. Introduction

Global warming effects upon water ecosystems have now been evident for years. The impact of climate change on freshwater availability was assessed both at the regional (Arnell, 1999; Lehner et al., 2006), and global scale (Döll et al., 2009; Sperna Weiland et al., 2012; Vörösmarty et al., 2000). Among others, several studies were carried out that highlighted significant warming in the European Alps, decreasing of snow and ice cover, and stream flows modification thereby (Bocchiola, 2014; Bocchiola & Diolaiuti, 2010; Fuso et al., 2021). Few studies focused on changes in water temperature, which is crucial for the distribution of biotic organisms in the rivers, featuring direct and indirect effects. Besides the direct influence upon dissolved oxygen (van Vliet et al., 2013; Webb et al., 2008), an increase in water temperature may provide the emergence of diseases, such as proliferative kidney disease PKD in freshwater fish (Carraro et al., 2017). PKD is a major threat to wild and farmed salmonid populations because of its lethal effect at high water temperatures. The disease was recognized as a frequent cause of the decline in fish populations over the last decades, even driving local extinctions of endemic and/or commercially important fish species (Borsuk et al., 2006).

When studying the thermal regime of rivers, attention was cast hitherto upon the link between water and air temperature. The latter can indeed be seen as a driver of the former because it affects heat flows to/from water (Edinger et al., 1968; Zhu et al., 2018). Thus, the projected air temperature increase under global warming will likely affect mountain stream temperatures, and living conditions of river species (Borgwardt et al., 2020; Isaak et al., 2010; Santiago et al., 2016). Stochastic models exist that link water and air temperature, and are easy to implement, thanks to the large diffusion of air temperature data (Caissie, 1998; Caissie et al., 2001). Further meteorological data are needed to apply more sophisticated deterministic models based on energy balance (Bustillo et al., 2013; Caissie et al., 2005). However, the latters are more appropriate to analyse anthropogenic activities directly impacting rivers, e.g., diversion channels, industrial flows, and presence of the reservoirs (Benyahya et al., 2007). Dams and minor barriers disrupt the hydrological and fluvial ecosystem connectivity, affecting the river environment, and thermal regime (Kędra & Wiejaczka, 2018). Particularly, diverted water is less susceptible to heating, given that often times diversion channels are buried in the ground. Then, the return of such colder water in the main river (typically at some length downstream, and at a lower altitude) would cause a sudden drop in water temperature. On the other hand, water flow left in the river has less thermal inertia due to decreased discharge, leading to higher temperatures in summer, and lower in winter (Meier et al., 2003). Thermal models depending upon air temperature only may not be always suitable, i.e. the effect of flow magnitude cannot be neglected (Toffolon & Piccolroaz, 2015), and more sophisticated heat exchange models are required, that make spatial dependence and effects of increasing flow downstream more explicit.

The EU Biodiversity strategy for 2030 (EC, 2020) states the need to re-establish freshwater ecosystems and the natural functions of rivers. In this context, the assessment of river habitat quality is a key factor (Canobbio et al., 2013; Lamouroux et al., 1998), and one expects that fish distribution/abundance will reflect riverine conditions on a larger spatial scale (Lamouroux & Cattanéo, 2006; VanCompernolle et al., 2019). Physical habitat models have been widely used to describe the connection between instream flow and habitat availability for different target species (Fornaroli et al., 2015). However, in addition to hydrological flows, water temperature is determinant for river species occurrence (Jonsson & Jonsson, 2009; Nukazawa et al., 2011). Thus, to simulate habitat suitability, it seems relevant to consider multiple habitat characteristics, and integrated frameworks that couple water temperature and hydraulic parameters may be considered (Morid et al., 2020).

The main goals of our study are 1) to propose a new physically based thermal model, called *Poli-Wat.Temp* to assess the water temperature of a river characterized by a complex geometry of withdrawal, and return to/from hydropower plants, and 2) to evaluate the combined effect of hydraulic, and thermal stress upon mountain river habitat, by elaborating a new index, which we call *River stress*.

We develop here the method and then we propose an application to a stretch of an Alpine river, the Serio catchment in northern Italy. We chose this catchment for two reasons, i.e. i) it nests several hydropower plants, displaying a complex geometry of diversion/return channels, affecting both hydrological and thermal regimes, and ii) it is populated by *Salmo trutta*, the presence of which is nowadays made possible by high dissolved oxygen and somewhat acceptable water temperature (Armour, 1994). The thermal model was calibrated using field data of air and water temperature, taken during surveys in several cross sections along the

Serio River. River discharge at several chosen locations along the stream was assessed using the semi-distributed, physically based hydrological model *Poli-Hydro* (Soncini et al., 2017) at the basin scale. For habitat quality assessment, we then used the so modelled discharges as an input to density-environmental functions for *Salmo trutta* at different stages (young, adult, and fries), calibrated recently for the Serio River (Fornaroli et al., 2016), to then evaluate the limiting effects of hydro-morphological variables, such as water depth, current velocity, substrate size, and composition, upon habitat conditions. We then propose a new index of river stress, by combining habitat suitability and water temperature, so obtaining a more credible habitat assessment under given climate conditions.

We projected water temperatures, and stream flows to the end of the XXI century, in response to climate change as projected under the socio-economic scenarios (SSP) of the most recent assessment report (AR6) of the Intergovernmental panel on climate change (IPCC), to highlight areas of increased stress, usable for future planning of adaptation strategies. The paper is organized as follows. The case study and available data are reported in section 2, where also the methods are discussed. The results of model calibration and subsequent application are discussed in Section 3. Discussion and conclusions are in sections 4, and 5, respectively.

2. Materials and Methods

2.1 Case study

Serio River is 124 km long, nested in Lombardy region (northern Italy), flowing in the provinces of Bergamo (BG) and Cremona (CR), to the outflow of the Adda River (Figure 1). It has a watershed of 1256 km^2, and the source is located at 2500 m asl nearby Torena mount, in the Orobic Prealps. Serio is a mountain river, with a mono-cursal bed, step-pools geometry, and coarse substrate. At ca. 600 m asl in Parre (BG), the river becomes more and more braiding, and gravel/sand bottomed. At ca. 100 m asl, it starts meandering with a very gentle slope, and fine substrate. Here we consider the river stretch upstream of Parre, as most relevant for water quality assessment, and as for the measurable presence of the target fish species.

The watershed is located within a temperate region, with a total precipitation of ca. 1300 mm per year, and mean temperature of +23.8 °C in July, and -1.5 °C in January. The river receives large precipitation in autumn and large snowmelt in spring. No ice melt contribution is present here, due to the absence of permanent glaciers in the area. The hydrological regime displays low discharges in January and February, mild flow in spring, and main floods in fall.

The Serio River is largely exploited for hydropower production. Seven run of river power plants are located along the river that we know of, in Valbondione to Parre stretch (Figure 1). The water collecting and returning points form 7 stretches, where the hydrological and thermal regime is altered with respect to natural conditions.

The considered reach is classified as a "high regard" area for fishing by the province of Bergamo (Gentili, 2009), where the most valued fish species is brown trout (*Salmo trutta*), protected from overfishing by a limitation in time and amount (Lombardy Region, 2003). Changes in precipitation and temperature may negatively affect the hydrological regime of the area (Armour, 1994; Groppelli, Confortola, et al., 2011; Viganò et al., 2015), leading to critical hydro-thermal conditions for the fish. It is therefore essential to study the impact of such present and potential future changes on river quality, to plan adaptation strategies for the safeguarding of the species and their ecosystem.

Here, we assessed the effect of climate change on river habitat within 8 stations of the upper Serio (Figure 1), where hydro-morphological and topographic surveys, together with electro-fishing samplings were carried out, as described e.g. in Viganò et al., (2015).

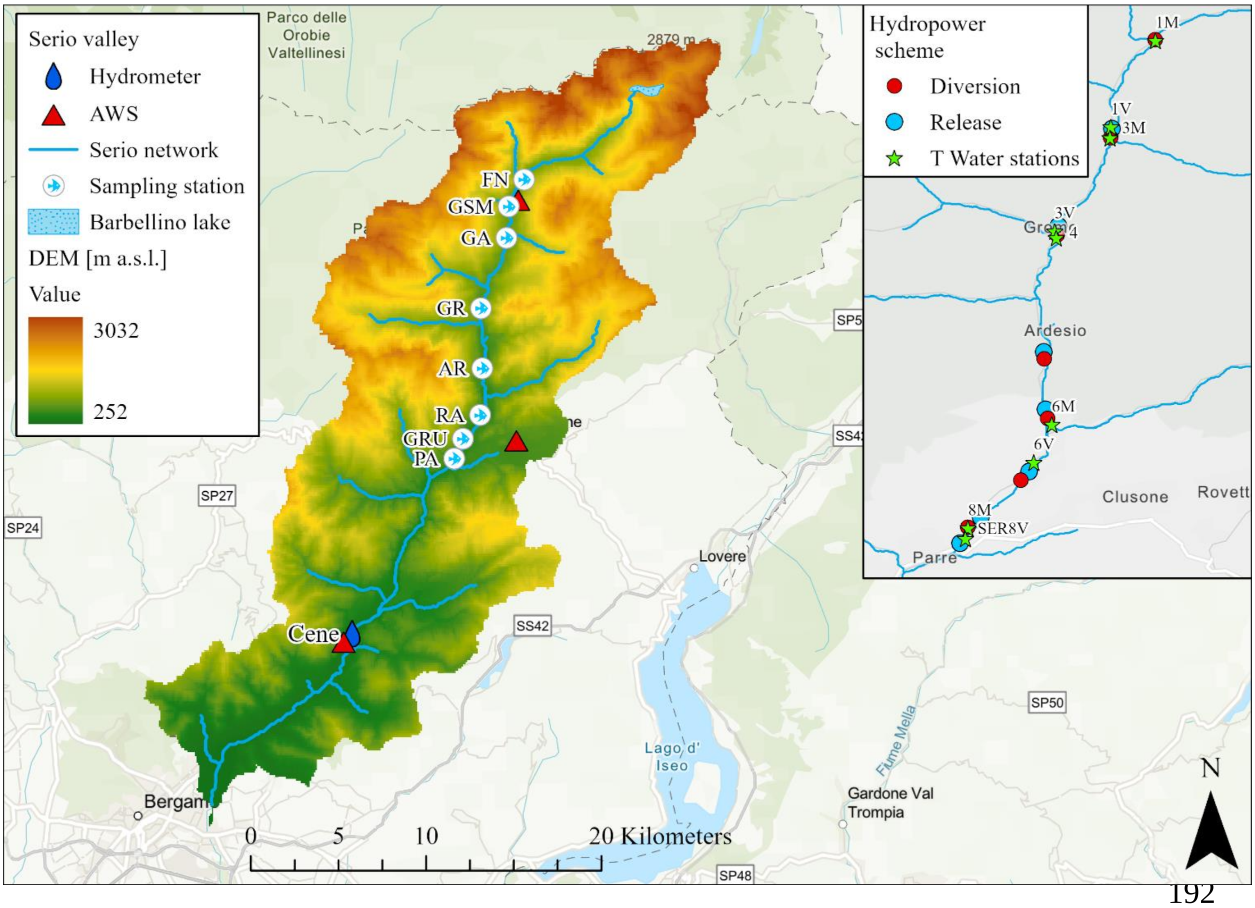


Figure 1. Catchment area of Serio River. We report the position of automatic weather stations (AWSs), hydrometric stations, sampling stations for fish habitat assessment, and water temperature sampling stations, as well as a scheme of the hydropower diversion-restitution system. Geographic Reference System WGS 84.

2.2 Data available

Daily series of precipitation and air temperature from 3 automatic weather stations (AWS) of ARPA Lombardy Authority were used here as inputs to the hydrological model Poli-Hydro (e.g. 9). The model was implemented with a spatial resolution of 100x100 m^2, for a 10-year control run period (CR), 2012-2021. Other inputs were the GIS map, i.e. digital elevation model (DEM) of the catchment (Earth data Available online: https://earthdata.nasa.gov/), and the land use maps from CORINE land cover (CLC 2018 — Copernicus Land Monitoring Service Available online: https://land.copernicus.eu/pan-european/corine-land-cover/clc2018). Daily discharges at Ponte Cene hydro station during the CR period were used for model calibration under natural regime conditions, while data of Minimum Instream Flow (MIF) and maximum operable discharge (Q_{HY}) for each hydropower station were used to switch from natural, to regulated hydrological regime (Table 1).

To setup the thermal model, water temperature data were gathered within the sites reported in Figure 1 (see Table 2), for three years (June 2018-October 2021), using iButton devices (range -5 to +26 °C, resolution: ±0.0625 °C, measurement interval 10 min). Water temperature data were downloaded, and a linear interpolation between consecutive measurements was performed to obtain a continuous trend of water temperature (one value per minute), and eventually daily mean, maximum and minimum temperature. Finally, density-environmental relationships for Salmo trutta at different stages (fry, juvenile, adult) as derived after sampling in eight stations along the river (Fornaroli et al., 2016) were used for river habitat assessment (Table 1).

Table 1. Fish sampling stations with acronym and location. For each station are reported the values of Minimum Instream Flow (MIF) and maximum operable discharge (Q_{HY}) of hydropower plant affecting the station.

Station	ID	Longitude	Latitude	Altitude m a.s.l.	MIF [m^3s^{-1}]	Q_{HY} [m^3s^{-1}]
Fiumenero	FN	9.96°	46.02°	788	0.4	4.5
Gromo San Marino	GSM	9.95°	46.01°	750	0.4	4.5
Gandellino	GA	9.94°	45.99°	687	0.6	4.5
Gromo	GR	9.93°	45.95°	604	0.9	9.7
Ardesio	AR	9.93°	45.92°	542	1	8
Rasini	RA	9.92°	45.90°	537	1.1	12
Grumella	GRU	9.91°	45.89°	495	1.3	11
Parre	PA	9.90°	45.88°	487	1.5	10.3

Table 2. Water temperature stations (from upstream to downstream). Coordinates in WGS84.

ID	Longitude	Latitude	Altitude m a.s.l.
1M	9.959°	46.021°	789
1V	9946°	45.996°	691
3M	9.946°	45.993°	692
3V	9.930°	45.966°	635
4	9.930°	45.964°	626
6M	9.929°	45.910°	516
6V	9.924°	45.899°	503
8M	9.905°	45.880°	491
8V	9.904°	45.877°	486

2.3 River suitability assessment

To assess the river suitability of Serio River several methods/models were applied here in cascade. For clarity, we report in Figure 2 a flowchart displaying the data and methods adopted here.

Using precipitation and air temperature data (P, T), and watershed GIS maps we setup the hydrological model *Poli-Hydro*, to derive daily discharges Q. We used then the modelled discharges as input to a habitat suitability model that defines fish potential density, used to evaluate habitat suitability in the sample locations. With the thermal model, based upon known the geometry of the hydropower system, and of the return (tail-race) system, we then used T, and the modelled discharge Q, to assess pointwise daily water temperature T_w. Then, we defined habitat suitability classes and water temperature thresholds for PKD. Next, we provided an indicator of the stress of the river *RS*, by matching hydraulic habitat suitability, with suitability based on water temperature, which we call *TS*. For future projections, we downscaled values from GCM scenarios to get future precipitation, and temperature, P_{fut} and T_{fut}. These were fed to *Poli-Hydro* to assess future discharges Q_{fut}. Still using the thermal model, we then exploited T_{fut}, Q_{fut}, to evaluate future scenarios of water temperature $T_{w,fut}$, and suitability thereby. Here, we assumed for simplicity that the present hydropower scheme would remain unchanged in the future. Finally, with the same approach above, we provided projections of the future river stress RS_{fut}.

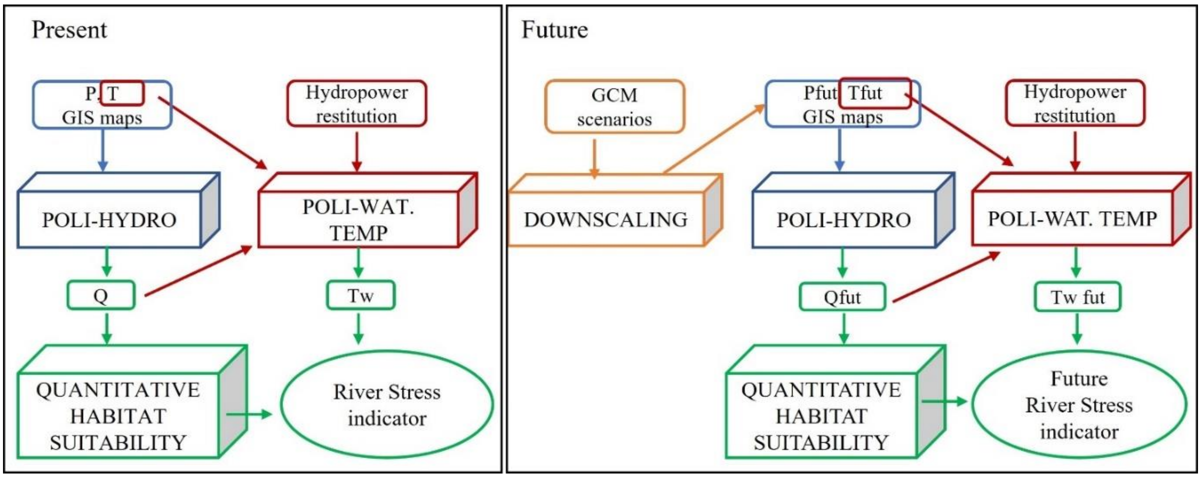


Figure 2. Flowchart of the methodology adopted for present and future river stress assessment.

2.4 Hydrological modelling

The *Poli-Hydro* hydrological model was already used, validated, and described in several studies hitherto (Soncini et al., 2017), where the reader is referred thereby for a detailed description. *Poli-Hydro* computes daily soil water balance for each cell within the catchment area (here defined with ARC-GIS software). The control variable is soil water content, inputs are given by liquid precipitation, air temperature, and snow/ice melt, and outputs are water fluxes in the river. Snow accumulation on the ground, in the form of Snow Water Equivalent (SWE) is assessed from precipitation, i.e. snowfall when temperature in one cell is below 0 °C. SWE melt is then evaluated with a mixed degree day formula (e.g. Pellicciotti et al., 2005). Temperature is distributed spatially using monthly vertical gradients as from observations. By doing so, the model can reconstruct for each cell rainfall, snow pack on the ground, snow/ice melt (however as reported, no ice surface is present in the catchment here), surface and subsurface flows. The latter are then routed (using a IUH function, i.e. Nash model) to the final outlet of each sub-basin, to obtain daily stream flow hydrographs. The model was calibrated here for natural discharge estimation, and then validated using goodness of fit statistics, i.e. *Bias*, and monthly *NSE* (Nash-Sutcliffe Efficiency) calculated against the observed discharges at Ponte Cene hydrometer, relatively undisturbed by flow regulation, and simulated discharges. To include water withdrawal from hydropower stations, for each location, we assumed that 90% of the discharge above minimum instream flow (i.e. ecological flow) MIF is diverted, until maximum operable flow (Equation 1).

$$\begin{aligned} Q &= Q_{nat} && if\ Q_{nat} < Q_{MIF} \\ Q &= (Q_{nat} - Q_{MIF}) \cdot 10\% + Q_{MIF} && if\ Q_{MIF} < Q_{nat} < Q_{HY} \\ Q &= Q_{nat} - Q_{HY} && if\ Q_{nat} > Q_{HY} \end{aligned} \tag{1}$$

Here Q is actual river discharge to be assessed, and Q_{nat} is natural discharge as evaluated by *Poli-Hydro*. Q_{MIF} is Minimum Instream Flow value, specific for each power plant, and Q_{HY} is maximum discharge conveyed to the power plants. As per regulation of Lombardy region, Q_{MIF} is provided for every plant (Table 1), and we used the proposed values accordingly, in the assumption that hydropower managers properly release Q_{MIF} downstream of intakes.

2.5 Hydraulic habitat assessment

To assess hydraulic based suitability, we used a habitat suitability model that defines potential density based upon a limiting factor approach, as recently proposed by (Fornaroli et al., 2016). These functions use water velocity/depth, substrate characteristics, availability of refuges, and mesohabitat type. The latter is divided in four categories, namely i) Shallow pool, ii) Deep pool, iii) Riffle, iv) Run, as retrieved within the 8 sampling sites (Figure 1, Table 1). Using the functions as developed in our study area (Fornaroli et al., 2016) we assessed the potential density (PD) (ind/m^2) with respect to discharge for the young and adult trout, and for fries, obtaining a potential number of individuals per square meters in each site, for each discharge level. So, we calculated *PD* for the CR period in each sampling site, and for each life stage of *Salmo trutta*. We then defined two classes of quality, i.e. poor and good, corresponding to the intervals for PD 40-60%, 60-100%, of the maximum value of daily potential density $PD_{max,}$ respectively. We chose 40% as a lower bound, because it was the lowest value resulting from our simulations. Thus, we added up the total number of days in each class, for the 4 seasons (winter, spring, summer, and fall) and we averaged over three different decades, i.e. CR (2012-2021) as a reference in the present conditions, a period one P1, half century (2046-2055), and a period two P2, end of century (2091-2100), to evaluate future river suitability.

2.6 Water temperature modelling

Here we developed a model for water temperature assessment, which we called *Poli-Wat.Temp*. This is a coupled model, interacting with *Poli-Hydro*, to take as an input estimated stream flows, and air temperature data. The *Poli-Wat.Temp* model uses a one-dimensional energy balance equation, suitable for shallow rivers where the vertical gradient of temperature can be neglected (Caissie et al., 2005), as follows:

$$\frac{\partial T_w}{\partial t} + v \cdot \frac{\partial T_w}{\partial x} - \frac{1}{A} \cdot \frac{\partial}{\partial x}\left(A \cdot D_L \cdot \frac{\partial T_w}{\partial x}\right) = \frac{B}{\theta \rho A} \cdot H_{tot} \tag{2}$$

Therein, T_w is the water temperature, v is the mean water velocity, x is the distance along the river axis, A is the cross section area, B is the river width, D_L is a dispersion coefficient in the flow direction, θ is the specific heat of water, ρ is the water density, H_{tot} is the total heat flux from the external environment to the river, including solar radiation, air temperature, evaporative heat fluxes, and net long-wave radiation. Here, we considered air temperature, and incident solar radiation as external sources of heat, that we modelled as linear functions of the air-water temperature gradient, and of the incident, clear sky solar radiation, respectively

$$H_{tot} = \alpha \cdot (T_{air} - T_w) + \beta \cdot Rad \tag{3}$$

The dispersion term in Eq. 2 $\partial(A \cdot D_L \cdot \partial T_w/\partial x)/\partial x$ may be generally neglected in alpine rivers, characterized by medium/high flow velocity, so that heat transfer along the x axis basically occurs by advection (Deas & Lowney, 2000) $v \cdot \partial T_w/\partial T_w$.

We solved Eq. 2 recursively, to evaluate heat fluxes from an upstream station to a downstream one, with temperature T_{w1}, and T_{w2} respectively, using a finite differences scheme, where ∂x was approximated with the distance L between the considered stations, and ∂t is 1 day.

Using a first-order upwind scheme, and approximating river channel shape with a rectangular one, roughly valid for naturally shaped rivers, such as Serio River here in several traits, we moved from Equation 2 to Equation 4, and then isolated $T_{w2,i2}$ to explicitly assess downstream temperature at day 2 (Eq. 5).

$$(T_{w1,i2} - T_{w1,i1})/\Delta t + v/L \cdot (T_{w2,i2} - T_{w1,i2}) = \frac{1}{\theta\rho h} \cdot \left(\alpha \cdot \left(T_{air} - T_{w1,i2}\right) + \beta \cdot Rad_{i2}\right) \tag{4}$$

$$T_{w2,i2} = T_{w1,i2} + \frac{L}{v\Delta t\theta\rho h}\left(\alpha \cdot \left(T_{air} - T_{w1,i2}\right) + \beta \cdot Rad_{i2}\right) - \frac{L}{v\Delta t}(T_{w1,i2} - T_{w1,i1}) \tag{5}$$

Therein $i1, i2$ indicate days 1 and 2, and h is the water depth. The water depth and the velocity v could be evaluated as (power) functions of discharge. In this space dependant formulation, one needs to fix an upstream initial condition for temperature. Therefore, we set the initial condition of the temperature at the largest lake upstream, i.e. Barbellino lake, where temperature changes are more gradual and season dependent. The Barbellino reservoir is an artificial lake located at 1870 m a.s.l., 9.3 km upstream of the first thermal station, where the outflow is regulated by a hydropower dam, 69 m tall. Serio River starts at the toe of the Serio waterfall (with a 315 m jump, the tallest waterfall in Italy) watered with the reservoir output. Generally, due to thermocline water temperature at a depth of 20+ m can be taken as constant, at +4 °C (Dodds & Whiles, 2017). However, withdrawal from the bottom outlet has a mixing effect that has been shown to impact *hypolimnion* (lake bottom) temperature (Nürnberg, 2007; Saber et al., 2020). Therefore, here we modelled Barbellino hypolimnion temperature using a sinusoidal function, well representing lake bottom temperature in other regulated lakes (48). Therein, the minimum water temperature can be fixed at +4 °C, and phase, amplitude, and mean values are related to seasonal air temperature as:

$$T_{wBar} = \gamma\bar{T}_y + \omega\left(\bar{T}_{sum} - \bar{T}_y\right) \cdot \sin\left(2\pi\frac{day - lag}{365} - \pi\right) \tag{6}$$

Therein, $\bar{T}_y$ and $\bar{T}_{sum}$ are annual, and July mean temperatures estimated at Barbellino lake, which we linked to average, and summer variation of water temperature, respectively. Also,

γ, ω, lag are calibration parameters. For model tuning, we used data of water temperature at the station of Fiumenero.

As mentioned above, along the river stem several hydropower plants divert water, modifying stream flows, and temperature thereby. To account for this, the thermal balance as from Eq. 5 was further modified to consider stream flow changes between different sections, due to i) hydrological flow increase (contributing catchment), ii) water diversion for hydropower, and iii) water return from hydropower (tail race channels). The water used for hydropower in Serio River is often collected in channels buried in the ground, i.e. largely insulated from the atmosphere, and restitution at lower altitudes occurs quite rapidly with respect to stream flow dynamics (i.e. with a shorter delay than the time required for the river flow to reach the same altitude). Accordingly, we made the hypothesis that diverted/returned water keeps the same temperature, i.e. the water temperature at the restitution point is the same as the (stream) temperature at the point of withdrawal. One can thereby assess water temperature downstream of a flow returning point (i.e. downstream of a tail race channel) as the weighted average of the upstream (in river) temperature, and the tail race temperature as

$$T_{w3} = \frac{T_{w1} \cdot Q_1 + T_{w2} \cdot Q_2}{Q_1 + Q_2} \tag{7}$$

Here, T_{w3} is the water temperature downstream the tail race, T_{w1}, T_{w2} are the temperatures of instream and diverted water, and Q_1, Q_2 are the discharge values thereby.

2.7 Critical temperature for thermal suitability

In this case of study, where *Salmo trutta* is abundant, and oxygen rate during our ten-year campaign was always found at saturation level due to the high water turbulence of many riffles/rapids, we chose as a target disease PKD, being particularly temperature dependant (Waldner et al., 2020), and a main threat for Alpine trouts (e.g. Wahli et al., 2007). To define the critical thresholds of water temperature for PKD we relied upon the most recent literature (Borgwardt et al., 2020; Carraro et al., 2017; Santiago et al., 2016), and we decided to use the criteria as set out by Borgwardt et al., (2020), considering water temperature T_w, and a corresponding consecutive duration d_{Tw}.

When the daily mean temperature is above $T_w \geq +15$ °C, a situation of i) *possible outbreak* of PKD occurs if the exceedance lasts for $d_{Tw} \geq 14$ consecutive days (Eq. 8), and a situation of ii) *low mortality* occurs when $d_{Tw} \geq 29$ consecutive days (Eq. 9). The most worrisome condition, i.e. iii) *high mortality*, takes place when the daily mean temperature exceeds $T_w \geq +18$ °C and $d_{Tw} \geq 26$ consecutive days (Eq. 10).

$$Possible\ outbreak\colon\ \ T_w\ \geq\ +15\ °\mathrm{C}\ \cap\ d_{Tw} \geq 14 \tag{8}$$

$$Low\ mortality\colon\ \ T_w\ \geq\ +15\ °\mathrm{C}\ \cap\ d_{Tw} \geq 29 \tag{9}$$

$$High\ mortality\colon\ \ T_w\ \geq\ +18\ °\mathrm{C}\ \cap\ d_{Tw} \geq 29 \tag{10}$$

2.8 River stress indicator

To provide a more comprehensive habitat assessment under present, and future climate, we constrained habitat suitability upon water temperature, by calculating a River Stress indicator RS, representing the number of days per year when the river is in stress conditions. RS is defined as the union of i) days of poorest river quality, e.g. number of days when PD is 40-60% of PD_{max}, and days when ii) water temperature is above the lowest threshold for PKD occurrence, e.g. possible outbreak, ideally more responsive to climate change.

$$RS = 0.4\,PD_{max} \leq PD\ \leq 0.6\,PD_{max}\ \ \cup\ \ (T_w\ \geq\ +15\ °\mathrm{C}\ \cap\ d_{Tw} \geq 14) \tag{11}$$

We calculated the total number of days when the river would be in poor quality conditions at each sampling site, for the 4 seasons, and we averaged this number on the three reference decades, CR (2012-2021), P1(2046-2055), and P2 (2091-2100).

2.9 Hydrological projections

To evaluate future air temperature to constrain hydrological scenarios we performed a downscaling of the outputs from six Global Circulation Models (GCMs), from the last Assessment Report 6 (AR6) of the IPCC, namely European EC-Earth3.0 (EC-Earth, 2019), CESM2 (Danabasoglu et al., 2020), ECHAM6.3 (Mauritsen et al., 2019), HADGEM3 (Ridley et al., 2018), MIRCOC6 (Kataoka et al., 2020), and CMCC-CM2 (Cherchi et al., 2019). For each model, we considered the 4 shared socio-economic pathways (SSPs) that are being used as part of the experiment Coupled Model Intercomparison Project Phase 6, CMIP 6, of the AR6 (O'Neill et al., 2016). SSP 1 and SSP 5 project a positive development of society, but while the latter would be at the expense of an economy based on fossil fuel, the former foresees a sustainable economy. The SSP 2 scenario follows the historical trend, while the SSP 3 and SSP 4 foresee a negative development of the social dynamics worldwide. Four

SSPs scenarios were used in this study, based on the Representative Concentration Pathways of the AR5, i.e., RCP 2.6, 4.5, and 8.5 scenarios, namely SSP 126, 245, 585, and an intermediate SSP370 scenario. Precipitation was spatially downscaled (i.e. from GCM cell to rain gauges), with a stochastic space random cascade model (Groppelli, Soncini, et al., 2011), while for temperature we used a correction with a mean monthly ΔT approach (Groppelli, Bocchiola, et al., 2011).

3. Results

3.1 Hydrological modelling and flow projections

Poli-Hydro model was calibrated to fix the necessary parameters of soil permeability, and snow melting for a calibration period 2015-2018, by matching *Q* values as measured at the Ponte Cene hydrometer (Figure 3). The bias between observed and modelled monthly stream flows was $Bias_{\%} = -7\%$, and NSE = 0.71. Similar statistics values were obtained for the validation period, 2019-2020 ($Bias_{\%} = -6\%$, NSE = 0.73). A table with the calibration parameter of *Poli-Hydro* model is given in the supplementary material.

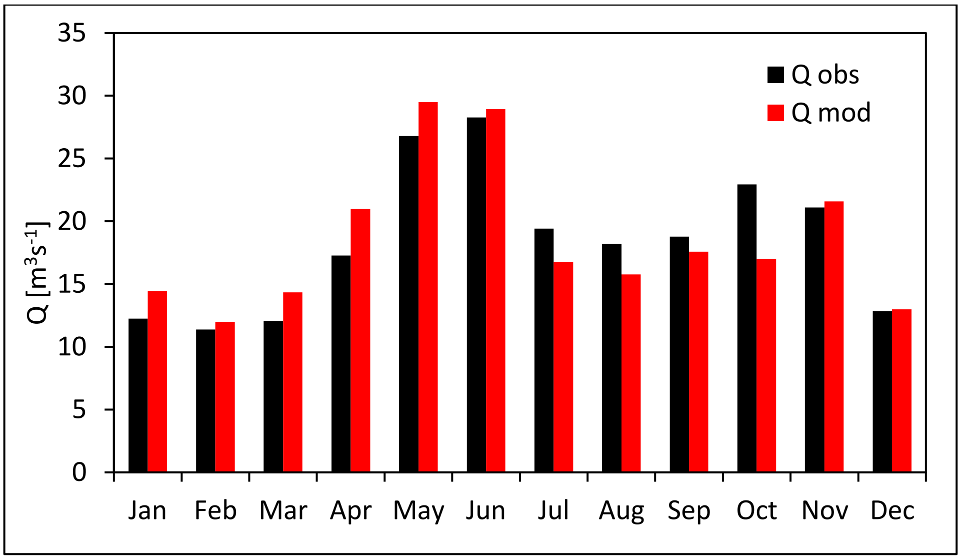


Figure 3. Mean monthly flows at Cene Ponte obs/mod during the period 2015-2018.

After model calibration, we used *Poli-Hydro* to assess projected flow discharges. We report in Figure 4 the projected mean monthly flow for each SSP, averaged over the 6 GCMs, at mid-century P1, and end of century P2, and comparison with discharges in CR period (2012-2021). The increase of liquid precipitation at the expense of solid precipitation in winter months would lead to an increase of stream flows therein. The decrease of discharge between

May and October would be due to decrease of precipitation and to a lack of snowmelt and increase of evapotranspiration. Overall, the average annual discharge (E[Q_y]) of 21.26 m^3s^{-1} in the CR period, would decrease in the future to E[Q_y] = 19.19 m^3s^{-1}, and E[Q_y] = 17.83 m^3s^{-1} for SSP 585 at P1, and P2, respectively.

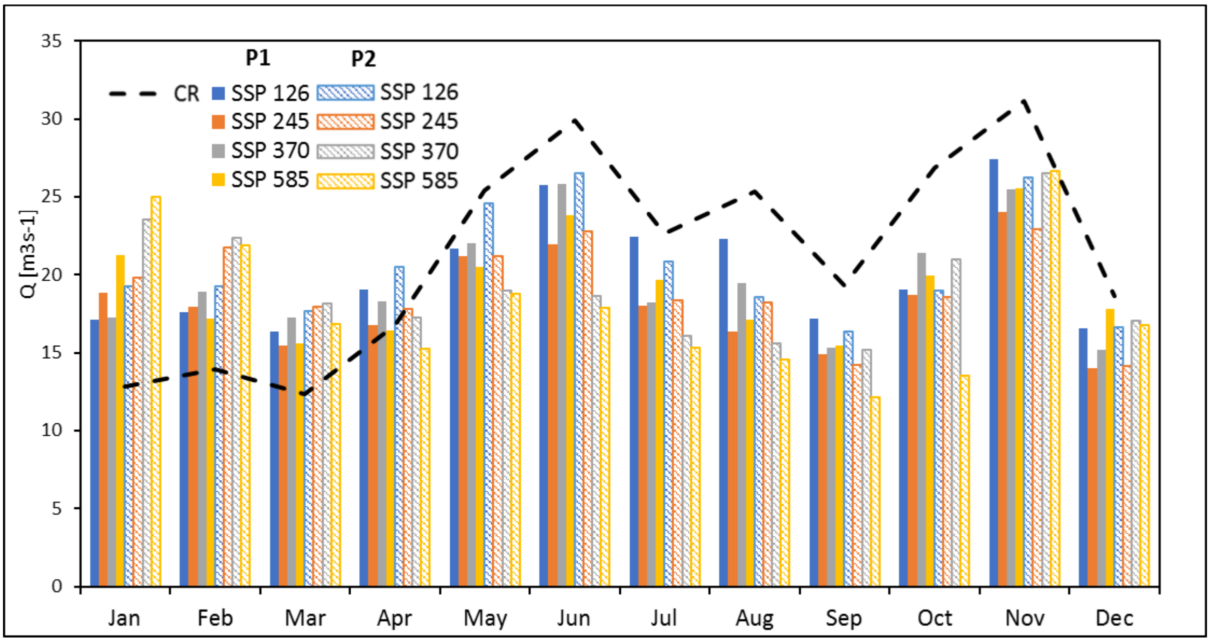


Figure 4. Projected mean monthly flows at Cene Ponte for each SSP at mid-century P1 (solid colour) and end-century P2 (striped colour). The black line represents the mean monthly discharge in the CR period.

3.2 Thermal modelling

Poli-Wat.Temp model calibration, namely for parameters α and β, was carried out by minimizing *Bias*$_{\%}$ and Random Mean Square Error, *RMSE***.** For calibration, starting from the measured water temperature at Fiumenero (1M), we applied the thermal model downstream, and then we corrected the parameters in order to fit the modelled water temperature to observed data in Parre (8V).

Then, we calibrated the parameters $\gamma, \omega, Lag,$ of Barbellino temperature model by applying *Poli-Wat.Temp* from Barbellino to the first station where we had measured data, i.e. Fiumenero. Here, we minimized *bias* and *RMSE* of the modelled temperature against the measured data at Fiumenero station (Figure 5). The calibration parameters for the *Poli-Wat.Temp* for Barbellino temperature are shown in the supplementary material (Table 5, Table 6).

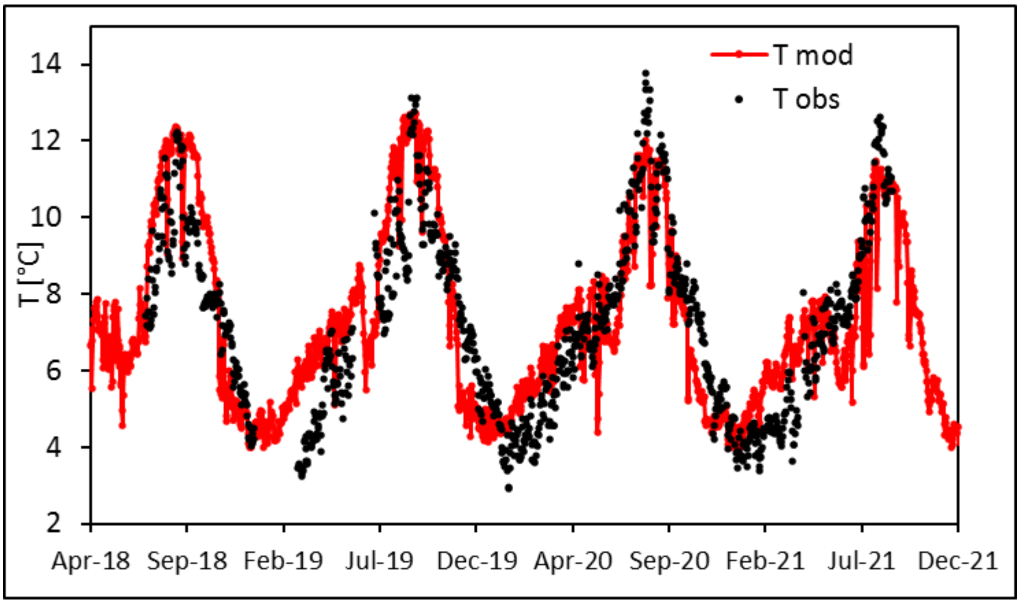


Figure 5. Time serie of estimated water temperature at Fiumenero station (red) vs observed ones (black).

Finally, we applied the thermal model from Barbellino to Parre, and we performed model validation, by matching for each station the computed values of water temperature with the measured ones and evaluating *bias* and *RMSE* thereby (Table 3).

Table 3. Values of bias and standard deviation [°C] of measured vs. modelled temperature at each station of Serio River.

Station	Bias	Std
1M	-0.31	2.06
1V	0.89	2.32
3V	0.07	1.44
3V	0.70	1.74
4	0.33	1.18
6M	-0.15	1.49
6V	-0.06	2.11
8M	-0.16	1.60
8V	-0.12	1.39

3.3 Thermal suitability

In Figure 6 we report the mean monthly temperature as simulated for the 8 river stations during the CR period (2012-2021) for the most critical month, i.e. August, when temperatures are the highest (and the flow the lowest). Although the average temperature is below the critical one for PKD, also in the most downstream stretch, sporadic exceeding of the threshold is found for the 3 most downstream stations, where PKD may burst, possibly with low impact.

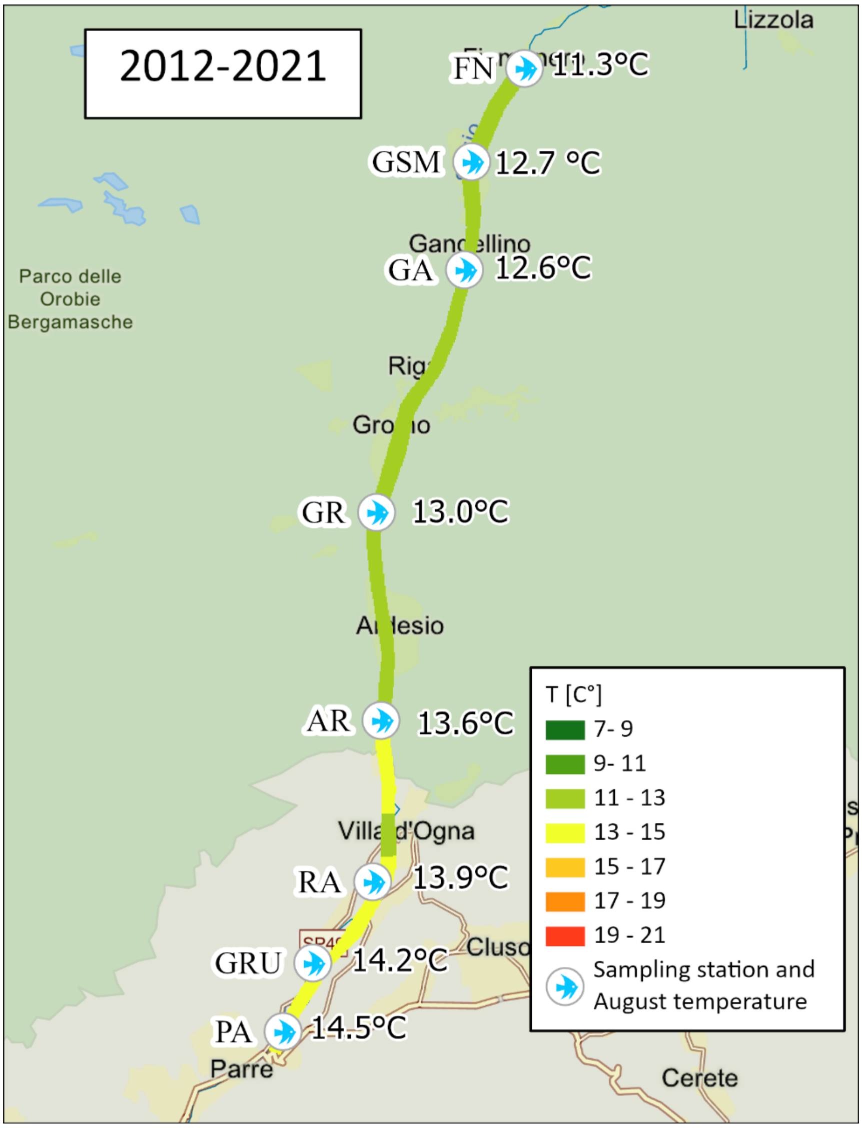
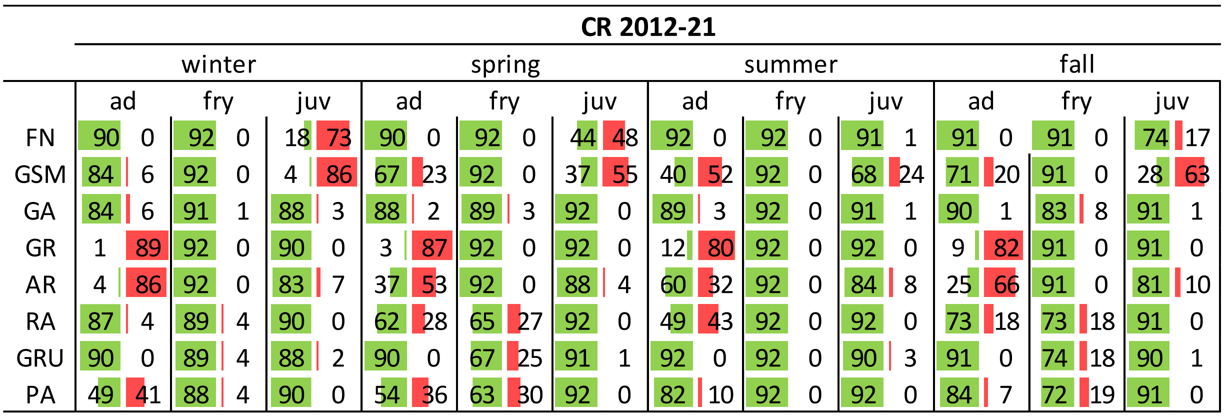


Figure 6. Average water temperature during the CR period (2012-2021) for the whole stretch (colour scale) and the sampling stations (text).

3.4 Habitat suitability

With *Poli-Hydro* model we simulated daily discharges within the 8 sampling locations, and we evaluated the corresponding PD in each station. In Figure 7 we reported the number of days per year, averaged along CR period, when trout PD falls in each of the two classes that we defined, i.e. good or poor, based upon the maximum value of daily potential density PD_{max}. We can see that PD is characterized by higher variability between the upstream and downstream sections, mainly for adults and juvenile, than for fry. But for adults, differently from fry and juvenile, most of the downstream sections show seemingly little suitable habitat conditions, in almost all seasons. Contrarily, for young trout, one finds low habitat suitability only in the two upstream sections, while overall quite acceptable flow conditions are found. This is true also for fry, except in downstream sections where the habitat is sometimes less suitable.



	CR 2012-21																							
	winter						spring						summer						fall					
	ad		fry		juv		ad		fry		juv		ad		fry		juv		ad		fry		juv	
FN	90	0	92	0	18	73	90	0	92	0	44	48	92	0	92	0	91	1	91	0	91	0	74	17
GSM	84	6	92	0	4	86	67	23	92	0	37	55	40	52	92	0	68	24	71	20	91	0	28	63
GA	84	6	91	1	88	3	88	2	89	3	92	0	89	3	92	0	91	1	90	1	83	8	91	1
GR	1	89	92	0	90	0	3	87	92	0	92	0	12	80	92	0	92	0	9	82	91	0	91	0
AR	4	86	92	0	83	7	37	53	92	0	88	4	60	32	92	0	84	8	25	66	91	0	81	10
RA	87	4	89	4	90	0	62	28	65	27	92	0	49	43	92	0	92	0	73	18	73	18	91	0
GRU	90	0	89	4	88	2	90	0	67	25	91	1	92	0	92	0	90	3	91	0	74	18	90	1
PA	49	41	88	4	90	0	54	36	63	30	92	0	82	10	92	0	92	0	84	7	72	19	91	0

Figure 7. The total number of days per year when trout density in each sample station falls within each class, i.e. good (green bar), and poor (red bar), for each season, averaged along the CR period, for each life stage of the trout. Bar width visually indicates the length of the period (over the length of the season, ca. 90 days).

3.5 River stress

We reported in Figure 8 the river stress indicator, for each sampling site, and trout life stage averaged over the CR. Since temperature is nearly always below the PKD critical threshold, the stress conditions for the river are mainly due to poor habitat suitability. One can see the (negative) contribution of temperature to RS only in downstream sections and in summer months, where sporadic exceedance of the thermal threshold is found.

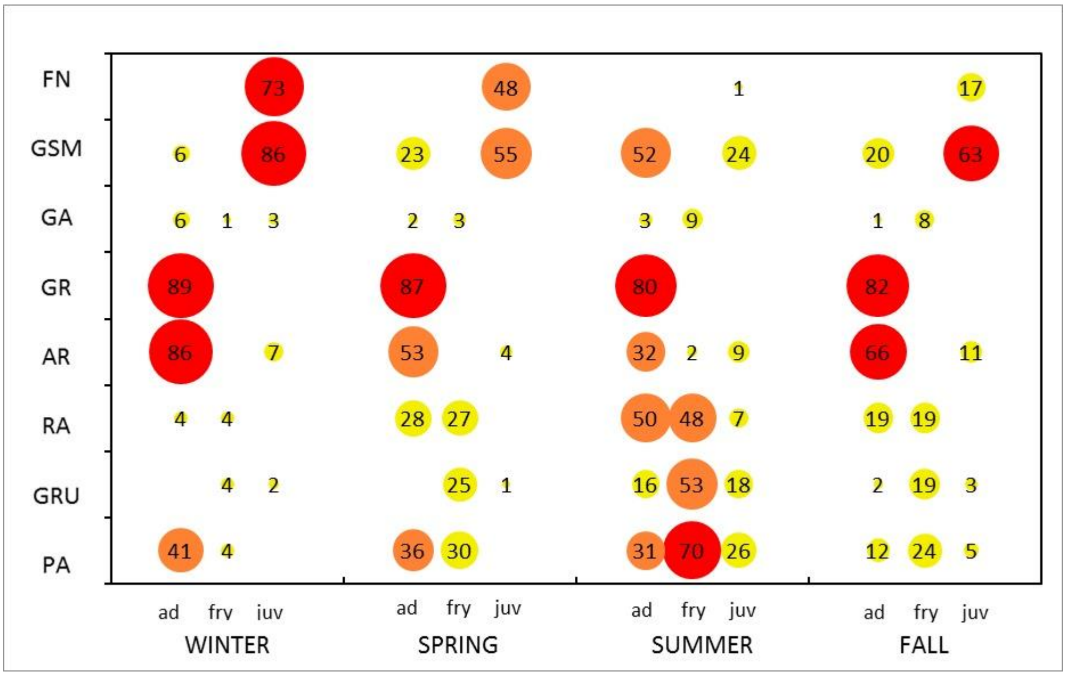


Figure 8. River Stress index, expressed as the number of days per year, for each season, averaged along the CR period, for each life stage of the trout, at each sampling point. Days 0-30 (yellow), days 30-60 (orange), and days 60-90 (red).

3.6 Future thermal suitability

The modelled water temperature in future scenarios is reported for the whole stretch in Figure 9 using average values of the 6 GCM models only for SSP126, and SSP585, as respectively the more optimistic, and pessimistic ones, in P1 and P2. One finds that in the worst-case scenario, the model estimated an increase up to +6.5 °C during August, which is again the most critical month, with likely severe consequences on trout health. Indeed, as the water temperature would increase, PKD outburst would become more and more frequent, and more severe. In Figure 10 we report the average number of days per year when the temperature would be above PKD threshold during CR, under all future scenarios. All scenarios exhibit possible outbreaks. However, while for mid-century P1 spreading of PKD would be limited to most downstream sections, during P2, under the worst scenarios PKD threshold would be exceeded for most of the summer, possibly leading to high mortality in downstream sections, and low mortality elsewhere in the reach.

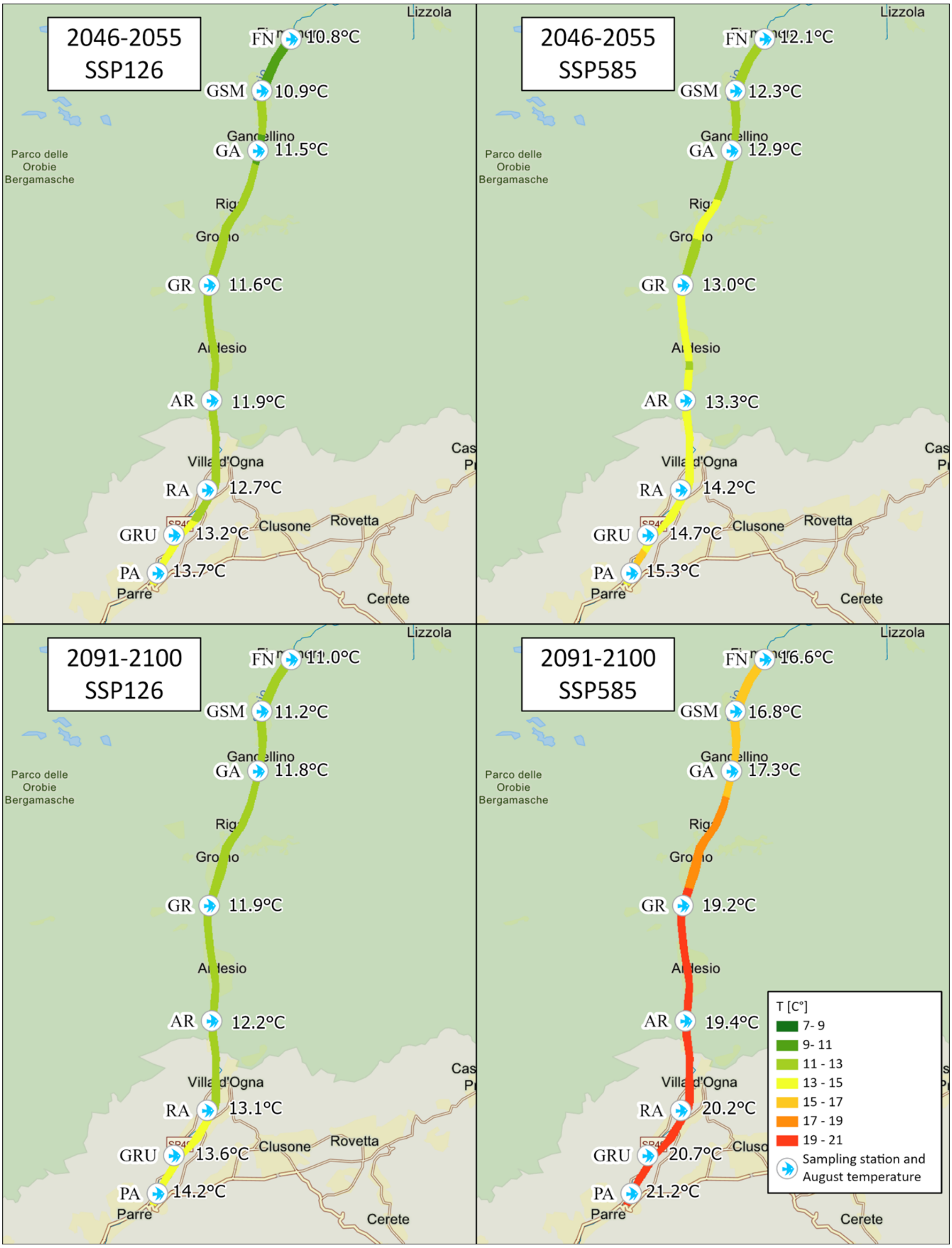
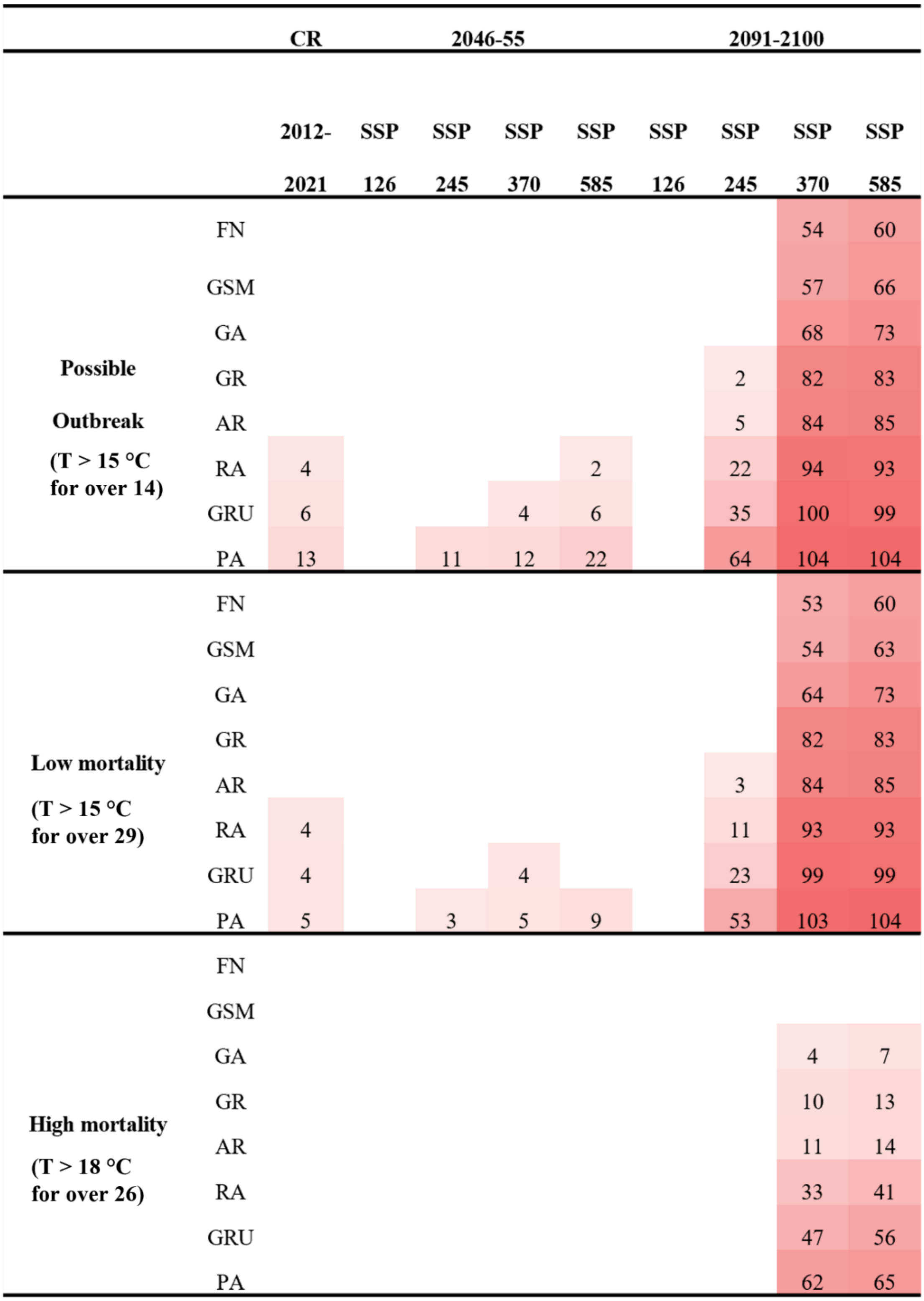


Figure 9. Average August water temperature for P1 and P2, and 2 scenarios, i.e. SSP 126 in 2046-55, SSP 585 in 2046-55, SSP 126 in 2091-2100, SSP 585 in 2091-2100.



		CR	2046-55				2091-2100			
		2012-2021	SSP 126	SSP 245	SSP 370	SSP 585	SSP 126	SSP 245	SSP 370	SSP 585
Possible Outbreak (T > 15 °C for over 14)	FN								54	60
	GSM								57	66
	GA								68	73
	GR							2	82	83
	AR							5	84	85
	RA	4				2		22	94	93
	GRU	6			4	6		35	100	99
	PA	13		11	12	22		64	104	104
Low mortality (T > 15 °C for over 29)	FN								53	60
	GSM								54	63
	GA								64	73
	GR								82	83
	AR							3	84	85
	RA	4						11	93	93
	GRU	4			4			23	99	99
	PA	5		3	5	9		53	103	104
High mortality (T > 18 °C for over 26)	FN									
	GSM									
	GA								4	7
	GR								10	13
	AR								11	14
	RA								33	41
	GRU								47	56
	PA								62	65

Figure 10. Outbreak of PKD in present and future scenarios in 8 considered stations, e.g., average days per year in critical conditions. Darker tones of red indicate worse conditions.

To assess hydro-morphological suitability, we evaluated PD for the 8 sampling sites during P1 and P2, for the two scenarios SSP126, and SSP585, thus providing the lower and the upper bound of the future suitability assessment. Then, we evaluated the number of days per year, averaged along the CR, P1, and P2, when such weighted PD for the river would fall within each class, for each season (Figure 11). Because winter discharge would increase in future scenarios (Figure 4), the water level would also increase, and accordingly adult fish would find more suitable conditions. This projected condition would be confirmed by the slight decrease, in future winters, in the number of days when PD for adult trout would be in the "poor" class. On the contrary, in spring and fall, the number of days in "poor" class would remain almost constant, while in summer the critical days would slightly increase. No evident trends are observed for juvenile and fry stages, which may face fewer criticalities.

P1 SSP 126

	winter						spring						summer						fall					
	ad		fry		juv		ad		fry		juv		ad		fry		juv		ad		fry		juv	
FN	71	19	90	0	45	45	49	43	92	0	73	19	28	64	92	0	92	0	71	20	71	20	71	20
GSM	80	10	90	0	15	75	71	21	92	0	52	40	50	43	92	0	92	0	80	11	80	11	80	11
GA	8	82	87	3	89	1	27	65	86	6	89	3	43	49	74	18	74	18	8	83	8	83	8	83
GR	6	84	90	0	90	0	17	75	92	0	92	0	32	60	92	0	92	0	6	85	6	85	6	85
AR	15	75	90	0	81	9	49	43	92	0	81	11	62	31	92	0	92	0	15	76	15	76	15	76
RA	83	7	84	6	90	0	71	21	75	17	92	0	57	35	59	33	59	33	83	8	83	8	83	8
GRU	90	0	85	5	89	1	92	0	77	15	88	4	92	0	62	30	62	30	90	1	90	1	90	1
PA	57	33	84	6	90	0	70	22	73	19	92	0	74	18	57	35	57	35	57	34	57	34	57	34

P1 SSP 585

	winter						spring						summer						fall					
	ad		fry		juv		ad		fry		juv		ad		fry		juv		ad		fry		juv	
FN	67	23	90	0	59	31	52	40	92	0	77	16	41	51	92	0	92	0	67	24	67	24	71	20
GSM	74	16	90	0	25	65	74	18	92	0	47	45	66	26	92	0	92	0	74	17	74	17	80	11
GA	15	76	83	7	89	1	21	71	88	4	87	5	28	64	82	10	82	10	15	77	15	77	8	83
GR	12	78	90	0	90	0	11	81	92	0	92	0	19	73	92	0	92	0	12	79	12	79	6	85
AR	25	65	90	0	81	9	43	49	92	0	79	13	46	46	92	0	92	0	25	66	25	66	15	76
RA	76	14	77	13	90	0	79	13	81	11	92	0	71	21	73	19	73	19	76	15	76	15	83	8
GRU	90	0	78	12	87	3	92	0	84	8	87	5	92	0	76	16	76	16	90	1	90	1	90	1
PA	76	14	74	16	90	0	72	20	76	16	92	0	78	14	69	23	69	23	76	15	76	15	57	34

P2 SSP 126

	winter						spring						summer						fall					
	ad		fry		juv		ad		fry		juv		ad		fry		juv		ad		fry		juv	
FN	69	21	90	0	51	39	43	49	92	0	77	15	32	60	92	0	92	0	69	22	69	22	69	22
GSM	78	12	90	0	20	71	68	24	92	0	59	33	51	41	92	0	92	0	78	13	78	13	78	13
GA	10	80	84	6	90	0	35	57	85	7	87	5	42	50	78	15	78	15	10	81	10	81	10	81
GR	8	82	90	0	90	0	20	72	92	0	92	0	29	63	92	0	92	0	8	83	8	83	8	83
AR	29	61	90	0	82	8	63	29	92	0	85	7	67	25	92	0	92	0	29	62	29	62	29	62
RA	80	10	81	9	90	0	64	28	68	24	92	0	60	32	64	28	64	28	80	11	80	11	80	11
GRU	90	0	81	9	87	3	92	0	73	19	88	4	92	0	67	25	67	25	90	1	90	1	90	1
PA	56	34	81	9	90	0	71	21	69	23	92	0	79	13	61	31	61	31	56	35	56	35	56	35

P2 SSP 585

	winter						spring						summer						fall					
	ad		fry		juv		ad		fry		juv		ad		fry		juv		ad		fry		juv	
FN	53	38	90	0	74	16	61	31	92	0	85	7	69	23	92	0	92	0	53	39	53	39	53	39
GSM	69	21	90	0	40	50	75	17	92	0	39	53	82	10	92	0	92	0	69	22	69	22	69	22
GA	23	67	79	11	89	2	14	78	88	4	89	3	10	82	89	4	89	4	23	68	23	68	23	68
GR	18	72	90	0	90	0	8	84	92	0	92	0	7	85	92	0	92	0	18	73	18	73	18	73
AR	48	42	90	0	80	10	44	48	92	0	78	15	42	50	92	0	92	0	48	43	48	43	48	43
RA	68	22	69	21	90	0	82	10	83	9	92	0	84	8	85	7	85	7	68	23	68	23	68	23
GRU	90	0	71	19	87	3	92	0	85	7	88	4	92	0	86	6	86	6	90	1	90	1	90	1
PA	79	11	65	25	90	0	75	17	80	12	92	0	85	7	83	9	83	9	79	12	79	12	79	12

Figure 11. Total number of days per year when PD along the river falls within each class, i.e. good (green), and poor (red), for each season, averaged on the three decades, CR, half century and end of

century, for each life stage of the trout. Bar width visually indicates the length of the period (over the length of the season, ca. 90 days).

3.7 Future river stress

In Figure 12 we report the RS index during P1 and P2, for the two scenarios SSP126, and SSP585. Differently from the findings for the CR period (Figure 8), here the combination of the habitat and thermal suitability seems crucial since it would lead to a worsening of river conditions when considering both the suitability functions, with respect to the approach of dealing with them separately (Figure 10, Figure 11). Whereas for adults the projected habitat suitability along the river would be undermined under all scenarios both in P1 and P2, for juvenile and fry the findings would be slightly less alarming (Figure 11). Contrarily, the RS index, by combining habitat suitability with the effect of projected water temperature increase, would project a picture with larger stress, leading under the worst-case scenarios to the highest stress conditions, in summer and fall seasons.

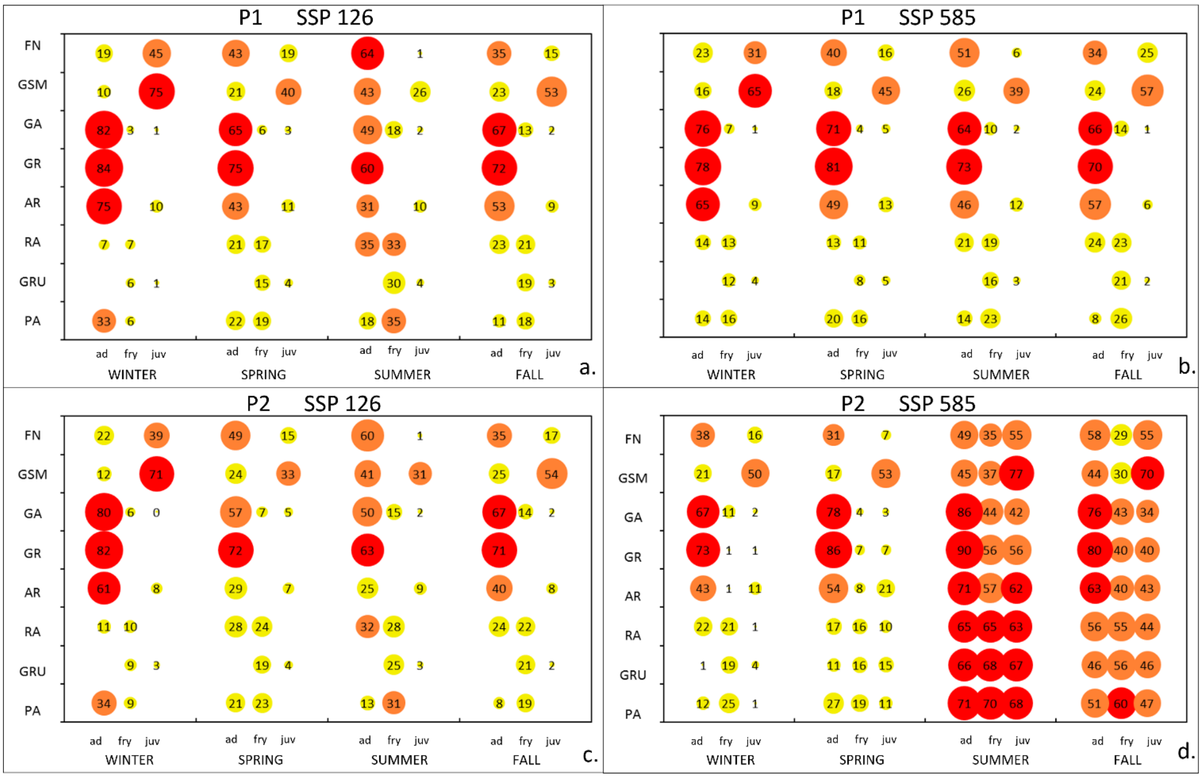


Figure 12. River Stress index, expressed in number of days per year, for each season, for each life stage of the trout, at each sampling point., averaged on P1 and P2, for 2 scenarios, i.e. (a) SSP 126 in 2046-55, (b) SSP 585 in 2046-55, (c) SSP 126 in 2091-2100, (d) SSP 585 in 2091-2100. Days 0-30 (yellow), days 30-60 (orange), days 60-90 (red).

4. Discussion

Suitability indexes depending upon stream flow magnitude, and timing are largely adopted to evaluate the effect of climate change on riverine habitat (Ayllón et al., 2009; Viganò et al., 2015). However, assessment of water temperature is likely essential, due to its effects on the physiology and behaviour of trout (Elliott & Elliott, 2010). The assessment of water temperature requires proper modelling, particularly in rivers exploited by human activity, where alteration of the thermal regime due to withdrawal, and release is still poorly understood (Dickson et al., 2012). We used here a physically based model, *Poli-Wat.Temp*, depending upon factors directly affecting thermal dynamics. We modelled daily water temperature, obtaining a *Bias* mod/obs smaller than 1 °C in each water temperature station, which is consistent with similar studies in nearby areas (Toffolon & Piccolroaz, 2015).

In future worst scenarios, we projected a significant temperature increase for water in most downstream areas during August, over +6.5 °C, which is even higher than the increase of air temperature as projected. This result is coherent e.g. with a recent study in the Columbia basin (Ficklin et al., 2014), where the lack of cold water coming from snow would lead to similar temperature outbreaks, and it is also consistent with the historic trend of Swiss streams temperature as observed, nearby +0.37 °C per decade *vs* +0.13 °C per decade for air temperature (Auer et al., 2007). Nevertheless, in other studies projected temperature increase would be milder (Agnetti et al., 2018; Michel et al., 2022), especially when using empirical models, possibly less recommended for projections in future scenarios (Leach & Moore, 2019). In these models, generally water temperature is linearly dependent on air temperature with slopes smaller than one (Erickson & Stefan, 1996). However, in physical models, the link with air temperature can be more complex, given the presence of other variables also depending upon air temperature, i.e. upstream water temperature like here, and the link between air/water temperatures is less predictable. Here we considered spatial dependence, thus water temperature is affected by upstream boundary conditions, e.g. water temperature in Barbellino lake, with its average linked linearly to annual air temperature. We did not consider here boundary/initial conditions as possibly given by other, smaller reservoirs in the high Serio valley, e.g. Valmorta, Avert. We nevertheless consider this choice as the best option here, since we do not possess data thereby for water temperature assessment. Furthermore, regarding the assessment of Barbellino temperature, the apparent lack of physical modelling of lake heating dynamics, crucial to correctly assess downstream temperature, possibly limits our analysis here. Indeed, most studies concerning lake temperature are related to *epilimnion* (i.e. the lake surface), where more data are available, and remote sensing can be used (Pareeth et al., 2016). Few studies try to model hypolimnion temperature (Prats & Danis, 2019), and we are not aware of any studies attempting to model lake temperature considering the effect of withdrawal upon lake mixing. Indeed, the morphology of the hydraulic structure impacts lake mixing, and so the vertical temperature profile is also affected.

According to our predictions of hydro-morphological suitability, we do not foresee very large trends therein for the next future. Like previous studies in the area (Viganò et al., 2015), small flow variations are projected in winter, when a slight increase in discharge, due to larger shares of liquid precipitation, would positively affect adult trout. We observed that potential trout density would never decrease below -40% of its maximum in our simulations, thus dramatic conditions linked to lack of water would not be encountered in Serio River, under our hypotheses. Moreover, the critical periods in response to hydrological and thermal conditions, i.e. winter and summer respectively, do not coincide. Thus, the combined indicator RS highlights that the critical periods in the year may be longer than when considering the two suitability indexes separately, as it would be expected. It is important to point out that *RS* we used here was calculated by merging the number of days when PD falls in the “poor” class and the number of days when the water temperature is above the threshold for the possible outbreak of PKD. If we had considered the intersection of the two sets, or a different criterion to define the critical threshold for temperature, probably the results would be less critical. However, we considered the lowest temperature threshold for PKD because it is the one likely to be most sensitive to climate change. Three years of water temperature monitoring (2018-2021) in the upper Serio catchment revealed an acceptable thermal habitat for *Salmo trutta*, since the water temperature was always below the chosen critical thresholds. The future projections show continuous, and evident worsening of the thermal habitat for trout, in particular for most downstream stations (RA, GRU, PA).

Other studies recently demonstrated the worsening of thermal conditions in temperate rivers due to climate change. Santiago et al. (2016) studied the effects of climate change on the thermal niche of brown trout in the Iberian Duero River basin. They showed that in the worst scenario (RCP 8.5), the loss of habitat of brown trout may reach -30% in the upstream part of the basin, at the end of the century. The thermal niche was assessed using a threshold based on the exceeding of +18 °C (daily mean), and projections showed an increase of ca. 3 and 9 folds of the number of consecutive days above the threshold, with RCP 4.5, and 8.5

respectively. Similarly, Borgwardt et al., (2020) projected the effects of climate change on Austrian brown trout at the country scale, assessing both physiological stress, and the potential emergence of diseases. Overall, they found that at the end of the century, RCP 8.5 would show an increase in both high mortality (+25%) and low mortality (+20%) conditions. In our case study, high mortality ($T_w > 18$ °C) is seldom, if ever, predicted since we studied a cold Alpine River. However, our results clearly show that the habitat of brown trout would face a more dramatic condition, with headwater areas becoming the only optimal niche for the conservation of the species.

We consider PKD as the most likely risk factor for trout, preliminarily neglecting a possible negative effect due to lack of food, or hypoxia. Indeed, several studies demonstrated that increasing temperatures enhance disease prevalence, severity and distribution, and PKD-related mortality (Okamura et al., 2011; Waldner et al., 2020). By contrast, rising temperatures do not seem to adversely affect food availability, because the secondary productivity of benthos generally increases (Albertson et al., 2018; Bonacina et al., 2022). Furthermore, as aforementioned, the oxygen rate in the Serio River was always found at saturation level, likely due to flow turbulence, and the maximum temperatures projected in the worst scenario (approximately +21 °C) did not visibly cause a decrease in oxygen below the concentration needed by trout (7 mg/l). Sub-Alpine and Alpine rivers are profoundly impacted by human infrastructures, both for hydroelectric and irrigation purposes, affecting the riverine thermal regime (Caissie, 2006). For this reason, we included here hydropower diversion in our study. To further explore climate change impacts on fish communities, more detailed investigations covering the effects of plants and dams on the thermal regime should be carried out at a regional scale.

This study helps to understand the magnitude of thermal impacts and explores measures to mitigate the effects of global warming. For instance, an increase in the minimum flow, especially during summer heat waves, could increase the thermal inertia of the river and reduce warming, decreasing the number of critical days, possibly at the cost of reducing hydropower production. Moreover, other strategies to reduce temperature raising could be implemented, such as the increase of vegetation cover along the river to enhance the shading and reduce the effect of solar radiation.

Here we considered as a target species the *Salmo trutta* since it is regarded as the most abundant, and economically viable fish species in Serio River. However, the marble trout (*Salmo marmoratus*), indigenous and sub-endemic of the Po Valley (Zerunian, 2003), has the same habitat preferences as the allopatric brown trout, and it may survive higher temperature thresholds, so in the future, it might likely face fewer criticalities. Marble trout is included in the Habitat Directive (92/43/CEE), and in the IUCN Red List of Threatened species (Crivelli, 2006). Another endemic species of the Po Valley is *Cottus gobio* (Elliott & Elliott, 1995) also included in the Habitat Directive (92/43/CEE) as well as in the IUCN Red list of vertebrate animals (Rondinini et al., 2013), and it has more flexible thermal preference compared to *Salmo trutta.* Thus, the conservation of the endangered species *Salmo marmoratus* and *Cottus gobio* may be fundamental to maintain healthy fish communities on subalpine rivers like Serio here, also under a climate change adaptation perspective.

5. Conclusions

This study introduces a new physical model to assess river water temperature with the presence of hydropower plants, and a synthetic *River Stress* index to consider both the effects of change in discharge and water temperature on riverine habitat. The proposed methodology was applied to the alpine Serio River in present and IPCC future scenarios, where future hydraulic habitat suitability is not expected to highlight large criticalities, while projections of stream temperature show more alarming findings.

This methodology can be applied to other Alpine rivers, also exploited for human activities and requiring quality assessment, pending basic information availability of hydrology, thermal regime, and fish abundance, as reported here. Even in lack of information, some findings may be portable to other areas, e.g. fish density functions for similar target species. Such analysis may help in i) evaluating seasonal criticalities for fish species, and ii) providing more sustainable withdrawal strategies and thus outlining a background for planning adaptation strategies.

Supplementary material

Table 1SM. Parameters for Poli-Hydro calibration.

Parameter	Unit	Description	Value	Method
DDS	[mmd^{-1} °C^{-1}]	Degree Day Snow	5	Literature [42]
t_g, t_s	[h]	Lag times, ground/surface	50, 400	Calibration, Hydrograph shape
n_g, n_s	[-]	Reservoirs, ground/surface	3, 3	Literature [41]
K	[mmd^{-1}]	Saturated conductivity	3	Calibration, flow volumes
k	[-]	Ground flow exponent	0.5	Calibration, flow volumes
θ_w, θ_s	[-]	Water content, wilting, field capacity	0.15, 0.45	Literature [41]

Table 2SM. Calibration parameter of the thermal model, Eq. (2)

Parameter	Unit	Value
α	$[JK^{-1}m^{-3}]$	20.94
β	$[s]$	41.87

Table 3SM. Calibration parameter of the Barbellino lake temperature model, Eq. (6)

Parameter	Unit	Value
γ	[-]	0.35
ω	[-]	0.5
Lag	[day]	105

CONCLUSION

CONCLUSION

This thesis concerned the water thermal regime of mountain streams, its drivers, and the effect on aquatic communities, in particular:

I. The mid-altitude streams of the Serio watershed revealed the extremely high thermal heterogeneity due to the interaction of different water sources and the effect of the presence of reservoirs. Such sharp thermal heterogeneity generates a mosaic of habitats available for the aquatic biota (Chapter 1).

II. The presence of run of river hydropower plants induces an increase in the rate of warming within the by-passed stretches and causes a water thermal discontinuity along the river (Chapter 2).

III. The effects of water temperature on macroinvertebrates reported in the literature are manifold with implications at different levels, from genes to communities, and involve multiple responses related to physiology, phenology, fitness, behaviour, community ecology, and evolution. The advances in the thermal macroinvertebrate bio-ecology suggest possible research directions (Chapter 3).

IV. Water temperature promotes changes in the dominance of periphyton groups and macroinvertebrate taxa throughout the year. The water thermal variability partially drives the macroinvertebrate community spatial dissimilarity, affecting especially cold stenothermal taxa and induces a phenological desynchronization in the populations of *Amphinemurae* sp. (Plecoptera) and *Serratella ignita* (Ephemeroptera) inhabiting streams with different water thermal regimes (Chapters 4 and 5).

V. Estimates of the brown trout habitat suitability in a regulated river under different climatic scenarios indicate a deterioration in the next decades especially due to warmer summers (Chapter 6).

Such findings raise further research questions and suggest management strategies, better detailed hereafter:

I. A continuous and detailed monitoring of water temperature in mountain watercourses is needed to describe the thermal spatiotemporal patterns of the stream networks, to quantify the thermal impacts of human infrastructures, and to provide reliable data for ecological research.

II. The inclusion of the thermal regime in environmental flow policies and bioassessment programs is essential to measure and quantify thermal alterations caused by water withdrawals with appropriate metrics and to develop indicators of thermal stress to be included in bioassessment programs to assess the impact of thermal changes. Moreover, it is important to explore measures to mitigate thermal impacts such as increasing environmental flow and tree canopy (i.e maintaining riparian vegetation) in summer periods.

III. The investigation of the responses of periphyton to environmental conditions is important being it the first level of the trophic chain. The taxonomic identification is needed to investigate the effect of water temperature on the community composition.

IV. The knowledge about macroinvertebrates inhabiting lotic systems, their life history traits (especially thermal preference), and their ecological functions is far to be complete. Exploring what is there and how it responds to environmental changes (such as temperature change) is needed to estimate threatened species, elaborate mitigation strategies, and develop conservation and restoration plans to preserve mountain streams.

V. Thermal variability and thermal average affect diversity by independent mechanisms; thus, any attempt to understand how temperature influences the aquatic biota should distinguish the two factors and disentangle the other confounding variables.

VI. Alpine regions are highly anthropized and the mountain freshwater system supplies also lowland areas providing water for households, industry, agriculture, and energy, besides supporting a high percentage of the biodiversity (~10% of the fauna in Italy); thus, thermal impacts and mitigation strategies should be placed within the human context.

References

Abati, S., Minciardi, M. R., Ciadamidaro, S., Fattorini, S., & Ceschin, S. (2016). Response of macrophyte communities to flow regulation in mountain streams. *Environmental Monitoring and Assessment*, *188*(7). https://doi.org/10.1007/s10661-016-5420-2

Abbott, J. K. (2013). Morph-specific and sex-spedfic temperature effects on morphology in the colour polymorphic damselfly Ischnura elegans. *Animal Biology*, *63*, 149–167. https://doi.org/10.1163/15707563-00002402

Abdullahi, B. A., & Laybourn-Parry, J. (1985). The effect of temperature on size and development in three species of benthic copepod. *Oecologia*, *67*, 295–297.

Acreman, M. C., & Ferguson, A. J. D. (2018). Environmental flows and the European Water Framework Directive. *Freshwater Biology*, (January 2010). https://doi.org/10.1111/j.1365-2427.2009.02181.x

Addo-Bediako, A., Chown, S. L., & Gaston, K. J. (2000). Thermal tolerance, climatic variability and latitude. *Proceedings of the Royal Society B: Biological Sciences*, *267*, 739–745. https://doi.org/10.1098/rspb.2000.1065

Agnetti, A., Tugnoli, F., Pecora, S., & Zolezzi, G. (2018). Prediction of the thermal regime of the Po river under climate change. In *Proceedings of the 5th IAHR Europe Congress — New Challenges in Hydraulic Research and Engineering* (pp. 673–674). https://doi.org/10.3850/978-981-11-2731-1

Aili, T., Soncini, A., Bianchi, A., Diolaiuti, G., D'Agata, C., & Bocchiola, D. (2019). Assessing water resources under climate change in high-altitude catchments: a methodology and an application in the Italian Alps. *Theoretical and Applied Climatology*, *135*(1–2), 135–156. https://doi.org/10.1007/s00704-017-2366-4

Alahuhta, J., Toivanen, M., & Hjort, J. (2020). Geodiversity–biodiversity relationship needs more empirical evidence. *Nature Ecology and Evolution*, *4*(1), 2–3. https://doi.org/10.1038/s41559-019-1051-7

Albertson, L. K., Ouellet, V., & Daniels, M. D. (2018). Impacts of stream riparian buffer land use on water temperature and food availability for fish. *Journal of Freshwater Ecology*, *33*(1), 195–210. https://doi.org/10.1080/02705060.2017.1422558

Allan, J. D., & Castillo, M. M. (2007). *Stream ecology*. (J. D. Allan & M. Castillo, Maria, Eds.) (Second). Dordrecht, The Netherlands: Springer.

Allen, A. P., Brown, J. H., & Gillooly, J. F. (2002). Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science*, *297*(5586), 1545–1548. https://doi.org/10.1126/science.1072380

Anderson, T. R., Hessen, D. O., Boersma, M., Urabe, J., & Mayor, D. J. (2017). Will invertebrates require increasingly carbon-rich food in a warming world? *The American Naturalist*, *190*(6), 725–742. https://doi.org/10.1086/694122

Angilletta, J. M. J. (2009a). Evolutionary thermal biology. In J. M. J. Angilletta (Ed.), *Thermal Adaptation: A Theoretical and Empirical Synthesis* (First, pp. 1–42). Oxford: Oxford University Press. https://doi.org/10.1093/acprof:oso/9780198570875.001.1

Angilletta, J. M. J. (2009b). Thermal heterogeneity. In J. M. J. Angilletta (Ed.), *Thermal Adaptation: A Theoretical and Empirical Synthesis* (First, pp. 1–33). Oxford: Oxford University Press. https://doi.org/10.1093/acprof:oso/9780198570875.001.1

Angilletta, M. J., Cooper, B. S., Schuler, M. S., & Boyles, J. G. (2002). The evolution of thermal physiology in ectotherms. *Journal of Thermal Biology*, 249–268. https://doi.org/10.2741/e148

Angilletta, M. J., Steury, T. D., & Sears, M. W. (2004). Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle. *Integrative and Comparative Biology*, *44*(6), 498–509. https://doi.org/10.1093/icb/44.6.498

APAT. (2007). *Annuario dei dati ambientali Edizione 2007*.

Arai, R., Nukazawa, K., Kazama, S., & Takemon, Y. (2015). Variation in benthic invertebrate abundance along thermal gradients within headwater streams of a temperate basin in Japan. *Hydrobiologia*, *762*, 55–63. https://doi.org/10.1007/s10750-015-2336-8

Arim, M., Marquet, P. A., & Jaksic, F. M. (2007). On the relationship between productivity and food chain length at different ecological levels. *The American Naturalist*, *169*(1), 62–72. https://doi.org/10.1086/510210

Arim, M., Bozinovic, F., & Marquet, P. A. (2007). On the relationship between trophic position, body mass and temperature: reformulating the energy limitation hypothesis. *Oikos*, *116*(9), 1524–1530. https://doi.org/10.1111/j.2007.0030-1299.15768.x

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. *Freshwater Biology*, *58*(5), 880–894. https://doi.org/10.1111/fwb.12094

Armour, C. L. (1994). *Evaluating temperature regimes for protection of Brown trout*. Washington.

Arnell, N. W. (1999). The effect of climate change on hydrological regimes in Europe: a continental perspective. *Global Environmental Change*, *9*(1), 5–23. https://doi.org/10.1016/S0959-3780(98)00015-6

Arscott, D. B., Tockner, K., & Ward, J. V. (2001). Thermal heterogeneity along a braided floodplain river (Tagliamento River, Northeastern Italy). *Canadian Journal of Fisheries and Aquatic Sciences*, *2373*, 2359–2373. https://doi.org/10.1139/cjfas-58-12-2359

Arthur, J. W., Zischke, J. A., & Ericksen, G. L. (1982). Effect of elevated water temperature on macroinvertebrate communities in outdoor experimental channels. *Water Research*, *16*, 1465–1477. https://doi.org/https://doi.org/10.1016/0043-1354(82)90245-7

Astorga, A., Heino, J., Luoto, M., & Muotka, T. (2011). Freshwater biodiversity at regional extent: determinants of macroinvertebrate taxonomic richness in headwater streams. *Ecography*, *34*, 705–713. https://doi.org/10.1111/j.1600-0587.2010.06427.x

Atkinson, D. (1994). Temperature and organism size-a biological law for ectotherms? *Advances in Ecological Research*, *25*, 1–58. https://doi.org/https://doi.org/10.1016/S0065-2504(08)60212-3

Atkinson, D. (1995). Effects of temperature on the size of aquatic ectotherms: exceptions to the general rule. *Journal of Thermal Biology*, *20*(1–2), 61–74. https://doi.org/10.1016/0306-4565(94)00028-H

Auer, I., Bohm, R., Jurkovic, A., Lipa, W., Orlik, A., Potzmann, R., et al. (2007). HISTALP – historical instrumental climatological surface time series of the Greater Alpine Region. *International Journal of Climatology*, *27*, 17–46. https://doi.org/10.1002/joc

Ayllón, D., Almodóvar, A., Nicola, G. G., & Elvira, B. (2009). Interactive effects of cover and hydraulics on brown trout habitat selection patterns. *River Research and Applications*, *25*, 1051–1065. https://doi.org/10.1002/rra.1215

Baker, R. L., & Feltmate, B. W. (1989). Depth selection by larval *Ischnura verticalis* (Odonata: Coenagrionidae): effects of temperature and food. *Freshwater Biology*, *22*, 169–175. https://doi.org/10.1111/j.1365-2427.1989.tb01093.x

Bálint, M., Domisch, S., Engelhardt, C. H. M., Haase, P., Lehrian, S., Sauer, J., et al. (2011). Cryptic biodiversity loss linked to global climate change. *Nature Climate Change*, *1*, 313–318. https://doi.org/10.1038/nclimate1191

Band, V. I., Valley, R., Gesierich, D., & Rott, E. (2004). Benthic algae and mosses from aquatic habitats in the catchment of a glacial stream (Rotmoos, Ötztal, Austria). *Ber. Nat.-Med. Verein Innsbruck*, *91*, 7–42.

Barbour, M. T., Gerritsen, J., Blaine, S. D., & Stribling, J. B. (1999). Rapid bioassessment protocols for use in streams and wadeable rivers: periphyton, benthic macroinvertebrates, and fish. *U.S. Environmental Protection Agency Policy*. Washington.

Barnett, T. P., Adam, J. C., & Lettenmaier, D. P. (2005). Potential impacts of a warming climate on water availability in snow-dominated regions. *Nature*, *438*, 303–309. https://doi.org/10.1038/nature04141

Barquín, J., & Death, R. G. (2011). Downstream changes in spring-fed stream invertebrate communities: The effect of increased temperature range? *Journal of Limnology*, *70*, 134–146. https://doi.org/10.3274/JL11-70-S1-10

Baselga, A. (2013a). Multiple site dissimilarity quantifies compositional heterogeneity among several sites, while average pairwise dissimilarity may be misleading. *Ecography*, *36*(2), 124–128. https://doi.org/10.1111/j.1600-0587.2012.00124.x

Baselga, A. (2013b). Separating the two components of abundance-based dissimilarity: Balanced changes in abundance vs. abundance gradients. *Methods in Ecology and Evolution*, *4*(6), 552–557. https://doi.org/10.1111/2041-210X.12029

Baselga, A. (2017). Partitioning abundance-based multiple-site dissimilarityinto components: balanced variation in abundance andabundance gradients. *Methods*, *8*, 799–808.

Baselga, A., Orme, D., Villeger, S., De Bortoli, J., Fabien, L., Logez, M., et al. (2022). Betapart.

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1). https://doi.org/10.18637/jss.v067.i01

Bayoh, M. N., & Lindsay, S. W. (2003). Effect of temperature on the development of the aquatic stages of *Anopheles gambiae* sensu stricto (Diptera: Culicidae). *Bullettin of Entomological Research*, *93*, 375–381. https://doi.org/10.1079/ber2003259

Beaufort, A., Curie, F., Moatar, F., Ducharne, A., Melin, E., & Thiery, D. (2016). T-NET, a dynamic model for simulating daily stream temperature at the regional scale based on a network topology. *Hydrological Processes*, *30*, 2196–2210. https://doi.org/10.1002/hyp.10787

Beck, W. M. (1955). Suggested method for repotting biotic data. *Sewage and Industrial Wastes*, *10*(10), 1193–1197.

Becquet, J., Lamouroux, N., Condom, T., Gouttevin, I., Forcellini, M., Launay, B., et al. (2022). Macroinvertebrate distribution associated with environmental variables in alpine streams. *Freshwater Biology*, *00*, 1–17. https://doi.org/10.1111/fwb.13977

Bennett, J. M., Sunday, J., Calosi, P., Villalobos, F., Martínez, B., Molina-Venegas, R., et al. (2021). The evolution of critical thermal limits of life on Earth. *Nature Communications*, *12*(1), 1–9. https://doi.org/10.1038/s41467-021-21263-8

Benyahya, L., Caissie, D., St-Hilaire, A., Ouarda, T. B. M. J., & Bobée, B. (2007). A review of statistical water temperature models. *Canadian Water Resources Journal*, *32*(3), 179–192. https://doi.org/10.4296/cwrj3203179

Beracko, P., & Revajová, A. (2019). Benthic life in karst spring—The life cycle and secondary production of benthic macroinvertebrates under the effects of constant water temperature. *Limnologica*, *74*, 51–60. https://doi.org/10.1016/j.limno.2018.11.002

Bergmann. (1847). *Ueber die verhältnisse der wärmeökonomie der thiere zu ihrer grösse*. (G. Studien, Ed.).

Bergström, I., Kortelainen, P., Sarvala, J., & Salonen, K. (2010). Effects of temperature and sediment properties on benthic CO_2 production in an oligotrophic boreal lake. *Freshwater Biology*, *55*, 1747–1757. https://doi.org/10.1111/j.1365-2427.2010.02408.x

Bernal, S., Lupon, A., Ribot, M., Sabater, F., & Martí, E. (2015). Riparian and in-stream controls on nutrient concentrations and fluxes in a headwater forested stream. *Biogeosciences*, *12*(6), 1941–1954. https://doi.org/10.5194/bg-12-1941-2015

Bernhardt, E. S., & Likens, G. E. (2004). Controls on periphyton biomass in heterotrophic streams. *Freshwater Biology*, *49*(1), 14–27. https://doi.org/10.1046/j.1365-2426.2003.01161.x

Besacier Monbertrand, A.-L., Timoner, P., Rahman, K., Burlando, P., Fatichi, S., Gonseth, Y., et al. (2019). Assessing the vulnerability of aquatic macroinvertebrates to climate warming in a mountainous watershed: supplementing presence-only data with species Traits. *Water*, *11*(4), 1–29. https://doi.org/10.3390/w11040636

Biggs, B. J. F. (1988). Artificial substrate exposure times for periphyton biomass estimates in rivers. *New Zealand Journal of Marine and Freshwater Research*, *22*(4), 507–515. https://doi.org/10.1080/00288330.1988.9516321

Biggs, B. J. F. (1995). The contribution of flood disturbance, catchment geology and land use to the habitat template of periphyton in stream ecosystems. *Freshwater Biology*, *33*(3), 419–438. https://doi.org/10.1111/j.1365-2427.1995.tb00404.x

Biggs, B. J. F. (1996). Hydraulic habitat of plants in streams. *Regulated Rivers: Research and Management*, *12*(2–3), 131–144. https://doi.org/10.1002/(sici)1099-

1646(199603)12:2/3<131::aid-rrr385>3.0.co;2-x

Biggs, B. J. F., & Smith, R. A. (2002). Taxonomic richness of stream benthic algae: effects of flood disturbance and nutrients. *Limnology and Oceanography, 47*(4), 1175–1186. https://doi.org/10.4319/lo.2002.47.4.1175

Birrell, J. H., Shah, A. A., Hotaling, S., Giersch, J. J., Williamson, C. E., Jacobsen, D., & Woods, H. A. (2020). Insects in high-elevation streams: life in extreme environments imperiled by climate change. *Global Change Biology*, *26*(12), 6667–6684. https://doi.org/10.1111/gcb.15356

Bocchiola, D. (2014). Long term (1921-2011) hydrological regime of Alpine catchments in Northern Italy. *Advances in Water Resources*, *70,* 51–64. https://doi.org/10.1016/j.advwatres.2014.04.017

Bocchiola, D., & Diolaiuti, G. (2010). Evidence of climate change within the Adamello Glacier of Italy. *Theoretical and Applied Climatology*, *100*(3), 351–369. https://doi.org/10.1007/s00704-009-0186-x

Bohle, H. W. (1972). The effect of temperature on embryogenesis and diapause of *Ephemerella ignita* (Poda) (Insecta, Ephemeroptera). *Oecologia*, *10*(3), 253–268. https://doi.org/10.1007/BF00368967

Bombelli, G. M., Soncini, A., Bianchi, A., & Bocchiola, D. (2019). Potentially modified hydropower production under climate change in the Italian Alps. *Hydrological Processes*, *33*(17), 2355–2372. https://doi.org/10.1002/hyp.13473

Bonacci, O., Trninic, D., & Bonacci, T. R. (2008). Analysis of the water temperature regime of the Danube and its tributaries in Croatia. *Hydrological Processes*, *22,* 1014–1021. https://doi.org/10.1002/hyp

Bonacina, L., Fasano, F., Mezzanotte, V., & Fornaroli, R. (2022). Effects of water temperature on freshwater macroinvertebrates: a systematic review. *Biological Reviews*, 000–000. https://doi.org/10.1111/brv.12903

Bonacina, L., Canobbio, S., & Fornaroli, R. (2022). Influence of the *Salmo (trutta) trutta* on the population structure, the growth, and the habitat preference of a *Cottus gobio* population. *River Research and Applications*, *38*(9), 1585–1600. https://doi.org/10.1002/rra.4018

Borgwardt, F., Unfer, G., Auer, S., Waldner, K., El-Matbouli, M., & Bechter, T. (2020). Direct and indirect climate change impacts on brown trout in Central Europe: how thermal regimes reinforce physiological stress and support the emergence of diseases.

Frontiers in Environmental Science, *8*, 1–14. https://doi.org/10.3389/fenvs.2020.00059

Borsuk, M. E., Reichert, P., Peter, A., Schager, E., & Burkhardt-Holm, P. (2006). Assessing the decline of brown trout (*Salmo trutta*) in Swiss rivers using a Bayesian probability network. *Ecological Modelling*, *192*(1–2), 224–244. https://doi.org/10.1016/j.ecolmodel.2005.07.006

Bottová, K., Derka, T., Beracko, P., & de Figueroa, J. M. T. (2013). Life cycle, feeding and secondary production of Plecoptera community in a constant temperature stream in Central Europe. *Limnologica*, *43*, 27–33. https://doi.org/10.1016/j.limno.2012.03.001

Bottová, K., Derka, T., & Svitok, M. (2013). Population dynamics of mayflies in a constant temperature spring stream in West Carpathians. *Limnologica*, *43*, 469–474. https://doi.org/10.1016/j.limno.2013.03.002

Bouton, N., Iserbyt, A., & Van Gossum, H. (2011). Thermal plasticity in life-history traits in the polymorphic blue-tailed damselfly, *Ischnura elegans*: no differences between female morphs. *Journal of Insect Science*, *11*, 1–11. https://doi.org/10.1673/031.011.11201

Bovill, W. D., Downes, B. J., & Lancaster, J. (2015). Caddisfly egg mass morphology mediates egg predation: potential costs to individuals and populations. *Freshwater Biology*, *60*, 360–372. https://doi.org/10.1111/fwb.12497

Bovill, W. D., Downes, B. J., & Lancaster, J. (2019). Variations in fecundity over catchment scales: implications for caddisfly populations spanning a thermal gradient. *Freshwater Biology*, *64*, 723–734. https://doi.org/10.1111/fwb.13257

Branco, C. C., & Necchi, O. (1996). Survey of stream macroalgae of eastern atlantic rainforest of São Paulo state, Southeastern Brazil. *Hydrobiologia*, *333*(3), 139–150. https://doi.org/10.1007/BF00013428

Branco, H. L., & Necchi, O. (1998). Distribution of stream macroalgae in three tropical drainage basins of southeastern Brazil. *Archiv Fur Hydrobiologie*, *142*(2), 241–256. https://doi.org/10.1127/archiv-hydrobiol/142/1998/241

Braune, E., Richter, O., Söndgerath, D., & Suhling, F. (2008). Voltinism flexibility of a riverine dragonfly along thermal gradients. *Global Change Biology*, *14*, 470–482. https://doi.org/10.1111/j.1365-2486.2007.01525.x

Brett, J. R. (1952). Temperature tolerance in young pacific salmon, genus Oncorhynchus. *Journal of the Fisheries Research Board of Canada*, *9*(6), 265–323. https://doi.org/10.1139/f52-016

Brighenti, S., Hotaling, S., Finn, D. S., Fountain, A. G., Hayashi, M., Herbst, D., et al. (2021).

Rock glaciers and related cold rocky landforms: Overlooked climate refugia for mountain biodiversity. *Global Change Biology*, *27*(8), 1504–1517. https://doi.org/10.1111/gcb.15510

Brittain, J. E. (1974). Studies on the lentic Ephemeroptera and Plecoptera of Southern Norway. *Norsk Entomologisk Tidsskr*, *21*, 135–154.

Brittain, J. E. (1977). The effect of temperature on the egg incubation period of *Taeniopteryx nebulosa* (Plecoptera). *Oikos*, *29*(2), 302–305. https://doi.org/https://doi.org/10.2307/3543618

Brittain, J. E. (1982). Biology of mayflies. *Annual Review of Entomology*, *27*, 119–147. https://doi.org/10.1146/annurev.en.27.010182.001003

Brittain, J. E. (1983). The influence of temperature on nymphal growth rates in mountain stoneflies (Plecoptera). *Ecology*, *64*(3), 440–446. https://doi.org/https://doi.org/10.2307/1939962

Brittain, J. E. (1990). Life history of Ephemeroptera and Plecoptera. In I. C. Campbell (Ed.), *Mayflies and Stoneflies: Life Histories and Biology. Proceedings of the 5th International Ephemeroptera Conference and the 9th International Plecoptera Conference* (pp. 1–12). Springer, Dordrecht.

Brittain, J. E., & Campbell, I. C. (1991). The effect of temperature on egg development in the australian mayfly genus *Coloburiscoides* (Ephemeroptera: Coloburiscidae) and its relationship to distribution and life history. *Journal of Biogeography*, *18*(2), 231. https://doi.org/10.2307/2845296

Brittain, J. E., & Eikeland, T. J. (1988). Invertebrate drift - A review. *Hydrobiologia*, *166*, 77–93. https://doi.org/10.1007/BF00017485

Brittain, J. E., & Milner, A. M. (2001). Ecology of glacier-fed rivers: current status and concepts. *Freshwater Biology*, *46*(12), 1571–1578. https://doi.org/10.1046/j.1365-2427.2001.00845.x

Brittain, J. E., & Mutch, R. A. (1984). The effect of water temperature on the egg incubation period of *Mesocapnia oenone* (Plecoptera) from the Canadian Rocky Mountains. *The Canadian Entomologist*, *116*, 549–554. https://doi.org/10.4039/Ent116549-4

Brock, T. D. (1978). *Thermophilic microorganis and life at high temperatures*. (M. P. Starr, Ed.). New York: Springer.

Brock, T. D. (1985). Life at high temperatures. *Science*, *230*(4722), 132–138. https://doi.org/10.1126/science.230.4722.132

Brown, G. W., & Krygier, J. T. (1970). Effects of clear-cutting on stream temperature. *Water Resource Reserch, 6*(4), 1133–1139.

Brown, L. E., & Hannah, D. M. (2008). Spatial heterogeneity of water temperature across an alpine river basin. *Hydrological Processes, 22*, 954–967. https://doi.org/10.1002/hyp

Brown, L. E., Hannah, D. M., & Milner, A. M. (2006). Thermal variability and stream flow permanency in an alpine river system. *River Research and Applications, 22*(4), 493–501. https://doi.org/10.1002/rra.915

Bruno, M. C., Siviglia, A., Carolli, M., & Maiolini, B. (2012). Multiple drift responses of benthic invertebrates to interacting hydropeaking and thermopeaking waves. *Ecohydrology, 6*(4), 511–522. https://doi.org/10.1002/eco.1275

Burgmer, T., Hillebrand, H., & Pfenninger, M. (2007). Effects of climate-driven temperature changes on the diversity of freshwater macroinvertebrates. *Oecologia*, *151*, 93–103. https://doi.org/10.1007/s00442-006-0542-9

Burkhardt-Holm, P., Giger, W., Guttinger, H., Ochsenbein, U., Peter, A., Scheurer, K., et al. (2005). Where have all the fish gone? *Environmental Science and Technology*, 13–14.

Burton, D. T., Richardson, L. B., & Margrey, S. L. P. R. (1976). Effects of low ΔT powerplant temperatures on estuarine invertebrates. *Journal of the Water Pollution Control Federation*, *48*(10), 2259–2272. https://doi.org/10.1016/0146-6291(77)90237-5

Bustillo, V., Moatar, F., Ducharne, A., Thiéry, D., & Poirel, A. (2013). A multimodel comparison for assessingwater temperatures under changing climate conditions via the equilibrium temperature concept: case study of the Middle Loire River, France. *Hydrological Processes*. https://doi.org/10.1002/hyp

Cadbury, S. L., Hannah, D. M., Milner, A. M., Pearson, C. P., & Brown, L. E. (2008). Stream temperature dynamics within a New Zealand glacierized river basin. *River Research and Applications*, *24*, 68–69. https://doi.org/10.1002/rra

Cairns, J., Heath, A. G., Parker, B. C., Cairns, J., Heath, A. G., & Parker, B. C. (1975). Temperature influence on chemical toxicity to aquatic organisms. *Water Pollution Control Federation*, *47*(2), 267–280.

Caissie, D. (1998). Stochastic modelling of water temperatures in a small stream using air to water relations. *Canadian Journal of Civil Engineering, 25*(43), 250–260. https://doi.org/10.1139/cjce-25-2-250

Caissie, D. (2006). The thermal regime of rivers: a review. *Freshwater Biology*, *51*, 1389–1406. https://doi.org/10.1111/j.1365-2427.2006.01597.x

Caissie, D., El-Jabi, N., & Satish, M. G. (2001). Modelling of maximum daily water temperatures in a small stream using air temperatures. *Journal of Hydrology*, *251*(1–2), 14–28. https://doi.org/10.1016/S0022-1694(01)00427-9

Caissie, D., Satish, M. G., & El-Jabi, N. (2005). Predicting river water temperatures using the equilibrium temperature concept with application on Miramichi River catchments (New Brunswick, Canada). *Hydrological Processes*, *19*(11), 2137–2159. https://doi.org/doi:10.1002/hyp.5684

Campaioli, S., Ghetti, Minelli, & Ruffo. (1994). *Manuale per il riconoscimento dei macroinvertebrati delle acque dolci italiane*. Provincia autonoma di Trento.

Cañedo-Argüelles, M., Gutiérrez-Cánovas, C., Acosta, R., Castro-López, D., Cid, N., Fortuño, P., et al. (2020). As time goes by: 20 years of changes in the aquatic macroinvertebrate metacommunity of Mediterranean river networks. *Journal of Biogeography*, *47*, 1861–1874. https://doi.org/10.1111/jbi.13913

Canobbio, S., Azzellino, A., Cabrini, R., & Mezzanotte, V. (2013). A multivariate approach to assess habitat integrity in urban streams using benthic macroinvertebrate metrics. *Water Science and Technology*, *67*(12), 2832–2837. https://doi.org/10.2166/wst.2013.166

Cantonati, M., Bertuzzi, E., Gerecke, R., Ortler, K., & Spitale, D. (2005). Long-term ecological research in springs of the Italian Alps: six years of standardised sampling. *Internationale Vereinigung Für Theoretische Und Angewandte Limnologie: Verhandlungen*, *29*(2), 907–911. https://doi.org/10.1080/03680770.2005.11902814

Cantonati, M., Gerecke, R., & Bertuzzi, E. (2006). Springs of the Alps - Sensitive ecosystems to environmental change: from biodiversity assessments to long-term studies. *Hydrobiologia*, *562*(1), 59–96. https://doi.org/10.1007/s10750-005-1806-9

Cantonati, M., Rott, E., Spitale, D., Angeli, N., & Komárek, J. (2012). Are benthic algae related to spring types? *Freshwater Science*, *31*(2), 481–498. https://doi.org/10.1899/11-048.1

Cantonati, M., Angeli, N., Bertuzzi, E., Spitale, D., & Lange-Bertalot, H. (2012). Diatoms in springs of the Alps: spring types, environmental determinants, and substratum. *Freshwater Science*, *31*(2), 499–524. https://doi.org/10.1899/11-065.1

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. *Ecology of Freshwater Fish*, *26*(2), 190–204.

https://doi.org/10.1111/eff.12267

Carolli, M., Bruno, M. C., Siviglia, A., & Maiolini, B. (2012). Responses of benthic invertebrates to abrupt changes of temperature in flume simulations. *River Research and Applications*, *28*, 678–691. https://doi.org/10.1002/rra

Carolli, M., Vanzo, D., Siviglia, A., Zolezzi, G., Bruno, M. C., & Alfredsen, K. (2015). A simple procedure for the assessment of hydropeaking flow alterations applied to several European streams. *Aquatic Sciences*, *77*(4), 639–653. https://doi.org/10.1007/s00027-015-0408-5

Carraro, L., Bertuzzo, E., Mari, L., Fontes, I., Hartikainen, H., Strepparava, N., et al. (2017). Integrated field, laboratory, and theoretical study of PKD spread in a Swiss prealpine river. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(45), 11992–11997. https://doi.org/10.1073/pnas.1713691114

Casado, A., Hannah, D. M., Peiry, J., & Campo, A. M. (2013). Influence of dam-induced hydrological regulation on summer water temperature: Sauce Grande River, Argentina. *Ecohydrology*, *535*, 523–535. https://doi.org/10.1002/eco.1375

Casas, J. J., Munoz, C. Z., Archila, F., & Tercedor, J. A. (2000). The effect of a headwater dam on the use of leaf bags. *Regulated Rivers: Research & Management*, *591*(6), 577–591. https://doi.org/https://doi.org/10.1002/1099-1646(200011/12)16:6<577::AID-RRR587>3.0.CO;2-P

Castella, E., Adalsteinsson, H., Brittain, J. E., Gislason, G. M., Lehmann, A., Lencioni, V., et al. (2001). Macrobenthic invertebrate richness and composition along a latitudinal gradient of European glacier-fed streams. *Freshwater Biology*, *46*, 1811–1831. https://doi.org/10.1046/j.1365-2427.2001.00860.x

Cattaneo, A., Kerimian, T., Roberge, M., & Marty, J. (1997). Periphyton distribution and abundance on substrata of different size along a gradient of stream trophy. *Hydrobiologia*, *354*(1–3), 101–110. https://doi.org/10.1023/a:1003027927600

CE. (2000). Water Frame Directive. *Official Journal of the European Communities*, *327*(1).

Céréghino, R., Cugny, P., & Lavandier, P. (2002). Influence of intermittent hydropeaking on the longitudinal zonation patterns of benthic invertebrates in a mountain stream. *International Review of Hydrobiology*, *87*(1), 47–60. https://doi.org/10.1002/1522-2632(200201)87:1<47::AID-IROH47>3.0.CO;2-9

Cerini, F., Stellati, L., Luiselli, L., & Vignoli, L. (2020). Long-term shifts in the communities of Odonata: effect of chance or climate change? *North-Western Journal of Zoology*, *16*(1), 1–6.

Chacón, M. M., Segnini, S., & Briceño, D. (2016). Temperatura y emergencia diaria de siete géneros de Ephemeroptera (Insecta) en un río de la Selva Nublada de los Andes Tropicales. *Revista de Biologia Tropical*, *64*(1), 117–130. https://doi.org/10.15517/rbt.v64i1.17919

Chadwick, M. A., & Feminella, J. W. (2001). Influence of salinity and temperature on the growth and production of a freshwater mayfly in the Lower Mobile River, Alabama. *Limnology and Oceanography*, *46*(3), 532–542. https://doi.org/10.4319/lo.2001.46.3.0532

Chandesris, A., Looy, K. Van, Diamond, J. S., & Souchon, Y. (2019). Small dams alter thermal regimes of downstream water. *Hydrology and Earth System Sciences*, *23,* 4509–4525. https://doi.org/https://doi.org/10.5194/hess-23-4509-2019

Chapman, R. F. (2013). *The insects structure and function*. (S. J. Simpson & A. E. Douglas, Eds.) (5th ed.). Cambridge University Press.

Chavez, M. Y., Mabry, K. E., McCauley, S. J., & Hammond, J. I. (2015). Differential larval responses of two ecologically similar insects (Odonata) to temperature and resource variation. *International Journal of Odonatology*, *18*(4), 297–304. https://doi.org/10.1080/13887890.2015.1082946

Cheney, K. N., Roy, A. H., Smith, R. F., Dewalt, R. E., & Murphy, S. (2019). Effects of stream temperature and substrate type on emergence patterns of Plecoptera and Trichoptera from Northeastern United States headwater streams. *Environmental Entomology*, *48*(6), 1349–1359. https://doi.org/10.1093/ee/nvz106

Cherchi, A., Fogli, P. G., Lovato, T., Peano, D., Iovino, D., Gualdi, S., et al. (2019). Global mean climate and main patterns of variability in the CMCC-CM2 coupled model. *Journal of Advances in Modeling Earth Systems*, *11*(1), 185–209. https://doi.org/10.1029/2018MS001369

Chessman, B. C. (2012). Biological traits predict shifts in geographical ranges of freshwater invertebrates during climatic warming and drying. *Journal of Biogeography*, *39*(5), 957–969. https://doi.org/10.1111/j.1365-2699.2011.02647.x

Chinnayakanahalli, K. J., Hawkins, C. P., Tarboton, D. G., & Hill, R. A. (2011). Natural flow regime, temperature and the composition and richness of invertebrate assemblages in streams of the Western United States. *Freshwater Biology*, *56*, 1248–1265. https://doi.org/10.1111/j.1365-2427.2010.02560.x

Chou, H., Pathmasiri, W., Deese-spruill, J., Sumner, S. J., Jima, D. D., Funk, D. H., et al. (2018). The good, the bad, and the lethal: gene expression and metabolomics reveal physiological mechanisms underlying chronic thermal effects in mayfly larvae (*Neocloeon triangulifer*). *Frontiers in Ecology and Evolution*, *6*(27), 1–11. https://doi.org/10.3389/fevo.2018.00027

Christidis, N., Jones, G. S., & Stott, P. A. (2015). Dramatically increasing chance of extremely hot summers since the 2003 European heatwave. *Nature Climate Change*, *5*(1), 46–50. https://doi.org/10.1038/nclimate2468

Clarke, A. (2003). Costs and consequences of evolutionary temperature adaptation. *Trends in Ecology and Evolution*, *18*(11), 573–581. https://doi.org/10.1016/j.tree.2003.08.007

Clarke, A. (2014). The thermal limits to life on Earth. *International Journal of Astrobiology*, *13*(2), 141–154. https://doi.org/10.1017/S1473550413000438

Clarke, A. (2017). *Principles of Thermal Ecology: Temperature, Energy, and Life*. Oxford: Oxford Academic. https://doi.org/https://doi.org/10.1093/oso/9780199551668.001.0001

Clarke, A., & Gaston, K. J. (2006). Climate, energy and diversity. *Proceedings of the Royal Society B: Biological Sciences*, *273*, 2257–2266. https://doi.org/10.1098/rspb.2006.3545

Čmrlec, K., Ivković, M., Šemnički, P., & Mihaljević, Z. (2013). Emergence phenology and microhabitat distribution of aquatic diptera community at the outlets of barrage lakes: effect of temperature, substrate and current velocity. *Polish Journal of Ecology*, *61*(1), 135–144.

Cogo, G. B., Martínez, J., Santos, S., & Graça, M. A. S. (2020). Caddisflies growth and size along an elevation/temperature gradient. *Hydrobiologia*, *847*, 207–216. https://doi.org/10.1007/s10750-019-04082-3

Colburn, E. A. (1983). Effect of elevated temperature on osmotic and ionic regulation in a salt-tolerant caddisfly from Death Valley, California. *Journal of Insect Physiology*, *29*(4), 363–369. https://doi.org/10.1016/0022-1910(83)90038-0

Coler, B. G., & Kondratieff, B. C. (1989). Emergence of Chironomidae (Diptera) from a delta-swamp receiving thermal effluent. *Hydrobiologia*, *174*(1), 67–77. https://doi.org/10.1007/BF00006059

Collier, K. J., & Smith, B. J. (2000). Interactions of adult stoneflies (Plecoptera) with riparian zones I. Effects of air temperature and humidity on longevity. *Aquatic Insects*, *22*(4), 275–284. https://doi.org/10.1076/0165-0424(200010)22:4;1-Y;FT275

Comiti, F. (2012). How natural are Alpine mountain rivers? Evidence from the Italian Alps.

Earth Surface Processes and Landforms, *37*, 693–707. https://doi.org/10.1002/esp.2267

Confortola, G., Soncini, A., & Bocchiola, D. (2013). Climate change will affect hydrological regimes in the Alps. *Revue de Géographie Alpine*, (101–3), 0–19. https://doi.org/10.4000/rga.2176

Contador, T., Kennedy, J., Ojeda, J., Feinsinger, P., & Rozzi, R. (2014). Life cycles of freshwater invertebrates and global climate change in the sub-Antarctic Magellanic ecoregion: long-term ecological research at the Omora Ethonobotanical Park, Biosphere Reserve Cape Horn (55° S). *Bosque*, *35*(3), 429–437. https://doi.org/10.4067/S0717-92002014000300018

Conti, L., Schmidt-Kloiber, A., Grenouillet, G., & Graf, W. (2014). A trait-based approach to assess the vulnerability of European aquatic insects to climate change. *Hydrobiologia*, *721*, 297–315. https://doi.org/10.1007/s10750-013-1690-7

Cooper, C. M. (1980). Effects of abnormal thermal stratification on a reservoir benthic macroinvertebrate community. *The American Midland Naturalist*, *103*(1), 149–154. https://doi.org/https://doi.org/10.2307/2425048

Corkum, L. D., & Hanes, E. C. (1992). Effects of temperature and photoperiod on larval size and survivorship of a burrowing mayfly (Ephemeroptera, Ephemeridae). *Canadian Journal of Zoology*, *70*, 256–263. https://doi.org/10.1139/z92-038

Coutant, C. C. (1987). Thermal preference: when does an asset become a liability? *Environmental Biology of Fisches*, *3*(18), 161–172.

Coutant, C. C. (1999). *Perspectives on temperature in the pacific northwest's fresh waters*. *Environmental Sciences Division* (Vol. 4849). Washington.

Cowx, I. G., Young, W. O., & Booth, J. P. (1987). Thermal characteristics of two regulated rivers in mid-wales, U.K. *Regulated Rivers: Research & Management*, *1*(1), 85–91. https://doi.org/10.1002/rrr.3450010109

Cox, T. J., & Rutherford, J. C. (2010). Thermal tolerances of two stream invertebrates exposed to diumally varying temperature. *New Zealand Journal of Marine and Freshwater Research*, *34*(2), 203–208. https://doi.org/10.1080/00288330.2000.9516926

Crisp, D. T., & Howson, G. (1982). Effect of air temperature upon mean water temperature in streams in the north Pennines and English Lake District. *Freshwater Biology*, *12*(4), 359–367. https://doi.org/10.1111/j.1365-2427.1982.tb00629.x

Crivelli, A. J. (2006). *Salmo marmoratus*. The IUCN Red List of threatened species.

Crozier, L. G., & Hutchings, J. A. (2014). Plastic and evolutionary responses to climate change in fish. *Evolutionary Applications*, *7*(1), 68–87. https://doi.org/10.1111/eva.12135

Culler, L. E., McPeek, M. A., & Ayres, M. P. (2014). Predation risk shapes thermal physiology of a predaceous damselfly. *Oecologia*, *176*, 653–660. https://doi.org/10.1007/s00442-014-3058-8

Cummins, K. W. (1974). Structure and function of stream ecosystems. *BioScience*, *24*(11), 631–641. https://doi.org/https://doi.org/10.2307/1296676

Currie, D. J. (1991). Energy and large-scale patterns of animal and plant species richness. *The American Naturalist*, *137*(1), 27–49. https://doi.org/10.1086/285144

Dallas, H., & Rivers-Moore, N. A. (2012). Critical thermal maxima of aquatic macroinvertebrates: towards identifying bioindicators of thermal alteration. *Hydrobiologia*, *679*, 61–76. https://doi.org/10.1007/s10750-011-0856-4

Dallas, H. F., & Ross-Gillespie, V. (2015). Sublethal effects of temperature on freshwater organisms, with special reference to aquatic insects. *Water SA*, *41*(5), 712–726. https://doi.org/10.4314/wsa.v41i5.15

Dallas, Helen F., & Ketley, Z. A. (2011). Upper thermal limits of aquatic macroinvertebrates: comparing critical thermal maxima with 96-LT50 values. *Journal of Thermal Biology*, *36*, 322–327. https://doi.org/10.1016/j.jtherbio.2011.06.001

Dallas, Helen F., & Rivers-Moore, N. (2014). Ecological consequences of global climate change for freshwater ecosystems in South Africa. *South African Journal of Science*, *110*(5–6), 1–11. https://doi.org/10.1590/sajs.2014/20130274

Danabasoglu, G., Lamarque, J. F., Bacmeister, J., Bailey, D. A., DuVivier, A. K., Edwards, J., et al. (2020). The community earth system model version 2 (CESM2). *Journal of Advances in Modeling Earth Systems*, *12*(2), 1–35. https://doi.org/10.1029/2019MS001916

Danks, H. V. (1978). Some effects of photoperiod, temperature, and food on emergence in three species of chironomidae (Diptera). *The Canadian Entomologist*, *110*, 289–300. https://doi.org/10.4039/Ent110289-3

Danks, H. V. (1987). *Insect dormancy: an ecological perspective*. (H. V. Danks, Ed.). Entomological Society of Canada.

Danks, H. V. (2002). The range of insect dormancy responses. *European Journal of Entomology*, *99*, 127–142. https://doi.org/10.14411/eje.2002.021

Darwin, C. (1959). *On the origin of species: by means of natural selection, or the* *preservation of favoured races in the struggle for life*. London. https://doi.org/10.4324/9781912281244

Deas, M. L., & Lowney, C. L. (2000). *Water temperature: modeling review*. *Central Valley*.

Death, R. G. (2010). Disturbance and riverine benthic communities: what has it contributed to general ecological theory? *River Research and Applications*, *26*, 15–25. https://doi.org/10.1002/rra

Death, R. G., & Zimmermann, E. M. (2005). Interaction between disturbance and primary productivity in determining stream invertebrate diversity. *Oikos*, *111*(2), 392–402. https://doi.org/10.1111/j.0030-1299.2005.13799.x

Demars, B. O. L., Russell Manson, J., Ólafsson, J. S., Gíslason, G. M., Gudmundsdóttir, R., Woodward, G., et al. (2011). Temperature and the metabolic balance of streams. *Freshwater Biology*, *56*, 1106–1121. https://doi.org/10.1111/j.1365-2427.2010.02554.x

Demars, B. O. L., Kemp, J. L., Friberg, N., Usseglio-Polatera, P., & Harper, D. M. (2012). Linking biotopes to invertebrates in rivers: biological traits, taxonomic composition and diversity. *Ecological Indicators*, *23*, 301–311. https://doi.org/10.1016/j.ecolind.2012.04.011

DeNicola, D. M. (1996). Periphyton responses to temperature at different ecological levels. In *Algal Ecology* (pp. 149–181). Elsevier. https://doi.org/10.1016/b978-012668450-6/50035-7

Diamond, J. S., Bernal, S., Boukra, A., Cohen, M. J., Lewis, D., Masson, M., et al. (2021). Stream network variation in dissolved oxygen: metabolism proxies and biogeochemical controls. *Ecological Indicators*, *131*, 108233. https://doi.org/10.1016/j.ecolind.2021.108233

Dickson, N. E., Carrivick, J. L., & Brown, L. E. (2012). Flow regulation alters alpine river thermal regimes. *Journal of Hydrology*, *464–465*, 505–516. https://doi.org/10.1016/j.jhydrol.2012.07.044

Dickson, T. R., & Walker, I. R. (2015). Midge (Diptera: Chironomidae and Ceratopogonidae) emergence responses to temperature: experiments to assess midges’ capacity as paleotemperature indicators. *Journal of Paleolimnology*, *53*, 165–176. https://doi.org/10.1007/s10933-014-9814-2

Dingemanse, N. J., & Kalkman, V. J. (2008). Changing temperature regimes have advanced the phenology of Odonata in the Netherlands. *Ecological Entomology*, *33*, 394–402. https://doi.org/10.1111/j.1365-2311.2007.00982.x

Dobrin, M., & Giberson, D. J. (2003). Life history and production of mayflies, stoneflies, and caddisflies (Ephemeroptera, Plecoptera, and Trichoptera) in a spring-fed stream in Prince Edward Island, Canada: evidence for population asynchrony in spring habitats? *Canadian Journal of Zoology*, *81*, 1083–1095. https://doi.org/10.1139/z03-091

Dodds, W., & Whiles, M. (2017). *Freshwater Ecology. Concepts and environmental applications of Limnology*. (W. Dodds & M. Whiles, Eds.) (Third). Elsevier. https://doi.org/https://doi.org/10.1016/C2016-0-03667-7

Dodds, W. K., Perkin, J. S., & Gerken, J. E. (2013). Human impact on freshwater ecosystem services: a global perspective. *Environmental Science and Technology*, *47*, 9061–9068. https://doi.org/10.1021/es4021052

Dodds, W. K., Bruckerhoff, L., Batzer, D., Schechner, A., Pennock, C., Renner, E., et al. (2019). The freshwater biome gradient framework: predicting macroscale properties based on latitude, altitude, and precipitation. *Ecosphere*, *10*(7). https://doi.org/10.1002/ecs2.2786

Doemel, W. N., & Brock, T. D. (1970). The upper temperature limit of *Cyanidium caldarium*. *Archiv Für Mikrobiologie*, *72*(4), 326–332. https://doi.org/10.1007/BF00409031

Dolédec, S., & Chessel, D. (1994). Co-inertia analysis: an alternative method for studying species–environment relationships. *Freshwater Biology*, *31*(3), 277–294. https://doi.org/10.1111/j.1365-2427.1994.tb01741.x

Döll, P., Fiedler, K., & Zhang, J. (2009). Global-scale analysis of river flow alterations due to water withdrawals and reservoirs. *Hydrology and Earth System Sciences*, *13*(12), 2413–2432. https://doi.org/10.5194/hess-13-2413-2009

Domish, S., Jahnig, S. C., & Haase, P. (2011). Climate-change winners and losers: stream macroinvertebrates of a submontane region in Central Europe. *Freshwater Biology*, *56*, 2009–2020. https://doi.org/https://doi.org/10.1111/j.1365-2427.2011.02631.x

Van Doorslaer, W., & Stoks, R. (2005a). Growth rate plasticity to temperature in two damselfly species differing in latitude: contributions of behaviour and physiology. *Oikos*, *111*, 599–605. https://doi.org/10.1111/j.1600-0706.2005.14335.x

Van Doorslaer, W., & Stoks, R. (2005b). Thermal reaction norms in two *Coenagrion damselfly* species: contrasting embryonic and larval life-history traits. *Freshwater Biology*, *50*, 1982–1990. https://doi.org/10.1111/j.1365-2427.2005.01443.x

Dorts, J., Grenouillet, G., Douxfils, J., Mandiki, S. N. M., Milla, S., Silvestre, F., & Kestemont, P. (2012). Evidence that elevated water temperature affects the reproductive physiology of the European bullhead *Cottus gobio*. *Fish Physiology and Biochemistry*, *38*(2), 389–399. https://doi.org/10.1007/s10695-011-9515-y

Dray, S., & Dufour, A. B. (2007). The ade4 package: implementing the duality diagram for ecologists. *Journal of Statistical Software*, *22*(4), 1–20. https://doi.org/10.18637/jss.v022.i04

Ducharne, A. (2008). Importance of stream temperature to climate change impact on water quality. *Hydrology and Earth System Sciences*, *12*(3), 797–810. https://doi.org/10.5194/hess-12-797-2008

Dudgeon, D., Ng, L. C. Y., & Tsang, T. P. N. (2020). Shifts in aquatic insect composition in a tropical forest stream after three decades of climatic warming. *Global Change Biology*, *26*, 6399–6412. https://doi.org/10.1111/gcb.15325

Durance, I., & Ormerod, S. J. (2007). Climate change effects on upland stream macroinvertebrates over a 25-year period. *Global Change Biology*, *13*, 942–957. https://doi.org/10.1111/j.1365-2486.2007.01340.x

Durance, I., & Ormerod, S. J. (2009). Trends in water quality and discharge confound long-term warming effects on river macroinvertebrates. *Freshwater Biology*, *54*, 388–405. https://doi.org/10.1111/j.1365-2427.2008.02112.x

Durrett, C. W., & Pearson, W. D. (1975). Drift of macroinvertebrates in a channel carrying heated water from a power plant. *Hydrobiologia*, *46*(1), 33–43. https://doi.org/10.1007/BF00038725

Eady, B. R., Rivers-Moore, N. A., & Hill, T. R. (2013). Relationship between water temperature predictability and aquatic macroinvertebrate assemblages in two South African streams. *African Journal of Aquatic Science*, *38*(2), 163–174. https://doi.org/10.2989/16085914.2012.763110

Ebner, J. N., Ritz, D., & von Fumetti, S. (2019). Comparative proteomics of stenotopic caddisfly Crunoecia irrorata identifies acclimation strategies to warming. *Molecular Ecology*, *28*, 4453–4469. https://doi.org/10.1111/mec.15225

EC-Earth Consortium (EC-Earth). (2019). EC-Earth-Consortium EC-Earth3-Veg model output prepared for CMIP6 ScenarioMIP. *Earth Syst. Grid Fed.* Retrieved from https://doi.org/https://doi.org/10.22033/ESGF/CMIP6.727

EC. (2020). *EU biodiversity strategy for 2030*. *European commission*. Bruxelles.

Echenique-Subiabre, I., Dalle, C., Duval, C., Heath, M. W., Couté, A., Wood, S. A., et al. (2016). Application of a spectrofluorimetric tool (bbe BenthoTorch) for monitoring potentially toxic benthic cyanobacteria in rivers. *Water Research*, *101*, 341–350. https://doi.org/10.1016/j.watres.2016.05.081

Edinger, J. E., Duttweiler, D. W., & Geyer, J. C. (1968). The response of water temperatures to meteorological conditions. *Water Resource Research*, *4*(5), 1137–1143. https://doi.org/https://doi.org/10.1029/WR004i005p01137

Edwards, R. ., Densem, J. W., & Russell, P. A. (1979). An assessment of the importance of temperature as a factor controlling the growth rate of brown trout in streams. *Journal of Animal Ecology*, *48*(2), 501–507. https://doi.org/https://doi.org/10.2307/4176

Elliott, J. M. (1972). Effect of temperature on the time of hatching in *Baetis rhodani* (Ephemeroptera: Baetidae). *Oecologia*, *9*, 47–51. https://doi.org/10.1007/BF00345242

Elliott, J. M. (1978). Effect of temperature on the hatching time of eggs of *Ephemerella ignita* (Poda) (Ephemeroptera: Ephemerellidae). *Freshwater Biology*, *8*, 51–58. https://doi.org/10.1111/j.1365-2427.1978.tb01425.x

Elliott, J. M. (1986). The effect of temperature on the egg incubation period of *Capnia bifrons* (Plecoptera: Capniidae) from Windermere (English lake district). *Ecography*, *9*(2), 113–116. https://doi.org/https://doi.org/10.1111/j.1600-0587.1986.tb01199.x

Elliott, J. M. (1987). Temperature-induced changes in the life cycle of *Leuctra nigra* (Plecoptera: Leuctridae) from a lake district stream. *Freshwater Biology*, *18*, 177–184. https://doi.org/10.1111/j.1365-2427.1987.tb01305.x

Elliott, J. M. (1988). Egg hatching and resource partitioning in stoneflies (Plecoptera): ten British species in the family Nemouridae. *The Journal of Animal Ecology*, *57*, 201–215. https://doi.org/10.2307/5057

Elliott, J. M., & Elliott, J. A. (1995). The critical thermal limits for the bullhead, *Cottus gobio*, from three populations in North-west England. *Freshwater Biology*, *33*, 411–418. https://doi.org/10.1111/j.1365-2427.1995.tb00403.x

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. *Journal of Fish Biology*, *77*(8), 1793–1817. https://doi.org/10.1111/j.1095-8649.2010.02762.x

Elliott, J. M., Gibbons, J. W., & Sharitz, R. R. (1975). Thermal ecology. *The Journal of Animal Ecology*, *44*(3), 926. https://doi.org/10.2307/3737

Elsaholi, M. (2011). Nutrient and light limitation of algal biomass in selected streams in Ireland. *Inland Waters*, *1*(2), 74–80. https://doi.org/10.5268/iw-1.2.341

Encalada, A. C., Flecker, A. S., Poff, N. L. R., Suárez, E., Herrera, G. A., Ríos-Touma, B., et al. (2019). A global perspective on tropical montane rivers. *Science*, *365*(6458), 1124–1129. https://doi.org/10.1126/science.aax1682

Erba, S., Melissano, L., & Buffagni, A. (2003). Life cycle of Baetidae (Ephemeroptera) in a North Italian prealpine stream. *Research Update on Ephemeroptera and Plecoptera*, 177–186.

Erickson, T. R., & Stefan, H. G. (1996). *Correlations of Oklahoma Stream temperatures with air temperatures*. *National Agricoltural water quality laboratory*. Minneapolis, Minnesota.

Estay, S. A., Lima, M., & Bozinovic, F. (2014). The role of temperature variability on insect performance and population dynamics in a warming world. *Oikos*, *123*(2), 131–140. https://doi.org/10.1111/j.1600-0706.2013.00607.x

European Committee for standardizations (CEN). (2014). *Water quality - Guidance for the identification and enumeration of benthic diatom samples from rivers and lakes*.

Evans, K. L., Warren, P. H., & Gaston, K. J. (2005). Species-energy relationships at the macroecological scale: a review of the mechanisms. *Biological Reviews*, *80*, 1–25. https://doi.org/10.1017/S1464793104006517

Everall, N. C., Johnson, M. F., Wilby, R. L., & Bennett, C. J. (2015). Detecting phenology change in the mayfly *Ephemera danica*: responses to spatial and temporal water temperature variations. *Ecological Entomology*, *40*, 95–105. https://doi.org/10.1111/een.12164

Eversham, B. C., & Cooper, J. M. (1998). Dragonfly species-richness and temperature: national patterns and latitude trends in Britain. *Odonatologica*, *27*(3), 307–316.

Fahy, E. (1973). Observations on the growth of Ephemeroptera in fluctuating and constant temperature conditions. *Proceedings of the Royal Irish Academy. Section B: Biological, Geological, and Chemical Science*, *73*, 133–149.

Farkas, A., Jakab, T., Müller, O., Móra, A., Lajter, I., & Dévai, G. (2013). Sex ratio in *Gomphidae* (Odonata) at emergence: is there a relationship with water temperature? *International Journal of Odonatology*, *16*(4), 279–287. https://doi.org/10.1080/13887890.2013.825937

Feld, C. K., & Hering, D. (2007). Community structure or function: effects of environmental stress on benthic macroinvertebrates at different spatial scales. *Freshwater Biology*, *52*, 1380–1399. https://doi.org/10.1111/j.1365-2427.2007.01749.x

Fenoglio, S., Bo, T., Battegazzore, M., & Morisi, A. (2005). Growth of *Oligoneuriella rhenana* (Imhoff, 1852) (Ephemeroptera: Oligoneuriidae) in two rivers with contrasting temperatures in NW Italy. *Zoological Studies, 44*(2), 271–274.

Fenoglio, S., Bo, T., Cucco, M., Mercalli, L., & Malacarne, G. (2010). Effects of global climate change on freshwater biota: a review with special emphasis on the Italian situation. *Italian Journal of Zoology, 77*(4), 374–383. https://doi.org/10.1080/11250000903176497

Fernandes, V. O., & Esteves, F. A. (2003). The use of indices for evaluating the periphytic community in two kinds of substrate in Imboassica lagoon, Rio de Janeiro, Brazil. *Brazilian Journal of Biology, 63*(2), 233–243.

Ferreira, V., Chauvet, E., & Canhoto, C. (2015). Effects of experimental warming, litter species, and presence of macroinvertebrates on litter decomposition and associated decomposers in a temperate mountain stream. *Canadian Journal of Fisheries and Aquatic Sciences*, *72*(2), 206–216. https://doi.org/10.1139/cjfas-2014-0119

Feuchtmayr, H., McKee, D., Harvey, I. F., Atkinson, D., & Moss, B. (2007). Response of macroinvertebrates to warming, nutrient addition and predation in large-scale mesocosm tanks. *Hydrobiologia*, *584*, 425–432. https://doi.org/10.1007/s10750-007-0588-7

Ficklin, D. L., Barnhart, B. L., Knouft, J. H., Stewart, I. T., Maurer, E. P., Letsinger, S. L., & Whittaker, G. W. (2014). Climate change and stream temperature projections in the Columbia River basin: habitat implications of spatial variation in hydrologic drivers. *Hydrology and Earth System Sciences*, *18*(12), 4897–4912. https://doi.org/10.5194/hess-18-4897-2014

Finn, D. S., Johnson, S. L., Gerth, W. J., Arismendi, I., & Li, J. L. (2022). Spatiotemporal patterns of emergence phenology reveal complex species-specific responses to temperature in aquatic insects. *Diversity and Distributions*, 1524–1541. https://doi.org/10.1111/ddi.13472

Fiorenzo, F., Mancino, G., Borghetti, M., & Ferrara, A. (2008). Spatial interpolation methods for monthly rainfalls and temperatures in Basilicata. *Forest*, *5*(1), 337–350. https://doi.org/10.3832/efor0550-0050337

Floury, M., Usseglio-Polatera, P., Ferreol, M., Delattre, C., & Souchon, Y. (2013). Global climate change in large European rivers: long-term effects on macroinvertebrate communities and potential local confounding factors. *Global Change Biology, 19*, 1085–1099. https://doi.org/10.1111/gcb.12124

Fochetti, R. (2012). Italian freshwater biodiversity: status, threats and hints for its conservation. *Italian Journal of Zoology*, *79*(1), 2–8. https://doi.org/10.1080/11250003.2011.620636

Fochetti, Romolo. (2020). Endemism in the Italian stonefly-fauna (Plecoptera). *Zootaxa*, *4722*(4), 381–388. https://doi.org/10.11646/zootaxa.4722.4.7

Fornaroli, R., Cabrini, R., Sartori, L., Marazzi, F., Vracevic, D., Mezzanotte, V., et al. (2015). Predicting the constraint effect of environmental characteristics on macroinvertebrate density and diversity using quantile regression mixed model. *Hydrobiologia*, *742*, 153–167. https://doi.org/10.1007/s10750-014-1974-6

Fornaroli, R., Cabrini, R., Sartori, L., Marazzi, F., Canobbio, S., & Mezzanotte, V. (2016). Optimal flow for brown trout: habitat – prey optimization. *Science of the Total Environment*, *566–567*, 1568–1578. https://doi.org/10.1016/j.scitotenv.2016.06.047

Fornaroli, R., Calabrese, S., Marazzi, F., Zaupa, S., & Mezzanotte, V. (2019). The influence of multiple controls on structural and functional characteristics of macroinvertebrate community in a regulated Alpine river. *Ecohydrology*, *12*, 1–12. https://doi.org/10.1002/eco.2069

Fornaroli, R., White, J. C., Boggero, A., & Laini, A. (2020). Spatial and temporal patterns of macroinvertebrate assemblages in the River Po catchment (Northern Italy). *Water*, *12*, 1–17. https://doi.org/10.3390/w12092452

Forseth, T., Hurley, M. A., Jensen, A. J., & Elliott, J. M. (2001). Functional models for growth and food consumption of Atlantic salmon parr, *Salmo salar*, from a Norwegian river. *Freshwater Biology*, *46*(2), 173–186. https://doi.org/10.1046/j.1365-2427.2001.00631.x

Forster, J., Hirst, A. G., & Atkinson, D. (2012). Warming-induced reductions in body size are greater in aquatic than terrestrial species. *PNAS*, *109*(47), 19310–19314. https://doi.org/10.1073/pnas.1210460109

Fox, J., Weisberg, S., Price, B., Adler, D., Bates, D., Baud-bovy, G., et al. (2022). Package ‘car.’

Fox, M. J., Muenchen, R., & Putler, D. (2022). Package ‘RcmdrMisc.’

Francoeur, S. N., Biggs, B. J. F., Smith, R. A., & Lowe, R. L. (1999). Nutrient limitation of algal biomass accrual in streams: seasonal patterns and a comparison of methods. *Journal of the North American Benthological Society*, *18*(2), 242–260. https://doi.org/10.2307/1468463

Franquet, E., Dolédec, S., & Chessel, D. (1995). Using multiviriate analyses for separating spatial and temporal effects within species-environment relationships. *Hydrobiologia*, *300–301*(1), 425–431. https://doi.org/10.1007/BF00024484

Fraser, R. H., & Currie, D. J. (1996). The species richness-energy hypothesis in a system where historical factors are thought to prevail: coral reefs. *The American Naturalist*, *148*(1), 138–159. https://doi.org/10.1086/285915

Friesen, M. K., Flannagan, J. F., & Lawrence, S. G. (1979). Effects of temperature and cold-storage on development time and viability of eggs of the burrowing mayfly *Hexagenia-rigida* (Ephemeroptera: Ephemeridae). *Canadian Entomologist*, *111*(6), 665–673.

Frouz, J., Ali, A., & Lobinske, R. J. (2002). Influence of temperature on developmental rate, wing length, and larval head capsule size of pestiferous midge *Chironomus crassicaudatus* (Diptera: Chironomidae). *Journal of Economic Entomology*, *95*(4), 699–705. https://doi.org/10.1603/0022-0493-95.4.699

Frutiger, A. (2004). Ecological impacts of hydroelectric power production on the River Ticino. Part 1: thermal effects. *Hydrobiologia*, 43–56. https://doi.org/10.1127/0003-9136/2004/0159-0043

Fuller, R. L., & Fry, T. J. (1991). The influence of temperature and food quality on the growth of Hydropsyche betteni (Trichoptera) and Simulium vittatum (Diptera). *Journal of Freshwater Ecology*, *6*(1), 75–86. https://doi.org/10.1080/02705060.1991.9665277

Fullerton, A. H., Torgersen, C. E., Lawler, J. J., Faux, R. N., Steel, E. A., Beechie, T. J., et al. (2015). Rethinking the longitudinal stream temperature paradigm: region-wide comparison of thermal infrared imagery reveals unexpected complexity of river temperatures. *Hydrological Processes*, *29*(22), 4719–4737. https://doi.org/10.1002/hyp.10506

Von Fumetti, S., Bieri-Wigger, F., & Nagel, P. (2017). Temperature variability and its influence on macroinvertebrate assemblages of alpine springs. *Ecohydrology*, *10*, 1–9. https://doi.org/https://doi.org/10.1002/eco.1878

Fureder, L., Vacha, C., Amprosi, K., Hansen, C., & Moritz, C. (2002). Reference conditions of alpine streams: physical habitat and ecology. *Water, Air, and Soil Pollution*, *2*, 275–294.

Füreder, L. (1999). High alpine streams: cold habitats for insect larvae. In R. Margesin & F. Schinner (Eds.), *Cold-Adapted Organisms. Ecology, Physiology, Enzymology and Molecular Biology* (pp. 181–196). Heidelberg: Springer. https://doi.org/10.1007/978-3-

662-06285-2_10

Füreder, L., & Niedrist, G. H. (2020). Glacial stream ecology: structural and functional assets. *Water (Switzerland)*, *12*(2), 8–10. https://doi.org/10.3390/w12020376

Fuso, F., Stucchi, L., Bonacina, L., Fornaroli, R., & Bocchiola, D. (2023). Evaluation of water temperature under changing climate and its effect on river habitat in a regulated Alpine catchment. *Journal of Hydrology*, *616*, 128816. https://doi.org/10.1016/j.jhydrol.2022.128816

Fuso, Flavia, Casale, F., Giudici, F., & Bocchiola, D. (2021). Future hydrology of the cryospheric driven lake como catchment in Italy under climate change scenarios. *Climate*, *9*(1), 1–24. https://doi.org/10.3390/cli9010008

Garen, D. C., & Marks, D. (2005). Spatially distributed energy balance snowmelt modelling in a mountainous river basin: Estimation of meteorological inputs and verification of model results. *Journal of Hydrology*, *315*(1–4), 126–153. https://doi.org/10.1016/j.jhydrol.2005.03.026

Gaston, K. J. (1996). Spatial covariance in the species richness of higher taxa. In M. E. Hochberg, M. E. Clobert, & R. Barbault (Eds.), *Aspects of the genesis and maintenance of biological diversity* (pp. 221–242). Oxford: University Oxford Press.

Gaston, K. J. (1999). Why Rapoport’s rule does not generalise. *Oikos*, *84*(2), 309–312.

Gaston, K. J., & Blackburn, T. M. (2000). *Pattern and process in macroecology*. *Pattern and Process in Macroecology*. Oxford: Blackwell Science. https://doi.org/10.1002/9780470999592

Gentili, G., Romano, A., Bucchini, A., & Bardazzi, M. (2001). Studio sull’ecologia dei laghi alpini della Provincia di Bergamo. Bergamo: Provincia di Bergamo.

Gentili, G., Romanò, A., & Porrini, S. (2009). *Fishery Planning of Bergamo Province*.

Gerecke, R., Cantonati, M., Spitale, D., Stur, E., & Wiedenbrug, S. (2011). The challenges of long-term ecological research in springs in the northern and southern Alps: indicator groups, habitat diversity, and medium-term change. *Journal of Limnology*, *70*(SUPPL.), 168–187. https://doi.org/10.3274/JL11-70-S1-13

Gesierich, D., & Kofler, W. (2010). Are algal communities from near-natural rheocrene springs in the Eastern Alps (Vorarlberg, Austria) useful ecological indicators? *Algological Studies*, *133*(April), 1–28. https://doi.org/10.1127/1864-1318/2010/0133-0001

Gibbins, C. N., Dilks, C. F., Malcolm, R., Soulsby, C., & Juggins, S. (2001). Invertebrate communities and hydrological variation in Cairngorm Mountain streams. *Hydrobiologia*, *462*, 205–219. https://doi.org/10.1023/A:1013102704693

Gibbons, J., & Sharitz, R. (1974). Thermal alteration of aquatic ecosystems. *The American Naturalist*, *62*, 660–669.

Gibbonson, J., & Sharitz, R. (1981). Thermal ecology: environmental teachings of a nuclear reactor site. *BioScience*, *31*(4), 293–298.

Gibeau, P., & Palen, W. J. (2020). Predicted effects of flow diversion by run-of-river hydropower on bypassed stream temperature and bioenergetics of salmonid fishes. *River Research and Applications*, *36*(9), 1903–1915. https://doi.org/10.1002/rra.3706

Giberson, D. J., & Rosenberg, D. M. (1992a). Effects of temperature, food quantity, and nymphal rearing density on life-history traits of a Northern population of *Hexagenia* (Ephemeroptera: Ephemeridae). *Journal of the North American Benthological Society*, *11*(2), 181–193. https://doi.org/https://doi.org/10.2307/1467384

Giberson, D. J., & Rosenberg, D. M. (1992b). Egg development in *Hexagenia limbata* (Ephemeroptera: Ephemeridae) from Southern Indian Lake, Manitoba: temperature effects and diapause. *Journal of the North American Benthological Society*, *11*(2), 194–203. https://doi.org/10.2307/1467385

Giersch, J. J., Jordan, S., Luikart, G., Jones, L. A., Hauer, F. R., & Muhlfeld, C. C. (2015). Climate-induced range contraction of a rare alpine aquatic invertebrate. *Freshwater Science*, *34*(1), 53–65. https://doi.org/10.1086/679490

Gillooly, J. F., & Dodson, S. I. (2000a). The relationship of egg size and incubation temperature to embryonic development time in univoltine and multivoltine aquatic insects. *Freshwater Biology*, *444*, 595–604. https://doi.org/10.1017/S095283690000710X

Gillooly, J. F., & Dodson, S. I. (2000b). The relationship of neonate mass and incubation temperature to embryonic development time in a range of animal taxa. *Journal of Zoology*, *251*(3), 369–375. https://doi.org/10.1017/S095283690000710X

Gilman, S. E., Urban, M. C., Tewksbury, J., Gilchrist, G. W., & Holt, R. D. (2010). A framework for community interactions under climate change. *Trends in Ecology and Evolution*, *25*, 325–331. https://doi.org/10.1016/j.tree.2010.03.002

Gintz, D., Hassan, M. A., & Schmidt, K. H. (1996). Frequency and magnitude of bedload transport in a mountain river. *Earth Surface Processes and Landforms*, *21*(5), 433–445. https://doi.org/10.1002/(SICI)1096-9837(199605)21:5<433::AID-ESP580>3.0.CO;2-P

Glazier, D. S. (2012). Temperature affects food-chain length and macroinvertebrate species richness in spring ecosystems. *Freshwater Science*, *31*(2), 575–585. https://doi.org/10.1899/11.058.1

Gong, Z., Xie, P., & Li, Y. (2002). Effect of temperature and photoperiod on hatching of eggs of *Tokunagayusurika akamusi* (Tokunaga) (Diptera: Chironomidae). *Journal of Freshwater Ecology*, *17*(1), 169–170. https://doi.org/10.1080/02705060.2002.9663881

Gordon, T. A. C., Neto-Cerejeira, J., Furey, P. C., & O'Gorman, E. J. (2018). Changes in feeding selectivity of freshwater invertebrates across a natural thermal gradient. *Current Zoology*, *64*(2), 231–242. https://doi.org/10.1093/cz/zoy011

Gore, J. A., & Banning, J. (2017). Discharge measurements and streamflow analysis. In F. R. Hauer & G. A. Lamberti (Eds.), *Methods in Stream Ecology* (Third, pp. 49–70). Elsevier. https://doi.org/10.1016/B978-0-12-416558-8.00003-2

Goslee, S. C., & Urban, D. L. (2007). The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software*, *22*(7), 1–19. https://doi.org/10.18637/jss.v022.i07

Gresens, S. E. (1997). Interactive effects of diet and thermal regime on growth of the midge Pseudochironomus richardsoni Malloch. *Freshwater Biology*, *38*, 365–373. https://doi.org/10.1046/j.1365-2427.1997.00248.x

Griffiths, D., Mcgonigle, C., & Quinn, R. (2014). Climate and species richness patterns of freshwater fish in North America and Europe. *Journal of Biogeography*, *41*(3), 452–463. https://doi.org/10.1111/jbi.12216

Groppelli, B., Confortola, G., Soncini, A., D., B., & Rosso, R. (2011). Assessment of future river habitat suitability under climate change scenarios in a mesoscale Alpine watershed of Italy (Serio River, Italian Alps). In *American Geophysical Union. Fall meeting*.

Groppelli, B., Soncini, A., Bocchiola, D., & Rosso, R. (2011). Evaluation of future hydrological cycle under climate change scenarios in a mesoscale Alpine watershed of Italy. *Natural Hazards and Earth System Science*, *11*(6), 1769–1785. https://doi.org/10.5194/nhess-11-1769-2011

Groppelli, B., Bocchiola, D., & Rosso, R. (2011). Spatial downscaling of precipitation from GCMs for climate change projections using random cascades: a case study in Italy. *Water Resources Research*, *47*(3), 1–18. https://doi.org/10.1029/2010WR009437

Grueber, C. E., Nakagawa, S., Laws, R. J., & Jamieson, I. G. (2011). Multimodel inference in ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology*, *24*(4), 699–711. https://doi.org/10.1111/j.1420-9101.2010.02210.x

Gustafson, M. P. (2008). Effects of thermal regime on mayfly assemblages in mountain streams. *Hydrobiologia*, *605*, 235–246. https://doi.org/10.1007/s10750-008-9357-5

Haase, P., Pilotto, F., Li, F., Sundermann, A., Lorenz, A. W., Tonkin, J. D., & Stoll, S. (2019). Moderate warming over the past 25 years has already reorganized stream invertebrate communities. *Science of the Total Environment*, *658*, 1531–1538. https://doi.org/10.1016/j.scitotenv.2018.12.234

Haidekker, A., & Hering, D. (2008). Relationship between benthic insects (Ephemeroptera, Plecoptera, Coleoptera, Trichoptera) and temperature in small and medium-sized streams in Germany: a multivariate study. *Aquatic Ecology*, *42*(3), 463–481. https://doi.org/10.1007/s10452-007-9097-z

Hamburger, K., Dall, P. C., & Lindegaard, C. (1994). Energy metabolism of *Chironomus anthracinus* (Diptera: Chironomidae) from the profundal zone of Lake Esrom, Denmark, as a function of body size, temperature and oxygen concentration. *Hydrobiologia*, *294*(1), 43–50. https://doi.org/10.1007/BF00017624

Hannah, D. M., & Garner, G. (2015). River water temperature in the United Kingdom: Changes over the 20th century and possible changes over the 21st century. *Progress in Physical Geography*, *39*(I), 68–92. https://doi.org/10.1177/0309133314550669

Hansson, L. A. (1992). Factors regulating periphytic algal biomass. *Limnology and Oceanography*, *37*(2), 322–328. https://doi.org/10.4319/lo.1992.37.2.0322

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. *Global Change Biology*, *12*(1), 10–26. https://doi.org/10.1111/j.1365-2486.2005.001051.x

Harper, P. P., & Pilon, J.-G. (1970). Annual patterns of emergence of some Quebec stoneflies (Insecta: Plecoptera). *Canadian Journal of Zoology*, *48*(4), 681–694. https://doi.org/10.1139/z70-126

Harris, T. D., & Graham, J. L. (2015). Preliminary evaluation of an in vivo fluorometer to quantify algal periphyton biomass and community composition. *Lake and Reservoir Management*, *31*(2), 127–133. https://doi.org/10.1080/10402381.2015.1025153

Harvell, C. D., Mitchell, C. E., Ward, J. R., Altizer, S., Dobson, A. P., Ostfeld, R. S., & Samuel, M. D. (2002). Climate warming and disease risks for terrestrial and marine biota. *Science*, *296*(5576), 2158–2162. https://doi.org/10.1126/science.1063699

Hassall, C., & Thompson, D. J. (2008). The effects of environmental warming on odonata: a review. *International Journal of Odonatology*, *11*(2), 131–153. https://doi.org/10.1080/13887890.2008.9748319

Hassall, Chirstopher, Thompson, D. J., French, G. C., & Harvey, I. F. (2007). Historical changes in the phenology of British Odonata are related to climate. *Global Change Biology*, *13*, 933–941. https://doi.org/10.1111/j.1365-2486.2007.01318.x

Hassall, Christopher. (2013). Time stress and temperature explain continental variation in damselfly body size. *Ecography*, *36*, 894–903. https://doi.org/10.1111/j.1600-0587.2013.00018.x

Hauer, F. R., & Lamberti, G. A. (2017). *Methods in stream ecology*. (F. Richard Hauer & G. A. Lamberti, Eds.) (Third, Vol. 1). San Diego, California: Elsevier. https://doi.org/10.2307/2266075

Hauer, F. R., & Resh, V. H. (2017). Macroinvertebrates. In F. R. Hauer & G. A. Lamberti (Eds.), *Methods in Stream Ecology* (Third, Vol. 1, pp. 297–319). San Diego, California, California: Elsevier. https://doi.org/10.1016/B978-0-12-416558-8.00015-9

Hawkins, B. A., Field, R., Cornell, H. V, Currie, D. J., Guégan, J., Kaufman, D. M., et al. (2003). Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, *84*(12), 3105–3117. https://doi.org/https://doi.org/10.1890/03-8006

Hawkins, C. P., Hogue, J. N., Decker, L. M., & Feminella, J. W. (1997). Channel morphology, water temperature, and assemblage structure of stream insects. *Journal of the North American Benthological Society*, *16*(4), 728–749. https://doi.org/10.2307/1468167

Hayashi, F. (1988). Life history variation in a dobsonfly, *Protohermes grandis* (Megaloptera: Corydalidae): effects of prey availability and temperature. *Freshwater Biology*, *19*, 205–216. https://doi.org/10.1111/j.1365-2427.1988.tb00343.x

Hayashi, F. (1996). Life cycle of *Protohermes immaculatus* (Megaloptera: Corydalidae) accelerated by warm water overflowing a dam. *Aquatic Insects*, *18*(2), 101–110. https://doi.org/10.1080/01650429609361609

Hedin, L. O., Von Fischer, J. C., Ostrom, N. E., Kennedy, B. P., Brown, M. G., & Philip Robertson, G. (1998). Thermodynamic constraints on nitrogen transformations and other biogeochemical processes at soil-stream interfaces. *Ecology*, *79*(2), 684–703. https://doi.org/10.1890/0012-9658(1998)079[0684:TCONAO]2.0.CO;2

Heggenes, J., Stickler, M., Alfredsen, K., Brittain, J. E., Adeva Bustos, A., & Huusko, A.

(2017). Stay cool: temperature changes and biological responses in hydropower-regulated northern river systems. *University College of Southeast Norway*, (21), 89.

Heino, J., Virkkala, R., & Toivonen, H. (2009). Climate change and freshwater biodiversity: detected patterns, future trends and adaptations in northern regions. *Biological Reviews*, *84*(1), 39–54. https://doi.org/10.1111/j.1469-185X.2008.00060.x

Hering, D., Moog, O., Sandin, L., & Verdonschot, P. F. M. (2004). Integrated assessment of running waters in Europe. *Integrated Assessment of Running Waters in Europe*, 1–20. https://doi.org/10.1007/978-94-007-0993-5

Hering, D., Schmidt-Kloiber, A., Murphy, J., Lücke, S., Zamora-Muñoz, C., López-Rodríguez, M. J., et al. (2009). Potential impact of climate change on aquatic insects: a sensitivity analysis for European caddisflies (Trichoptera) based on distribution patterns and ecological preferences. *Aquatic Sciences*, *71*(1), 3–14. https://doi.org/10.1007/s00027-009-9159-5

Herzog, R., & Hadrys, H. (2017). Long-term genetic monitoring of a riverine dragonfly, *Orthetrum coerulescens* (Odonata: Libellulidae): direct anthropogenic impact versus climate change effects. *PLOS ONE*, *12*(5), 1–14. https://doi.org/10.1371/journal.pone.0178014

Hester, E. T., & Doyle, M. W. (2011). Human impacts to river temperature and their effects on biological processes: a quantitative synthesis. *Journal of the American Water Resources Association*, *47*(3), 571–587. https://doi.org/10.1111/j.1752-1688.2011.00525.x

Hewitt, G. M. (1999). Post-glacial re-colonization of European biota. *Biological Journal of the Linnean Society*, *68*(1–2), 87–112. https://doi.org/10.1111/j.1095-8312.1999.tb01160.x

Hicks, M. (2002). *Evaluating criteria for the protection of aquatic life in Washington’s surface water quality standards*.

Hieber, M., Robinson, C. T., Rushforth, S. R., & Uehlinger, U. (2001). Algal communities associated with different alpine stream types. *Arctic, Antarctic, and Alpine Research*, *33*(4), 447–456. https://doi.org/10.1080/15230430.2001.12003454

Hieber, M., Robinson, C. T., Uehlinger, U., & Ward, J. V. (2005). A comparison of benthic macroinvertebrate assemblages among different types of alpine streams. *Freshwater Biology*, *50*(12), 2087–2100. https://doi.org/10.1111/j.1365-2427.2005.01460.x

Hildrew, A. G., & Edington, J. M. (1979). Factors facilitating the coexistence of

Hydropsychid caddis larvae (Trichoptera) in the same river system. *The Journal of Animal Ecology*, *48*(2), 557. https://doi.org/10.2307/4180

Hildrew, A. G., & Giller, P. S. (1994). Patchiness, species interactions and disturbance in the stream benthos. *Aquatic Ecology: Scale, Pattern and Process*, 21–62.

Hill, W. R., & Dimick, S. M. (2002). Effects of riparian leaf dynamics on periphyton photosynthesis and light utilisation efficiency. *Freshwater Biology*, *47*(7), 1245–1256. https://doi.org/10.1046/j.1365-2427.2002.00837.x

Hill, W. R., Ryon, M. G., & Schilling, E. M. (1995). Light limitation in a stream ecosystem: responses by primary producers and consumers. *Ecology*, *76*(4), 1297–1309.

Hines, J., Reyes, M., & Gessner, M. O. (2016). Density constrains cascading consequences of warming and nitrogen from invertebrate growth to litter decomposition. *Ecology*, *97*(7), 1635–1642. https://doi.org/10.1002/ecy.1447

Hock, R., Bliss, A., Marzeion, B. E. N., Giesen, R. H., Hirabayashi, Y., Huss, M., et al. (2019). GlacierMIP-A model intercomparison of global-scale glacier mass-balance models and projections. *Journal of Glaciology*, *65*(251), 453–467. https://doi.org/10.1017/jog.2019.22

Hoeppli, J. (1926). Studies of free-living nematodes from the thermal waters of Yellostone Park.

Holt, E. A., & Miller, S. W. (2010). Bioindicators: using organisms to measure environmental impacts. *Nature Education Knowledge*, *3*(10), 8.

Horne, B. D., Rutherford, E. S., & Wehrly, K. E. (2004). Simulating effects of hydro-dam alteration on thermal regime and wild steelhead recruitment in a stable-flow Lake Michigan tributary. *River Research and Applications*, *20*(2), 185–203. https://doi.org/10.1002/rra.746

Horne, C. R., Hirst, A. G., & Atkinson, D. (2015). Temperature-size responses match latitudinal-size clines in arthropods, revealing critical differences between aquatic and terrestrial species. *Ecology Letters*, *18*(4), 327–335. https://doi.org/10.1111/ele.12413

Horne, C. R., Hirst, A. G., & Atkinson, D. (2018). Insect temperature–body size trends common to laboratory, latitudinal and seasonal gradients are not found across altitudes. *Functional Ecology*, *32*(4), 948–957. https://doi.org/10.1111/1365-2435.13031

Horner, R. R., & Welch, E. B. (1981). Stream periphyton development in relation to current velocity and nutrients. *Canadian Journal of Fisheries and Aquatic Sciences*, *38*(4), 449–457. https://doi.org/10.1139/f81-062

Horner, R. R., Welch, E. B., Seeley, M. R., & Homer, R. R. (1990). Responses of periphyton to changes in current velocity, suspended sediment and phosphorus concentration. *Freshwater Biology*, *24*, 215–232. https://doi.org/10.1111/J.1365-2427.1990.TB00704.X

Hotaling, S., Shah, A. A., McGowan, K. L., Tronstad, L. M., Giersch, J. J., Finn, D. S., et al. (2020). Mountain stoneflies may tolerate warming streams: evidence from organismal physiology and gene expression. *Global Change Biology*, *26*, 5524–5538. https://doi.org/10.1111/gcb.15294

Howell, D. A., & Voshell, J. J. R. (1982). The effects of body weight and temperature on the metabolic-rate of *Hydropsyche Venularis* nanks (Trichoptera, Hydropsichidae). *Comp. Biochem. Physiol.*, *71*, 401–405. https://doi.org/10.1016/0300-9629(82)90425-X

Huang, E., Chen, Y., Fang, M., Zheng, Y., & Yu, S. (2021). Environmental drivers of plant distributions at global and regional scales. *Global Ecology and Biogeography*, *30*, 697–709. https://doi.org/10.1111/geb.13251

Huey, R. B., & Stevenson, R. D. (1979). Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *Integrative and Comparative Biology*, *19*, 357–366. https://doi.org/10.1093/icb/19.1.357

Humboldt, V. (1808). *Ansichten der Natur mit wissenschaftlichen Erlauterungen*. Tubingen, Germany: J. G. Cotta.

Humpesch, U. H. (1979). Life cycles and growth rates of *Baetis* spp. (Ephemeroptera: Baetidae) in the laboratory and in two stony streams in Austria. *Freshwater Biology*, *9*, 467–479. https://doi.org/10.1111/j.1365-2427.1979.tb01531.x

Humpesch, U. H. (1980a). Effect of temperature on the hatching time of eggs of five *Ecdyonurus* spp. (Ephemeroptera) from Austrian streams and English streams, rivers and lakes. *Journal of Animal Ecology*, *49*(1), 317–333.

Humpesch, U. H. (1980b). Effect of temperature on the hatching time of parthenogenetic eggs of five *Ecdyonurus* spp. and two *Rhithrogena* spp. (Ephemeroptera) from Austrian streams and English rivers and lakes. *British Ecological Society*, *49*(1), 927–937. https://doi.org/https://doi.org/10.2307/4236

Humpesch, U. H. (1981). Effect of temperature on larval growth of *Ecdyonurus dispar* (Ephemeroptera: Heptageniidae) from two English lakes. *Freshwater Biology*, *11*(5), 441–457. https://doi.org/10.1111/j.1365-2427.1981.tb01276.x

Humpesch, U. H. (1982). Effect of fluctuating temperature on the duration of embryonic development in two *Ecdyonurus* spp. and *Rhithrogena cf. hybrida* (Ephemeroptera) from

Austrian streams. *Oecologia*, *55*(3), 285–288. https://doi.org/10.1007/BF00376913

Humpesch, U. H., & Elliott, J. M. (1980). Effect of temperature on the hatching time of eggs of three *Rhithrogena* spp. (Ephemeroptera) from Austrian streams and an English stream and river. *The Journal of Animal Ecology*, *49*(2), 643–661. https://doi.org/10.2307/4269

Huryn, A. D. (1996). Temperature-dependent growth and life cycle of *Deleatidium* (Ephemeroptera: Leptophlebiidae) in two high-country streams in New Zealand. *Freshwater Biology*, *36*(2), 351–361. https://doi.org/10.1046/j.1365-2427.1996.00098.x

Hutchinson, G. E., & MacArthur, R. (1959). A theoretical ecological model of size distributions among species of animals. *The American Naturalist*, *93*(869), 117–125. https://doi.org/https://doi.org/10.1086/282063

Hynes, H. B. N. (1970). *The Ecology of Running Waters*. Toronto: University of Toronto Press. https://doi.org/10.4319/lo.1971.16.3.0593

Ichikawa, Y., Yokoi, T., & Watanabe, M. (2017). Thermal factors affecting egg development in the wandering glider dragonfly, *Pantala flavescens* (Odonata: Libellulidae). *Applied Entomology and Zoology*, *52*(1), 89–95. https://doi.org/10.1007/s13355-016-0457-9

Imholt, C., Gibbins, C. N., Malcolm, I. A., Langan, S., & Soulsby, C. (2010). Influence of riparian cover on stream temperatures and the growth of the mayfly *Baetis rhodani* in an upland stream. *Aquatic Ecology*, *44*, 669–678. https://doi.org/10.1007/s10452-009-9305-0

Ingram, B. R. (1976). Effects of photoperiod and temperature on abnormal wing-pad development in two species of Odonata. *Canadian Journal of Zoology*, *54*(7), 1103–1110. https://doi.org/10.1139/z76-125

Isaak, D. J., Luce, C. H., Rieman, B. E., Nagel, D. E., Peterson, E. E., Horan, D. L., et al. (2010). Effects of climate change and wildfire on stream temperatures and salmonid thermal habitat in a mountain river network. *Ecological Applications*, *20*(5), 1–22. https://doi.org/https://doi.org/10.1890/09-0822.1

Ivković, M., Miliša, M., Previšić, A., Popijač, A., & Mihaljević, Z. (2013). Environmental control of emergence patterns: case study of changes in hourly and daily emergence of aquatic insects at constant and variable water temperatures. *International Review of Hydrobiology*, *98*, 104–115. https://doi.org/10.1002/iroh.201301483

Jackson, F. L., Fryer, R. J., Hannah, D. M., & Malcolm, I. A. (2020). Predictions of national-scale river temperatures: a visualisation of complex space–time dynamics. *Hydrological Processes*, *34*, 2823–2825. https://doi.org/10.1002/hyp.13761

Jackson, H. M., Gibbins, C. N., & Soulsby, C. (2007). Role of discharge and temperature variation in determining invertebrate community structure in a regulated river. *River Research and Applications*, *23*, 651–669. https://doi.org/10.1002/rra

Jacobsen, D., & Dangles, O. (2017). *Ecology of high altitude waters*. (Oxford editor Press, Ed.).

Jacobsen, D., Shultz, R., & Encalada, A. (1997). Structure and diversity of stream invertebrate assemblages: the influence of temperature with altitude and latitude. *Freshwater Biology*, *38*, 247–261. Retrieved from http://ida.lib.uidaho.edu:3278/doi/10.1046/j.1365-2427.1997.00210.x/pdf

Jacobsen, D., Rostgaard, S., & Vásconez, J. J. (2003). Are macroinvertebrates in high altitude streams affected by oxygen deficiency? *Freshwater Biology*, *48*(11), 2025–2032. https://doi.org/10.1046/j.1365-2427.2003.01140.x

Jacobsen, D., Cauvy-Fraunie, S., Andino, P., Espinosa, R., Cueva, D., & Dangles, O. (2014). Runoff and the longitudinal distribution of macroinvertebrates in a glacier-fed stream: Implications for the effects of global warming. *Freshwater Biology*, *59*(10), 2038–2050. https://doi.org/10.1111/fwb.12405

Johansson, M. P., Quintela, M., & Laurila, A. (2016). Genetic divergence and isolation by thermal environment in geothermal populations of an aquatic invertebrate. *Journal of Evolutionary Biology*, *29*, 1701–1712. https://doi.org/10.1111/jeb.12902

Johnson, S. L., & Jones, J. A. (2000). Stream temperature responses to forest harvest and debris flows in western Cascades, Oregon. *Canadian Journal of Fisheries and Aquatic Sciences*, *57*, 30–39. https://doi.org/10.1139/cjfas-57-s2-30

Jones, L. A., Muhlfeld, C. C., & Hauer, F. R. (2017). Temperature. In F. R. Hauer & G. A. Lamberti (Eds.), *Methods in Stream Ecology* (Third, Vol. 1, pp. 109–120). San Diego, California: Elsevier. https://doi.org/10.1016/B978-0-12-416558-8.00006-8

Jonsson, B., & Jonsson, N. (2009). A review of the likely effects of climate change on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular reference to water temperature and flow. *Journal of Fish Biology*, *75*(10), 2381–2447. https://doi.org/10.1111/j.1095-8649.2009.02380.x

Jonsson, M., Hedström, P., Stenroth, K., Hotchkiss, E. R., Vasconcelos, F. R., Karlsson, J., & Byström, P. (2015). Climate change modifies the size structure of assemblages of emerging aquatic insects. *Freshwater Biology*, *60*, 78–88. https://doi.org/10.1111/fwb.12468

Joos, N. (2003). *Spatial-temporal distribution of periphyton in the lower parts of the River Thur: the influence of morphology, hydraulics and hydrology*.

Jordan, S., Giersch, J. J., Muhlfeld, C. C., Hotaling, S., Fanning, L., Tappenbeck, T. H., & Luikart, G. (2016). Loss of genetic diversity and increased subdivision in an endemic alpine stonefly threatened by climate change. *PLOS ONE*, *11*(6), 1–13. https://doi.org/10.1371/journal.pone.0157386

Jourdan, J., O'Hara, R. B., Bottarin, R., Huttunen, K. L., Kuemmerlen, M., Monteith, D., et al. (2018). Effects of changing climate on European stream invertebrate communities: a long-term data analysis. *Science of the Total Environment*, *621*(April), 588–599. https://doi.org/10.1016/j.scitotenv.2017.11.242

Junker, J. R., Cross, W. F., Benstead, J. P., Huryn, A. D., Hood, J. M., Nelson, D., et al. (2020). Resource supply governs the apparent temperature dependence of animal production in stream ecosystems. *Ecology Letters*, *23*, 1809–1819. https://doi.org/10.1111/ele.13608

Kahlert, M., & McKie, B. G. (2014). Comparing new and conventional methods to estimate benthic algal biomass and composition in freshwaters. *Environmental Science: Processes and Impacts*, *16*(11), 2627–2634. https://doi.org/10.1039/c4em00326h

Kamberovic, J., Plenković-Moraj, A., Borojevic, K. K., Udovic, M. G., Žutinic, P., Hafner, D., & Cantonati, M. (2019). Algal assemblages in springs of different lithologies (ophiolites vs. limestone) of the Konjuh Mountain (Bosnia and Herzegovina). *Acta Botanica Croatica*, *78*(1), 66–81. https://doi.org/10.2478/botcro-2019-0004

Karouna-Renier, N. K., & Zehr, J. P. (1999). Ecological implications of molecular biomarkers: assaying sub-lethal stress in the midge *Chironomus tentans* using heat shock protein 70 (HSP-70) expression. *Hydrobiologia*, *401*, 255–264. https://doi.org/10.1023/A:1003730225536

Karr, J. R., & Dudley, D. R. (1981). Ecological perspective on water quality goals. *Environmental Management*, *5*(1), 55–68. https://doi.org/10.1007/BF01866609

Kassambara, A., & Mundt, F. (2020). Factoextra: extract and visualize the results of multivariate data analyses.

Kataoka, T., Tatebe, H., Koyama, H., Mochizuki, T., Ogochi, K., Naoe, H., et al. (2020). Seasonal to decadal predictions with MIROC6: description and basic evaluation. *Journal of Advances in Modeling Earth Systems*, *12*(12), 1–25. https://doi.org/10.1029/2019MS002035

Kaushal, S. S., Likens, G. E., Jaworski, N. A., Pace, M. L., Sides, A. M., Seekell, D., et al. (2010). Rising stream and river temperatures in the United States. *Frontiers in Ecology and the Environment, 8*(9), 461–466. https://doi.org/10.1890/090037

Kędra, M., & Wiejaczka, Ł. (2018). Climatic and dam-induced impacts on river water temperature: assessment and management implications. *Science of the Total Environment*, *626*, 1474–1483. https://doi.org/10.1016/j.scitotenv.2017.10.044

Kelleher, C., Wagener, T., Gooseff, M., McGlynn, B., McGuire, K., & Marshall, L. (2012). Investigating controls on the thermal sensitivity of Pennsylvania streams. *Hydrological Processes*, *26*(5), 771–785. https://doi.org/10.1002/hyp.8186

Killian, J. C., & Lutz, P. E. (1985). Photoperiodic and thermal effects on nymphal development in *Epitheca (Tetragoneuria) cynosura* (Odonata: Libellulidae). *Environmental Entomology*, *14*(6), 142–145. https://doi.org/10.1093/ee/14.2.142

Kim, K. S., Chou, H., Funk, D. H., Jackson, J. K., Sweeney, B. W., & Buchwalter, D. B. (2017). Physiological responses to short-term thermal stress in mayfly (*Neocloeon triangulifer*) larvae in relation to upper thermal limits. *Journal of Experimental Biology*, *220*, 2598–2605. https://doi.org/10.1242/jeb.156919

Kingsolver, J. G., & Huey, R. B. (2008). Size, temperature, and fitness: three rules. *Evolutionary Ecology Research*, *10*(2), 251–268.

Kinouchi, T. (2007). Impact of long-term water and energy consumption in Tokyo on wastewater effluent: implications for the thermal degradation of urban streams. *Hydrological Processes*, *1216*, 1207–1216. https://doi.org/10.1002/hyp

Kishi, D., Murakami, M., Nakano, S., & Maekawa, K. (2005). Water temperature determines strength of top-down control in a stream food web. *Freshwater Biology, 50*, 1315–1322. https://doi.org/10.1111/j.1365-2427.2005.01404.x

Knispel, S., & Lubini, V. (2015). Assessing the stability of stonefly (Plecoptera) biodiversity in the Swiss National Park. *Mitteilungen Der Schweizerischen Entomologischen Gesellschaft*, *88*(2015), 257–271. https://doi.org/10.5281/zenodo.33951

Konrad, C. P., Brasher, A. M. D., & May, J. T. (2008). Assessing streamflow characteristics as limiting factors on benthic invertebrate assemblages in streams across the western United States. *Freshwater Biology, 53*, 1983–1998. https://doi.org/10.1111/j.1365-2427.2008.02024.x

Krajenbrink, H. J., White, J. C., Dunbar, M. J., & Wood, P. J. (2021). Macroinvertebrate and diatom community responses to thermal alterations below water supply reservoirs. *River*

Research and Applications, 1–18. https://doi.org/10.1002/rra.3922

Kreiling, A., Govoni, D. P., & Kristja, B. K. (2022). Invertebrate communities in springs across a gradient in thermal regimes. *PLOS ONE*, 1–20. https://doi.org/10.1371/journal.pone.0264501

Krishnaraj, R., & Pritchard, G. (1995). The influence of larval size, temperature, and components of the functional response to prey density on growth rates of the dragonflies *Lestes disjunctus* and *Coenagrion resolutum* (Insecta: Odonata). *Canadian Journal of Zoology*, *73*(9), 1672–1680. https://doi.org/10.1139/z95-199

Küry, D., Lubini, V., & Stucki, P. (2017a). Index to evaluate the vulnerability to climate change of mayfly, stonefly and caddisfly species in alpine springs. In *Conference Volume: 6th Symposium for Research in Protected Areas* (pp. 357–360).

Küry, D., Lubini, V., & Stucki, P. (2017b). Temperature patterns and factors governing thermal response in high elevation springs of the Swiss Central Alps. *Hydrobiologia*, *793*(1), 185–197. https://doi.org/10.1007/s10750-016-2918-0

Lamberti, G. A., & Steinman, A. D. (1997). A comparison of primary production in stream ecosystems. *Journal of the North American Benthological Society*, *16*(1), 95–104. https://doi.org/10.2307/1468241

Lamberti, G. A., Ashkenas, L. R., Gregory, S. V, & Steinman, A. D. (1987). Effects of three herbivores on periphyton communities in laboratory streams. *Journal of the North American Benthological Society*, *6*(2), 92–104. https://doi.org/https://doi.org/10.2307/1467219

Lambret, P., Hilaire, S., & Stoks, R. (2017). Egg hatching phenology and success of *Lestes macrostigma* in two temporary brackish ponds. *International Journal of Odonatology*, *20*(1), 1–12. https://doi.org/10.1080/13887890.2016.1269690

Lamouroux, N., & Cattanéo, F. (2006). Fish assemblages and stream hydraulics: consistent relations across spatial scales and regions. *River Research and Applications*, *22*(7), 727–737. https://doi.org/10.1002/rra.931

Lamouroux, N., Capra, H., & Pouilly, M. (1998). Predicting habitat suitability for lotic fish: linking statistical hydraulic models with multivariate habitat use models. *Regulated Rivers: Research and Management*, *14*(1), 1–11. https://doi.org/10.1002/(SICI)1099-1646(199801/02)14:1<1::AID-RRR472>3.0.CO;2-D

Lancaster, J., & Downes, B. J. (2010). Linking the hydraulic world of individual organisms to ecological processes: putting ecology into ecohydraulics. *River Research and*

Applications, *26*, 385–403. https://doi.org/10.1002/rra

Lande, R. (1980). Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution, 34*(2), 292–305. https://doi.org/https://doi.org/10.2307/2407393

Lange, K., Meier, P., Trautwein, C., Schmid, M., Robinson, C. T., Weber, C., & Brodersen, J. (2018). Basin-scale effects of small hydropower on biodiversity dynamics. *Frontiers in Ecology and the Environment*, *16*(7), 397–404. https://doi.org/10.1002/fee.1823

Langford, T. E. (1975). The emergence of insects from a British River, warmed by power station cooling-water. *Hydrobiologia*, *47*(1), 91–133. https://doi.org/10.1007/bf00036746

Larned, S. T. (2010). A prospectus for periphyton: recent and future ecological research. *Journal of the North American Benthological Society*, *29*(1), 182–206. https://doi.org/10.1899/08-063.1

Larned, S. T., & Santos, S. R. (2000). Light and nutrient-limited periphyton in low order streams of Oahu, Hawaii. *Hydrobiologia*, *432*(1–3), 101–111. https://doi.org/10.1023/a:1004074004416

Leach, J. A., & Moore, R. D. (2019). Empirical stream thermal sensitivities may underestimate stream temperature response to climate warming. *Water Resources Research*, *55*(7), 5453–5467. https://doi.org/10.1029/2018WR024236

Legendre, P. (2019). A temporal beta-diversity index to identify sites that have changed in exceptional ways in space–time surveys. *Ecology and Evolution, 9*(6), 3500–3514. https://doi.org/10.1002/ece3.4984

Leggott, M., & Pritchard, G. (1985). The effect of temperature on rate of egg and larval development in populations of Argia vivida Hagen (Odonata: Coenagrionidae) from habitats with different thermal regimes. *Canadian Journal of Zoology*, *63*, 2578–2582. https://doi.org/10.1139/z85-384

Lehner, B., Döll, P., Alcamo, J., Henrichs, T., & Kaspar, F. (2006). Estimating the impact of global change on flood and drought risks in Europe: a continental, integrated analysis. *Climatic Change*, *75*(3), 273–299. https://doi.org/10.1007/s10584-006-6338-4

Lencioni, V. (2004). Survival strategies of freshwater insects in cold environments. *Journal of Limnology*, *63*, 45–55. https://doi.org/10.4081/jlimnol.2004.s1.45

Lencioni, V., Bernabò, P., Cesari, M., Rebecchi, L., & Cesari, M. (2013). Thermal stress induces HSP70 proteins synthesis in larvae of the cold stream non-biting midge Diamesa cinerella Meigen. *Archives of Insect Biochemistry and Physiology*, *83*(1), 1–14.

https://doi.org/10.1002/arch.21088

Lessard, J. L., & Hayes, D. B. (2003). Effects of elevated water temperature on fish and macroinvertebrate communities below small dams. *River Research and Applications, 19,* 721–732. https://doi.org/10.1002/rra.713

Li, F., Cai, Q., & Liu, J. (2009). Temperature-dependent growth and life cycle of <i>Nemoura sichuanensis<i> (Plecoptera: Nemouridae) in a Chinese mountain stream. *International Review of Hydrobiology*, *94*(5), 595–608. https://doi.org/10.1002/iroh.200911180

Li, F., Chung, N., Bae, M. J., Kwon, Y. S., & Park, Y. S. (2012). Relationships between stream macroinvertebrates and environmental variables at multiple spatial scales. *Freshwater Biology*, *57*(10), 2107–2124. https://doi.org/10.1111/j.1365-2427.2012.02854.x

Li, F., Chung, N., Bae, M. J., Kwon, Y. S., Kwon, T. S., & Park, Y. S. (2013). Temperature change and macroinvertebrate biodiversity: assessments of organism vulnerability and potential distributions. *Climatic Change*, *119,* 421–434. https://doi.org/10.1007/s10584-013-0720-9

Li, J., Johnson, S., & Sobota, J. (2011). Three responses to small changes in stream temperature by autumn-emerging aquatic insects. *Journal of the North American Benthological Society*, *30*(2), 474–484. https://doi.org/10.1899/10-024.1

Lillehammer, A. (1985). Temperture influence on egg incubation period and nymphal growth on the stoneflies *Leucra digitata* and *L. fusca* (Plecoptera: Leuctridae). *Entomologia Generalis, 11*(1–2), 59–67.

Lillehammer, A. (1986). The effect of temperature on the egg incubation period and nymphal growth of two Nemoura species (Plecoptera) from Subarctic Fennoscandia. *Aquatic Insects*, *8*(4), 223–235. https://doi.org/10.1080/01650428609361257

Lindeman, R. L. (1942). The trophic-dynamic aspect of ecology. *Ecology*, *23*(4), 399–417.

Lombardy Region. Regolamento regionale 22/9/2003 (2003).

Lopez-Martinez, G., Elnitsky, M. A., Benoit, J. B., Lee, R. E., & Denlinger, D. L. (2008). High resistance to oxidative damage in the Antarctic midge *Belgica antarctica*, and developmentally linked expression of genes encoding superoxide dismutase, catalase and heat shock proteins. *Insect Biochemistry and Molecular Biology, 38,* 796–804. https://doi.org/10.1016/j.ibmb.2008.05.006

López-Rodríguez, M. J., de Figueroa, J. M. T., & Alba-Tercedor, J. (2009). The life history of *Serratella ignita* (Poda, 1761) (Insecta: Ephemeroptera) in a temporary and permanent

Mediterranean stream. *Aquatic Sciences*, *71*(2), 179–188. https://doi.org/10.1007/s00027-009-9211-5

Lowe, C. H., & Vance, V. J. (1955). Acclimation of the critical thermal maximum of the reptile *Urosaurus ornatus*. *Science, 122*(3158), 73–74. https://doi.org/10.1126/science.122.3158.73

Lowney, C. L. (2000). Stream temperature variation in regulated rivers: evidence for a spatial pattern in daily minimum and maximum magnitudes. *Water Resources Research*, *36*(10), 2947–2955.

Lutterschmidt, W. I., & Hutchison, V. H. (1997). The critical thermal maximum: history and critique. *Canadian Journal of Zoology, 75*, 1561–1574. https://doi.org/10.1139/z97-783

Lutz, P. E. (1974). Effects of temperature and photoperiod on larval development in *Tetragoneuria cynosura* (Odonata: Libellulidae). *Ecology, 55*(2), 370–377. https://doi.org/10.2307/1935224

Mackay, R. J. (1984). Life history patterns of *Hydropsyche bronta* and *H. morosa* (Trichoptera: Hydropsychidae) in summer-warm rivers of southern Ontario. *Canadian Journal of Zoology*, *62*(2), 271–275. https://doi.org/10.1139/z84-044

MacPhee, S. A., Arnott, S. E., & Keller, W. (2011). Lake thermal structure influences macroinvertebrate predation on crustacean zooplankton. *Journal of Plankton Research, 33*(10), 1586–1595. https://doi.org/10.1093/plankt/fbr046

Madden, N., Lewis, A., & Davis, M. (2013). Thermal effluent from the power sector: an analysis of once-through cooling system impacts on surface water temperature. *Environmental Research Letters*, *8*, 1–8. https://doi.org/10.1088/1748-9326/8/3/035006

Magurran, A. E., Dornelas, M., Moyes, F., & Henderson, P. A. (2019). Temporal β diversity—A macroecological perspective. *Global Ecology and Biogeography*, *28*(12), 1949–1960. https://doi.org/10.1111/geb.13026

Maheu, A., St-Hilaire, A., Caissie, D., & El-Jabi, N. (2016). Understanding the thermal regime of rivers influenced by small and medium size dams in easter Canada. *River Research and Applications*. https://doi.org/10.1002/rra.3046

Maier, K. J., Kosalwat, P., & Knight, A. W. (1990). Culture of *Chironomus decorus* (Diptera: Chironomidae) and the effect of temperature on its life history. *Environmental Entomology*, *19*(6), 1681–1688. https://doi.org/10.1093/ee/19.6.1681

Maiolini, B., & Lencioni, V. (2001). Longitudinal distribution of macroinvertebrate assemblages in a glacially influenced stream system in the Italian Alps. *Freshwater*

Biology, *46*(12), 1625–1639. https://doi.org/10.1046/j.1365-2427.2001.00849.x

Mao, L., Cavalli, M., Comiti, F., Marchi, L., Lenzi, M. A., & Arattano, M. (2009). Sediment transfer processes in two Alpine catchments of contrasting morphological settings. *Journal of Hydrology*, *364*(1–2), 88–98. https://doi.org/10.1016/j.jhydrol.2008.10.021

Marcarelli, A. M., Baxter, C. V., Mineau, Madeleine, M., & Hall, R. O. (2011). Quantity and quality: unifying food web and ecosystem perspectives on the role of resource subsidies in freshwaters. *Ecology*, *92*(6), 1215–1225. https://doi.org/https://doi.org/10.1890/10-2240.1

Marcogliese, D. J. (2016). The distribution and abundance of parasites in aquatic ecosystems in a changing climate: more than just temperature. *Integrative and Comparative Biology*, *56*(4), 611–619. https://doi.org/10.1093/icb/icw036

Markarian, R. K. (1980). A study of the relationship between aquatic insect growth and water temperature in a small stream. *Hydrobiologia*, *75*, 81–95. https://doi.org/10.1007/BF00006565

Marten, M. (1990). Interspecific variation in temperature dependence of egg development of five congeneric stonefly species (*Protonemura* Kempny, 1898, Nemouridae, Plecoptera). *Hydrobiologia*, *199*, 157–172. https://doi.org/10.1007/BF00005607

Martín-Folgar, R., de la Fuente, M., Morcillo, G., & Martínez-Guitarte, J. L. (2015). Characterization of six small HSP genes from *Chironomus riparius* (Diptera, Chironomidae): differential expression under conditions of normal growth and heat-induced stress. *Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology*, *188*, 76–86. https://doi.org/10.1016/j.cbpa.2015.06.023

Martin, W. J., Garten, C. T., & Gentry, J. B. (1976). Thermal tolerances of dragonfly nymphs. I. Sources of variation in estimating critical thermal maximum. *Physiological Zoology*, *49*(2), 200–205. https://doi.org/10.1086/physzool.49.2.30152540

Martins, R. T., Melo, A. S., Gonçalves, J. F., Campos, C. M., & Hamada, N. (2016). Effects of climate change on leaf breakdown by microorganisms and the shredder *Phylloicus elektoros* (Trichoptera: Calamoceratidae). *Hydrobiologia*, *789*, 31–44. https://doi.org/10.1007/s10750-016-2689-7

Martins, R. T., Gonçalves, J. F., Campos, C. M., Lopes, A., Piedade, M. T. F., & Hamada, N. (2020). Leaf consumption by invertebrate aquatic shredders in the Amazon: effects of climate change and microbial conditioning. *Limnology*, *21*(2), 257–266. https://doi.org/10.1007/s10201-020-00609-z

Mauritsen, T., Bader, J., Becker, T., Behrens, J., Bittner, M., Brokopf, R., et al. (2019). Developments in the MPI-M Earth system model version 1.2 (MPI-ESM1.2) and its response to increasing CO2. *Journal of Advances in Modeling Earth Systems*, *11*(4), 998–1038. https://doi.org/10.1029/2018MS001400

Mbaka, J. G., & Mwaniki, M. W. (2015). A global review of the downstream effects of small impoundments on stream habitat conditions and macroinvertebrates. *Environmental Reviews*, *23*(3), 257–262. https://doi.org/10.1139/er-2014-0080

McAuliffe, J. R. (1984). Resource depression by a stream herbivore: effects on distributions and abundances of other grazers. *Oikos*, *42*(3), 327. https://doi.org/10.2307/3544401

McCafferty, W. P., & Pereira, C. (1984). Effects of developmental thermal regimes on two mayfly species and their taxonomic interpretation. *Annals of the Entomological Society of America*, *77*(1), 69–87. https://doi.org/10.1093/aesa/77.1.69

McCarty, J. D., Cross, W. F., Albertson, L. K., Tumolo, B. B., & Sklar, L. S. (2022). Life histories and production of three Rocky Mountain aquatic insects along an elevation-driven temperature gradient. *Hydrobiologia*, *849*(16), 3633–3652. https://doi.org/10.1007/s10750-022-04978-7

McCauley, S. J., Hammond, J. I., Frances, D. N., & Mabry, K. E. (2015). Effects of experimental warming on survival, phenology, and morphology of an aquatic insect (Odonata). *Ecological Entomology*, *40*, 211–220. https://doi.org/10.1111/een.12175

McCauley, S. J., Hammond, J. I., & Mabry, K. E. (2018). Simulated climate change increases larval mortality, alters phenology, and affects flight morphology of a dragonfly. *Ecosphere*, *9*(3), 1–14. https://doi.org/10.1002/ecs2.2151

McConnell, W. J., & Singler, W. F. (1999). Chlorophyll and productivity in a mountain river. *Limnology and Oceanography*. https://doi.org/https://doi.org/10.4319/lo.1959.4.3.0335

McIntosh, M. D., Benbow, M. E., & Burky, A. J. (2002). Effects of stream diversion on riffle macroinvertebrate communities in a Maui, Hawaii, stream. *River Research and Applications*, *18*(6), 569–581. https://doi.org/10.1002/rra.694

McKie, B.G., & Cranston, P. S. (2005). Size matters: systematic and ecological implications of allometry in the responses of chironomid midge morphological ratios to experimental temperature manipulations. *Canadian Journal of Zoology*, *83*(4), 553–568. https://doi.org/10.1139/Z05-051

McKie, Brendan G., & Pearson, R. G. (2006). Environmental variation and the predator-specific responses of tropical stream insects: effects of temperature and predation on survival and development of Australian Chironomidae (Diptera). *Oecologia*, *149*, 328–339. https://doi.org/10.1007/s00442-006-0454-8

McKie, Brendan G., Cranston, P. S., & Pearson, R. G. (2004). Gondwanan mesotherms and cosmopolitan eurytherms: effects of temperature on the development and survival of Australian Chironomidae (Diptera) from tropical and temperate populations. *Marine and Freshwater Research*, *55*, 759–768. https://doi.org/10.1071/MF04023

Medlyn, B. E., Dreyer, E., Ellsworth, D., Forstreuter, M., Harley, P. C., Kirschbaum, M. U. F., & Roux, X. L. E. (2002). Temperature response of parameters of a biochemically based model of photosynthesis. II. A review of experimental data. *Plant, Cell and Environments*, *25*, 1167–1179. https://doi.org/https://doi.org/10.1046/j.1365-3040.2002.00891.x

Meier, W., Bonjour, C., Wüest, A., & Reichert, P. (2003). Modeling the effect of water diversion on the temperature of mountain streams. *Journal of Environmental Engineering*, *129*(8), 755–764. https://doi.org/10.1061/(asce)0733-9372(2003)129:8(755)

Melbourne, B. A., & Daniel, P. J. (2003). A low-cost sensor for measuring spatiotemporal variation of light intensity on the streambed. *Journal of the North American Benthological Society*, *22*(1), 143–151. https://doi.org/https://doi.org/10.2307/1467983

Mendonça, F. Z., Bernardy, J. V., Oliveira, C. E. K., Oliveira, P. B. G., & De Marco, P. (2018). Temperature effect on the development of tropical dragonfly eggs. *Neotropical Entomology*, *47*, 484–491. https://doi.org/10.1007/s13744-017-0546-7

Menéndez, M., Descals, E., Riera, T., & Moya, O. (2012). Effect of small reservoirs on leaf litter decomposition in Mediterranean headwater streams. *Hydrobiologia*, *691*(1), 135–146. https://doi.org/10.1007/s10750-012-1064-6

Merritt, R. W., Cummins, K. W., & Berg, M. B. (2017). Trophic relationships of macroinvertebrates. In F. R. Hauer & G. A. Lamberti (Eds.), *Methods in Stream Ecology* (Third, Vol. 1, pp. 413–433). Elsevier. https://doi.org/10.1016/B978-0-12-416558-8.00020-2

Messager, M. L., Lehner, B., Grill, G., Nedeva, I., & Schmitt, O. (2016). Estimating the volume and age of water stored in global lakes using a geo-statistical approach. *Nature Communications*, *7*, 1–11. https://doi.org/10.1038/ncomms13603

Michel, A., Råman Vinnå, L., Bouffard, D., Epting, J., Huwald, H., Schaefli, B., et al. (2021). *Evolution of stream and lake water temperature under climate change*. Federal Office for the Environment (FOEN). https://doi.org/10.16904/envidat.207

Michel, A, Schaefli, B., Wever, N., Zekollari, H., Lehning, M., & Huwald, H. (2022). Future water temperature of rivers in Switzerland under climate change investigated with physics-based models. *Hydrology and Earth System Sciences*, *26*(4), 1063–1087. https://doi.org/10.5194/hess-26-1063-2022

Michel, Adrien, Brauchli, T., Lehning, M., Schaefli, B., & Huwald, H. (2020). Stream temperature and discharge evolution in Switzerland over the last 50 years: annual and seasonal behaviour. *Hydrology and Earth System Sciences*, *24*, 115–142. https://doi.org/10.5194/hess-24-115-2020

Milner, A. M., & Petts, G. E. (1994). Glacial rivers: physical habitat and ecology. *Freshwater Biology*, *32*, 295–307. https://doi.org/10.1111/j.1365-2427.1994.tb01127.x

Milner, A. M., Brittain, J. E., Castella, E., & Petts, G. E. (2001). Trends of macroinvertebrate community structure in glacier-fed rivers in relation to environmental conditions: a synthesis. *Freshwater Biology*, *46*, 1833–1847.

Milner, A. M., Brittain, J. E., Brown, L. E., & Hannah, D. M. (2010). Water sources and habitat of Alpine streams. *Alpine Waters*, (2010), 175–191. https://doi.org/10.1007/978-3-540-88275-6_9

Milner, Alexander M, Brown, L. E., & Hannah, D. M. (2009). Hydroecological response of river systems to shrinking glaciers. *Hydrological Processes*, *23*, 62–77. https://doi.org/10.1002/hyp.7197

Minckley, W. L., & Minckley, C. O. (1986). *Cyprinodon pachycephalus*, a new species of pupfish (Cyprinodontidae) from the Chihuahuan desert of Northern México. *Copeia*, *1*, 184–192. https://doi.org/10.2307/1444904

Mirauda, D., Greco, M., & Moscarelli, P. (2011). *Practical methods for water discharge measurements in fluvial sections*. *WIT Transactions on ecology and the environment* (Vol. 146). https://doi.org/10.2495/RM110301

Mochizuki, S., Kayaba, Y., & Tanida, K. (2006). Larval growth and development in the caddisfly *Cheumatopsyche brevilineata* under natural thermal regimes. *Entomological Science*, *9*, 129–136. https://doi.org/10.1111/j.1479-8298.2006.00160.x

Modlin, R. F., & Jayne, R. D. (1981). The effect of temperature on the oxygen consumption of three species of *Isoperla* (Plecoptera: Perlodidae). *Journal of Freshwater Ecology*, *1*(3), 299–306. https://doi.org/10.1080/02705060.1981.9664045

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.

Mondy, N., Cathalan, E., Hemmer, C., & Voituron, Y. (2011). The energetic costs of case construction in the caddisfly *Limnephilus rhombicus*: direct impacts on larvae and delayed impacts on adults. *Journal of Insect Physiology*, *57*(1), 197–202. https://doi.org/10.1016/j.jinsphys.2010.11.009

Montejano, G., & Absalon, I. (2009). *Caracterizaciòn del habitat acuatico asociado al pez Cypeinodes (nsp.) julimes*.

Moody, E. K., Rugenski, A. T., Sabo, J. L., Turner, B. L., & Elser, J. J. (2017). Does the growth rate hypothesis apply across temperatures? Variation in the growth rate and body phosphorus of Neotropical benthic grazers. *Frontiers in Environmental Science*, *5*, 1–11. https://doi.org/10.3389/fenvs.2017.00014

Moore, J. W., & Schindler, D. E. (2008). Biotic disturbance and benthic community dynamics in salmon-bearing streams. *Journal of Animal Ecology*, *77*, 275–284. https://doi.org/10.1111/j.1365-2656.2007.01336.x

Moore, M. K., & Townsend, V. R. (1998). The interaction of temperature, dissolved oxygen and predation pressure in an aquatic predator-prey system. *Oikos*, *81*, 329–336. https://doi.org/10.2307/3547053

Morgan, L. V. (2016). Biogeography of river algae. In O. Necchi (Ed.), *River Algae* (pp. 1–279). Spriger. https://doi.org/10.1007/978-3-319-31984-1

Morid, R., Shimatani, Y., & Sato, T. (2020). An integrated framework for prediction of climate change impact on habitat suitability of a river in terms of water temperature, hydrological and hydraulic parameters. *Journal of Hydrology*, *587*, 124936. https://doi.org/10.1016/j.jhydrol.2020.124936

Morin, A., Lamoureux, W., & Busnarda, J. (1999). Empirical models predicting primary productivity from chlorophyll a and water temperature for stream periphyton and lake and ocean phytoplankton. *Journal of the North American Benthological Society*, *18*(3), 299–307. https://doi.org/10.2307/1468446

Mosisch, T. D., Bunn, S. E., Davies, P. M., & Marshall, C. J. (1999). Effects of shade and nutrient manipulation on periphyton growth in a subtropical stream. *Aquatic Botany*, *64*(2), 167–177. https://doi.org/10.1016/S0304-3770(99)00014-5

Muhlfeld, C. C., Cline, T. J., Giersch, J. J., Peitzsch, E., Florentine, C., Jacobsen, D., & Hotaling, S. (2020). Specialized meltwater biodiversity persists despite widespread deglaciation. *Proceedings of the National Academy of Sciences of the United States of*

America, *117*(22). https://doi.org/10.1073/pnas.2001697117

Muller, K. (1954). *Investigations on the organic drift in North Swedish streams*. *Institute of Freshwater Research, Drottningholm* (Vol. 35).

Munari, C. (2011). Effects of the 2003 European heatwave on the benthic community of a severe transitional ecosystem (Comacchio Saltworks, Italy). *Marine Pollution Bulletin*, *62*, 2761–2770. https://doi.org/10.1016/j.marpolbul.2011.09.011

Mustonen, K. R., Mykrä, H., Marttila, H., Sarremejane, R., Veijalainen, N., Sippel, K., et al. (2018). Thermal and hydrologic responses to climate change predict marked alterations in boreal stream invertebrate assemblages. *Global Change Biology*, *24*(6), 2434–2446. https://doi.org/10.1111/gcb.14053

Nakagawa, S., Johnson, P. C. D., & Schielzeth, H. (2017). The coefficient of determination R2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *Journal of the Royal Society Interface*, *14*(134). https://doi.org/10.1098/rsif.2017.0213

Navarro, F. K. S. P., & Gonçalves Júnior, J. F. (2017). Effect of leaf decomposition stage and water temperature on fragmentation activity of a shredder invertebrate species in lotic ecosystems. *Iheringia. Serie Zoologia*, *107,* 1–6. https://doi.org/10.1590/1678-4766e2017017

Nebeker, A. V. (1971). Effect of high winter water temperatures on adult emergence of aquatic insects. *Water Research*, *5*(9), 777–783. https://doi.org/10.1016/0043-1354(71)90100-X

Necchi, O., Branco, C. C. Z., Simão, R. C. G., & Branco, L. H. Z. (1995). Distribution of stream macroalgae in the northwest region of São Paulo State, southeastern Brazil. *Hydrobiologia*, *299*(3), 219–230. https://doi.org/10.1007/BF00767329

Nelson, D., Benstead, J. P., Huryn, A. D., Cross, W. F., Hood, J. M., Johnson, P. W., et al. (2017). Shifts in community size structure drive temperature invariance of secondary production in a stream-warming experiment. *Ecology*, *98*(7), 1797–1806. https://doi.org/10.1002/ecy.1857

Newbold, J. D., Sweeney, B. W., & Vannote, R. L. (1994). A model for seasonal synchrony in stream mayflies. *Journal of the North American Benthological Society*, *13*(1), 3–18. https://doi.org/10.2307/1467261

Niedrist, G. H., & Füreder, L. (2020). Real-time warming of alpine streams: (re)defining invertebrates’ temperature preferences. *River Research and Applications*, 1–11.

https://doi.org/10.1002/rra.3638

Nilsson-Örtman, V., Stoks, R., Block, M. De, & Johansson, F. (2012). Generalists and specialists along a latitudinal transect: patterns of thermal adaptation in six species of damselflies. *Ecology*, *93*(6), 1340–1352.

Nilsson-Örtman, V., Stoks, R., De Block, M., & Johansson, F. (2013). Latitudinal patterns of phenology and age-specific thermal performance across six *Coenagrion* damselfly species. *Ecological Monographs*, *83*(4), 491–510. https://doi.org/10.1890/12-1383.1

Nilsson-Örtman, V., Stoks, R., De Block, M., Johansson, H., & Johansson, F. (2013). Latitudinally structured variation in the temperature dependence of damselfly growth rates. *Ecology Letters*, *16*, 64–71. https://doi.org/10.1111/ele.12013

Nilsson-Örtman, V., Stoks, R., & Johansson, F. (2014). Competitive interactions modify the temperature dependence of damselfly growth rates. *Ecology*, *95*(5), 1394–1406. https://doi.org/10.1890/13-0875.1

Nukazawa, K., Shiraiwa, J. ichi, & Kazama, S. (2011). Evaluations of seasonal habitat variations of freshwater fishes, fireflies, and frogs using a habitat suitability index model that includes river water temperature. *Ecological Modelling*, *222*, 3718–3726. https://doi.org/https://doi.org/10.1016/j.ecolmodel.2011.09.005

Nürnberg, G. K. (2007). Lake responses to long-term hypolimnetic withdrawal treatments. *Lake and Reservoir Management*, *23*(4), 388–409. https://doi.org/10.1080/07438140709354026

Nyquist, C., Vondracek, B., & Ferrington, L. (2020). The influence of an in-stream thermal gradient on chironomid emergence during winter. *Hydrobiologia*, *847*(15), 3153–3167. https://doi.org/10.1007/s10750-020-04281-3

O’Neill, B. C., Tebaldi, C., Van Vuuren, D. P., Eyring, V., Friedlingstein, P., Hurtt, G., et al. (2016). The scenario model intercomparison project (ScenarioMIP) for CMIP6. *Geoscientific Model Development*, *9*(9), 3461–3482. https://doi.org/10.5194/gmd-9-3461-2016

Oberdoff, T., Guégan, J. -F, & Hugueny, B. (1995). Global scale patterns of fish species richness in rivers. *Ecography*, *18*(4), 345–352. https://doi.org/10.1111/j.1600-0587.1995.tb00137.x

Oberdorff, T., Tedesco, P. A., Hugueny, B., Leprieur, F., Beauchard, O., Brosse, S., & Dürr, H. H. (2011). Global and regional patterns in riverine fish species richness: a review. *International Journal of Ecology*, 2–12. https://doi.org/10.1155/2011/967631

Ocaña, A. (1991). Relationship between nematode species and the physico-chemical characteristics of spring waters. II. Temperature. *Nematol. Medit, 19*, 25–28.

Odum, E. (1962). Relationship between structure nd function in the ecosystem. *Japanese Journal of Ecology*, *12*(3), 108–118. https://doi.org/https://doi.org/10.18960/seitai.12.3_108

Odum, E. P. (1968). Energy flow in ecosystems: a historical review. *American Zoologist*, *8*(1), 11–18.

Odum, H. T. (1973). Energy, ecology and economics. *Ambio*, *2 (6)*, 220–227.

Okamura, B., Hartikainen, H., Schmidt-Posthaus, H., & Wahli, T. (2011). Life cycle complexity, environmental change and the emerging status of salmonid proliferative kidney disease. *Freshwater Biology*, *56*(4), 735–753. https://doi.org/10.1111/j.1365-2427.2010.02465.x

Olden, J. D., & Naiman, R. J. (2010). Incorporating thermal regimes into environmental flows assessments: modifying dam operations to restore freshwater ecosystem integrity. *Freshwater Biology*, 86–107. https://doi.org/10.1111/j.1365-2427.2009.02179.x

Olden, J. D., & Poff, N. L. (2003). Redundancy and the choice of hydrologic indices for characterizing streamflow regimes. *River Research and Applications*, *19*(2), 101–121. https://doi.org/10.1002/rra.700

Opik, H., & Rolfe, S. (2005). *The physiology of flowering plants* (Fourth). Cambridge: Cambridge University Press. https://doi.org/http://dx.doi.org/10.1017/CBO9781139164450

Orr, H. G., Simpson, G. L., des Clers, S., Watts, G., Hughes, M., Hannaford, J., et al. (2015). Detecting changing river temperatures in England and Wales. *Hydrological Processes*, *29*, 752–766. https://doi.org/10.1002/hyp.10181

Orr, S. E., & Buchwalter, D. B. (2020). It’s all about the fluxes: temperature influences ion transport and toxicity in aquatic insects. *Aquatic Toxicology*, *221*, 1–7. https://doi.org/10.1016/j.aquatox.2020.105405

Ouahsine, H., Céréghino, R., & Lavandier, P. (1996). Influence of temperature and macrophytes development on the larval population dynamics of *Epeorus sylvicola* Pict (Ephemeroptera) in a torrential river of the «Haut-Atlas de Marrakech» (Morocco). *Annales de Limnologie*, *32*(1), 27–31. https://doi.org/10.1051/limn/1996002

Padfield, D., Lowe, C., Buckling, A., Ffrench-Constant, R., Jennings, S., Shelley, F., et al. (2017). Metabolic compensation constrains the temperature dependence of gross primary production. *Ecology Letters*, *20*, 1250–1260. https://doi.org/10.1111/ele.12820

Pagano, T., Bida, M., & Kenny, J. E. (2014). Trends in levels of allochthonous dissolved organic carbon in natural water: a review of potential mechanisms under a changing climate. *Water, 6*(10), 2862–2897. https://doi.org/10.3390/w6102862

Pandian, T. J., Mathavan, S., & Jeyagopl C. P. (1979). Influence of temperature and body weight on mosquito predation by the dragonfly nymphs *Mesogomphus lineatus*. *Hydrobiologia*, *62*(2), 99–104. https://doi.org/https://doi.org/10.1007/BF00037502

Pareeth, S., Salmaso, N., Adrian, R., & Neteler, M. (2016). Homogenised daily lake surface water temperature data generated from multiple satellite sensors: a long-term case study of a large sub-Alpine lake. *Scientific Reports, 6*, 1–14. https://doi.org/10.1038/srep31251

Parlamento italiano. Decreto legislativo 152/2006 (2006).

Parliament, E. Directive 2006/44/EC of the European Parliament and of the Council, 264 Official Journal of the European Union § (2006).

Patrick, C. J., McGarvey, D. J., Larson, J. H., Cross, W. F., Allen, D. C., Benke, A. C., et al. (2019). Precipitation and temperature drive continental-scale patterns in stream invertebrate production. *Science Advances*, *5*(4), 1–9. https://doi.org/10.1126/sciadv.aav2348

Pedreros, P., Guevara-Mora, M., Stehr, A., Araneda, A., & Urrutia, R. (2020). Response of macroinvertebrate communities to thermal regime in small Mediterranean streams (Southern South America): implications of global warming. *Limnologica*, *81*, 125763. https://doi.org/10.1016/j.limno.2020.125763

Pekárová, P., Miklánek, P., Halmová, D., Onderka, M., Pekár, J., Kucárová, K., et al. (2011). Long-term trend and multi-annual variability of water temperature in the pristine Bela River basin (Slovakia). *Journal of Hydrology*, *400*, 333–340. https://doi.org/10.1016/j.jhydrol.2011.01.048

Pellicciotti, F., Brock, B., Strasser, U., Burlando, P., Funk, M., & Corripio, J. (2005). An enhanced temperature-index glacier melt model including the shortwave radiation balance: development and testing for Haut Glacier d’Arolla, Switzerland. *Journal of Glaciology, 51*(175), 573–587. https://doi.org/10.3189/172756505781829124

Pepin, N., Bradley, R. S., Diaz, H. F., Baraer, M., Caceres, E. B., Forsythe, N., et al. (2015). Elevation-dependent warming in mountain regions of the world. *Nature Climate Change*, *5*, 424–430. https://doi.org/10.1038/nclimate2563

Permanent Secretariat of the Alpine Convention. (2009). *Water and water management* *issues. Report on the state of the Alps*.

Perry, S. A., Perry, W. B., & Stanford, J. A. (1987). Effects of thermal regime on size, growth rates and emergence of two species of stoneflies (Plecoptera: Taeniopterygidae, Pteronarcyidae) in the Flathead River, Montana. *The American Midland Naturalist*, *117*(1), 83–93. https://doi.org/10.2307/2425710

Péry, A. R. R., & Garric, J. (2006). Modelling effects of temperature and feeding level on the life cycle of the midge *Chironomus riparius*: an energy-based modelling approach. *Hydrobiologia*, *553*(1), 59–66. https://doi.org/10.1007/s10750-005-1284-0

Peszek, Ł., Kawecka, B., & Robinson, C. T. (2022). Long-term response of diatoms in high-elevation streams influenced by rock glaciers. *Ecological Indicators*, *144*(June). https://doi.org/10.1016/j.ecolind.2022.109515

Petruzziello, A., Bonacina, L., Marazzi, F., Zaupa, S., Mezzanotte, V., & Fornaroli, R. (2021). Effects of high-altitude reservoirs on the structure and function of lotic ecosystems: a case study in Italy. *Hydrobiologia*, *848*, 1455–1474. https://doi.org/10.1007/s10750-020-04510-9

Petts, G. E., & Bickerton, M. (1994). Influence of water abstraction on the macroinvertebrate community gradient within a glacial stream system: La Borgne d'Arolla, Valais, Switzerland. *Freshwater Biology*, *32*, 375–386. https://doi.org/10.1111/j.1365-2427.1994.tb01133.x

Petts, G. E., & Gurnell, A. M. (2005). Dams and geomorphology: research progress and future directions. *Geomorphology*, *71*(1–2), 27–47. https://doi.org/10.1016/j.geomorph.2004.02.015

Picard, C., Floury, M., Seyedhashemi, H., Morel, M., Pella, H., Lamouroux, N., et al. (2022). Direct habitat descriptors improve the understanding of the organization of fish and macroinvertebrate communities across a large catchment. *PLOS ONE*, *17*(9 September), 1–22. https://doi.org/10.1371/journal.pone.0274167

Piccolroaz, S., Calamita, E., Majone, B., Gallice, A., Siviglia, A., & Toffolon, M. (2016). Prediction of river water temperature: a comparison between a new family of hybrid models and statistical approaches. *Hydrological Processes*, *30*(21), 3901–3917. https://doi.org/10.1002/hyp.10913

Pickup, J., & Thompson, D. J. (1990). The effects of temperature and prey density on the development rates and growth of damselfly larvae (Odonata: Zygoptera). *Ecological Entomology*, *15*, 187–200. https://doi.org/10.1111/j.1365-2311.1990.tb00800.x

Pielou, E. C. (1975). *Ecological diversity*. (Wiley, Ed.). New York.

Piggott, J. J., Townsend, C. R., & Matthaei, C. D. (2015). Climate warming and agricultural stressors interact to determine stream macroinvertebrate community dynamics. *Global Change Biology, 21,* 1887–1906. https://doi.org/10.1111/gcb.12861

Pires, M. M., Périco, E., Renner, S., & Sahlén, G. (2018). Predicting the effects of future climate change on the distribution of an endemic damselfly (Odonata, Coenagrionidae) in subtropical South American grasslands. *Journal of Insect Conservation*, *22*(2), 303–319. https://doi.org/10.1007/s10841-018-0063-y

Pitman, K. J., Moore, J. W., Sloat, M. R., Beaudreau, A. H., Bidlack, A. L., Brenner, R. E., et al. (2020). Glacier retreat and Pacific salmon. *BioScience*, *70*(3), 220–236. https://doi.org/10.1093/biosci/biaa015

Pizarro, H., & Alemanni, M. E. (2005). Variables físico-químicas del agua y su influencia en la biomasa del perifiton en un tramo inferior del Río Luján (Provincia de Buenos Aires). *Ecología Austral*, *15*, 73–88.

Poff, L. N., Pyne, M. I., Bledsoe, B. P., Cuhaciyan, C. C., & Carlisle, D. M. (2010). Developing linkages between species traits and multiscaled environmental variation to explore vulnerability of stream benthic communities to climate change. *Journal of the North American Benthological Society*, *29*(4), 1441–1458. https://doi.org/10.1899/10-030.1

Poff, N. L. R. (1996). A hydrogeography of unregulated streams in the United States and an examination of scale-dependence in some hydrological descriptors. *Freshwater Biology*, *36*, 71–79. https://doi.org/10.1046/j.1365-2427.1996.00073.x

Poff, N. L. R. (1997). Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society*, *16*(2), 391–409. https://doi.org/10.2307/1468026

Poff, N. L. R., Olden, J. D., Vieira, N. K. M., Finn, D. S., Simmons, M. P., & Kondratieff, B. C. (2006). Functional trait niches of North American lotic insects: traits-based ecological applications in light of phylogenetic relationships. *Journal of the North American Benthological Society*, *25*(4), 730–755. https://doi.org/10.1899/0887-3593(2006)025[0730:FTNONA]2.0.CO;2

Poff, N. Leroy, & Zimmerman, J. K. H. (2010). Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. *Freshwater Biology*, *55*, 194–205. https://doi.org/10.1111/j.1365-2427.2009.02272.x

Poff, N. LeRoy, Tharme, R. E., & Arthington, A. H. (2017). *Evolution of environmental fows assessment science, principles, and methodologies*. *Water for the Environment*. https://doi.org/10.1016/B978-0-12-803907-6.00011-5

Poikane, S., Kelly, M., & Cantonati, M. (2016). Benthic algal assessment of ecological status in European lakes and rivers: challenges and opportunities. *Science of the Total Environment*, *568*, 603–613. https://doi.org/10.1016/j.scitotenv.2016.02.027

Polášková, V., Bojková, J., Polášek, M., Šorfová, V., & Horsák, M. (2022). Water temperature stability modulates insect thermal responses at spring fens. *Hydrobiologia*, (0123456789). https://doi.org/10.1007/s10750-022-05008-2

Polato, N. R., Gill, B. A., Shah, A. A., Gray, M. M., Casner, K. L., Barthelet, A., et al. (2018). Narrow thermal tolerance and low dispersal drive higher speciation in tropical mountains. *PNAS*, *115*(49), 12471–12476. https://doi.org/10.1073/pnas.1809326115

Porcal, P., Koprivnjak, J. F., Molot, L. A., & Dillon, P. J. (2009). Humic substances-part 7: the biogeochemistry of dissolved organic carbon and its interactions with climate change. *Environmental Science and Pollution Research*, *16*, 714–726. https://doi.org/10.1007/s11356-009-0176-7

Pörtner, H. O., & Peck, M. A. (2010). Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. *Journal of Fish Biology*, *77*, 1745–1779. https://doi.org/10.1111/j.1095-8649.2010.02783.x

Potapova, M. G., & Charles, D. F. (2002). Benthic diatoms in USA rivers: distributions along spatial and environmental gradients. *Journal of Biogeography*, *29*(2), 167–187. https://doi.org/10.1046/j.1365-2699.2002.00668.x

Power, M. E., & Stewart, A. J. (1987). Disturbance and recovery of an algal assemblage following flooding in an Oklahoma stream. *The American Midland Naturalist*, *117*(2), 333–345. https://doi.org/10.2307/2425975

Prats, J., & Danis, P. A. (2019). An epilimnion and hypolimnion temperature model based on air temperature and lake characteristics. *Knowledge and Management of Aquatic Ecosystems*, *420*(8). https://doi.org/10.1051/kmae/2019001

Prats, J., Val, R., Armengol, J., & Dolz, J. (2010). Temporal variability in the thermal regime of the lower Ebro River (Spain) and alteration due to anthropogenic factors. *Journal of Hydrology*, *387*, 105–118. https://doi.org/10.1016/j.jhydrol.2010.04.002

Preece, R. M., & Jones, H. A. (2002). The effect of Keepit dam on the temperature regime of the Namoi River, Australia. *River Research and Applications*, *18*(4), 397–414.

https://doi.org/10.1002/rra.686

Pritchard, G., & Pelchat, B. (1977). Larval growth and development of *Argia vivida* (Odonata: Coenagrionidae) in warm sulphur pools at Banff, Alberta. *Canadian Entomologist*, *109*(12), 1563–1570. https://doi.org/https://doi.org/10.4039/Ent1091563-12

Pritchard, G., & Zloty, J. (1994). Life histories of two *Ameletus* mayflies (Ephemeroptera) in two mountain streams: the influence of temperature, body size, and parasitism. *Journal of the North American Benthological Society*, *13*(4), 557–568. https://doi.org/https://doi.org/10.2307/1467851

Pritchard, G., Harder, L. D., & Mutch, R. A. (1996). Development of aquatic insect eggs in relation to temperature and strategies for dealing with different thermal environments. *Biological Journal of the Linnean Society*, *58*(2), 221–244. https://doi.org/10.1111/j.1095-8312.1996.tb01432.x

Procter, D. L. C. (1973). The effect of temperature and photoperiod on larval development in Odonata. *Canadian Journal of Zoology*, *51*(11), 1165–1170. https://doi.org/10.1139/z73-169

Pyne, M. I., & Poff, N. L. R. (2017). Vulnerability of stream community composition and function to projected thermal warming and hydrologic change across ecoregions in the western United States. *Global Change Biology*, *23*(1), 77–93. https://doi.org/10.1111/gcb.13437

Quenta-Herrera, E., Daza, A., Lazzaro, X., Jacobsen, D., Dangles, O., & Cauvy-Fraunié, S. (2021). Aquatic biota responses to temperature in a high Andean geothermal stream. *Freshwater Biology*, *66*(10), 1889–1900. https://doi.org/10.1111/fwb.13798

Quenta Herrera, E., Casas, J., Dangles, O., & Pincebourde, S. (2018). Temperature effects on ballistic prey capture by a dragonfly larva. *Ecology and Evolution*, *8*(8), 4303–4311. https://doi.org/10.1002/ece3.3975

Quinn, J. M., & Hickey, C. W. (1990). Characterisation and classification of benthic invertebrate communities in 88 new zealand rivers in relation to environmental factors. *New Zealand Journal of Marine and Freshwater Research*, *24*(3), 387–409. https://doi.org/10.1080/00288330.1990.9516432

Quinn, J. M., Hickey, C. W., & Linklater, W. (1996). Hydraulic influences on periphyton and benthic macroinvertebrates: simulating the effects of upstream bed roughness. *Freshwater Biology*, *35*(2), 301–309. https://doi.org/10.1046/j.1365-2427.1996.d01-

466.x

R Core Team. (2020). R: A Language and Environment for Statistical Computing. Retrieved from www.R-project.org

Raddum, G. G. (1985). Effects of winter warm reservoir release on benthic stream invertebrates. *Hydrobiologia*, *122*, 105–111. https://doi.org/10.1007/BF00032096

Rader, R., & Ward, J. (1990). Mayfly growth and population density in constant and variable temperature regimes. *The Great Basin Naturalist*, *50*(2), 97–106.

Rahbek, C., Borregaard, M. K., Colwell, R. K., Dalsgaard, B., Holt, B. G., Morueta-Holme, N., et al. (2019). Humboldt's enigma: what causes global patterns of mountain biodiversity? *Science*, *365*(6458), 1108–1113. https://doi.org/10.1126/science.aax0149

Rajwa-Kuligiewicz, A., Bialik, R. J., & Rowiński, P. M. (2015). Dissolved oxygen and water temperature dynamics in lowland rivers over various timescales. *Journal of Hydrology and Hydromechanics*, *63*(4), 353–363. https://doi.org/10.1515/johh-2015-0041

Rantanen, M., Karpechko, A. Y., Lipponen, A., Nordling, K., Hyvärinen, O., Ruosteenoja, K., et al. (2022). The Arctic has warmed nearly four times faster than the globe since 1979. *Communications Earth and Environment*, *3*, 1–10. https://doi.org/10.1038/s43247-022-00498-3

Raptis, C. E., van Vliet, M. T. H., & Pfister, S. (2016). Global thermal pollution of rivers from thermoelectric power plants. *Environmental Research Letters*, *11*(10). https://doi.org/10.1088/1748-9326/11/10/104011

Rasmussen, J. B. (1982). The effect of thermal effluent, before and after macrophyte harvesting, on standing crop and species composition of benthic macroinvertebrate communities in Lake Wabamun, Alberta. *Canadian Journal of Zoology*, *60*(12), 3196–3205. https://doi.org/10.1139/z82-405

Reice, S. R. (1994). Nonequilibrium determinants of biological community structure. *American Scientist*, *82*(5), 424–435.

Rempel, R. S., & Carter, J. C. H. (1986). An experimental study on the effect of elevated temperature on the heterotrophic and autotrophic food resources of aquatic insects in a forested stream. *Canadian Journal of Zoology*, *64*(11), 2457–2466. https://doi.org/10.1139/z86-366

Rempel, R. S., & Carter, J. C. H. (1987). Temperature influences on adult size, development, and reproductive potential of aquatic Diptera. *Canadian Journal of Fisheries and Aquatic Sciences*, *44*(10), 1743–1752. https://doi.org/10.1139/f87-213

Resh, V. H. (2008). Which group is best? Attributes of different biological assemblages used in freshwater biomonitoring programs. *Environmental Monitoring and Assessment*, *138*(1–3), 131–138. https://doi.org/10.1007/s10661-007-9749-4

Rex, M. A., Crame, J. A., Stuart, C. T., & Clarke, A. (2005). Large-scale biogeographic patterns in marine mollusks: a confluence of history and productivity? *Ecology*, *86*(9), 2288–2297. https://doi.org/10.1890/04-1056

Reynolds, S. K., & Benke, A. C. (2005). Temperature-dependent growth rates of larval midges (Diptera: Chironomidae) from a southeastern U.S. stream. *Hydrobiologia*, *544*, 69–75. https://doi.org/10.1007/s10750-004-8334-x

Richter, O., Suhling, F., Müller, O., & Kern, D. (2008). A model for predicting the emergence of dragonflies in a changing climate. *Freshwater Biology*, *53*, 1868–1880. https://doi.org/10.1111/j.1365-2427.2008.02012.x

Ridley, J., Menary, M., Kuhlbrodt, T., Andrews, M., & Andrews, T. (2018). MOHC HadGEM3-GC31-LL model output prepared for CMIP6 CMIP. *Earth System Grid Federation*. https://doi.org/https://doi.org/10.22033/ESGF/CMIP6.419

Rier, S. T., & Stevenson, R. J. (2002). Effects of light, dissolved organic carbon, and inorganic nutrients on the relationship between algae and heterotrophic bacteria in stream periphyton. *Hydrobiologia*, *489*, 179–184. https://doi.org/10.1023/A:1023284821485

Rivers-Moore, N. A., Dallas, H. F., & Ross-Gillespie, V. (2012). Life history does matter in assessing potential ecological impacts of thermal changes on aquatic macroinvertebrates. *River Research and Applications*, *29*(9), 1100–1109. https://doi.org/10.1002/rra

Robert, P., & Escoufier, Y. (1976). A unifying tool for linear multivariate statistical methods: the RV- coefficient. *Journal of the Royal Statistical Society*, *25*(3), 257–265.

Robinson, C. T., & Rushforth, S. R. (1987). Effects of physical disturbance and canopy cover on attached diatom community structure in an Idaho stream. *Hydrobiologia*, *154*(1), 49–59. https://doi.org/10.1007/BF00026830

Robinson, C. T., Uehilinger, U., & Gessner, M. O. (2000). Nutrient limitation. In J. V. Ward & U. Uehlingher (Eds.), *Ecology of a Glacial Flood Plain* (pp. 231–241). Springer. https://doi.org/10.1007/978-94-017-0181-5_14

Robinson, C. T., Uehlinger, U., & Hieber, M. (2001). Spatio-temporal variation in macroinvertebrate assemblages of glacial streams in the Swiss Alps. *Freshwater Biology*, *46*(12), 1663–1672. https://doi.org/10.1046/j.1365-2427.2001.00851.x

Robinson, C. T., Tonolla, D., Imhof, B., Vukelic, R., & Uehlinger, U. (2016). Flow intermittency, physico-chemistry and function of headwater streams in an Alpine glacial catchment. *Aquatic Sciences, 78*(2), 327–341. https://doi.org/10.1007/s00027-015-0434-3

Rogowski, D. L., & Stewart, K. R. (2016). Effects of increased temperature on a Trichoptera (Hydropsychidae) from premontane forest streams in Southern Costa Rica. *Tropical Ecology*, *57*(1), 57–68.

Rondinini, C., Battistoni, A., Peronace, V., & Teofili, C. Lista rossa dei vertebrati italiani, 56 WWF Italia. Settore Diversità Biologica § (2013). Retrieved from www.iucn.it

Rosemond, A. D. (1993). Interactions among irradiance, nutrients, and herbivores constrain a stream algal community. *Oecologia*, *94*(4), 585–594. https://doi.org/10.1007/BF00566976

Rosenzweig, M. L. (2010). *Species diversity in space and times*. (Cambridge University Press, Ed.), *Species diversity in space and times* (Second). Cambridge. https://doi.org/https://doi.org/10.1017/CBO9780511623387

Rosero-López, D., Walter, M. T., Flecker, A. S., Ontaneda, D. F., & Dangles, O. (2021). Standardization of instantaneous fluoroprobe measurements of benthic algal biomass and composition in streams. *Ecological Indicators*, *121*, 107185. https://doi.org/10.1016/j.ecolind.2020.107185

Rosillon, D. (1988). Food preference and relative influence of temperature and food quality on life history characteristics of a grazing mayfly, Ephemerella ignita (Poda). *Canadian Journal of Zoology*, *66*(6), 1474–1481. https://doi.org/10.1139/z88-214

Ross-Gillespie, V., Picker, M. D., Dallas, H. F., & Day, J. A. (2018). The role of temperature in egg development of three aquatic insects *Lestagella penicillata* (Ephemeroptera), *Aphanicercella scutata* (Plecoptera), *Chimarra ambulans* (Trichoptera) from South Africa. *Journal of Thermal Biology*, *71*, 158–170. https://doi.org/10.1016/j.jtherbio.2017.11.008

Rott, E., & Wehr, J. D. (2016). The spatio-temporal development of macroalgae in rivers. In O. Necchi (Ed.), *River Algae* (pp. 1–279). Springer. https://doi.org/10.1007/978-3-319-31984-1

Rott, E., Cantonati, M., Füreder, L., & Pfister, P. (2006). Benthic algae in high altitude streams of the Alps - A neglected component of the aquatic biota. *Hydrobiologia*, *562*(1), 195–216. https://doi.org/10.1007/s10750-005-1811-z

Rotvit, L., & Jacobsen, D. (2013). Temperature increase and respiratory performance of macroinvertebrates with different tolerances to organic pollution. *Limnologica*, *43*, 510–515. https://doi.org/10.1016/j.limno.2013.04.003

Saber, A., James, D. E., & Hayes, D. F. (2020). Long-term forecast of water temperature and dissolved oxygen profiles in deep lakes using artificial neural networks conjugated with wavelet transform. *Limnology and Oceanography*, *65*(6), 1297–1317. https://doi.org/10.1002/lno.11390

Saltveit, S. J., & Brittain, J. E. (2016). Contrasting life cycle strategies in mountain and lowland populations of the stonefly, *Amphinemura standfussi*. *Biology of Inland Waters*, 43–50.

Saltveit, S. J., Bremnes, T., & Brittain, J. E. (1994). Effect of changed temperature regime on the benthos of Norwegian regulated river. *Regulated Rivers: Research&menagement*, *9*, 93–102.

Sandin, L., Schmidt-Kloiber, A., Svenning, J. C., Jeppesen, E., & Friberg, N. (2014). A trait-based approach to assess climate change sensitivity of freshwater invertebrates across Swedish ecoregions. *Current Zoology*, *60*(2), 221–232. https://doi.org/10.1093/czoolo/60.2.221

Santiago, J. M., García de Jalón, D., Alonso, C., Solana, J., Ribalaygua, J., Pórtoles, J., & Monjo, R. (2016). Brown trout thermal niche and climate change: expected changes in the distribution of cold-water fish in central Spain. *Ecohydrology, 9*(3), 514–528. https://doi.org/10.1002/eco.1653

Sarvala, J. (1979). Effect of temperature on the duration of egg, nauplius and copepodite development of some freshwater benthic Copepoda. *Freshwater Biology, 9*, 515–534. https://doi.org/10.1111/j.1365-2427.1979.tb01536.x

Sawchyn, W. W., & Church, N. S. (1973). The effects of temperature and photoperiod on diapause development in the eggs of four species of *Lestes* (Odonata: Zygoptera). *Canadian Journal of Zoology, 51*, 1257–1265. https://doi.org/10.1139/z73-179

Scherr, M. A., Wooster, D. E., & Rao, S. (2010). Effects of temperature on growth rate and behavior of *Epeorus albertae* (Ephemeroptera: Heptageniidae) nymphs. *Environmental Entomology, 39*(6), 2017–2024. https://doi.org/10.1603/EN09247

Schmeller, D. S., Weatherdon, L. V., Loyau, A., Bondeau, A., Brotons, L., Brummitt, N., et al. (2018). A suite of essential biodiversity variables for detecting critical biodiversity change. *Biological Reviews, 93*(1), 55–71. https://doi.org/10.1111/brv.12332

Schmidt-Kloiber, A., & Hering, D. (2015). www.freshwaterecology.info - An online tool that unifies, standardises and codifies more than 20,000 European freshwater organisms and their ecological preferences. *Ecological Indicators*, *53*, 271–282. https://doi.org/10.1016/j.ecolind.2015.02.007

Schmitt, T. (2007). Molecular biogeography of Europe: pleistocene cycles and postglacial trends. *Frontiers in Zoology*, *4*, 1–13. https://doi.org/10.1186/1742-9994-4-11

Schülting, L., Feld, C. K., & Graf, W. (2016). Effects of hydro and thermopeaking on benthic macroinvertebrate drift. *Science of the Total Environment*, *573*, 1472–1480. https://doi.org/10.1016/j.scitotenv.2016.08.022

Seyedhashemi, H., Moatar, F., Vidal, J. P., Diamond, J. S., Beaufort, A., Chandesris, A., & Valette, L. (2021). Thermal signatures identify the influence of dams and ponds on stream temperature at the regional scale. *Science of the Total Environment*, *766*, 142667. https://doi.org/10.1016/j.scitotenv.2020.142667

Seyedhashemi, H., Vidal, J., Diamond, J. S., Thiéry, D., Monteil, C., Hendrickx, F., et al. (2022). Regional, multi-decadal analysis on the Loire River basin reveals that stream temperature increases faster than air temperature. *Hydrology and Earth System Sciences*, *26*, 2583–2603. https://doi.org///doi.org/10.5194/hess-26-2583-2022

Shah, A. A., Gill, B. A., Encalada, A. C., Flecker, A. S., Funk, W. C., Guayasamin, J. M., et al. (2017). Climate variability predicts thermal limits of aquatic insects across elevation and latitude. *Functional Ecology*, *00*, 1–10. https://doi.org/10.1111/1365-2435.12906

Shah, A. A., Bacmeister, E. M. S., Rubalcaba, J. G., & Ghalambor, C. K. (2020). Divergence and constraint in the thermal sensitivity of aquatic insect swimming performance. *Current Zoology*, *66*(5), 555–564. https://doi.org/10.1093/cz/zoaa040

Sherberger, F. F., Benfield, E. F., Dickson, K. L., & Cairns, J. (1977a). Effects of thermal shocks on drifting aquatic insects: a laboratory simulation. *Journal of the Fisheries Research Board of Canada*, *34*(4), 529–536. https://doi.org/10.1139/f77-084

Sherberger, F. F., Benfield, E. F., Dickson, K. L., & Cairns, J. (1977b). Effects of thermal shocks on drifting aquatic insects: A laboratory simulation. *Journal of the Fisheries Research Board of Canada*, *34*(4), 529–536. https://doi.org/10.1139/f77-084

Shoup, L., & Houghton, D. (2013). The effect of acclimation temperature on the critical thermal maximum of a cold-water population of *Pteronarcys dorsata* (Say) (Plecoptera: Pteronarcyidae). *The Great Lakes Entomologist*, *46*(3 & 4), 3.

Silva, D. P., Dias, A. C., Lecci, L. S., & Simião-Ferreira, J. (2019). Potential effects of future climate changes on Brazilian cool-adapted stoneflies (Insecta: Plecoptera). *Neotropical Entomology*, *48*(1), 57–70. https://doi.org/10.1007/s13744-018-0621-8

Sinsabaugh, R. L. (1997). Large-scale trends for stream benthic respiration. *Journal of the North American Benthological Society*, *16*(1), 119–122. https://doi.org/https://doi.org/10.2307/1468244

Smith, K., & Lavis, M. E. (1975). Environmental influences on the temperature of a small upland stream. *Oikosikos*, *26*, 228–236.

Smith, M., Odum, E., & Sharitz, R. (2001). *Savannah River Ecology Laboratory*: a model for a cooperative partnership between a university and the federal government. In G. W. Barrett & T. L. Barrett (Eds.), *Holistic Science: the evolution of the Georgia Institute of Ecology* (pp. 95–127). New York: Taylor & Francis.

Smolar-Žvanut, N., & Mikoš, M. (2014). Impact de la régularisation du débit causée par les barrages hydroélectriques sur la communauté périphytique de la rivière Soca, Slovénie. *Hydrological Sciences Journal*, *59*(5), 1032–1045. https://doi.org/10.1080/02626667.2013.834339

Smolinský, R., & Gvoždík, L. (2014). Effect of temperature extremes on the spatial dynamics of predator-prey interactions: a case study with dragonfly nymphs and newt larvae. *Journal of Thermal Biology*, *39*(1), 12–16. https://doi.org/10.1016/j.jtherbio.2013.11.004

Śniegula, S., Golab, M. J., & Johansson, F. (2019). Size-mediated priority and temperature effects on intra-cohort competition and cannibalism in a damselfly. *Journal of Animal Ecology*, *00*, 1–12. https://doi.org/10.1111/1365-2656.12947

Söderström, O. (1988). Effects of temperature and food quality on life-history parameters in *Parameletus chelifer* and *P. minor* (Ephemeroptera): a laboratory study. *Freshwater Biology*, *20*, 295–303. https://doi.org/10.1111/j.1365-2427.1988.tb00455.x

Sommer, C., Malz, P., Seehaus, T. C., Lippl, S., Zemp, M., & Braun, M. H. (2020). Rapid glacier retreat and downwasting throughout the European Alps in the early 21st century. *Nature Communications*, *11*, 1–10. https://doi.org/10.1038/s41467-020-16818-0

Soncini, A., Bocchiola, D., Azzoni, R. S., & Diolaiuti, G. (2017). A methodology for monitoring and modeling of high altitude Alpine catchments. *Progress in Physical Geography*, *41*(4), 393–420. https://doi.org/10.1177/0309133317710832

Söndgerath, D., Rummland, J., & Suhling, F. (2012). Large spatial scale effects of rising temperatures: modelling a dragonfly's life cycle and range throughout Europe. *Insect Conservation and Diversity*, *5*, 461–469. https://doi.org/10.1111/j.1752-

4598.2011.00182.x

Sparks, T. H., Jeffree, E. P., & Jeffree, C. E. (2000). An examination of the relationship between flowering times and temperature at the national scale using long-term phenological records from the UK. *International Journal of Biometeorology, 44,* 82–87. https://doi.org/10.1007/s004840000049

Sperna Weiland, F. C., Van Beek, L. P. H., Kwadijk, J. C. J., & Bierkens, M. F. P. (2012). Global patterns of change in discharge regimes for 2100. *Hydrology and Earth System Sciences, 16*(4), 1047–1062. https://doi.org/10.5194/hess-16-1047-2012

Srivastava, D. S., & Lawton, J. H. (1998). Why more productive sites have more species: an experimental test of theory using tree-hole communities. *The American Naturalist, 152*(4), 510–529. https://doi.org/10.1086/286187

Starr, S. M., & McIntyre, N. E. (2020). Effects of water temperature under projected climate change on the development and survival of Enallagma civile (Odonata: Coenagrionidae). *Environmental Entomology*, *49*(1), 230–237. https://doi.org/10.1093/ee/nvz138

Stegen, J. C., Enquist, B. J., & Ferriere, R. (2009). Advancing the metabolic theory of biodiversity. *Ecology Letters, 12*(10), 1001–1015. https://doi.org/10.1111/j.1461-0248.2009.01358.x

Stendera, S., Adrian, R., Bonada, N., Cañedo-Argüelles, M., Hugueny, B., Januschke, K., et al. (2012). Drivers and stressors of freshwater biodiversity patterns across different ecosystems and scales: a review. *Hydrobiologia, 696*(1), 1–28. https://doi.org/10.1007/s10750-012-1183-0

Stewart, B. A., Close, P. G., Cook, P. A., & Davies, P. M. (2013). Upper thermal tolerances of key taxonomic groups of stream invertebrates. *Hydrobiologia*, *718,* 131–140. https://doi.org/10.1007/s10750-013-1611-9

Stoks, R., Swillen, I., & De Block, M. (2012). Behaviour and physiology shape the growth accelerations associated with predation risk, high temperatures and southern latitudes in *Ischnura damselfly* larvae. *Journal of Animal Ecology*, *81*(5), 1034–1040. https://doi.org/10.1111/j.1365-2656.2012.01987.x

Stoks, R., Geerts, A. N., & De Meester, L. (2014). Evolutionary and plastic responses of freshwater invertebrates to climate change: realized patterns and future potential. *Evolutionary Applications*, *7*(1), 42–55. https://doi.org/10.1111/eva.12108

Storey, A. W. (1987). Influence of temperature and food quality on the life history of an epiphytic chironomid. *Entomologica Scandinavica Supplements*, *29*(1980), 339–347.

Strange, C. D. (1985). The effect of temperature on the egg development of *Protonemura meyeri* Pictet (Plecoptera; Nemouridae). In *Proceedings of the Royal Irish Academy.* (Vol. 85B, pp. 101–106). Royal Irish Academy.

Suhling, F., Suhling, I., & Richter, O. (2015). Temperature response of growth of larval dragonflies – an overview. *International Journal of Odonatology*, *18*(1), 15–30. https://doi.org/10.1080/13887890.2015.1009392

Sunday, J. M., Bates, A. E., & Dulvy, N. K. (2011). Global analysis of thermal tolerance and latitude in ectotherms. *Proceedings of the Royal Society B: Biological Sciences*, *278,* 1823–1830. https://doi.org/10.1098/rspb.2010.1295

Sundermann, A., Antons, C., Cron, N., Lorenz, A. W., Hering, D., & Haase, P. (2011). Hydromorphological restoration of running waters: effects on benthic invertebrate assemblages. *Freshwater Biology*, *56,* 1689–1702. https://doi.org/10.1111/j.1365-2427.2011.02599.x

Šupina, J., Bojková, J., & Boukal, D. S. (2020). Warming erodes individual-level variability in life history responses to predation risk in larvae of the mayfly *Cloeon dipterum*. *Freshwater Biology*, *65,* 2211–2223. https://doi.org/10.1111/fwb.13619

Sutton, R. T., Dong, B., & Gregory, J. M. (2007). Land/sea warming ratio in response to climate change: IPCC AR4 model results and comparison with observations. *Geophysical Research Letters*, *34,* 2–6. https://doi.org/10.1029/2006GL028164

Swaegers, J., Spanier, K. I., & Stoks, R. (2020). Genetic compensation rather than genetic assimilation drives the evolution of plasticity in response to mild warming across latitudes in a damselfly. *Molecular Ecology*, *29*(24), 4823–4834. https://doi.org/10.1111/mec.15676

Sweeney, B. W. (1978). Bioenergetic and developmental response of a mayfly to thermal variation. *Limnology and Oceanography*, *23*(3), 461–477. https://doi.org/https://doi.org/10.4319/lo.1978.23.3.0461

Sweeney, B. W., & Vannote, R. L. (1978). Size variation and the distribution of hemimetabolous aquatic insects: two thermal equilibrium hypotheses. *Science*, *200*(4340), 444–446. https://doi.org/10.1126/science.200.4340.444

Sweeney, B. W., & Vannote, R. L. (1984). Influence of food quality and temperature on life history characteristics of the parthenogenetic mayfly, *Cloeon triangulifer*. *Freshwater Biology*, *14,* 621–630. https://doi.org/10.1111/j.1365-2427.1984.tb00181.x

Sweeney, B. W., Vannote, R. L., & Dodds, P. J. (1986a). Effects of temperature and food quality on growth and development of a mayfly *Leptophlebia intermedia*. *Canadian Journal of Fisheries and Aquatic Sciences*, *43*, 12–18. https://doi.org/https://doi.org/10.1139/f86-00

Sweeney, B. W., Vannote, R. L., & Dodds, P. J. (1986b). The relative importance of temperature and diet to larval development and adult size of the winter stonefly, *Soyedina carolinensis* (Piecoptera: Nemouridae). *Freshwater Biology*, *16*, 39–48. https://doi.org/10.1111/j.1365-2427.1986.tb00946.x

Sweeney, B. W., Funk, D. H., Camp, A. A., Buchwalter, D. B., & Jackson, J. K. (2018). Why adult mayflies of *Cloeon dipterum* (Ephemeroptera: Baetidae) become smaller as temperature warms. *Freshwater Science*, *37*(1), 64–81. https://doi.org/10.1086/696611

Tachet, H., Richoux, P., Bournaud, M., & Usseglio-Polatera, P. (2010). *Invertébrés d'eau douce: systématique, biologie, écologie*. (CNRS éditions, Ed.).

Tan, H., Hirst, A. G., Atkinson, D., & Kratina, P. (2021). Body size and shape responses to warming and resource competition. *Functional Ecology*, *00*, 1–10. https://doi.org/10.1111/1365-2435.13789

Tang, E. P. Y., Tremblay, R., & Vincent, W. F. (1997). Cyanobacterial dominance of polar freshwater ecosystems: are high-latitude mat-formers adapted to low temperature? *Journal of Phycology*, *33*(2), 171–181. https://doi.org/10.1111/j.0022-3646.1997.00171.x

Tansey, M. R., & Brock, T. D. (1972). The upper temperature limit for eukaryotic organisms. *Proceedings of the National Academy of Sciences of the United States of America*, *69*(9), 2426–2428. https://doi.org/10.1073/pnas.69.9.2426

Taylor, M., & Figgis, P. (2007). Protected areas: buffering nature against climate change. In *Proceedings of a WWF and IUCN World Commission on Protected Areas symposium* (pp. 18–19).

Teets, N. M., Kawarasaki, Y., Lee, R. E., & Denlinger, D. L. (2013). Expression of genes involved in energy mobilization and osmoprotectant synthesis during thermal and dehydration stress in the Antarctic midge, *Belgica antarctica*. *Journal of Comparative Physiology B*, *183*, 189–201. https://doi.org/10.1007/s00360-012-0707-2

Tennessen, K. ., Miller, J. L., & Price, J. H. (1982). Hatching success of eggs of *Hexagenia bilineata* (Ephemeroptera) exposed to brief thermal shock. *Journal of Thermal Biology*, *7*, 133–137. https://doi.org/https://doi.org/10.1016/0306-4565(82)90001-8

Thompson, D. J. (1978). Towards a realistic predator-prey model: the effect of temperature on the functional response and life history of larvae of the damselfly, *Ischnura elegans*. *Journal of Animal Ecology*, *47*(3), 757–767. https://doi.org/https://doi.org/10.2307/3669

Tierno de Figueroa, M. J., Fenoglio, S., Lòpez-Rodrìguez, M. J., Sànchez-Castillo, P., & Fochetti, R. (2013). Freshwater biodiversity in the rivers of the Mediterranean Basin. *Hydrobiologia*, *719*, 137–186. https://doi.org/10.1007/s10750-012-1281-z

Timoner, P., Marle, P., Castella, E., & Lehmann, A. (2020). Spatial patterns of mayfly, stonefly and caddisfly assemblages in Swiss running waters in the face of global warming. *Ecography*, *43*, 1–14. https://doi.org/10.1111/ecog.04808

Toffolon, M., & Piccolroaz, S. (2015). A hybrid model for river water temperature as a function of air temperature and discharge. *Environmental Research Letters*, *10*, 114011. https://doi.org/10.1088/1748-9326/10/11/114011

Tonn, W. M. (1990). Climate change and fish communities: a conceptual framework. *Transactions of the American Fisheries Society*, *119*, 337–352. https://doi.org/10.1577/1548-8659(1990)119<0337

Tougeron, K. (2019). Diapause research in insects: historical review and recent work perspectives. *Entomologia Experimentalis et Applicata*, *167*(1), 27–36. https://doi.org/10.1111/eea.12753

Townsend, C. R., Scarsbrook, M. R., Doledec, S., & Dolédec, S. (1997). Quantifying disturbance in streams: alternative measures of disturbance in relation to macroinvertebrate species traits and species richness. *Journal of the North American Benthological Society*, *16*(3), 531–544. https://doi.org/10.2307/1468142

Townsend, C. R., Dolédec, S., & Scarsbrook, M. R. (1997). Species traits in relation to temporal and spatial heterogeneity in streams: a test of habitat templet theory. *Freshwater Biology*, *37*(2), 367–387. https://doi.org/10.1046/j.1365-2427.1997.00166.x

Trottier, R. (1971). Effect of temperature on the life-cycle of anax junzus (Odonata: Aeshnidae) in Canada. *The Canadian Entomologist*, *103*, 1671–1683. https://doi.org/10.4039/Ent1031671-12

Trottier, R. (1973). Influence of temperature and humidity on the emergence behaviour of anax junius (Odonata: Aeshnidae). *The Canadian Entomologist*, *105*(7), 975–984. https://doi.org/10.4039/Ent105975-7

Turner, D., & Williams, D. D. (2005). Sexual dimorphism and the influence of artificial elevated temperatures on body size in the imago of *Nemoura trispinosa* (Plecoptera: Nemouridae). *Aquatic Insects*, *27*(4), 243–252.

https://doi.org/10.1080/01650420500336566

Turner, J. R. G. (2004). Explaining the global biodiversity gradient: energy, area, history and natural selection. *Basic and Applied Ecology*, *5*(5), 435–448. https://doi.org/10.1016/j.baae.2004.08.004

Tüzün, N., Op de Beeck, L., Brans, K. I., Janssens, L., & Stoks, R. (2017). Microgeographic differentiation in thermal performance curves between rural and urban populations of an aquatic insect. *Evolutionary Applications*, *10*, 1067–1075. https://doi.org/10.1111/eva.12512

Uehlinger, U. (1991). Spatial and temporal variability of the periphyton biomass in a prealpine river (Necker, Switzerland). *Archiv Für Hydrobiologie*, *123*(2), 219–237. https://doi.org/10.1127/archiv-hydrobiol/123/1991/219

Uehlinger, U. (2006). Annual cycle and inter-annual variability of gross primary production and ecosystem respiration in a floodprone river during a 15-year period. *Freshwater Biology*, *51*(5), 938–950. https://doi.org/10.1111/j.1365-2427.2006.01551.x

Uehlinger, U., Zah, R., & Bürgi, H. (1998). The Val Roseg project: temporal and spatial patterns of benthic algae in an Alpine stream ecosystem influenced by glacier runoff. In *IAHS publication* (Vol. 248, pp. 419–424).

Uehlinger, U., Malard, F., & Ward, J. V. (2003). Thermal patterns in the surface waters of a glacial river corridor (Val Roseg, Switzerland). *Freshwater Biology*, *48*(2), 284–300. https://doi.org/10.1046/j.1365-2427.2003.01000.x

VanCompernolle, M., Knouft, J. H., & Ficklin, D. L. (2019). Hydrologic and thermal conditions occupied by a species within a single watershed predict the geographic extent of occurrence of freshwater fishes. *Ecohydrology*, *12*(3), 1–8. https://doi.org/10.1002/eco.2071

Vannote, R. L., & Sweeney, B. W. (1980). Geographic analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. *The American Naturalist*, *115*(5), 667–695.

Vannote, R. L., Minshall, G. W., Cummins, K., Sedell, J. R., & Cushing, C. E. (1980). The River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences*, *37*(1), 130–137.

Vanzo, D., Siviglia, A., Carolli, M., & Zolezzi, G. (2016). Characterization of sub-daily thermal regime in alpine rivers: quantification of alterations induced by hydropeaking. *Hydrological Processes*, *30*(7), 1052–1070. https://doi.org/10.1002/hyp.10682

Vasseur, D. A., & McCann, K. S. (2005). A mechanistic approach for modeling temperature-dependent consumer-resource dynamics. *The American Naturalist*, *166*(2), 184–198. https://doi.org/10.1086/431285

Verberk, W. C. E. P., Atkinson, D., Hoefnagel, K. N., Hirst, A. G., Horne, C. R., & Siepel, H. (2021). Shrinking body sizes in response to warming: explanations for the temperature–size rule with special emphasis on the role of oxygen. *Biological Reviews*, *96*(1), 247–268. https://doi.org/10.1111/brv.12653

Viganò, G., Confortola, G., Fornaroli, R., Cabrini, R., Canobbio, S., Mezzanotte, V., & Bocchiola, D. (2015). Effects of future climate change on a river habitat in an Italian Alpine catchment. *Journal of Hydrologic Engineering*. https://doi.org/10.1061/(ASCE)HE.1943-5584.0001293

Villalobos-Jiménez, G., & Hassall, C. (2017). Effects of the urban heat island on the phenology of Odonata in London, UK. *International Journal of Biometeorology*, *61*(7), 1337–1346. https://doi.org/10.1007/s00484-017-1311-7

Vinson, M. R., & Hawkins, C. P. (2003). Broad-scale geographical patterns in local stream insect genera richness. *Ecography*, *26*(6), 751–767. https://doi.org/10.1111/j.0906-7590.2003.03397.x

van Vliet, M. T. H., Franssen, W. H. P., Yearsley, J. R., Ludwig, F., Haddeland, I., Lettenmaier, D. P., & Kabat, P. (2013). Global river discharge and water temperature under climate change. *Global Environmental Change*, *23*, 450–464. https://doi.org/10.1016/j.gloenvcha.2012.11.002

Voelz, N. J., Poff, N. L., & Ward, J. V. (1994). Differential effects of a brief thermal disturbance on caddisflies (Trichoptera) in a regulated river. *The American Midland Naturalist*, *132*(1), 173–182. https://doi.org/10.2307/2426211

Vogt, C., Pupp, A., Nowak, C., Jagodzinski, L. S., Baumann, J., Jost, D., et al. (2007). Interaction between genetic diversity and temperature stress on life-cycle parameters and genetic variability in midge *Chironomus riparius* populations. *Climate Research*, *33*, 207–214. https://doi.org/10.3354/cr033207

Vörösmarty, C. J., Green, P., Salisbury, J., & Lammers, R. B. (2000). Global water resources: vulnerability from climate change and population growth. *Science*, *289*, 284–288. https://doi.org/10.1126/science.289.5477.284

Wagner, R. (1990). Influence of temperature, photoperiod and nutrition on growth and consumption of *Chaetopteryx Villosa* (Trichoptera). *Ecography*, *13*(3), 247–254.

https://doi.org/https://doi.org/10.1111/j.1600-0587.1990.tb00615.x

Wagner, R. (2005). The influence of stream water temperature on size and weight of caddisflies (Insecta, Trichoptera) along the Breitenbach 1983-1991. *Archiv Für Hydrobiologie*, *163*(1), 65–79. https://doi.org/10.1127/0003-9136/2005/0163-0065

Wahli, T., Bernet, D., Steiner, P. A., & Schmidt-Posthaus, H. (2007). Geographic distribution of Tetracapsuloides bryosalmonae infected fish in Swiss rivers: an update. *Aquatic Sciences*, *69*(1), 3–10. https://doi.org/10.1007/s00027-006-0843-4

Waldner, K., Bechter, T., Auer, S., Borgwardt, F., El-Matbouli, M., & Unfer, G. (2020). A brown trout (*Salmo trutta*) population faces devastating consequences due to proliferative kidney disease and temperature increase: a case study from Austria. *Ecology of Freshwater Fish*, *29*(3), 465–476. https://doi.org/10.1111/eff.12528

Wallace, A. R. (1976). *The geographical distribution of animals; with a study of the relations of living and extinct faunas as elucidating the past changes of the Earth's surface*. New York: Harper&Brothers.

Wanders, N., van Vliet, M. T. H., Wada, Y., Bierkens, M. F. P., & van Beek, L. P. H. (Rens. (2019). High-resolution global water temperature modeling. *Water Resources Research*, *55*, 2760–2778. https://doi.org/10.1029/2018WR023250

Ward, J. V., & Stanford, J. A. (1979). Ecological factors controlling stream zoobenthos with emphasis on thermal modification of regulated streams. In J. V. Ward & J. A. Stanford (Eds.), *The ecology of regulated streams* (pp. 35–55). New York: Springer. https://doi.org/10.1007/978-1-4684-8613-1_4

Ward, J. V., & Stanford, J. A. (1982). Thermal responses in the evolutionary ecology of aquatic insects. *Annual Review of Entomology*, *27*, 97–117. https://doi.org/10.1146/annurev.en.27.010182.000525

Ward, J. V. (1976). Effects of thermal constancy and seasonal temperature displacement on community structure of stream macroinvertebrates. In *Thermal Ecology symposium* (Vol. 2, pp. 302–307). Augusta, Georgia.

Waring, R. H., & Running, S. W. (1998). *Forest Ecosystems. Analysis at multiple scales*. (R. H. Waring & S. W. Running, Eds.) (Third). San Diego, California: Elsevier.

Waringer, J., & Graf, W. (2013). Key and bibliography of the genera of European Trichoptera larvae. *Zootaxa*, *3640*(2), 101–151. https://doi.org/10.11646/zootaxa.3640.2.1

Watanabe, N. C., Mori, I., & Yoshitaka, I. (1999). Effect of water temperature on the mass emergence of the mayfly, Ephoron shigae, in a Japanese river (Ephemeroptera:

Polymitarcyidae). *Freshwater Biology*, *41*, 537–541. https://doi.org/10.1046/j.1365-2427.1999.00398.x

Waters, T. F. (1965). Interpretation of invertebrate drift in streams. *Ecology*, *46*(3), 327–334. https://doi.org/https://doi.org/10.2307/1936336

Wawrzyniak, V., Piégay, H., & Poirel, A. (2012). Longitudinal and temporal thermal patterns of the French Rhône River using Landsat ETM+ thermal infrared images. *Aquatic Sciences*, *74*(3), 405–414. https://doi.org/10.1007/s00027-011-0235-2

Webb, B. W. (1996). Trends in stream and river temperature. *Hydrological Processes*, *10*, 205–226. https://doi.org/https://doi.org/10.1002/(SICI)1099-1085(199602)10:2<205::AID-HYP358>3.0.CO;2-1

Webb, B. W., & Nobilis, F. (1995). Long term water temperature trends in Austrian rivers. *Hydrological Sciences Journal*, *40*(1), 83–96. https://doi.org/10.1080/02626669509491392

Webb, B. W., & Walling, D. E. (1993). Longer-term water temperature behaviour in an upland stream. *Hydrological Processes*, *7*, 19–32. https://doi.org/10.1002/hyp.3360070104

Webb, B. W., & Walling, D. E. (1997). Complex summer water temperature behaviour below a UK regulating reservoir. *Regulated Rivers: Research and Management*, *13*(5), 463–477. https://doi.org/10.1002/(SICI)1099-1646(199709/10)13:5<463::AID-RRR470>3.0.CO;2-1

Webb, B. W., Hannah, D. M., Moore, R. D., Brown, L. E., & Franz, N. (2008). Recent advances in stream and river temperature tesearch. *Hydrological Processes*, *22*, 902–918. https://doi.org/10.1002/hyp

Weber, C. (1973). *Biological field and laboratory methods for measuring the quality of surface waters and effluents. National environmental research center office of research and development.*

Wellborn, G. A., & Robinson, J. V. (1996). Effects of a thermal effluent on macroinvertebrates in a Central Texas reservoir. *The American Midland Naturalist*, *136*(1), 110–120. https://doi.org/10.2307/2426636

White, J. C., Hannah, D. M., House, A., Beatson, S. J. V., Martin, A., & Wood, P. J. (2016). Macroinvertebrate responses to flow and stream temperature variability across regulated and non-regulated rivers. *Ecohydrology*, *10*(1), 1–21. https://doi.org/10.1002/eco.1773

White, J. C., House, A., Punchard, N., Hannah, D. M., Wilding, N. A., & Wood, P. J. (2018).

Macroinvertebrate community responses to hydrological controls and groundwater abstraction effects across intermittent and perennial headwater streams. *Science of the Total Environment, 610–611*, 1514–1526. https://doi.org/10.1016/j.scitotenv.2017.06.081

Whitton, B. A. (2012). Changing approaches to monitoring during the period of the 'Use of algae for monitoring rivers' symposia. *Hydrobiologia*, *695*, 7–16. https://doi.org/10.1007/s10750-012-1121-1

Wiley, M. J., & Kohler, S. L. (1980). Positioning changes of mayfly nymphs due to behavioral regulation of oxygen consumption. *Canadian Journal of Zoology*, *58*(4), 618–622. https://doi.org/10.1139/z80-088

Will K. W., & Resh V. H. (2008). Phylogenetic relationships and evolutionary adaptations of aquatic insects. In *An Introduction to the Aquatic Insects of North America* (pp. 139–156).

Winterbourn, M. J., Cadbury, S., Ilg, C., & Milner, A. M. (2008). Mayfly production in a New Zealand glacial stream and the potential effect of climate change. *Hydrobiologia, 603*(1), 211–219. https://doi.org/10.1007/s10750-007-9273-0

Wojtalik, T. A., & Waters, T. F. (1970). Some effects of heated water on the drift of two species of stream invertebrates. *Transactions of the American Fisheries Society*, *99*(4), 782–788. https://doi.org/10.1577/1548-8659(1970)99<782:seohwo>2.0.co;2

Wonglersak, R., Fenberg, P. B., Langdon, P. G., Brooks, S. J., & Price, B. W. (2020). Temperature-body size responses in insects: a case study of British Odonata. *Ecological Entomology*, *45*, 795–805. https://doi.org/10.1111/een.12853

Wood, S. N. (2022). Package 'mgcv.' *CRAN*. https://doi.org/https://doi.org/10.1201/9781315370279

Woods, H. A. (1999). Egg-mass size and cell size: effects of temperature on oxygen distribution. *American Zoologist*, *39*, 244–252. https://doi.org/10.1093/icb/39.2.244

Woods, T., Kaz, A., & Giam, X. (2021). Phenology in freshwaters: a review and recommendations for future research. *Ecography*, 1–14. https://doi.org/10.1111/ecog.05564

Woodward, G., Dybkjær, J. B., Ólafsson, J. S., Gíslason, G. M., Hannesdóttir, E. R., & Friberg, N. (2010). Sentinel systems on the razor's edge: effects of warming on Arctic geothermal stream ecosystems. *Global Change Biology*, *16*(7), 1979–1991. https://doi.org/10.1111/j.1365-2486.2009.02052.x

Worthington, T. A., Shaw, P. J., Daffern, J. R., & Langford, T. E. L. (2015). The effects of a thermal discharge on the macroinvertebrate community of a large British river: implications for climate change. *Hydrobiologia*, *753*, 81–95. https://doi.org/10.1007/s10750-015-2197-1

Wright, D. H. (1983). Species-energy theory: an extension of species-area theory. *Oikos*, *41*(3), 496. https://doi.org/10.2307/3544109

Wright, L. L., Mattice, J. S., & Beauchamp, J. J. (1982). Effect of temperature and sex on growth patterns in nymphs of the mayfly *Hexagenia hilineata* in the laboratory. *Freshwater Biology*, *12*, 535–545. https://doi.org/10.1111/j.1365-2427.1982.tb00645.x

Wrona, F. J., Prowse, T. D., Reist, J. D., Hobbie, J. E., Lévesque, L. M. J., & Vincent, W. F. (2006). Climate change effects on aquatic biota, ecosystem structure and function. *Ambio*, *35*(7), 359–369. https://doi.org/10.1579/0044-7447(2006)35[359:CCEOAB]2.0.CO;2

Xenopoulos, M. A., Lodge, D. M., Alcamo, J., Märker, M., Schulze, K., & Van Vuuren, D. P. (2005). Scenarios of freshwater fish extinctions from climate change and water withdrawal. *Global Change Biology*, *11*(10), 1557–1564. https://doi.org/10.1111/j.1365-2486.2005.001008.x

Xu, Y., Guo, X., Dan, Y., Yang, Z., Ma, J., Liu, D., & Xu, Y. (2021). Impact of cascade reservoirs on continuity of river water temperature: a temperature trend hypothesis in river. *Hydrological Processes*, *35*(1), 1–13. https://doi.org/10.1002/hyp.13994

Zarfl, C., Lumsdon, A. E., Berlekamp, J., Tydecks, L., & Tockner, K. (2015). A global boom in hydropower dam construction. *Aquatic Sciences*, *77*(1), 161–170. https://doi.org/10.1007/s00027-014-0377-0

Zemp, M., Huss, M., Thibert, E., Eckert, N., McNabb, R., Huber, J., et al. (2019). Global glacier mass changes and their contributions to sea-level rise from 1961 to 2016. *Nature*, *568*, 382–386. https://doi.org/10.1038/s41586-019-1071-0

Zerunian, S. (2002). *Condannati all'estinzione? Biodiversità, biologia, minacce e strategie di conservazione dei pesci d'acqua dolce indigeni in Italia*. (Esagricole, Ed.).

Zerunian, S. (2003). Piano d'azione generale per la conservazione dei pesci d'acqua dolce italiani. *Quaderni*.

Zhu, S., Nyarko, E. K., & Hadzima-Nyarko, M. (2018). Modelling daily water temperature from air temperature for the Missouri River. *PeerJ*, *2018*(6), 1–19. https://doi.org/10.7717/peerj.4894

Zimmerman, M. C., & Wissing, T. E. (1978). Effects of temperature on gut-loading and gut-clearing times of the burrowing mayfly, Hexagenia limbata. *Freshwater Biology*, *8*, 269–277. https://doi.org/10.1111/j.1365-2427.1978.tb01447.x

Živić, I., Živić, M., Bjelanović, K., Milošević, D., Stanojlović, S., Daljević, R., & Marković, Z. (2014). Global warming effects on benthic macroinvertebrates: a model case study from a small geothermal stream. *Hydrobiologia*, *732*, 147–159. https://doi.org/10.1007/s10750-014-1854-0

Zolezzi, G., Siviglia, A., Toffolon, M., & Maiolini, B. (2011). Thermopeaking in Alpine streams: event characterization and time scales. *Ecohydrology*, *576*, 564–576. https://doi.org/10.1002/eco

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R. Springer*.

Zwick, P. (1996). Capacity of discontinuous egg development and its importance for the geographic distribution of the warm water stenotherm, *Dinocras cephalotes* (Insecta: Plecoptera: Perlidae). *Annales de Limnologie*, *32*(3), 147–160. https://doi.org/10.1051/limn/1996014

Publications

Bonacina, L., Fasano, F., Mezzanotte, V., & Fornaroli, R. (2022). Effects of water temperature on freshwater macroinvertebrates: a systematic review. *Biological Reviews*, 000–000. https://doi.org/10.1111/brv.12903

Bonacina, L., Canobbio, S., & Fornaroli, R. (2022). Influence of the *Salmo (trutta) trutta* on the population structure, the growth, and the habitat preference of a *Cottus gobio* population. *River Research and Applications*, *38*(9), 1585–1600. https://doi.org/10.1002/rra.4018

Fehlinger, L., Misteli, B., Morant, D., Juvigny-Khenafou, N., Cunillera-Montcusí, D., Chaguaceda, F., … Bonacina, L., et al. (2022). The ecological role of permanent ponds in Europe: a review of dietary linkages to terrestrial ecosystems via emerging insects. *Inland Waters*, 1–47. https://doi.org/10.1080/20442041.2022.2111180

Fuso, F., Stucchi, L., Bonacina, L., Fornaroli, R., & Bocchiola, D. (2023). Evaluation of water temperature under changing climate and its effect on river habitat in a regulated Alpine catchment. *Journal of Hydrology*, *616*, 128816. https://doi.org/10.1016/j.jhydrol.2022.128816

Petruzziello, A., Bonacina, L., Marazzi, F., Zaupa, S., Mezzanotte, V., & Fornaroli, R. (2021). Effects of high-altitude reservoirs on the structure and function of lotic ecosystems: a case study in Italy. *Hydrobiologia*, *848*, 1455–1474. https://doi.org/10.1007/s10750-020-04510-9

Bonacina, L. & Tirozzi, P. (2022). La biodiversità che non potremo conoscere. *Triennale di Milano* (https://triennale.org/magazine/biodiversita-pupak)

Bonacina, L. (2021). Water and Stones. *On the rocks. Geological film festival*. https://www.youtube.com/watch?v=EgSMDRENU2E&ab_channel=ONTHEROCKS

Conferences

Bonacina, L., Fornaroli, R., Cauvy-Fraunié, S. (2022). Thermal regime effects on alpine stream macroinvertebrates. Oral communication. *International Mountain Conference*. Innsbruck.

Bonacina, L., Mezzanotte, V., Fornaroli, R. (2022). Water temperature variability and macroinvertebrate assemblages in subalpine streams. Oral communication. *Incontro Dottorandi in Ecologia e Scienze dei Sistemi Acquatici (A.I.O.L., S.It.E).* Cagliari. Virtual Meeting.

Bonacina, L., Vezzoli, G., Mezzanotte, V., Fornaroli, R. (2021). Channel morphology, sediment characterization and bedload transport of steep alpine streams. A case study in the Orobic Alps (Italy). Poster. *BeGeo Scientists*. Napoli.

Bonacina, L., Boggero, A., Mezzanotte, V., Fornaroli, R. (2021). Effects of Temperature on freshwater macroinvertebrates. Oral communication. *Water Resources and Wetlands*. Tulcea. Virtual Meeting.

Bonacina, L., Fornaroli, R., Mezzanotte, V., Marazzi, F. (2021). Linking flow disturbance and phytobenthos communities' dynamics in Alpine streams. Poster. *SEFS12, Symposium for European Freshwater Sciences.* Dublin. Virtual Meeting.

Bonacina, L., Fornaroli R., Mezzanotte V., Marazzi F. (2021). Ecological effects of flow disturbance on phytobenthos communities in natural and regulated alpine streams. Poster. *European Geoscience Union*. Vienna. Virtual Meeting.

Bonacina, L., Canobbio, S., Fornaroli, R. (2021). Influence of the predator *Salmo trutta trutta* on the habitat preference, community structure and growth rate of a *Cottus gobio* population. Oral communication. *XXV Congresso Associazione Italiana di Oceanografia e Limnologia*. Peschiera del Garda. Virtual Meeting.

Bonacina, L., Fornaroli, R., Marazzi, F., Mezzanotte, V. (2021). Thermal regime of alpine streams: controls and ecological effects on the biological community in natural and regulated streams. Oral communication. *Incontro Dottorandi in Ecologia e Scienze dei Sistemi Acquatici (A.I.O.L., S.It.E).* Napoli. Virtual Meeting.

Fornaroli, R., Bonacina, L., Marazzi, F., Mezzanotte, V. (2019). The thermal regime of Alpine streams: natural controls and effect of hydroelectric power production. *European Geoscience Union*. Vienna.