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Decline of European grayling (*Thymallus thymallus* L.) populations in Belgian rivers: What are the main environmental factors involved?

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ABSTRACT

This study investigated population trends of the European grayling (*Thymallus thymallus* L.) across Belgian rivers in relation to environmental changes. Freshwater biodiversity has been declining dramatically and facing many threats those past decades. Among freshwater species, the European grayling is present throughout Europe, but its populations have declined across their distribution area. It is an exigent fish species, having specific physiological and ecological needs that are in the frontline of many consequences of human activities, with climate change bringing additional pressures. This study aimed to assess the decline of graylings and to determine the most impactful environmental factors. We analysed data from fishing events from 2000 to 2022 and environmental data of the Walloon region of Belgium. When comparing the first two decades of the 2000 s, the fishing data highlighted a decline of 42.8 % of grayling population abundance. In parallel, water flow tended to decrease with a higher occurrence of very low-flow, and maximum water temperature tended to increase with higher occurrence of days with water temperature > 18 °C. Indeed, there was an average of 18.6 additional days at very low water flow and an average of 9.6 additional days at water temperature > 18 °C. These parameters showed an impact on graylings abundance giving the significant correlation found between them. This study quantifies the rate of grayling's decline in Belgium and the change of water flow and temperature over time, and it highlights the environmental variables that have shown an influence on European grayling abundance.

1. Introduction

Freshwater ecosystems are among the most diverse on earth but are greatly impacted and threatened by human activities. They face a biodiversity decline that occurs faster than that of terrestrial ecosystems, with fish and amphibians as the groups of freshwater vertebrates that are the most threatened (Albert et al., 2021). With only 40 % of European river water bodies evaluated as having a "good status" (Schürings et al., 2024), European freshwater ecosystems are still facing threats for the conservation of their biodiversity, and 39 % of European freshwater fish species are currently facing extinction (Darwall & Freyhof, 2015). Among these species is the European grayling (*Thymallus thymallus* L.), a salmonid species of the subfamily Thymallinae. It is encountered in central and northern Europe and present as a holobiotic potamodromous fish in well-oxygenated rivers with a maximum summer water temperature of 23 °C (Bruslé & Quignard, 2006). European grayling has witnessed a decline in its populations across Europe in recent decades. This decline, albeit poorly quantified, has been linked to general river degradation, such as habitat loss, pollution, or flow regulation, but also to human activities such as overfishing (Cattanéo et al., 2014; Hayes et al., 2021; Horká et al., 2015; Kodela et al., 2023; Ovidio et al., 2004) and, most recently, to climate change with, for example, increases of water temperature (Cattanéo et al., 2014; Mruk et al., 2024; Mueller et al., 2020; Trimmel et al., 2018; Wild et al., 2023). Such anthropogenic degradations also have impacted other specialised potamodromous fish species, such as the nase (*Chondrostoma nasus* L.), the brown trout (*Salmo trutta* L.), and the barbel (*Barbus barbus* L.) (Borsuk et al., 2006; Britton & Pegg, 2011; Ovidio & Nzau Matondo, 2024).

The European grayling is a sensitive freshwater species that completes its entire life cycle in rivers and can migrate more than 40 km in some regions (Junge et al., 2014). Graylings are therefore impacted by river fragmentation, with a lower obstacle-clearing capacity than the trout (Baudoin et al., 2014; Ovidio et al., 2007) and different life stages needing specific habitat conditions. Indeed, in spring when the water temperature reaches 7–8 °C, eggs are buried a few centimetres in the gravel of riffles and need good water circulation within the substrate to

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provide enough oxygen during development (Kodela et al., 2023; Ovidio et al., 2004). Egg incubation lasts about 20 days at 8–10 °C (150–220 degree days), and the larvae will stay in the gravel until absorption of their yolk reserve (Bruslé & Quignard, 2006; Kodela et al., 2023; Nykänen, 2004). Young will then move to areas with fine substrate and slow water flow along the riverbanks and will then slowly go to deeper areas with more coarse substrate and rapid water flow. Adults will generally be found in strong currents in areas with coarse substrate at variable depths (Auer et al., 2023; Bruslé & Quignard, 2006; Nykänen, 2004). As a result, European grayling demands a broad diversity of habitats and flow facies (Mallet et al., 2000). Moreover, the species is also one of the most sensitive to pollution (Uiblein, 2001). It is also very sensitive to increases in water temperature, with a reduction of its activity starting between 18–20 °C, cessation of activities above 20 °C, and mortality above 23 °C (Bašić et al., 2018; Bruslé & Quignard, 2006) which is below the thermal limits of the brown trout, the Atlantic salmon (*Salmo salar* L.), and most other freshwater fish species (Bašić et al., 2018; Bruslé & Quignard, 2006; Pletterbauer et al., 2016).

Water temperature plays an important role in several physical and chemical habitat properties (Trimmel et al., 2018) but most importantly in physiological parameters of ectotherm species such as fishes (Auer et al., 2023; Tissot & Souchon, 2010). Excessively high temperatures decrease oxygen saturation and can lead to a high physiological demand and stress, while low temperatures can decrease muscle efficiency and impact the swimming capacity of the fish (Auer et al., 2023; Melcher et al., 2013; Ovidio et al., 2007; Trimmel et al., 2018). Water temperature also plays a key role in fish growth and in initiating migration, with graylings beginning their reproductive migration in early spring as water temperature increases to 7–8 °C (Kodela et al., 2023; Ovidio et al., 2004). Water flow fluctuations can modify temperature but also sediment structure, oxygen content, and habitat availability, influence the amount of drifting prey (Bašić et al., 2018; Marsh et al., 2022) and impact the ability to pass obstacles (Ovidio et al., 2007). Reproductive migration of European grayling generally occurs when water flows decrease after winter floods, which, if occurring before egg burial, could be beneficial for development (Ovidio et al., 2004). If floods occur after egg burial, they can possibly expel eggs or larvae from the spawning gravel (Bašić et al., 2018). Due to climate change, both water flow and water temperature are expected to evolve towards more extreme events, thus putting additional pressure on freshwater fish (Forzieri et al., 2014; Sabater et al., 2023; Trimmel et al., 2018).

An anthropic pressure associated with land cover, the riparian forest, is known to have a buffering effect by retaining various compounds such as sediments, organic matter, and pollutants from neighbouring lands (Brogna et al., 2018; Damanik-Ambarita et al., 2018; Stutter et al., 2012). It can be one of the most influential factors to regulate water temperature (Bierschenk et al., 2019), depending on zone width, vegetation density, and average tree height, which will affect radiation fluxes, evaporation, and heat fluxes. This, among other things, reduces solar radiation on the river (Tissot & Souchon, 2010; Trimmel et al., 2018). As for pollution, land cover, and more precisely artificialised areas with wastewater discharge and less infiltration, but also agricultural areas discharging sediment, pesticide residues, and nutrients such as nitrogen and phosphorus are two primary sources of water quality degradation. Both affecting fish and other freshwater organisms (Brogna et al., 2018; Damanik-Ambarita et al., 2018; Elosegi et al., 2010; Green et al., 2022; Kovalenko, 2019) as well as fish community composition with a shift of sensitive species towards more tolerant species (Bierschenk et al., 2019).

In Belgium, the European grayling was reevaluated from “Vulnerable” to “In Danger” in the International Union for Conservation of Nature (IUCN) Red List for Wallonia in 2022 (Thiry, 2022) without any explanation of why nor any precise knowledge of the species’ population dynamics since the beginning of 2000. Most of all, the European Union (EU) Water Framework Directive, which started in 2000 with the goal to halt deterioration and attain “good status” for all European rivers (Directive 2000/60/EC), should have prevented the degradation of conditions these past years. In addition, a focus on environmental parameters impacting European grayling populations is lacking in the literature. Moreover, the European grayling is one of the first species to face the effect of extreme temperature events in addition to all other pressures, making it a species of interest to preserve many others. The goal of our study was to evaluate the population dynamics of the European grayling in the Walloon region of Belgium between 2000 and 2022, based on electric fishing data, and to evaluate how water flow, water temperature, riparian habitat, and land-use data have evolved in the watersheds where European grayling is found. We combine these two approaches to highlight the environmental parameters that could be the most problematic for the species in order to provide leads to further research or conservation actions.

2. Materials and methods

2.1. Study area

The datasets used in this study contain data that were collected in the nine watersheds where European grayling populations are or were present in Belgium between 2000 and 2022. This area is located in the Walloon region in western Europe (Fig. 1), mostly in the Meuse River basin, and covers an area of 11424 km^2.

2.2. Fishing data

The fishing data were provided by the Service Publique de Wallonie (SPW) – Département d’Etude du Milieu Naturel et Agricole (DEMNA). The data were generated from electric fishing mostly done by Belgian universities and government to evaluate the ecological status of water bodies within the Framework of the EU Water Directive (2000/60/EC), which creates a pluri-annual and multi-species dataset. The fishing is done on an average river sector of 150 m length, with two consecutive passages.

For each fishing event, data for the following variables were recorded: date; location; total number of individuals; total European grayling biomass; number of individuals per size class (< 13 cm = juveniles 0+, 13–23 cm = juveniles 1+, > 23 cm = adults); and the width and length of the fishing sector. In this way, data could be averaged by year or period and scale (water body, watershed, Wallonia). Each locality was linked to its water body’s code to enable connection with other datasets. In addition, the data were only kept for sites with a minimal presence of one individual over the period in order to eliminate locations where European grayling is not naturally present. There were 197 sites and 402 fishing events (2.04 fishing events/site). To temporally homogenise the dataset, all values were averaged by water body, resulting in a total number of 74 water bodies (5.43 fishing events/water body).

2.3. Water flow and water temperature data

The AQUALIM hydrological measurement network (SPW – DCENN) gives continuous information on water height, flow, and temperature across Wallonia. The flow data began about 1980 and the temperature data in 2011. For this study, we used only stations that were present in the study area, i.e., 112 stations for water temperature and 149 stations for water flow. Each station was associated with a water body and measured the daily mean water flow or the daily mean water temperature. From this information, we calculated for each station:

- Qmean/min/maxMod: the annual modulated average, minimal, and maximal water flow;
- Tmean/min/max: the annual average, minimal, and maximal water temperature;
- NdaysSupP95: the number of days with a flow above P95 (= the flow rate exceeded 5 % of the time for the station over the entire period);

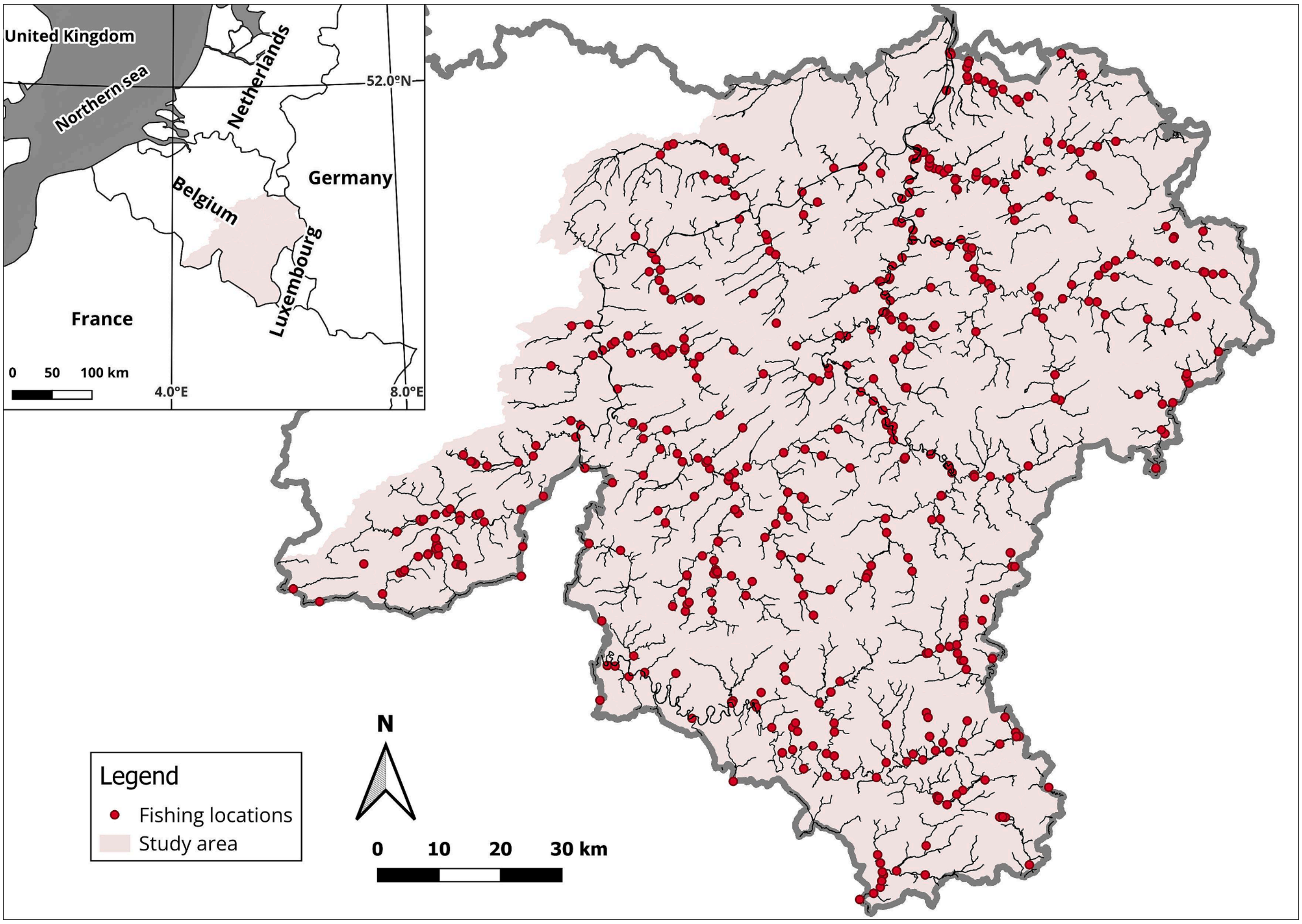

Fig. 1. Study area and location of fishing sites (red dots) in the Wallon region of Belgium. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

- NdaysInfP5: the number of days with a flow below P5 (= the flow rate exceeded 95 % of the time for the station over the entire period);
- MAM7: the minimal modulated water flow rate of a 7-day moving average over the year;
- Ndays18/20/23: the number of days with water temperature 18.0–19.9 °C, 20.0–22.9 °C, or ≥ 23 °C.

2.4. Riparian and land-use data

The riparian area was characterised by PARIS (River Action Programmes using an Integrated, Sector-based approach), which aims to integrate, in time and space, different parameters and information for all the management measures specific to the linear stretch of a watercourse, on the scale of the sectors (SPW, 25/0802022). The dataset received from SPW-DCENN gave information on the hydromorphology and riparian area of public rivers of Wallonia. The data are available at the scale of hydromorphologically homogeneous sectors within sub-watersheds. The information used here was generated by remote sensing. The dataset contained, for each water body, the mean proportion of riparian vegetation up to 6 m from the bank in 2015 (RipaGrowth) and the mean proportion of shading (ShadeIndex) received using the highest position of the sun over the year, taking into account the position and height of the trees.

The land-use data came from the 2022 land cover map of Life Watch Belgium and are based on 2-m pixels classification with a precision of 94.8 % (Radoux et al., 2022). The land cover classes were grouped, and tree groups were categorised as "%Artificialised" (dense and low artificialised area, naked soil, naked soil and mixed vegetation), "% Crops" (periodically herbaceous, mixed vegetation cover with crops in the majority), or "%Forest" (deciduous, coniferous, deciduous and coniferous, recently perturbed forested area).

2.5. Data analysis

The different datasets were managed with R software (v4.4.2). For the statistical analysis, normality of the different variables was tested by the test of Shapiro-Wilk (function: "stats::shapiro.test()"; v4.4.2). The Mann-Kendall test ("trend::mk.test()"; v1.1.6) was used to evaluate if a trend was present over the period for non-parametric data, and a linear regression ("stats::lm()") was used for parametric data. In addition, average values of the different parameters were compared between two periods (2000–2010 and 2011–2022 or 2011–2016 and 2017–2022) with Wilcoxon (W) test ("stats::wilcox.test()") or Student's *t*-test (*T* test: "stats::t.test()"), depending on the normality of the data.

In order to evaluate the impact of the variables on European grayling abundance per ha, different types of models and distribution were tried. Unfortunately, due to the data's complexity and lack of sampling homogeneity, no model could fit our dataset. Consequently, a Kendall correlation analysis (method = "kendall"; "stats::cor.test()") was used to highlight the variables significantly correlated with European grayling abundance per ha. In addition, a Principal Component Analysis (PCA: "FactoMineR::PCA()"; v2.11) was performed on the variables effectively correlated and only with values from 2011 to 2022 (as a consequence of the water temperature dataset beginning in 2011). A PERMANOVA ("vegan::adonis2()"; v.2.6) was performed between the periods 2011–2015 and 2016–2022 after creating a distance matrix ("stats::dist()") from the PCA coordinates. For all tests, a significance level of 0.05 was considered.

3. Results

3.1. Population dynamics of the European grayling

European grayling abundance per ha in Wallonia decreased significantly ($p < 0.001$, $R^2 = 0.415$) since 2000 (Fig. 2a), declining from 98.5 to 56.4 individuals/ha. Biomass per ha also diminished significantly ($S = -95$, $n = 23$, $p = 0.013$) from 7.6 to 3.6 kg/ha. When comparing four periods (2000–2005, 2006–2010, 2011–2015, and 2016–2022), a decrease in population of 53.9 % was observed between 2000 and 2005 and 2016–2022, and when comparing the first and second decade (2000–2010 vs 2011–2022), a decrease of 42.8 % occurred. These trends apply to all size groups except the smallest, with a significant decrease of juveniles 1+ ($S = -87$, $n = 23$, $p = 0.023$) and adults ($S = -113$, $n = 23$, $p = 0.003$). Juveniles 0 + represented the higher proportion in each period, followed by juveniles 1 + and adults, respectively (Fig. 2b).

3.2. Dynamics of water flow and water temperature

QmeanMod ($p = 0.003$, $R^2 = 0.348$) and MAM7 ($p = 0.004$, $R^2 = 0.334$) significantly decreased between 2000 and 2022. In parallel, NdaysInfP5 increased significantly ($S = 97$, $p = 0.011$, $n = 23$) over the same period (Fig. 3a). These trends are confirmed with a significant difference between average values from 2000 to 2010 and 2011–2022 (Table 1). Average MAM7 decreased from 0.2 to 0.16 ($W = 434113$; $p < 0.001$), average QminMod decreased from 0.18 to 0.15 ($W = 487368$; $p < 0.001$), and average NdaysInfP5 increased from 6.9 to 25.4 days ($W = 250462$; $p < 0.001$). In addition, QmeanMod decreased from 1.03 to 0.98 ($W = 437368$; $p = 0.001$), QmaxMod increased from 8.92 to 10.08 ($W = 370589$; $p = 0.006$), and average NdaysSupP95 increased from 17.3 to 18.6 days ($T = -2.238$; $p = 0.025$) (Table 1).

No significant trend was found for the different water temperature variables over the period 2011–2022, but significant differences between average values from 2011 to 2016 and 2017–2022 were detected (Table 2). Average Tmax increased from 19.3 to 19.8 °C ($W = 74130$; $p < 0.001$), average Ndays18 increased from 9.4 to 15.5 days ($W = 74130$; $p < 0.001$), average Ndays20 increased from 2.6 to 5.7 days ($W = 73182$; $p < 0.001$), and Ndays23 increased from 0.2 to 0.6 days ($W = 87879$; $p < 0.001$). A longer time period could have shown a significant trend when considering the dynamics of average number of days at

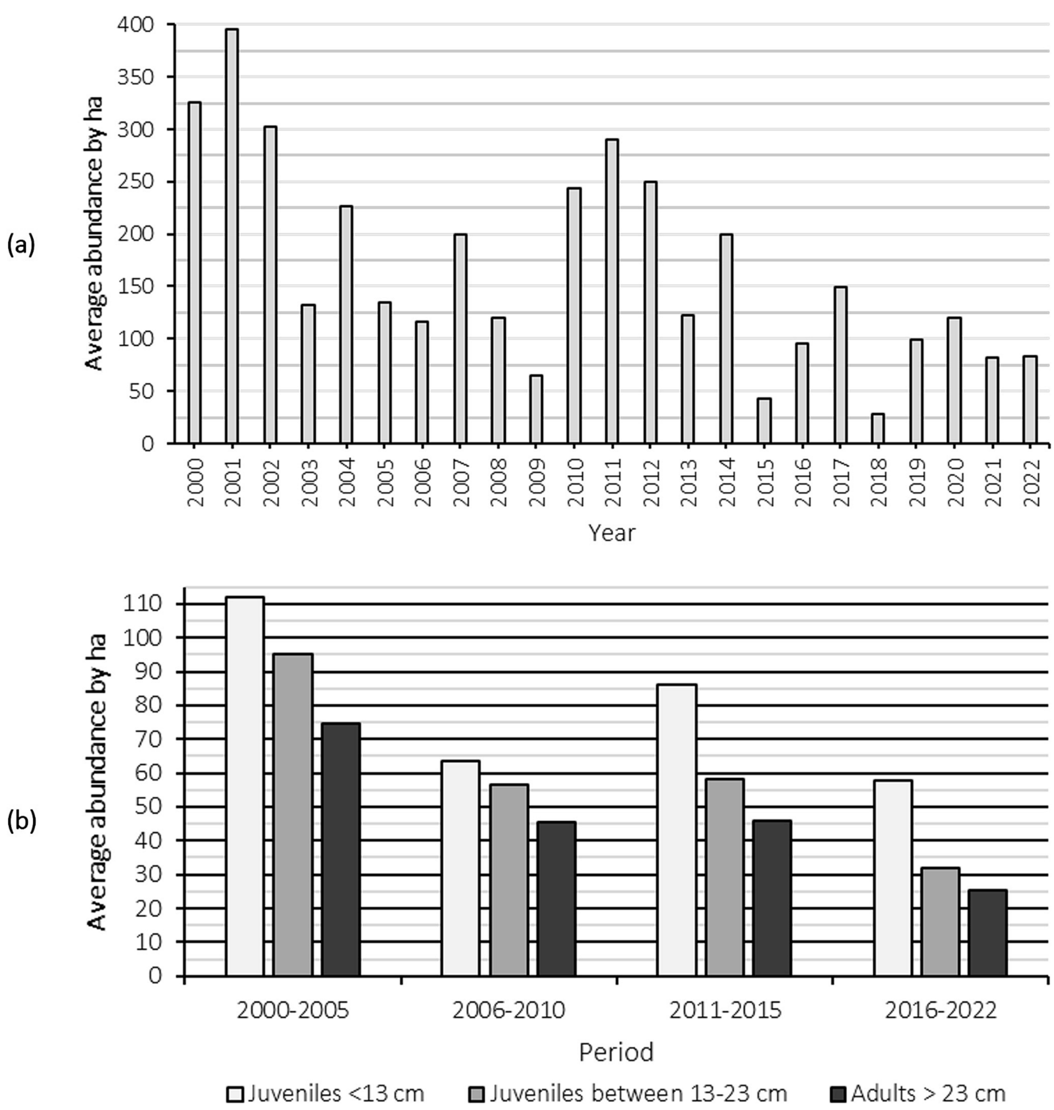

Fig. 2. (a) Dynamic between 2000 and 2022 of European grayling abundance per ha, and (b) dynamic of abundance per ha for three size groups (< 13 cm, between 13 and 23 and > 23 cm) across four time periods.

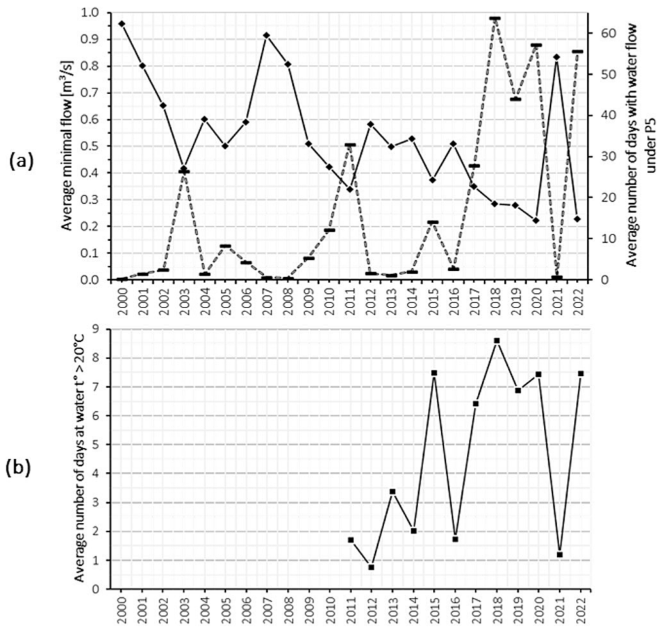

Fig. 3. Dynamics between 2000 and 2022 of (a) the average minimal water flow (solid line) and the average number of days at water flow < P5 (dashed line) and (b) the average number of days at water temperature over 20 °C.

Table 1
Results of the Wilcoxon test (or Student's *t*-test) comparing the average values of two periods (2000–2010 and 2011–2022) for the average modulated minimal (QMinMod), mean (QMeanMod) and maximal (QMaxMod) water flow, and for the average number of days with water flow > P95 (NdaysSupP95) and with water flow < P5 (NdaysInfP5).

Variable	Wilcoxon test (* *t* test)	2000–2010 average	2011–2022 average
QMinMod	W = 487,368; p < 0.001	0.184	0.153
QMeanMod	W = 437163; p = 0.001	1.034	0.975
QMaxMod	W = 370,589; p = 0.006	8.918	10.084
MAM7	W = 434,113; p < 0.001	0.200	0.164
NdaysSupP95 [days]	*T = −2.238; p = 0.025	17.328	18.560
NdaysInfP5 [days]	W = 250462; p < 0.001	6.854	25.401

water temperature over 20 °C (Fig. 3b).

3.3. *Impacting factors*

European grayling abundance was significantly correlated with six of eight environmental variables (Table 3). QminMod, QmeanMod, and MAM7 were positively correlated with abundance, but only the correlation with QmeanMod was significant. On the other hand, NdaysInfP5, Ndays23, the proportion of artificialised area, and the shade index were significantly negatively correlated with European grayling abundance.

Based on the correlated environmental variables, the first two dimensions of the Principal Component Analysis (Dimension 1 = 30.43 %; Dimension 2 = 22.12 %) explain 52.6 % of the total variance (Table 4) and indicate a positive correlation between European grayling abundance and QminMod but a negative correlation with NdaysInfP5 and Ndays23 (Fig. 4). As for the artificialised proportion and the shade index, the relationship appears more complex and dependent on the dimension. A significant difference is observed between data from 2011 to 2015 and from 2016 to 2022 (PERMANOVA: p = 0.008; R^2 = 0.041), although the two ellipses overlap (Fig. 4).

Table 2
Results of the Wilcoxon test comparing the average values of two periods (2000–2010 and 2011–2022) for the average minimal (Tmin), mean (Tmean) and maximal (Tmax) water temperature, and for the average number of days at water temperature 18 °C ≤ T < 20 °C (Ndays18), at water temperature 20 °C ≤ T < 23 °C (Ndays20) and at water temperature T ≥ 23 °C (Ndays23).

Variable	Wilcoxon test	2011–2016 average	2017–2022 average
Tmin [°C]	W = 112,782; p < 0.001	2.454	1.951
Tmean [°C]	W = 84,753; p = 0.007	10.683	10.701
Tmax [°C]	W = 78587; p < 0.001	19.295	19.746
Ndays18 [days]	W = 74,130; p < 0.001	9.399	15.522
Ndays20 [days]	W = 73,182; p < 0.001	2.549	5.721
Ndays23 [days]	W = 87,879; p < 0.001	0.211	0.565

Table 3
Significant (p < 0.05) results from the Kendall correlation test between each of eight environmental variables and European grayling abundance. With "QMinMod" the average modulated minimal water flow, "QMeanMod" the average modulated mean water flow, "NdayInfP5" the average number of days with water flow < P5, "MAM7" the minimal modulated water flow rate of a 7-day moving average over the year, "Nday23" the number of days with water temperature ≥ 23 °C, "%Artificialised" the proportion of artificialised area, "ShadeIndex" the mean proportion of shading and "RipaGrowth" the mean proportion of riparian vegetation up to 6 m from the bank in 2015.

Variable	z	p	Tau
QMinMod	1.808	0.071	0.066
QMeanMod	2.536	0.011	0.093
NdayInfP5	−2.214	0.027	−0.088
MAM7	1.865	0.062	0.068
Nday23	−3.076	0.002	−0.218
%Artificialised	−3.068	0.002	−0.114
ShadeIndex	−2.156	0.031	−0.080
RipaGrowth	−3.807	0<.001	−0.141

Table 4
Principal Component Analysis parameters for environmental variables correlated with European grayling abundance per ha in Wallonia, Belgium.

	Dim.1	Dim.2
Variance	1.826	1.327
Cumulative % of variance	30.432	52.557
Variable		
Abundance/ha	0.193	−0.281
QMinMod	0.845	−0.065
NdayInfP5	−0.656	0.417
Nday23	−0.314	0.640
%Artificialized	0.607	0.539
Shade index	−0.421	−0.609

4. Discussion

This study analyses an original and robust dataset of 402 fishing events conducted during the period 2000–2022, which captured a total of 10,981 European grayling. The creation of this important dataset was made possible by the electric fishing done to evaluate the ecological status of water bodies since the early 2000 s (EU Water Framework Directive 2000/60/EC), which provides a precious systematic dataset that can help us assess fish population trends. Unfortunately, these data

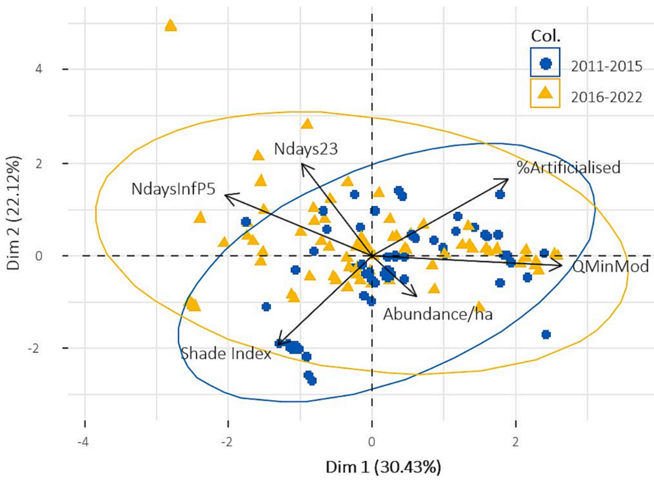

Fig. 4. Principal Component Analysis of five environmental variables significantly or nearly significantly correlated with European grayling abundance per ha in Wallonia, Belgium during two time periods. The ellipses have a confidence level of 95 %.

are underused, and *meta*-analysis is rarely done on them as mentioned by Mueller et al. (2018). One explanation could be the lack of spatial and temporal homogeneity in the dataset. With the change of sampling sites during the period or the high number of sites to evaluate, combined with the number of people and time needed to achieve the fishing, it results in not all sites being evaluated each year. As a consequence, some sites were studied much less than others over the study period. To compensate for this spatiotemporal problem, we homogenised the data by keeping the information at the water body level. It also made it easier to combine with environmental datasets. Despite these considerations, the dataset used is quite unique and of great interest for quantifying changes in European grayling populations in association with environmental factors.

Quantifying the decline of species is essential to evaluate their conservation status. The IUCN Red List is, indeed, based on the rate of decline (Benitez et al., 2022). To date, the European grayling is still considered a “least concern” species in the IUCN Red List, which also indicates that the quantification of its decline is lacking (IUCN, 2023). To the authors’ knowledge, our study is the first to quantify the decline of European grayling populations in southern Belgium over a continuous 23-year time period (2000–2022) by using data from the electric fishing done for the EU Water Framework Directive. Our dataset shows a clear decline between the first and second decades of the 2000 s with a 42.8 % loss of individuals and a 52.6 % loss of biomass. As the only comparison on the same spatial scale, Mueller et al. (2018) indicated a decline of 41.7 % in Bavarian streams of Germany between 1989 and 1997 and 2004–2013, and Mruk et al. (2024) measured a decline of 58.3 % when comparing a 2009 survey with previous studies dating from 1926 and 1982 in the Tisza River and its tributaries in the Transcarpathian region of Ukraine. When looking at the population dynamics of the different size groups between 2000 and 2022, the decline was evident in all groups, although not significantly for the size group < 13 cm, which is the group of young fish less than a year old. This observation highlights that all life stages are at risk of different stressors, even if the abundance of adults could be misjudged by the fact that fishing events mostly occured after the spawning season. Indeed, having a short lifespan, up to 6–7 years in this region (Droll et al., 2025)), older adults may die once reproduction is completed.

Environmental conditions have also evolved over the past decades, and climate change brings more frequent extreme climatic events (Forzieri et al., 2014; Sabater et al., 2023; Sanderson et al., 2012). Our study used water flow data from 149 measurement stations (23 years) and water temperature data from 112 measurement stations (12 years) in the study area. The hydrological conditions have evolved towards more or longer low water flow events, with an increase of more than three times the number of days at very low water flow (water flow below the P5) for the second decade of the 2000 s. High water flow events have also increased but to a lesser extent, with 1.2 extra days at very high water flow (water flow above the P95) for the second decade of the 2000 s. To the hydrological regime can be added the change of water temperature over time, which tends globally to warmer conditions (Melcher et al., 2013; Wedekind & Küng, 2010). Our study, even though it only considers a 12-year period, shows a higher number of days with a mean water temperature above 18 °C, with 9.6 additional days for 2016–2022 compared to 2011–2015. In addition, we observed an increase in the average maximal water temperature by 0.45 °C. A study by Melcher et al. (2013) showed an increase of 4 °C between 1975 and 2010 for mean August temperature in grayling areas of two Austrian rivers. Generally, drought events, which bring lower water flow and possibly higher water temperatures, have become more frequent and longer than before (Trnka et al., 2016).

Both water flow and water temperature variables show a significant correlation with grayling abundance. Low water flow and days with water temperature above 23 °C, which are hydrological conditions often occurring simultaneously, are correlated to European grayling abundance, and both have significantly changed over the years. Water flow and water temperature, in their extremes, bring negative consequences (Bănăduc et al., 2021; Marsh et al., 2022; Sabater et al., 2023) and can be highly problematic depending on when they occur during the biological cycle. Excessively high water flow can be problematic for young stages that do not yet have good swimming ability, and it can expel eggs or larvae from the spawning substrate (Bašić et al., 2018; Marsh et al., 2022; Nykänen, 2004). Very low water flows are linked to a reduction of available habitats and possibly increased water temperature (Marsh et al., 2022). Generally, wide variations of water flow alter temperature, sediment structure, oxygen content, and habitat availability (Bašić et al., 2018). An increase in water temperature, even if beneficial for larval growth in some cases (Auer et al., 2023; Bašić et al., 2018; Marsh et al., 2022), can highly promote the onset of disease (Melcher et al., 2013) and has a negative impact on European grayling survival at 18 °C and above, with water temperature higher than 23 °C known to be lethal for grayling (Bašić et al., 2018; Bruslé & Quignard, 2006). Higher temperature during eggs and larval development can add stress if the sediment load is already important by decreasing oxygen level, and lower water flow will decrease oxygen input into the spawning substrate (Wild et al., 2023, 2024). The impact of higher temperature has also been shown to be problematic for fall-spawning salmonids like the brown trout, with a lower reproductive success, depending more on cool water temperature during this life stage (Sternecker et al., 2014; Wild et al., 2023). Moreover, a rapid change in temperature will induce physiological and behavioural changes that may require several hours to several days and will increase energy consumption (Auer et al., 2023). In our study, we highlight that extreme events (very low water flow, very high water flow, and water temperatures > 18 °C) have become more frequent and are putting additional pressure on freshwater organisms, especially on sensitive fish species such as the European grayling. Indeed, extreme events complement the loss of river and facies heterogeneity and diversity, which decreases habitat availability (Elosegi et al., 2010), and the presence of migratory barriers that impact river connectivity, which becomes even more problematic when graylings need to find refuge areas to escape thermal or hydric adversities or when migrating to reproduce (Hayes et al., 2021). Extreme events are all the more damaging for graylings that need a variety of habitats for their different life stages (Auer et al., 2017; Mallet et al., 2000; Nykänen, 2004) and having a weaker behavioural plasticity and obstacle-clearing capacity than trout (Ovidio et al., 2007).

Land-use and anthropogenic activities also have their part in altering river conditions because urban landscapes, industrial zones, agricultural lands, and natural areas (riverbanks, forests) are known to influence water quality (Bierschenk et al., 2019; Brogna et al., 2018; Damanik-Ambarita et al., 2018; Elosegi et al., 2010; Mueller et al., 2020; Schürings et al., 2024). Indeed, many studies have already shown that the physicochemical and hydromorphological changes caused by land-use affect the diversity and abundance of freshwater organisms and fish populations (Bowes et al., 2023; Brogna et al., 2018; Damanik-Ambarita et al., 2018). Croplands, with their inputs of organic matter and other anthropogenic stressors, can directly influence fish community composition (Bierschenk et al., 2019; Mueller et al., 2020). In our study, no clear impact of land-use was noted, probably due to the fact that the information was likely not precise enough, but also may be due to the more complex and indirect impact of land-use parameters, which can take more time to bring about their consequences. We used an average value at the water body level, not at the site level, because of the lack of temporal homogeneity of sampling sites. Another approach, keeping data at a more precise spatial level combined with an homogenised fishing dataset could give us information on land-use factors and the combination of factors that are most impactful on the decline of European grayling populations in its distribution range. As Mueller et al. (2020) and Bierschenk et al. (2019) highlighted, the stress added by land-use and human activities have to be taken more into consideration to preserve freshwater biodiversity, as they can add to other factors and certainly act in synergy, which emphasises the need for more holistic approaches when evaluating impacting factors.

As many studies highlight, measures must be taken to prevent the further decline of freshwater fish populations, and focusing more precisely on European grayling as an umbrella species could benefit it. In general, the enhancement of knowledge on the habitat requirements of the different life stages of the European grayling would be a good basis to improve their protection, as the literature is dearth on this topic. We showed that extreme water flow and water temperature events are significantly correlated to European grayling abundance. Even if we cannot directly act on these climatic events, measures can be taken to allow graylings to find refuge areas when they occur. Being able to locate and prevent the destruction of these protective places (e.g., resurgence zones, deeper zones, and current refuge zones) and the key habitats such as spawning areas would be a first step. Better knowledge of the potential predators (i.e., the great cormorant (*Phalacrocorax carbo*)) and their impact on European grayling populations would be of considerable interest to assess the extent to which they play a role in European grayling decline. It is also crucial to limit the artificialisation of river banks, the dredging of riverbeds and to maintain adequate banks that benefit graylings, mainly the young stages, and to find places where the impact of changes in flow can be mitigated (Bănăduc et al., 2021; Cattanéo et al., 2014). It would also be interesting to reassess the impact of the various barriers to the free movement of fish and to carry out improvements at problematic points. As for land use, it is important to protect rivers by encouraging natural land use in the surrounding area, particularly by planting woodlands that provide shade, maintain riverbanks, and reduce inputs of sediment and nutrients (Bierschenk et al., 2019; Brogna et al., 2018; Damanik-Ambarita et al., 2018; Stutter et al., 2012; Wild et al., 2023). In addition, we must not only try to limit thermal discharges during extreme thermal conditions (Auer et al., 2023) but also eliminate or reduce the number of wastewater discharges and keep rivers and watersheds as natural as possible since the European grayling is a very sensitive species (Bowes et al., 2023; Bruslé & Quignard, 2006; Elosegi et al., 2010; Hayes et al., 2021; Uiblein, 2001). Despite high human population density and a high proportion of man-made areas in the distribution area of the European grayling, it is essential to take adverse environmental factors into account when planning future regional land developments.

5. Conclusion

This study precisely quantified the decline of European grayling populations in the Walloon region of Belgium over a 23-year continuous time period. It linked some environmental factors to this decline, with lower water flow and longer duration of high water temperature having a negative correlation with European grayling abundance. The parameter dynamics of both variables were evaluated over the 23 years and showed an increasing number of days at very low water flow and with water temperature higher than 18 °C. This study was made possible by the important dataset procured by the electric fishing events done to evaluate the biological state of water bodies, but also by the measurement station network present throughout the study area, which gave to us valuable data on water flow and water temperature over time. Freshwater biodiversity still needs protection measures, and there are still many things we should achieve to reach “good status” for all water bodies across Europe.

CRediT authorship contribution statement

Chloé Vom Berge: Writing – original draft, Project administration, Methodology, Investigation, Data curation. **Michaël Ovidio:** Writing – original draft, Supervision. **Jean-Philippe Benitez:** Writing – original draft, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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