Current and projected impacts of the parasite *Tetracapsuloides bryosalmonae* (causative to proliferative kidney disease) on Central European salmonid populations under predicted climate change

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Abstract

1. Proliferative kidney disease (PKD) caused by the myxozoan parasite *Tetracapsuloides bryosalmonae* is an emerging salmonid disease implicated in recent declines in salmonid populations. Laboratory experiments have shown that the clinical symptoms of PKD exacerbate with increasing temperature. However, empirical evidence for a relationship between climate change and PKD driven declines in wild salmonid stocks is scarce.

2. The current study uses both empirical data and ecological niche modelling to extrapolate future changes in temperature and precipitation on the spread of PKD in relation to changes in suitability of rivers for its primary bryozoan and secondary salmonid hosts.

3. A 20-year dataset on brown trout density using standardised method shows a decline of more than 50% in the population of the river Wutach, south-western Germany at 536–755 m elevation. The decline coincides with higher prevalence of PKD. This decline was temperature related and driven by reduced local survival of parr to yearlings. Kidney hyperplasia was highest at low elevations and correlated negatively with trout density.

4. Niche models based on state-wide data show strong overlap in the areas suitable for *T. bryosalmonae* and its primary bryozoan hosts, and a strong link with temperature. Projections based on moderate to high emission-case climate change scenarios predict a 50%–82% decrease in the area suitable for salmonids within this century, linked to PKD.

5. The empirical data identify temperature-mediated PKD as the underlying cause of the population decline. This relationship was corroborated by the niche modelling results. The highest losses are expected in projected salmonid suitable areas where salmonid habitats currently overlap with areas suitable for *T. bryosalmonae*.
6. With ongoing climate change, both current and future populations are at severe risk to *T. bryosalmonae* and its associated disease PKD. Conservation efforts of salmonid stocks are dependent on climate mitigation and measures to help salmonids adapt to the disease.

**KEYWORDS**
bryozoans, global warming, Proliferative kidney disease, population decline, trout

## 1 | INTRODUCTION

Salmonids are ecologically important species to river ecosystems and a highly appreciated target for commercial and recreational fisheries (Arlinghaus et al., 2015; Baer & Brinker, 2010; Pander & Geist, 2013; Račinska et al., 2015). However, it is increasingly evident via both professional fisheries and anglers that European populations of various salmonid species are in decline (Burkhardt-Holm et al., 2005; ICES, 2019; Waldner et al., 2020). The causes of these declines are multiple and involve both local and global changes in environmental factors. Local causes include structural degradation through obstruction of waterways and the operations of water power stations, and deterioration in water quality due to influxes of wastewater, nutrients, and other contaminants from human activities (Burkhardt-Holm & Zehnder, 2018). An important global factor implicated in the decrease in salmonid populations is anthropogenic climate change, which will increase water use and water temperatures, and alter precipitation (Bölscher et al., 2013; Borgwardt et al., 2020; Hari et al., 2006; Masson-Delmotte et al., 2018). First attempts to mitigate local impacts include restoration and rewilding of rivers (Roni, 2019), which together with stocking programmes have restored salmon to the Rhine catchment (Schneider, 2011). However, considering emergent climate change such local conservation programmes have, at best, only temporary effects on population density, and long-term stocking might even negatively impact stock fitness of trout populations (Baer et al., 2007; Baer & Rösch, 2008; Derry et al., 2019; Fraser, 2008; Harbicht et al., 2014). Therefore, effects of climate change must be taken into account in programmes for salmonid conservation.

Globally speaking, salmonids are often the dominant species in cool, clear, and well-oxygenated waters. Although adults are able to adapt to a relatively wide range of temperatures, the embryonal and early developmental stages are highly stenothermal, and require low temperatures for optimal development (Elliott & Elliott, 2010; Klemetsen et al., 2003). Correspondingly in Europe, both brown trout (*Salmo trutta*), and Atlantic salmon (*Salmo salar*) spawn in autumn or early winter and their parr (young of the year) grow up in rhithral streams, i.e. mountainous headwaters characterised by swift currents, cool water and high levels of dissolved oxygen (Crisp, 1996). The grayling (*Thymallus thymallus*), has a broader thermal tolerance than brown trout (Haugen & Vellestad, 2000; Jungwirth & Winkler, 1984) and spawn in spring on gravel banks downstream of the rhithral zone (Crisp, 1996). Still, in summer, water temperatures might rise above physiological thresholds of these species, causing stress and increasing susceptibility to pathogens (Borgwardt et al., 2020; Gallana et al., 2013; Klemetsen et al., 2003).

The last 2 decades have seen increasing reports of mass mortality events and population declines in salmonids, related to extended periods of high temperatures (Arndt et al., 2019; Burkhardt-Holm & Zehnder, 2018; Schager et al., 2007; Sterud et al., 2007). Although the precise cause of these events is difficult to ascertain (Hutchins et al., 2018), the affected populations are often infected by the multicellular myxozoan parasite *Tetracapsuloides bryosalmonae*, which is the causative agent of the potentially fatal proliferative kidney disease (PKD) (Clifton-Hadley & Feist, 1989; Lahnsteiner et al., 2011; Lewisch et al., 2018; Wahl et al., 2002). *Tetracapsuloides bryosalmonae* has a complex life cycle in which the parasite requires the presence of a bryozoan primary host (e.g. *Fredericella sultana* in Europe) and a salmonid secondary host (Grabner & El-Matbouli, 2008, 2010; Longshaw & Feist, 2000; Okamura et al., 2011) for reproduction and to disperse and establish new colonies. In Europe, the brown trout has been identified as the most common secondary host for *T. bryosalmonae*, but salmon and grayling are also widely infected (Mo et al., 2011; Schmidt-Posthaus et al., 2017; Sobociński et al., 2018; Sterud et al., 2007). Spores released from infected bryozoan colonies are infective to salmonids, while spores released from a fish host are infective to bryozoans (Feist et al., 2001; Morris & Adams, 2006; Tops & Okamura, 2003). Some evidence suggests that *T. bryosalmonae* is able to spread within colonies of *F. sultana* by intra-clonal propagation (Morris & Adams, 2006), but fish to fish transmission of the parasite does not occur (D’Silva et al., 1984; Fergusson & Ball, 1979).

The macroscopic expression of PKD is kidney hyperplasia (swelling) resulting from damage and inflammation of the haematopoietic kidney tissue (Bettge et al., 2009; Bruneaux et al., 2017; Clifton-Hadley et al., 1987). In severe cases, PKD results in anaemia and increased mortality (Schager et al., 2007; Schubiger et al., 2003). Cage experiments in a summer-cold rhithral stream have estimated PKD induced mortality to be about 15% in parr of brown trout (Schmidt-Posthaus et al., 2015, 2017). Moreover, it has been suggested that conditional effects inflicted by PKD (see Bruneaux et al., 2017) might affect the return rates of anadromous salmonid species (Kent et al., 1995). The pathogenicity of PKD is temperature dependent...
(Clifton-Hadley et al., 1986; Okamura et al., 2011; Rubin et al., 2019; Strepparava et al., 2018). Therefore, it was suggested that recent declines in salmonid stocks were the result of elevated mortality caused by PKD under climate change (Burkhardt-Holm et al., 2002; Burkhardt-Holm & Zehnder, 2018; Carraro et al., 2017; Lewisch et al., 2018; Waldner et al., 2020). However, evidence for a relationship between climate warming and parasite-mediated declines in wild salmonid stocks is still based on few laboratory (Strepparava et al., 2018) and field studies (Bruneaux et al., 2017; Carraro et al., 2017; Waldner et al., 2020). Moreover, the current compelling evidence for population decline in wild trout in Europe comes from an analysis of long-term angling catch statistics (Burkhardt-Holm et al., 2002), which lack a standardised catch per unit effort over the study period.

To address the paucity of evidence for PKD-mediated population declines and to better understand the challenges that salmonid populations face in a changing world, the following research questions were posed: (1) To what extent is infection with *T. bryosalmonae* implicated in current changes in brown trout populations (case study)? (2) What is the prevalence of infections with *T. bryosalmonae* in salmon, brown trout, and graying populations, and which geographic and temperature variables are related to the pathogenicity of PKD (spatial survey)? (3) How is the prevalence of salmonid infection with *T. bryosalmonae* linked to the distribution of bryozoan primary hosts (spatial survey)? (4) Based on the interplay of research questions 2 and 3: how will anticipated climate change in terms of temperature and precipitation affect the potential PKD and salmonid distribution in the future (ecological niche modelling)?

A long-term standardised catch per unit effort dataset on brown trout density (20 years) combined with measurements of PKD was used to analyse the first research question. The results of this analysis form the basis for the other research questions, which were addressed in an intensive 4-year spatial survey that was conducted in south-western Germany, recording primary (bryozoan) and secondary (salmonid fish) hosts of *T. bryosalmonae*. These were combined with available weather data in ecological niche modelling to infer probabilities of PKD presence under current and future conditions. Actual PKD presence was ascertained through molecular detection of the parasite using quantitative polymerase chain reaction (qPCR) and macroscopic evaluation of kidney hyperplasia. Based on the literature it was hypothesised that: (1) PKD is limited to salmonid populations at lower elevations that currently already experience warm-summer climate conditions; (2) the spread of the parasite *T. bryosalmonae* would be linked to the distribution of its primary bryozoan hosts; and (3) predicted climate change will lead to environmental conditions that favour the spread and pathogenicity of *T. bryosalmonae*.

The developed ecological niche models were used to predict risks to the salmonid populations under different global change scenarios.

## 2 METHODS

### 2.1 Study area and study species

The study was carried out in the federal state of Baden-Württemberg, southwestern Germany. The state is rich in mid-elevation mountainous areas from which rhithral rivers drain into the catchments of the Rhine or the Danube (Figure 1a). In the small rhithral rivers, salmonids, especially brown trout and graying, are the dominant fish species. Brown trout mostly populate steep headwater sections with 100% oxygen saturation and cool temperatures; whereas graying inhabit the transitional sections between mountains and lowlands, where rivers flow more steadily and include areas with deeper water. Following significant efforts to restock the Rhine with salmon following a long period of absence, adult salmon are swimming up the upper Rhine again and regularly enter tributary streams in the Black Forest (Monnerjahn, 2011). Salmonid aquaculture is widespread in the study area, playing an important role in the local economy, and stocking programmes, especially for brown trout, are abundant. Thus, the state conducts active monitoring for trout diseases and a programme to track PKD as an emerging disease. In the past few decades, there has been no evidence of large-scale trout mortality in the study area that could be assigned to parasite or pathogen infections other than PKD.

### 2.2 Study design (1) Wutach case study

Since the cessation of stocking in year 2000, the fisheries management of the rivers Wutach and Gutach (Figure 1a) has been based on natural reproduction of local brown trout accompanied with low fishing pressure (Baer & Brinker, 2010). From 2001 to 2008; and 2013 to 2019 electrofishing surveys were carried out annually in early July along 100-m stretches of river at four locations on the Wutach and one location on the Gutach (Table 1). The detailed methods used in these surveys are described by Baer and Brinker (2010). Due to unsuitable field conditions (small summer floods) no sampling was carried out at the Gutach location in June 2016 and 2018. Sampling involved two electrofishing runs (EFKO 8000, straight DC, 300–600 V, EFKO Fischfanggeräte GmbH) made by wading at each location, with stop nets installed at the end and beginning of the sampling section. All captured fish were measured to the nearest cm (total length TL), placed in an aerated tank and released after the second electro-fishing run. All trout were divided into age classes, based on length distribution (in June) as follows: parr (also commonly referred to as young of the year or 0+) 50–99 mm, yearling (also referred to as 1+) 100–199 mm, and older fish (hereafter referred to as adults) with TL above 199 mm. Data for local summer/autumn air temperatures (July–October) over the study period were obtained for the nearest available weather station (no. 5731, Wütöschingen) through the climate data centre of the Germany’s National Meteorological Service, the DWD (for data see Figure S1).
Data from the electrofishing campaigns were compared with T. bryosalmonae data collected along the Wutach, the Gutach, and an additional upstream tributary of the Gutach, the Josbach. PKD data in terms of parasite prevalence and the degree of kidney hyperplasia were collected from three periods (June; July–August; September–October, Table 1b). The methods for scoring of kidney hyperplasia and parasite analyses procedures are given below (see Section 2.3.3).
2.3 Study design (2) Current and future risk assessment of PKD in salmonids

2.3.1 Spatial surveys of T. bryosalmonae and bryozoans over a wide range of salmonid habitats

Sampling was carried out during the summers of 2014–2019 at 140 locations on rivers in Baden-Württemberg. Sampling locations were chosen from those used for on-going spatial surveys being carried out under the European Water Framework Directive (Van de Bund, 2009), and conservation programmes (Natura 2000: Verschuuren, 2002). From these locations (Figure 1c), a total of 1,240 parr brown trout; 91 parr and yearling grayling; and 34 parr and yearling salmon were sampled and examined for presence of T. bryosalmonae, and kidney changes (hyperplasia) were scored as a proxy for the clinical pathology known as PKD. Direct current electrofishing was performed under the general allowance granted to the Fisheries Research Station to collect fish in Baden-Württemberg and in agreement with local fishing authorities. Upon capture, fish were stunned by a blow to the head and expertly killed immediately by a cardiac stab according to the German Animal Protection Law (§ 4) and the ordinance of the slaughter and killing of animals (Tierschutzschlachtverordnung § 13). Their kidneys were either scored immediately for hyperplasia, then dissected and kept in tissue storage medium (RNAlater, Sigma-Aldrich Chemie GmbH), or the fish were frozen (−80°C) for later preparation and scoring of the kidneys. Methods for scoring hyperplasia and parasite analyses are given below (see Section 2.3.3).

In addition, in 2017–2018, 110 locations in the study area were searched for colonies of bryozoans (Figure 1b, methods based on Fontes, 2015). At these locations, a river stretch with an average of 150 m of length and 2 m width, and with structures suitable for colonisation by bryozoans (e.g. tree roots, dead wood, and/or boulders) was inspected for 30 min. During the search, structures were lifted and examined for bryozoans. On average, 10 tree roots and 45 stones were examined but this varied considerably with sample location depending on habitat conditions. When bryozoans were found, a sample was taken for stereomicroscopic (Zeiss Stemi 508, Carl Zeiss Microscopy GmbH/Motic RED39Z, MoticEurope) inspection of zooids, polypide structure and flotoblasts. Species were identified according to Wood and Okamura (2005).

2.3.2 Niche models

To assess the potential distribution of T. bryosalmonae and its primary (bryozoan) and secondary (salmonid) hosts, niche models were constructed at a resolution of 30 arcsec (approx. 0.6 km² in the research area), that related climate and environmental conditions (overview in Table S1 and Figure S3) at presence sites to the available environment in the study area(background) using the MaxEnt algorithm (version 3.4.1. Phillips et al., 2006). Bioclimatic data (seasonal temperature and precipitation data) were obtained from BioClim (http://www.worldclim.org, Hijmans et al., 2005). To minimise collinearity among bioclimatic variables for Baden-Württemberg, principal component regression analysis was used, followed by the best-regressor approach as described in Dormann et al., (2013). Using this approach, five variables were selected to represent variation in temperature: mean diurnal range (bio2), isothermality (bio3), temperature seasonality (bio4),...
mean summer temperature (bio10), and mean winter temperature (bio11). A further two variables were retained as predictors for precipitation, namely mean summer precipitation (bio18) and mean winter precipitation (bio19). Environmental data in the model included slope (calculated from elevation maps using the gdal slope plugin in QGIS version 3.4), land cover (categorical variable, Hansen et al., 1998), and the Human Influence Index (HII). The HII is a composite measure of anthropogenic impacts on the environment (Last of the Wild Data Version 2, 2005), and provides a gradient from near-natural to disturbed environments. A similar set of candidate predictors has previously been used in Baden-Württemberg to model ecological niches for freshwater macroinvertebrates (Chucholl, 2017). To add a measure of stream size to the model, Strahler order classifications were extracted from the European catchments and Rivers network system provided by the European Environment Agency (Ecrins, version 1, June 2012, Denmark). The Strahler order ranges from a value of 1 for small headwaters to a value of 8 for large rivers.

The MaxEnt training and prediction area was limited to grid cells (30 arcsec) covering surface waters. Species presence records for *T. bryosalmonae* (positive locations: *N* = 105) and its bryozoan hosts (positive locations for *F. sultana*: *N* = 45; *Plumatella emarginata*: *N* = 25) were derived from the state-wide spatial survey (see above). Additional presence records from fish hosts (grayling: *N* = 183; brown trout: *N* = 1,846) were extracted from a database of the Federal State of Baden-Württemberg, which contains more than 20,000 georeferenced records of fish occurrence. No niche model was calculated for salmon, as records of free salmon sightings are scarce and the species currently shows no equilibrium distribution within the study area. The historic distribution of salmon was restricted to the Upper Rhine catchment and ongoing reintroduction efforts are consequently focussed on tributaries such as the Murg, Kinzig, and Dreisam (Figure 1c). To correct for uneven sampling effort across the investigation area, a sampling bias grid was specified in MaxEnt, which indicated relative sampling effort based on the number of sampling sites per cell (Elith et al., 2011).

For further analysis, output from the logistic model was converted into binary presence-absence maps using the 10th percentile training presence threshold (10thPTP) to assess the core distribution area with a suitable environment for the different species. In addition, the equate entropy of thresholded and original distributions threshold (EETOD) was used, to acquire less conservative predictions than the 10thPTP. The thresholded presence–absence maps for salmonids (brown trout and grayling) and the two most abundant bryozoan host species (*F. sultana* and *P. emarginata*) were subsequently superimposed to arrive at combined presence-absence maps for secondary and primary hosts. The combined maps of predicted suitable habitat for primary and secondary hosts were then overlayed with the environmental suitability map for *T. bryosalmonae* in order to identify areas at risk of further disease outbreaks (i.e. areas with high suitability for both primary and secondary hosts, and *T. bryosalmonae*).

To forecast future presence probabilities of *T. bryosalmonae* and its primary and secondary hosts, the final models were projected to 2050 and 2070 according to predicted climate conditions, using pessimistic and moderate climate change scenarios to cover the most likely outcomes of future global change (http://www.worldclim.org, Giorgetta et al., 2013). The pessimistic prediction was represented by the fossil fuel intensive climate change scenario with highest changes in temperature and precipitation (Representative Concentration Pathways 8.5 W/m² = RCP 8.5) based on the MPI-ESM LR model. For our moderate scenario, we used the MPI-ESM LR model of the emissions reductions climate change scenario (RCP 4.5) that may unfold if climate mitigation policies are put into place and climate tipping points are not reached.

### 2.3.3 | Macroscopic and molecular evaluation of kidney samples

The degree of kidney hyperplasia was scored as an indicator of the clinical disease known as PKD. Kidney hyperplasia scores were made as follows, according to Clifton-Hadley et al., (1986): 0 no kidney change; (1) some grey nodules visible; (2) large grey nodules in part of the kidney; (3) large part of the kidney swollen with large grey nodules; (4) whole kidney swollen.

DNA was extracted from the preserved kidneys using a commercial kit (PureLink™ Genomic DNA Mini Kit, Invitrogen). The procedures (i.e. digestion, binding to spin column, washing, and elution) were carried out according to the manufacturer’s instructions with small modifications. Approximately 50 μg kidney tissue was added to a 1.5-ml tube containing buffer and two 2.4-mm diameter metal beads (OMNI International). Tissue was homogenised for 3 s at maximum speed (Bead Ruptor 4, OMNI International). The homogenate was digested for 3 hr at 55°C with continuous mixing (150 rpm) on a thermomixer (Mixer HC, Starlab). DNA was extracted from the homogenate using the buffers and spin columns provided in the kit. DNA was eluted from the spin column with 75 μl of elution buffer and DNA quantity and purity was measured on a spectrophotometer (NanoDrop 2000c, Thermo Fisher Scientific). Sample concentrations were standardised to 300 ng/μl DNA for real-time qPCR.

For molecular detection of the parasite *T. bryosalmonae*, the method of Bettge et al., (2009) was followed using the primers PKDtaq1 and PKDtaq1. A probe with 6-carboxyfluorescein (FAM) on the 5’ side was applied as a fluorescent reporter and tetramethylrhodamine (TAMRA) was used as quencher at the 3’ side.

### TABLE 2 | Primers and probe used for real-time quantitative polymerase chain reaction

<table>
<thead>
<tr>
<th>Primer name</th>
<th>Sequence (5’–3’)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>PKDtaq1</td>
<td>GGGAGATTGTTGGCATTTTTAAAAG</td>
<td>Bettge et al. (2009)</td>
</tr>
<tr>
<td>PKDtaq2</td>
<td>GCCATGAGCTGTCCAAATCG</td>
<td></td>
</tr>
<tr>
<td>ProbePKD</td>
<td>FAM-CAAAATTGGAGACGTCC GACTACGA-TAMRA</td>
<td></td>
</tr>
</tbody>
</table>
(Table 2). Primers and probes were synthesised by Eurofins Genomics (Ebersberg). All analyses were carried out in duplicates on 96 well reaction plates (MicroAmp, Applied Biosystems). Additional standardised samples with known quantities of parasite DNA (10-fold dilution series from pooled positive and negative samples. Samples were extracted from kidney tissue) and a blank were also run on each plate. The following components were added to each well: 2 μl of template (600 ng DNA), standard or blank, 1 pmol of each primer, 0.4 pmol of probe, and 10 μl of TaqMan master mix (TaqMan Universal Master Mix II, no UNG, Applied Biosystems) and ultra-pure water (Invitrogen) to attain a final volume of 20 μl. Plates were homogenised promptly, using a plate centrifuge (MPS1000, Labnet) and a standard qPCR was carried out on a QuantStudio 3 (Applied Biosystems). Threshold values higher than 32 cycles were not considered to be positive to *T. bryosalmonae* because earlier research showed that at high cycles unspecific sequences might be amplified (Bettge et al., 2009). Sanger sequencing (Eurofins Genomics) of an isolate of the DNA using the primers 514F-new and 776R (Hartikainen et al., 2014) of the standard, and that of sporesacks that were obtained from a local colony of *F. sultana* confirmed a 100% match with *T. bryosalmonae* (GenBank accession numbers: MW269859 and MW269860).

### 2.4  |  Data analysis and statistics

A SpatiaLite Database (SpatiaLite version 4.3.0, managed on SQLite Studio version 3.2.1) was used to log georeferenced spatial data of parasite and bryozoan abundance. The spatial data were processed using QGIS (version 3.12.0) and R (version 3.6.2 running in Jupyter Notebook, packages: sf and raster). Ecological niche modelling was done using MaxEnt (version 3.4.0). The sample bias layer was produced using kde2 in R (package: MASS). The area under the receiver operating characteristic curve (AUC) is given to assess the accuracy of the MaxEnt models. Values range between 0.5 for random prediction to 1.0 for perfect prediction (Elith et al., 2011). AUC values lower than 0.7 indicate low accuracy, whereas AUC values higher than 0.7 represent adequate discrimination capacity (Pearce & Ferrier, 2000; Swets, 1988). Graphs of the distributions were drawn with R (packages: graphics, ggplotify, grid, gridExtra, and Rcolorbrewer).

The population density of brown trout in study 1 was estimated per age-class from the two fishing runs using the method of Carle and Strub (1978) as implemented in the R package FSA. This method estimates the total fish captured from the numbers of fish captured during the first fishing run and the fraction of the fish captured during the second fishing run. Further statistics were calculated in JMP Pro (version 15.1.0, SAS Institute Inc.). Population density data showed a log normal distribution. Linear mixed models and standard least squares statistics were carried out on log transformed data. A linear mixed model was calculated to test changes in population density over a period of 20 years, with density data averaged per decade. Due to the large variation between sample locations and between years, pooling of data was done to decrease the variance in the calculated values of population density. Regression methods would yield similar outcomes but are less intuitive to describe quantitatively. Sample location and age class were added as subject variables with period as repeated covariance structure (spatial) in this model.

### 3  |  RESULTS

#### 3.1  |  Study 1: PKD and brown trout populations in the Wutach and Gutach

#### 3.1.1  |  Changes in brown trout population density during the study period

Brown trout population densities showed a significant positive relationship with elevation of the sampling location (mixed model, pooled per period: $F = 11.8, df = [1,9], p = 0.0074$). The three sampled locations of the river Wutach situated above 600 m above mean

![Graph](image)

**FIGURE 2**  Population density age class of brown trout for the different sampling years. Electrofishing was carried out in June. Age was estimated based on the local total length distribution: parr = 50 – 99 mm, yearlings = 100 – 199 mm and adults above 199 mm. Each data point per sampling date expresses a sampling location in the Wutach and Gutach in the Black Forest. The black line represents the arithmetic mean of population density with grey shaded areas representing the 95% confidence interval.
sea level (mamsl) showed the greatest densities of yearling and adult fish. The greatest overall densities of parr were found in the highest location in the Gutach (Table S3). During the sampling period from 2002 to 2019, population densities showed a significant decrease (Figure 2; mixed model, pooled per period: $F = 13.2$, $df = 13$, $p = 0.0054$), amounting to 51.9% over the two sampling periods (Table S3). This decrease was not significantly different between different age-classes, or between elevations (interactions between age, elevation, and period: $p > 0.48$).

The year to year variation in parr density was significantly correlated with the variation in yearling density the following year (Figure 3a, log-transformed LM: $r^2 = 0.59$, $N = 36$, $p < 0.0001$), and the residual recruitment of this relationship decreased significantly over the years (Figure 3b, log transformed LM: $r^2 = 0.69$, $N = 8$, $p = 0.011$). This indicates a strong decrease in local survival of parr and accounts for the decrease in population density over the study period. Furthermore, local air temperatures increased over the study periods (climate data centre of the Germany’s National Meteorological Service, DWD, station no. 5731, Wutöschingen: Figure S1), and showed a significantly negative relationship with elevation and time of year, as that found for parasite prevalence (logistic regression: effect elevation, $\chi^2 = 20.0$, $p < 0.0001$; effect month, $\chi^2 = 77.2$, $p < 0.0001$; interaction, $\chi^2 = 6.0$, $p = 0.014$). The increase in hyperplasia showed a relative delay of about 2 months compared to increases in parasite prevalence (Figure 4a vs. Figure 4b). The severity of hyperplasia (Figure 4c) also increased in the season and was negatively related to elevation (ordinal logistic regression: effect elevation, $\chi^2 = 25.1$, $p < 0.0001$; effect month, $\chi^2 = 74.8$, $p < 0.0001$; interaction, $\chi^2 = 4.2$, $p = 0.040$). The most severe kidney changes (scores of 3–5) were only found at the lower locations (Figure 4c).

### 3.1.2 Occurrence of *T. bryosalmonae* in the investigation area

The prevalence of *T. bryosalmonae* in brown trout was negatively related with elevation of the sampling location (logistic regression: $\chi^2 = 108.1$, $p < 0.0001$, for bryozoans see Table S4). Whereas up to 100% of brown trout at the lower sampling locations on the Wutach (Wutach_4 and Wutach_3) tested positive for the parasite, none of those caught at the most upstream sampling location, the Josbach, tested positive (Figure 4a). A significant increase in *T. bryosalmonae* prevalence was evident from early summer to autumn (Figure 4a, logistic regression: $\chi^2 = 90.5$, $p < 0.0001$). This increase was steepest in the lower sampling localities on the Wutach (Wutach_4 and Wutach_3) but absent on the Josbach (interaction elevation and month, logistic regression: $\chi^2 = 12.0$, $p < 0.001$).

The percentage of brown trout showing kidney hyperplasia showed a similar relationship with elevation and time of year, as that found for parasite prevalence (logistic regression: effect elevation, $\chi^2 = 20.0$, $p < 0.0001$; effect month, $\chi^2 = 77.2$, $p < 0.0001$; interaction, $\chi^2 = 6.0$, $p = 0.014$). The increase in hyperplasia showed a relative delay of about 2 months compared to increases in parasite prevalence (Figure 4a vs. Figure 4b). The severity of hyperplasia (Figure 4c) also increased in the season and was negatively related to elevation (ordinal logistic regression: effect elevation, $\chi^2 = 25.1$, $p < 0.0001$; effect month, $\chi^2 = 74.8$, $p < 0.0001$; interaction, $\chi^2 = 4.2$, $p = 0.040$). The most severe kidney changes (scores of 3–5) were only found at the lower locations (Figure 4c).

### 3.1.3 Relationship between PKD and changes in salmonid density

The three measurements for PKD, i.e. prevalence of *T. bryosalmonae*, prevalence and severity of kidney hyperplasia, all showed a negative relationship with brown trout population density (parasite prevalence: $\chi^2 = 14.0$, $p < 0.001$; hyperplasia prevalence: $\chi^2 = 5.7$, $p = 0.017$; hyperplasia grade: $\chi^2 = 5.7$, $p = 0.017$).

### 3.2 Study 2: Current and future risk assessment of PKD in salmonids

#### 3.2.1 *T. bryosalmonae* and kidney hyperplasia

In total, fish sampled from 110 out of 140 locations in the study area tested positive for *T. bryosalmonae*. Parasite prevalence was
significantly different between species, at 23.5% for salmon, 60.7% for brown trout, and 81.3% for grayling ($\chi^2 = 38.3$, $df = 2$, $p < 0.001$). In fish that tested positive, the prevalence of kidney hyperplasia was lowest in salmon, at 25.0%, compared to 57.9% in brown trout and 33.8% in grayling ($\chi^2 = 18.8$, $df = 2$, $p < 0.001$). This difference was also reflected in the degree of hyperplasia, which was lowest in salmon and highest in brown trout (mild kidney changes [index 1–2] vs. all kidney changes; salmon: 100%, grayling: 72%, brown trout: 41.2%; $\chi^2 = 10.7$, $df = 2$, $p = 0.005$). All fish showing kidney hyperplasia also tested positive for *T. bryosalmonae* using qPCR.

As can be seen from Figure 1c,d, *T. bryosalmonae* was widely distributed over the investigation area. However, a significant difference was found between the distribution of elevations where salmonids were sampled and that of elevations where salmon tested positive for *T. bryosalmonae* (Figure 5, Kolmogorov–Smirnov test, $D = 0.57$, $p = 0.036$, one-sided). The parasite-free higher elevations (higher than 600–700 m asl: Figure 5) were mostly found in the mountainous Black Forest and on the north side of Swabian Alb plateau (24 of 30 locations without *T. bryosalmonae*: Figure 1b,c).

3.2.2 | Bryozoan hosts for *T. bryosalmonae*

Stereoscopic identification of the bryozoan samples showed two species of bryozoans to be the most abundant, both of which have been implicated as hosts for *T. bryosalmonae*. These species were *Fredericella sultana*, found at 45 locations (Figure 1b), and *P. emarginata*, at 24 locations (Figure 1b). In 23% (13 of 56) of these locations, both species were found together. Other species found to co-occur with *F. sultana* were *Plumatella fruticosa* in 10 locations (Figure 1b), and *Paludicella articulata* at three locations. Most of the sampling locations where no bryozoan colonies were found are located in mountainous areas of the Black Forest and the Swabian Alb (26 of 40 sample sites without bryozoans, Figure 1b).

3.2.3 | Distribution patterns of primary hosts: bryozoans

Areas of predicted environmental suitability for *F. sultana* ($AUC = 0.679 \pm 0.192$ [mean \pm SD]) and *P. emarginata* ($AUC = 0.690 \pm 0.276$ [mean \pm SD]) are depicted in Figure 6b,c. Temperature and precipitation variables made the largest contribution to the niche model for *F. sultana* (Figure S3), for which the probability of presence correlated positively with variation in diurnal range and seasonality of temperature, and showed a peak at mean summer air temperatures of approximately 17°C and
winter temperatures of approximately 0°C. Furthermore, the model showed *F. sultana* to be more likely to occur in areas with high summer precipitation and low winter precipitation. Coniferous forest and wooded grasslands correlated negatively with *F. sultana* presence. *Plumatella emarginata* showed generally similar environmental preferences as were found for *F. sultana*, but was more strongly associated with river sections with steeper gradients. It also was less associated with forest and more with grasslands and urban areas (Figure S3). Overall, 66.2%–84.1% of the grid cells were estimated to be suitable to either one or both of the bryozoan species (10thPTP–EETOD rule, Figure 6b,c). The model predicted that higher elevated areas of the Black Forest and north-eastern Baden-Württemberg and lowland stretches of the Rhine and Neckar rivers are unsuitable for either species of bryozoans (Figure 6).

### 3.2.4 Distribution patterns of secondary hosts: Salmonids

Areas of predicted environmental suitability for the main secondary hosts of *T. bryosalmonae*, i.e. brown trout (test AUC = 0.712 ± 0.047 [mean ± SD]) and grayling (test AUC = 0.896 ± 0.029 [mean ± SD]), are shown in Figure 6d,e. The probability of brown trout and grayling presence was mostly affected by the variables stream size (Strahler order) and slope. Brown trout are associated more closely with steep headwater streams, while grayling are predicted to occur mostly in larger rhithral streams. For brown trout (Figure 6c), precipitation (21.7%) and temperature (20.4%) both contributed notably to predicted habitat suitability. In terms of air temperature, cool conditions appear to be favourable in summer, while optimum winter values are
around 0°C. By contrast, the probability of grayling presence was related positively to precipitation (30.5% contribution) and human impact (15.6% contribution). The combined predicted distribution of these two species covered 53.9% to 77.8% (10thPTP–EETOD rule, Figure 6d,e) of the grid cells in the study area. Unsuitable areas tended to be situated in the west and the north-east of the federal state area (Figure 6d,e, and Table S2).

3.2.5 | Distribution pattern of PKD

The niche model for *T. bryosalmonae* is shown in Figure 6a (test $\text{AUC} = 0.728 \pm 0.096$ [mean $\pm$ SD]). Probability of presence is seen to be determined mostly by temperature variables (53.4% contribution; Figure S3). Of these predictors, mean summer temperature showed the highest contribution (26.3%) and was related positively to parasite occurrence. Precipitation also made an important contribution to the model, with *T. bryosalmonae* being most abundant in areas with average summer rainfall (18.8%). Finally, the parasite seems to be more abundant in rural areas (contributions of HII: 7.9%, and land cover: 16.2%). The model predicted a distribution covering 52.4% to 70.3% (10thPTP–EETOD rule) of the grid cells in the study area, suggesting high environmental suitability for *T. bryosalmonae* in areas of lower elevation in Baden-Württemberg (Figure 6a).

Comparing the predicted distribution of *T. bryosalmonae* (Figure 6a) to that of its primary (Figure 6b,c) and secondary (Figure 6d,e) hosts shows an overlap of 88.5% and 63.6%, respectively (using the core suitable area based on the 10thPTP rule). Figure 7 shows an overlay of the distribution maps (10thPTP rule) projected for salmonids (greens and dark brown) and *T. bryosalmonae* (dark brown + light brown) and indicates areas where salmonid populations are relatively protected against outbreaks of PKD (green),

![FIGURE 7 Overlay of projected distribution maps of Tetracapsuloides bryosalmonae (colours: light brown + dark brown) and salmonids (Salmo trutta and Thymallus thymallus: in colours green + dark brown) for current and different future climate change scenarios. Projections are plotted for current climate conditions, and for two climate change scenarios represented via their RCP value (representative concentration pathways = 4.5 and 8.5 W/m²) in 2050 and 2070. Core suitable areas were calculated using the 10 percentile training presence rule in Maxent [Colour figure can be viewed at wileyonlinelibrary.com]](image-url)
areas suitable for both primary and secondary hosts but not to the parasite (light green), and areas where outbreaks are likely to occur as conditions for primary and secondary hosts and the parasite are favourable (dark brown). The main safe areas for salmonids, where outbreaks of PKD are unlikely, are predicted in the highland rivers of the Black Forest and some rivers on the north of the Swabian Alb (Figure 7a). Northern and eastern regions of the Black Forest seem to contain habitat suitable to primary and secondary hosts, i.e. areas where *T. bryosalmonae* might potentially spread and thus reach salmonid areas that have previously been protected from PKD.

### 3.2.6 Predicted future risk for salmonid populations

Model projections using forecast climate conditions (Figure 8: RCP 4.5: a → b → c; RCP 8.5: a → d → e) show a strong decline in the areas suitable for salmonids, while areas suited for *T. bryosalmonae* are unaffected or affected to a much lesser extent. The average over both climate models predicts a 40.9%–72.3% decrease in brown trout populations over the next 50 years and an initial increase of 11.0% in grayling populations followed by a decrease of 25.9%. Taken together, this amounts to a 69.1% decrease in the area suitable for salmonid populations by 2070 as a result of climate change (Figure 8a). By contrast, the total area predicted to be suitable for *T. bryosalmonae*, does not change significantly by 2070 (Figure 8b). The two climate change scenarios differ strongly in their prediction for 2070, as the pessimistic RCP 8.5 scenario leaves very few areas suitable to salmonids while the moderate RCP 4.5 scenario spares relevant refuges of suitable habitat at higher elevations (Figure 8c vs. 8d and 9a). The models indicate that areas currently showing a high risk on PKD (dark brown areas in Figure 8a) are the ones that will be progressively lost to salmonid populations by 2050–2070 due to climate change. The models further predict that the fraction of potential salmonid range that is safe from *T. bryosalmonae* infections, i.e. the safe area, will remain low (Figure 8d). Meanwhile, the fraction of potential salmonid range suitable to *T. bryosalmonae* and its bryozoan hosts, i.e. the high-risk area, shows no decline in the future.
and is predicted to significantly increase under the pessimistic RCP 8.5 scenario (Figure 8c).

4 | DISCUSSION

The aims of this study were to determine whether emerging temperature-mediated PKD of salmonids is related to changes in salmonid populations, and to predict the extent to which the disease will affect populations under different climate change scenarios. By carrying out a long-term time series study in a typical salmonid river in southern Germany, the Wutach, this study provides the first empirical evidence for an alarming 51.9%-decline in brown trout populations in just the last 2 decades. In the studied locations, brown trout populations have declined over a wide range of elevations, in parallel with a temperature correlated reduction in local recruitment from yearlings, despite temperature values remaining in the suitable range. Furthermore, these declines are strongly related to an increased prevalence of Tetracapsuloides bryosalmonae, the causative agent of PKD. The prevalence of both PKD and kidney hyperplasia was increased at lower elevations where river temperatures are higher, and were negatively related to brown trout densities.

The results of the spatial survey showed widespread parasite infections in salmon, grayling, and brown trout. The few locations where infections were rarely detected were exclusively situated in mountainous area at elevations above 600 m asl, which is in line with an earlier publication of Wahl et al. (2008). Ecological niche modelling based on current and future climate data shows that the distribution of the parasite strongly overlaps with that of its primary hosts, namely the two most abundant bryozoans in the region, F. sultana and P. emarginata, and that this poses risks to current salmonid populations. Future climate change scenarios indicate a strong decline in the area of habitat suitable for salmonids, with the strongest decreases occurring in areas where salmonids are already exposed to T. bryosalmonae.

4.1 | How are brown trout populations affected by PKD?

Previous studies in the Wutach have shown that both density and yield of brown trout were constant or even slightly increasing at the start of the century (Baer & Brinker, 2010). This trend has clearly changed over the last 2 decades, and the data presented here show a 51.9% decrease in trout densities over a wide range of elevations in the river. All measures of T. bryosalmonae infection in brown trout that were taken during the second part of the study period, i.e. parasite prevalence, kidney hyperplasia percentage and kidney hyperplasia grade correlated negatively with brown trout population density. To the best knowledge of the authors, no other possible negative impact factors, such as predation by cormorants, fish dying through pollution events, or stream modifications occurred in the Wutach during the study period. Thus, the most likely cause of the observed decline in brown trout populations is the cumulative effect of PKD interacting with abiotic factors intrinsic to the river system.

Few studies have reported PKD outbreaks in trout in southern Germany (Arndt et al., 2019; Hoffmann & Dangschat, 1981), and no PKD linked mortality of wild salmonids has been reported in the area. One possibility is that mortality is under-reported due to the disease mostly affecting young fish (Schager et al., 2007) and due to the general difficulty in observing and measuring parasite-induced mortality in the field (Rousset et al., 1996). Temperature driven PKD induced population decline is multifaceted, involving many indirect effects on survival (Burkhardt-Holm & Zehnder, 2018). For example, PKD may make fish more susceptible to existing environmental stressors (Bruneaux et al., 2017) such as warmer than average summers (Borsuk et al., 2006; Hari et al., 2006; Rubin et al., 2019), pollution (Bailey et al., 2018), or secondary infection with other pathogens (Arndt et al., 2019; Chimlonczyk et al., 2002; Hedrick et al., 1993). PKD compromised condition (Bruneaux et al., 2017) could potentially decrease survival through subsequent metabolic challenging periods like winter (recruitment) or migration (Kent et al., 1995). PKD may also indirectly increase mortality by rendering diseased parr more vulnerable to predators as behavioural responses wither when the disease advances and fish become anaemic (Bruneaux et al., 2017). Of the factors examined, a general rise in temperature is most likely to be interacting with PKD in the Wutach, where ambient temperatures increased by 1°C over the period of the population decline (DWD data, Figure S1). However, it is important to note that temperatures across the study area remained in the optimal range for endemic salmonids (Elliott & Elliott, 2010; Klemetsen et al., 2003). Taken together, PKD and increasing temperatures explain the significant decrease in recruitment of yearlings in the Wutach over the study period (see also Carraro et al., 2017). Two previous exposure trials in this same river have estimated PKD related mortality of brown trout parr to be 15% (Schmidt-Posthaus et al., 2015, 2017). Reduced parr survival in the river due to PKD would cascade to subsequent age classes, and this probably plays a main role explaining the observed general decrease in brown trout numbers.

The pattern of population decline in the Wutach seems to be delayed in time compared to the slow decline reported for brown trout in Switzerland by angler statistics during the last quarter of the 20th century (Burkhardt-Holm et al., 2002). PKD was hypothesised to be a major factor in the Swiss brown trout decline as it started in rivers at lower elevation with favourable conditions for the spread of T. bryosalmonae and become generalised when river temperatures increased by 1°C between 1985 and 1990 (Hari et al., 2006). Eventually brown trout catches in Swiss rivers were estimated to have declined by 66.4% in the 2 decades to 2000 (Hari et al., 2006), while angling yields of brown trout in the Wutach remained stable. The delay might possibly be explained by the near-natural state of the latter river and the concomitantly greater resilience of its fish populations to environmental stressors (Baer & Brinker, 2010). The current 51.9% decrease in brown trout density in the Wutach in the last decade is suggestive of a recent upstream spread of T. bryosalmonae. The pending increase in temperatures due to climate change make it increasingly essential
for surviving salmonid populations in rivers such as the Wutach to have secure access to head waters, small tributaries or other areas with relatively cool and well oxygenated water, where the effects of *T. bryosalmonae* infection tend to be mild (Rubin et al., 2019; Streparava et al., 2018; Wahl et al., 2008).

### 4.2 Distribution of *T. bryosalmonae* in relation to its primary host

The spatial study found the parasite *T. bryosalmonae* to be widespread in salmonids in rhithral rivers in the investigation area, with the exception of mountainous rivers at elevations over 600 mabsl. This corresponds well with previous studies (Wahl et al., 2008) and with proposed temperature limits for spore release (Tops et al., 2006). Carraro et al., (2018) and Rubin et al., (2019) suggest river temperatures over 15°C are most favourable for the spread of the parasite and for the development of PKD in brown trout, and the current results support these theories, as summer mean air temperatures in the study zone are about 1.5°C lower in areas above 600 mabsl than in areas below 600 mabsl elevation. As the primary interest in the current study was in analysing effects of climatic variables, air temperature was entered as variable in the ecological niche modelling of the spread of *T. bryosalmonae*, rather than elevation. Higher summer air temperatures (optimum at 17-18°C) show a positive relationship with the spread of PKD in the investigation area. Increased *T. bryosalmonae* prevalence in trout was also found in areas most impacted by human land use. This might be due to greater sensitivity of salmonids to the parasites in these areas, as increased water pollution has been implicated in greater prevalences of PKD in brown trout in several previous studies (Bailey et al., 2018; El-Matbouli & Hoffmann, 2002). Moreover, eutrophication due to increased wastewater may result in increased bryozoan growth (Hartikainen et al., 2009), which in turn drives parasite spore production.

As salmonids can acquire PKD only through infection with spores of *T. bryosalmonae* released from infected bryozoans (Feist et al., 2001; Morris & Adams, 2006; Tops & Okamura, 2003), the spread of the disease is limited by the distribution of the main primary hosts *F. sultana* and *P. emarginata* (Hartikainen et al., 2014; Longshaw & Feist, 2000; Okamura & Wood, 2002). However, the range may be slightly extended through fish migration and drifting of parasite spores. Both bryozoan species were found to be widely distributed in the investigation area, overlapping in range with PKD. *Fredericella sultana* was the most abundant bryozoan species found in rivers, possibly reflecting its ability to produce sessile dormant stages, so-called statoblasts, which survive through winter (Brown, 1933). The elevated mountainous areas of the investigation area were found to be less favourable for bryozoans and this is probably an effect of lower temperature. Both *F. sultana* and *P. emarginata* start to grow when average water temperatures rise to 10–15°C (Vohmann et al., 2009). Bryozoan colonies were patchily distributed, often found between or under large rock slabs or boulders. The number of colonies found in this study was within the range of those found in the Wulka catchment in Austria (Waldner et al., 2020).

### 4.3 Sensitivity of salmonid populations to PKD

While the brown trout is the primary fish host of *T. bryosalmonae* in Europe (Grabner & El-Matbouli, 2008), the current results also show significant proportions of salmon and grayling testing positive for the parasite. Of these species, parasite prevalence and kidney hyperplasia were lowest in salmon parr. Previous data pertaining to the sensitivity of salmon to PKD are limited to a study in Norwegian rivers that showed high fry mortality due to PKD (Sterud et al., 2007). Salmon have a complex and variable life-cycle, which for populations in the sampled region entails seaward migrations in summer, through warm potamal rivers, a period at sea, and a migration back to rhithral rivers for spawning (Monnerjahn, 2011). In the current study, 23.5% of investigated salmon parr were infected with the parasite. It is not known whether these infected fish could still successfully perform migration. Chronic infections with *T. bryosalmonae* are known to occur in brown trout (Abd-Elfattah et al., 2014; Soliman et al., 2018) and the parasite has been implicated in a disease of adult trout, proliferative darkening syndrome (Arndt et al., 2019). Thus, even if salmon parr were to survive a first infection in colder rhithral waters, they may still experience symptoms later in life which could limit their chances during the highly demanding potamal migration, when aerobic performance and thermal tolerance are critical (Bruneaux et al., 2017).

Parasite prevalence in grayling was found to be distinctly high, higher even than in brown trout (81.3% vs. 60.7%). Similar high parasite prevalence has been reported in rivers in Finland (Vasemägi et al., 2017). However, in experiments in which grayling were kept in similar conditions and temperatures to brown trout, the former was found to be more resilient to *T. bryosalmonae* infections and not to spread spores of the parasite (Grabner & El-Matbouli, 2008; Schmidt-Posthaus et al., 2017). Indeed, despite high prevalence, grayling in the current study showed markedly less hyperplasia than brown trout (33.8% vs. 57.9%). Furthermore, grayling exhibiting PKD-like kidney hyperplasia were sampled at some locations in the Danube, where summer temperatures are not favourable for brown trout. Thus, grayling is clearly sensitive to PKD although at higher temperatures than found for brown trout, but up to date the species is not considered to spread spores of *T. bryosalmonae* (Grabner & El-Matbouli, 2008). Clearly, the dynamics of *T. bryosalmonae* infection in the different salmonid species, including grayling, should be considered separately in order to learn how to manage the consequences of PKD in the decline of salmonid populations in general.

### 4.4 Future estimated changes in salmonid populations and PKD

The future impact of PKD on brown trout, grayling, and salmon populations is greatly dependent on how water temperature, precipitation, and evaporation change in the context of the climate crisis (Borgwardt et al., 2020; Masson-Delmotte et al., 2018). Water temperatures in central Europe have already increased by 1-2°C (Daufresne & Boët, 2007; Kędra, 2020; Michel et al., 2020; Webb & Nobilis, 2007) and patterns
of precipitation have changed in quality (increasingly torrential rain, less snow) and seasonality (decreases in summer, increases in winter) (Masson-Delmotte et al., 2018). Under these conditions, salmonids are estimated to have already lost half of their population density (Arndt et al., 2019; Burkhardt-Holm & Zehnder, 2018; Waldner et al., 2020). This time-series study shows, for the first time empirically, a decline in brown trout density in the investigated area, and links this decline to PKD. The prognoses of moderate to pessimistic high emission-case climate change scenarios predicting that global temperatures would increase a further 1–3°C in the 21st century (Masson-Delmotte et al., 2018), do not portend a break in this trend. Further losses to salmonid populations, both in density and in suitable habitat are thus to be expected. The presented data support this expectation and warn of a near exponential loss of salmonid habitat under more pessimistic high-emission scenarios.

Fifty years into the pessimistic climate change scenario (RCP 8.5), even the salmonid habitats at high elevation in the study area will become suitable for both bryozoans and T. bryosalmonae. Then, one must expect that more than 85% of the current habitat will turn unsuitable for salmonids. Under the moderate-case climate change scenario (RCP 4.5), the predicted loss of suitable habitat lowers to 50%. Overlapping maps of habitat suitability for salmonids and T. bryosalmonae indicate that this habitat loss is extensive at lower elevations where salmonids already suffer a high probability of exposure to PKD and experience more severe grades of kidney hyperplasia. By contrast, losses of suitable habitat at lower elevations will be slightly compensated by an increase in suitable habitat at higher elevations (Borgwardt et al., 2020). Even if these elevated areas are small and therefore not relevant for fishery utilisation, they are less suitable to bryozoans and T. bryosalmonae, which means they might remain suitable for salmonids and provide a refuge even under significant warming.

Globally freshwater ecosystems and biodiversity are in strong decline, prompting Tickner et al., (2020) to call for emergency action plans to accelerate the implementation of conservation, restoration and improvement of water quality and connectivity measures. In line with this call, it is imperative for salmonid conservation that the connectivity is restored and maintained between different sections of rivers and streams, so that suitable habitat at higher elevations remains accessible as potential future refuge, both in terms of climate suitability and exposure to PKD. Furthermore, maintaining T. bryosalmonae-free headwaters will be especially important for survival of young salmonids in a warming world as PKD is more severe at higher temperatures. These populations should be protected from parasite infection by awareness programmes preventing cross contamination from rivers that already have the parasite. Other measures should focus on minimising environmental stressors on infected populations by providing more shade, lowering pollution, and maintaining cold-water refuges. The prognoses for habitat suitability underline that such conservation efforts to protect and restore salmonid populations, including the salmon but also for currently abundant species such as brown trout and grayling, should include an assessment of climate change. It is likely that the predicted and ongoing decline in trout density will result in increased efforts to restock salmonids. Especially after hot and dry summers like that of 2018 in Europe, such efforts might be essential for conserving trout populations. Pre-stocking acclimatisation to local environmental conditions was found to be beneficial to stock survival (Baer & Brinker, 2008). It is unknown whether such acclimatisation included exposure to local parasites such as T. bryosalmonae. Studies into benefits of local adaptation of salmonids to parasites should guide conservation measures. Together, the significant efforts being made to re-wild rivers, to build viable salmonid stocks, and to reduce the damage from diseases such as PKD to existing salmonid populations, will only produce desired results when climate change is mitigated to at least the more moderate-case climate change scenario.

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CONFLICT OF INTEREST

The authors report no conflicts of interests.

DATA AVAILABILITY STATEMENT

The georeferenced collected data on which this paper is based cannot be made publicly available due to German privacy protection regulation.

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