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Inland freshwater aquaculture in a warming world

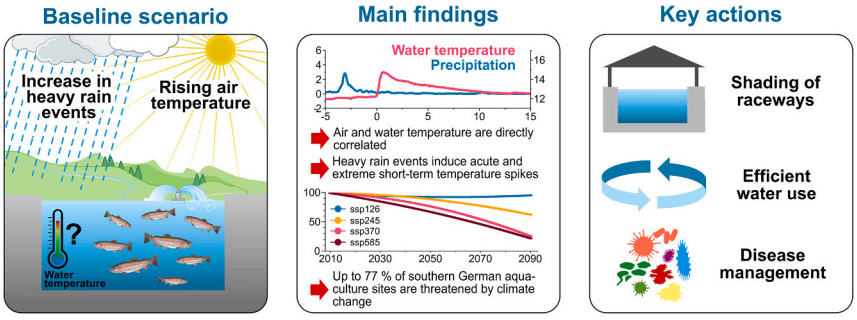
Tamara Wind [a,*], Albert Ros [a], Christoph Chucholl [a], Samuel Roch [a], Mark Schumann [a], Carsten Schulz [b], Alexander Brinker [a,c]

[a] Fisheries Research Station of Baden-Wuerttemberg, Argenweg 50/1, 88085 Langenargen, Germany
[b] Christian-Albrechts-University Kiel, Olshausenstraße 40, 24098 Kiel, Germany
[c] University of Konstanz, Mainaustraße 252, 78464 Konstanz, Germany

HIGHLIGHTS

- Temperature dynamics were predicted under four projected climate change scenarios.
- Water temperature rises significantly less in shaded facilities.
- Extreme rain events could induce increases in water temperature of up to 5 °C.
- 37–77 % of cold-water facilities face suboptimal climate conditions in the future.
- Management options are proposed as key actions to preserve cold-water aquaculture.

GRAPHICAL ABSTRACT



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ABSTRACT

Climate change potentially threatens the sustainable production of highly valued cold-water fish species in flow-through systems, such as salmonids. By analysing the relationship of water temperature to hydrological characteristics, air temperature, solar exposure, and precipitation, this study predicted temperature dynamics of five temperate cold-water aquaculture facilities under four projected climate change scenarios. Air temperature was found to be directly associated with facility site water temperature, and based on rational assumptions, two of the five facilities were predicted to face critical warming by mid-century. Extreme precipitation events induced acute short-term increases in water temperature of up to 5 °C. Significantly lower warming, roughly equal to the projected climate change–induced increase, was seen with artificial shading lowering temperature by 1 °C. Complementary niche modelling revealed that 37–77 % of current cold-water facilities will likely incur suboptimal climate conditions by the end of the century. Shading of raceways, more efficient water use, and disease management are proposed as key actions to preserve cold-water aquaculture.

1. Introduction

Aquaculture has been identified as a key sustainable food producing sector as it has the potential to use renewable resources such as fish meal or soy for the production of protein-rich and healthy food (Cottrell et al., 2020; Gephart and Golden, 2022; Hilborn et al., 2018). The majority of these professional facilities are directly connected to, or strongly embedded in the aquatic environment. Therefore successful production largely depends on a stable water supply with limited variation in its physical conditions (Ebeling and Timmons, 2010). Especially in the

* Corresponding author at: Fisheries Research Station of Baden-Wuerttemberg, Argenweg 50/1, 88085 Langenargen, Germany.
E-mail address: alexander.brinker@lazbw.bwl.de (A. Brinker).

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production of stenotherm cold-water fishes like salmonids, climate change might severely affect key water parameters. Consequently, in northern and central Europe, where the focus lies on this practice, aquaculture is particularly vulnerable to the impact of climate change (Brämick, 2021; Fornshell et al., 2012; Hough, 2022). Current climate-change is expected to increase both frequency and intensity of drought and extreme rainfall events, and average temperatures in Europe are rising at a rate exceeding the global mean change of 1.09 °C (Brasseur et al., 2017; IPCC, 2023; Wilke, 2013). Such extreme weather events affect water temperature and oxygen availability and influence, directly or indirectly, disease susceptibility and growth of cultured animals (Fry, 1971; Pugovkin, 2019). Consequently, fish farming must adapt to such changing conditions as the future climate will exceed the historic climatic range in which aquaculture has developed in Europe (Gutiérrez et al., 2021; Osman et al., 2021).

Depending on intensity and temporal scale, changes in water temperature can exert both positive and negative effects on aquaculture. Temperatures in the range of 20 to 30 °C are considered as incipient lethal temperatures, with temperatures above resulting in an acute thermal shock for most salmonid species. Still salmonids may acclimate to temperatures above their upper incipient lethal temperature when water temperatures increase slowly (Jonsson, 2023). Such long-term increases, which are considered to be of great importance in aquaculture, can be associated with climate change. Risks resulting from those increases are likely to outweigh any benefits of traditional cold-water fish farming. For example, while higher temperatures during winter are positively correlated with growth of rainbow trout (Morgan et al., 2001), warmer summers may be detrimental if water temperature exceeds the upper thermal limit for growth of the reared stock (Ebeling and Timmons, 2010; Jonsson, 2023). If high temperatures persist over an extended period, thermal stress can result in physiological changes that may negatively affect fish fitness (Alfonso et al., 2021). Warmer conditions, especially in summer, can cause changes in behaviour and feeding efficiency and increase energy demand, leading to reduced growth and survival (Hjeltnes et al., 2008; Rottman et al., 1992; Wedemeyer, 1996). Excessive summer warming endangers cold-water fish welfare and increases susceptibility to disease and pathogens (Alfonso et al., 2021; Schreckenbach, 2002). A striking example of this is proliferative kidney disease, an emerging disease in salmonids associated with high mortality at elevated temperatures (Ros et al., 2021).

Water temperature in freshwater aquaculture facilities is directly affected by air temperature and solar radiation on the water surface (Adam and Sullivan, 1989). Heavy rain on warm days may result in an acute rise in water temperature when water falling on heated surfaces runs into the water source, and fish stress can be exacerbated by increased inflow of suspended solids (Courtice et al., 2022; Jacquin et al., 2020; Zhao et al., 2018). Summer drought reducing the availability of water, also carries significant risks (FAO, 2018). With low inflow of fresh water, concentration of metabolic end products like CO_2 and NH_3 might quickly exceed tolerable levels (Zhao et al., 2018). Additionally, water will remain longer in the system, absorbing more heat from the surroundings. As a result, the water temperature will warm even faster (Adam and Sullivan, 1989).

The adverse effects of climate change on water supply and quality raise the question of the extent to which cold-water aquaculture will be sustainable, and what measures might be undertaken to increase resilience of fish production to weather extremes, warming, and altered precipitation patterns. Few studies have investigated the consequences and risks of ongoing climate change on aquaculture. Given the rapid pace of such changes and the pivotal role of aquaculture in food production, this question needs to be addressed (Basen et al., 2022a, 2022b; FAO, 2018).

Using a dataset with high temporal resolution, we assessed in this study the effects of current and projected climate change on intra-daily, daily and monthly temperature regimes in five typical cold-water aquaculture facilities in central Europe. In the first part, parameters that influence local temperature, such as differences in shading at the study sites, are described in relation to intra-daily and daily variations in weather conditions on water temperatures. A model was then created that plotted historical trends in monthly hydrological characteristics (air temperature, solar radiation and precipitation) against water temperatures at the sites. This model was used to test the impact of four climate change scenarios ranging from effective climate protection to worst-case global warming on cold-water aquaculture of the near future. To further test these relationships on a regional-spatial scale, the locations of professional fish farms in southern Germany were used to infer the environmental niche supporting that supports current land-based cold-water aquaculture. Niche parameters were projected to future climate conditions to assess the environmental suitability for land-based cold-water aquaculture under expected climate change. Based on the warming trend in Europe, it was hypothesized that climate change has already caused water in aquaculture facilities to reach temperature thresholds close to the critical thermal maximum of salmonid species reared in aquaculture facilities (Perry et al., 2005). Findings and recommendations from this study will help inform decision making on effective adaptation and mitigation measures like increased use of shading in cold-water aquaculture in the face of rapid climate change.

2. Material and methods

2.1. Study site characteristics

High resolution water temperature data were acquired from five flow-through salmonid aquaculture facilities (sites A to E) located in south-western Germany, an important central European salmonid farming region (Fig. S1). Study sites were selected to cover a broad range of environmental and production conditions. All facilities received water from a groundwater spring or headwater stream with multiple small springs before reaching facilities. Husbandry systems in fish holding facilities consisted of raceways with rearing compartments being either earthen or concrete ponds. Study site C has five natural ponds connected in line, while compartments of sites A, B, D and E consist of concrete basins. Study sites A and E each have a tssingle raceway, B has two parallel raceways and study site D four parallel raceways. Raceways of sites D and E were completely shaded by a roof. The raceway volume ranged from 300 to 2000 m^3 and flow rate through the system varied from 20 to 300 L/s (Table TS1). These characteristics of the study sites, including calculations of energy input from the environment, and raceway volumes can be found in Table TS1.

2.2. Data collection and management

Water temperature (*Tw*, °C) at the sites was continuously recorded at one- or two-minute intervals. Data for all sites were available for the period from 2017 through 2021. For sites that recorded *Tw* in multiple compartments (B, C, D), only data from the most downstream compartment is presented, as these exhibit greatest warming. The data was used to

1) chart hourly and daily fluctuations in water temperature relative to local weather conditions;
2) investigate historic temperature trends by extrapolating the obtained relationships to historical weather data from the Germany's National Meteorological Service database (Deutscher Wetterdienst, DWD, https://opendata.dwd.de/, accessed July 2022); and.
3) calculate future patterns of water temperature under projected climate change based on simulated weather data extracted from the WorldClim database (https://www.worldclim.org/data/index.html, accessed July 2022).

To investigate drivers of short-term fluctuations in water temperature, the following weather data were extracted from the DWD data

portal (https://opendata.dwd.de; accessed July 2022): precipitation (*P*), solar impact (*S*), and ambient air temperature (*Ta*).

Data of local precipitation (mm/5 min) were extracted from georeferenced grids hourly. Heavy rain events were defined as precipitation ≥7.5 mm in 30 min, per the DWD definition (DWD, 2023), with a cumulative sum of precipitation calculated backward and forward (R package data.table, function frollsum) (Dowle et al., 2015) at each data point. The difference between the two values was calculated.

Air temperature (°C) on a 5 min scale and sunshine duration (min/h) were obtained from the nearest weather station, and temperature data on a monthly scale were extracted from georeferenced grids available from the DWD data portal. Solar position (altitude above the horizon in radians) was calculated for each study site using the R package "suncalc" (Thieurmel and Elmarhraoui, 2019). Solar exposure in min/h was calculated by correcting sunshine duration for sun position using the formula sin(sun elevation in rad).

Extreme change in water temperature was defined as Δt ≥1 °C within 30 min. In order to identify these events, a running average of the temperature was calculated over the data 30 min before and 30 min after each data point (R package data.table, function frollmean), and the difference between the two obtained values was calculated. Past and future estimates of water temperature were derived from the WorldClim historical monthly weather and future climate data (www.worldclim.org, accessed July 2022).

For future climate, four Shared Socioeconomic Pathways (SSP), SSP126, SSP245, SSP370, and SSP585, of the Max Planck Institute Earth System Model were extracted [MPI-ESM1.2 high resolution (Gutjahr et al., 2019)]. These scenarios cover a range from worst- to best-case climate change scenarios, with intermediate scenarios (SSP245 and SSP370) being the most realistic outcomes based on current climate conservation policies and pledges (Masson-Delmotte et al., 2021). In this dataset, precipitation (mm/month) as well as maximum and minimum air temperatures (°C) were available for each year from 1960 through 2017 and estimated for 20-year periods from 2021 through 2100.

2.3. Statistical analysis

Data was managed and analysed with R version 4.2 (R Core Team, 2022) using packages "data.table", "forecast", "dplyr", "raster" (Hijmans, 2022), and "suncalc" (Thieurmel and Elmarhraoui, 2019).

To assess the effect of extreme precipitation events on water temperature, a pre- and post-event temporal analysis of extreme precipitation events and peak water temperature was carried out using local precipitation and water temperature averaged on a 5 min scale.

To assess the effect of artificial shading on water temperature, the diurnal temperature range ($\Delta T = wt_{max} - wt_{min}$) in July and August was plotted with respect to shade (shaded *vs.* unshaded) and solar conditions (cloud *vs.* sun) in a linear model with interaction term and study site as random factors.

To test for drivers of daily fluctuations in water temperature, a linear auto-regressive integrated moving average (ARIMA) model was calculated by averaging data on a daily scale. The auto-regressive and moving average parameters correct for temporal processes of inhibition and attenuation in the temperature dynamics. Publicly accessible data were collected for local precipitation, air temperature, and solar exposure, calculated as sunshine duration corrected for sun position (duration x π/altitude). Sun hours and precipitation were lag-shifted with a factor 1 to obtain data of the previous day (lead function). The ARIMA was used to correct for autocorrelation in the high-resolution temporal water temperature models:

$$Y_t = \beta_0 + \left(\sum\nolimits_{i=1}^{n} \beta_i X_{ti}\right)^2 + \gamma_t$$

$$\gamma_t = \sum\nolimits_{j=1}^{2} \varphi_i \gamma_{t-j} + \epsilon_t - \sum\nolimits_{k=1}^{2} \theta_i \epsilon_{t-k}$$

where Y_t is a time series of water temperature, and X_{t1}, X_{t2} … X_{tn} are potential drivers of variation in Y_t. These include four dummy variables representing variation among the five study sites (each of levels 0 and 1) and three continuous variables: precipitation (*P*), solar exposure (*S*) and air temperature (*Ta*). Second order interaction terms were added by crossing each variable. β_0 = coefficient of the intercept and β_1 … β_n are the corresponding model coefficients. The residual variation in water temperature γ_t was corrected for autocorrelation using ARIMA. The Bayesian information criterion (BIC) was used to select the optimal ARIMA model. The final model included two orders of partial autocorrelation parameters, φ_i, and moving average parameters, θ_i. Discharge has been identified as an important variable in driving water temperature variation in free flowing water (Bal et al., 2014). However as flow was regulated at a constant rate in the different facilities (see Table TS1) this effect is captured by the variation between study sites *via* the dummy variables in the model.

To estimate past and future water temperature based on available precipitation and air temperature data (historical weather data and projections from a global climate model), a linear model was calculated using the R standard function *lm* to predict monthly water temperatures:

$$wt = \beta_0 + \left(\sum\nolimits_{i=1}^{4} \beta_i X_i\right)^2 + \epsilon$$

where wt = water temperature, X_1 = location (factor), X_2 = maximum air temperature, X_3 = minimum air temperature, and X_4 = precipitation. All second order interactions among predictors were included in the model.

2.4. Future environmental suitability for salmonid aquaculture

Complementary to the site-specific analysis, an environmental niche model (ENM) was used to describe the environmental niche supporting current salmonid aquaculture in temperate Europe and to assess environment suitability for salmonid aquaculture under projected end-of-century climate. Although ENMs are primarily used to forecast species distribution, they can be applied to socio-economic activity linked to distinct environmental conditions. Based on the extraordinarily long history of cold-water aquaculture in southern Germany (Brämick, 2023), aquaculture facilities were considered to exhibit equilibrium distribution, *i.e.* they are commonly present in environmentally suitable areas and absent from those unsuitable, a fundamental assumption for correlative ENMs (Phillips et al., 2006).

The ENM was constructed in MaxEnt v. 3.4.1. and calibrated on locations of 107 cold-water aquaculture facilities in southern Germany, compiled from publicly accessible information (Fig. S2). MaxEnt relies on a machine-learning maximum entropy framework to relate environmental conditions at farm sites to the background environment of the area obtained by sampling 10,000 random locations. The established relationships were used to characterize environmental suitability for cold-water aquaculture throughout the region. In contrast to most other ENM methods, MaxEnt does not require *a priori* assumptions about absences, allowing for seamless application to the presence-only dataset used in this study, and is more stable in the presence of correlated predictor variables (Elith et al., 2011; Merow et al., 2013; Wisz et al., 2008).

Environmental suitability for salmonid aquaculture was predicted from five bioclimatic variables and four landscape-related variables that were previously shown to affect distribution of temperate fish species (Basen et al., 2022a, 2022b) and obtained at a resolution of 30 arc seconds. Bioclimatic variables included isothermality (bio3), maximum temperature of warmest month (bio5), minimum temperature of coldest month (bio6), precipitation of wettest month (bio13), and precipitation seasonality (bio15). Data were obtained from the WordClim database (Fick and Hijmans, 2017) for near-current (1970–2000) and projected

end-of-century (2081–2100) conditions across SSP126, SSP245, SSP370, and SSP585. Landscape-related variables included terrain *roughness* and *northness* (http://www.earthenv.org/ (Amatulli et al., 2018); the *human footprint*, a composite measure of *population density*, *built-up environments*, and *agriculture* (Venter et al., 2016, 2023); as well as *hydrological substrate*, a categorical variable of four levels: pore aquifers, combined pore and fractured aquifers, fractured and karst aquifers, and aquitards and aquicludes (https://www.bgr.bund.de/had; HY1000 © BGR Hannover 2019). All of these variables were expected to influence potential environmental suitability for salmonid aquaculture and justification for inclusion is summarized in Supplement Table TS2.

All MaxEnt settings were left at default, with the exception of the regularization multiplier, which was set to 1.5 to provide better generalization of the model and to avoid overfitting (Basen et al., 2022a; Phillips et al., 2006). Model performance was evaluated by the area under the receiver operating characteristic curve (AUC). The AUC ranges from 0.5 (random prediction) to 1 (perfect prediction), with values 0.7–0.8 indicating fair performance and values >0.8 indicating good to excellent performance (Araújo et al., 2005). AUC was calculated for the final model, using all aquaculture facilities for training, and for 20 replicate runs fitted with cross-validation to assess performance on test data. The response curves of the predictor variables were inspected for plausible behaviour, and the final model output for near-current conditions was visually checked for its power to capture the location of known salmonid aquaculture facilities. To calculate the proportion of current salmonid culture facilities that will remain in suitable areas under projected future climate conditions, the equate entropy of thresholded and original distributions (EETOD) threshold was used to distinguish suitable from unsuitable areas.

3. Results

3.1. Intraday fluctuations in water temperature

In the two warmest months, July and August, daily variation in water temperatures (ΔT) at the study sites showed a steep increase from sunrise to 14.00 CET with distinct differences among study sites in night to day change on sunny days (Fig. S3). The increase in water temperature lagged about 2 h behind the increase of air temperature. Study sites A and C showed the greatest ΔT, ranging from 2.43 to 3.73 °C, while sites D and E showed lowest, 1.60–1.78 °C (Table 1). On cloudy days, ΔT was lower at all sites compared to sunny days (Table 1).

3.2. Effect of shading on intraday temperature fluctuations

The impact of solar exposure on ΔT was modulated by artificial shading (Table 1) as indicated by a significant interaction term between shading and weather conditions (analysis of deviance with type II Wald F test: $F_{3,463} = 8.866$, $p = 0.03$). On sunny days, the intraday temperature increased less at shaded ($\Delta T_{[shaded]} = 1.7 \pm 0.4$ SE) than at unshaded sites ($\Delta T_{[unshaded]} = 2.7 \pm 0.3$ SE), whereas on cloudy days this difference in increase was less pronounced ($\Delta T_{[shaded]} = 0.8 \pm 0.4$ SE and $\Delta T_{[unshaded]} = 1.4 \pm 0.3$ SE).

3.3. Effect of extreme precipitation events on water temperature

Extreme water temperature fluctuations, defined as >1 °C within 30 min, varied with study site (Table 2) and was highest at sites B and E, where it occurred on 2.7–6.0 % of days in May through October 2017–2021. Extreme water temperature fluctuations were rare (0.1–1.2 % of days) at other sites.

The large majority (92.5 %) of extreme precipitation events (>3.75 mm per 30 min) occurred May through October, on 2.8–3.9 % of days. In most cases, extreme water temperature changes did not correlate with precipitation events, except for sites B and E, which showed 13.0 % and 3.7 % overlap of these events, respectively.

Table 1
Number of observation days ($N_{sun/cloud}$), daily maximum water temperature (TMax; mean ± SD), and intraday increase in water temperature (ΔT; mean ± SD) relative to sun or cloud conditions at the five cold-water aquaculture facilities (A–E) during July and August (2017–2021). Sunny days were defined as days with >11.8 h of sunshine in summer and cloudy days as those with <1.7 h of sunshine in summer.

Study site	N_{sun}	$TMax_{sun}$ (°C)	ΔT_{sun} (°C)	N_{cloud}	$TMax_{cloud}$ (°C)	ΔT_{cloud} (°C)
A	45	12.94 ± 0.67	2.43 ± 0.58	57	11.63 ± 0.46	0.92 ± 0.36
B	42	13.15 ± 0.81	2.00 ± 0.66	54	12.63 ± 0.93	1.17 ± 0.79
C	43	19.32 ± 1.43	3.73 ± 0.56	63	16.6 ± 2.10	2.07 ± 1.28
D[a]	49	10.56 ± 0.62	1.60 ± 0.53	80	9.66 ± 0.35	0.63 ± 0.26
E[a]	25	15.93 ± 0.96	1.78 ± 0.68	11	14.26 ± 1.41	1.01 ± 0.48

[a] Completely shaded by a roof.

Site B showed the greatest overlap of extreme precipitation with extreme temperature variation, and *a posteriori* analysis of these overlapping cases consistently showed a rain event (not always extreme) prior to each temperature increase. On average, 3 h 10 min were between peak precipitation and beginning of temperature increase (Fig. 1a). Within an hour post-onset of these extreme temperature events, the temperature increased 1.5–5.0 °C, with the magnitude of increase being significantly positively related to the cumulative rainfall 3.5 to 2.5 h before the start of the temperature rise (Fig. 1b; $n = 26$, $R = 0.618$, $p < 0.001$).

3.4. Drivers of daily variation in water temperature

A daily time series dataset was compiled to analyse the impact of weather variables on water temperature at the five study sites. The dataset showed a significant residual auto-regressive component (Durban-Watson test DW = 0.47, $p < 0.001$), and ARIMA modelling revealed a 2nd order autoregressive process including two moving average terms. Correcting for these terms resulted in a significant explanatory fit between water temperature values and the predicted values from the ARIMA model (fitted *vs.* observed data: $R^2_{adj} = 0.98$, $p < 0.001$; ARIMA coefficients: AR1, AR2, MA1, and MA2: $p < 0.001$, Table TS3).

A significant and positive effect of air temperature, solar exposure, and a cooling effect of precipitation on water temperature was observed (summed z-values using Stouffer's method; air temperature, $z = 49.5$, $p < 0.001$; solar exposure, $z = 5.60$, $p < 0.001$; precipitation, $z = -7.36$, $p < 0.001$; Table TS3). Additionally, precipitation showed a significant interaction with air temperature ($z = 3.04$, $p = 0.002$; Table TS3), which manifested as a positive effect of precipitation on water temperature at low air temperatures and a slightly negative effect of precipitation on water temperatures at high air temperatures.

The water/air temperature relationship differed significantly among

Table 2
Average frequency of extreme precipitation events and temperature increases at cold-water aquaculture facilities (A–E) April through October 2017–2021. Overlap indicates co-occurrence of events relative to the days with extreme precipitation events. N_{Days} = number of days in analysis.

Study site	N_{Days}	Days with extreme precipitation events (%)	Days with extreme temperature increase (%)	Overlap (%)
A	917	3.37	0.11	0.00
B	920	2.83	5.98	12.99
C	888	3.48	1.23	0.00
D	918	3.91	0.22	0.00
E	592	3.91	2.70	3.70

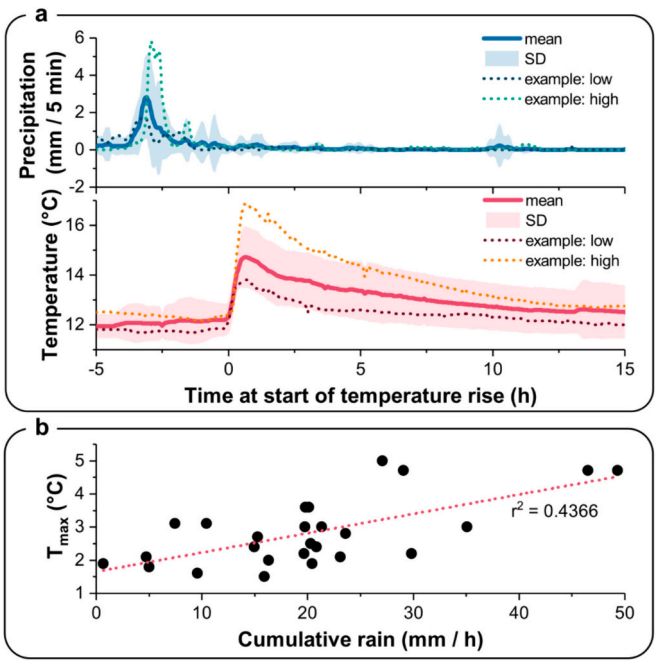

Fig. 1. Relationship of precipitation with water temperature at study site B on days with water temperature increase >1 °C per 30 min.
a: Comparative time sequence of precipitation and water temperature (time set as zero at the onset of temperature increase; n = 26). Mean values of low and high extreme events (n = 3 and 4, respectively) of precipitation and temperature are shown as dotted lines. SD = standard deviation.
b: Correlation of peak water temperature (T_{max}) with preceding cumulative rainfall (n = 26).

facilities (Table TS3). A *post-hoc* analysis with site-specific coefficients correlated with facility characteristics showed significantly stronger impact of air temperature at sites with lower discharge values (Spearman rank correlation, S = 40, p = 0.017) and lower flow rate through the facility (Spearman rank correlation, S = 39.5, $p < 0.01$). Solar exposure showed a near-significant negative relationship with artificial shading (Welch t-test, t = 3.13, df = 2.8, p = 0.058). No other relationships were significant ($p > 0.1$).

3.5. Past and future site-specific water temperature under climate change

The regression model explained about 91 % of the variation in water temperature in the facilities over the course of the five-year study period ($p < 0.001$, n = 168, Table TS4). Estimates of past water temperature based on local WorldClim climate data suggest that mean water temperature at the study sites has increased by 1 °C since the 1970s (Fig. 2). Under projected climate change, site-specific water temperatures are likely to increase by up to 3 °C by the end of the century. The magnitude of predicted local temperature change generally parallels the magnitude of projected climate change, with the best-case scenario, SSP126, leading to a slight decrease in water temperature and the worst-case scenario, SSP585, resulting in the most extreme warming. Intermediate scenarios (SSP345 and SSP370) predict a temperature increase of <1 to >2 °C, depending on site.

3.6. Environmental suitability for salmonid aquaculture under climate change

The final MaxEnt model, using all aquaculture sites for training, featured an AUC of 0.74, while average test AUC for the 20 replicate runs with cross-validation was 0.65 (±0.11). All response curves exhibit plausible, linear, or unimodal behaviour (Fig. S4) and at the applied EETOD threshold, the final model was able to capture all of the known aquaculture sites, indicating overall poor to fair performance. The model predictions were primarily influenced by terrain roughness (permutation importance, 28 %), bio13 (permutation importance, 20 %), and human footprint (permutation importance, 17 %). Temperature-related predictors (bio3, bio5, and bio6) accounted for 16 % permutation importance.

Under projected climate change, environmental suitability for salmonid aquaculture in southern Germany is decreasing, with the magnitude of decrease being strongly affected by the applicable SSP (Fig. 3). Under worst-case and business-as-usual scenarios (SSP585 and SSP370, respectively), >70 % of current aquaculture sites are likely to experience end-of-century climates that fall outside the niche that currently supports cold-water aquaculture. This proportion decreases to <30 % under the SSP245 scenario.

This study quantitatively investigates the vulnerability of land-based cold-water aquaculture to ongoing climate change and addresses its potential mitigation. Significant climate-related risks to traditional production of cold-water salmonids were identified. As expected, site-specific water temperatures have increased since the previous century and can realistically be assumed to approach critical thresholds in the more exposed facilities by the end of this century. Further, extreme precipitation events, predicted to increase in frequency and intensity, are shown to induce acute short-term increases in water temperature up to 5 °C, making rearing conditions unstable. Consistent with the site-specific analyses, generic niche modelling suggests that a considerable proportion of cold-water facilities are likely to face end-of-century climate conditions incompatible to salmonid culture. Far-sighted effective adaption is a key challenge for continuing salmonid production.

3.7. Temperature-related risks

Rearing of salmonids, rainbow trout in particular, is optimal at

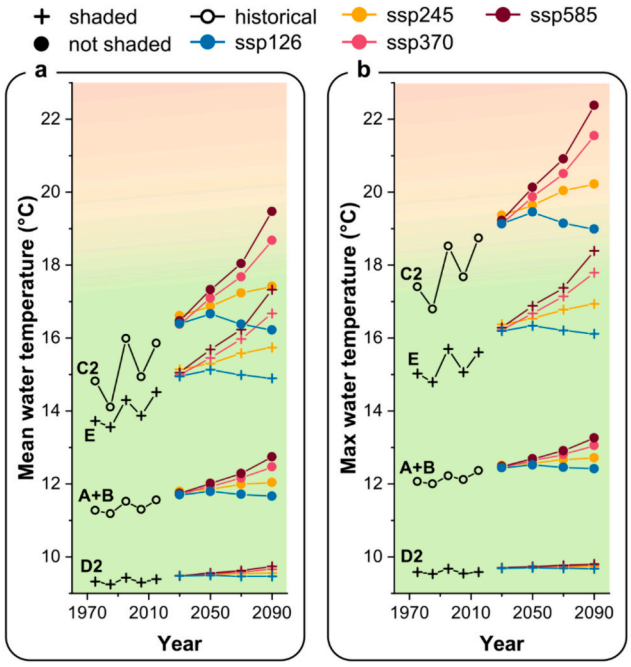

Fig. 2. Estimated mean daily water temperatures July and August at the cold-water aquaculture facilities (A–E) under historic (1960–2017, data in 10-year increments) and projected future climate (2021–2100, data in 20-year increments) under climate change scenarios SSP126–SSP585. a) mean daily temperature at the study sites; b) mean maximum daily temperature at the study sites. Background fill indicates the temperature range for rearing juvenile and maintenance of adult rainbow trout (green: optimal temperature, red: detrimental/chronic stress temperature) (Jonsson, 2023).

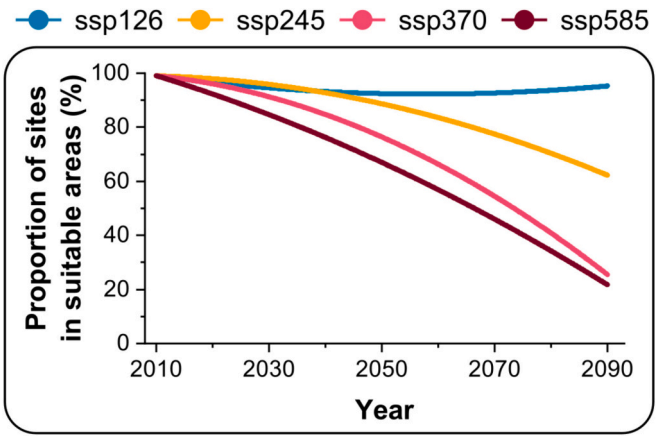

Fig. 3. Proportion of present aquaculture sites ($n = 107$) in southern Germany within areas predicted to be suitable for cold-water aquaculture (environmental niche model, AUC = 0.74) under projected climate change across four scenarios.

10–19 °C (Ebeling and Timmons, 2010; Jonsson et al., 2001; Myrick and Cech, 2004). Without mitigation measures, climate change is likely to place exposed facilities outside this range.

While rearing of juvenile trout is most efficient at 10–15 °C, optimal growth of adult trout without negative health effects is attained at 13–17 °C (Ebeling and Timmons, 2010; Jonsson, 2023; Myrick and Cech, 2004). Temperatures above 17 °C are manageable for most salmonids when oxygen supply is sufficient, while temperatures above 20 °C are unsuitable for most salmonid species (Ebeling and Timmons, 2010; Myrick and Cech, 2004), although there is restricted possibility for temperature acclimation. Experiments showed that fish reared in warmer environments are more resistant to the physiological effects of higher water temperatures (Jonsson, 2023). Since juvenile fish require cooler conditions, they are usually reared near the raceway inflow, with adult fish kept near the outflow where water is warmer, and the load of metabolic end products is higher.

At the five study sites, daily mean water temperature typically stayed within the 9–17 °C range (Table TS5). During the warmest months, July and August, temperature increase on sunny days could reach 3.7 °C, resulting in areas with maximum temperature of 19 °C. Warming of >2 °C in an hour was occasionally recorded at all facilities. These peak temperatures and rapid fluctuations constitute a significant management challenge, as metabolic rate in fish is closely tied to water temperature, and warmer water increases fish oxygen requirements while reducing oxygen solubility (Johnston and Dunn, 1987; Xing et al., 2014).

The ARIMA modelling showed air temperature, solar exposure, and precipitation to be the chief drivers of daily water temperature fluctuation, and the regression analysis corroborated air temperature and precipitation as major drivers of monthly mean water temperature. Water temperature was in all cases positively correlated with air temperature, although the precise relationship of weather conditions with water temperature was site-specific and dependent on facility parameters like flow rate and shading. Since detailed data on discharge and water volume were missing, those factors were not considered in the ARIMA model. Nevertheless, their effect can be tremendous. Discharge can vary with precipitation and result in a different pace of water warming, especially during sunny days. The more water flows through the system, the less it will warm within a certain time. Same holds for the water volume. The bigger the water volume, the longer it takes to heat the water.

Warmer air is a predictable consequence of climate change. The studied aquaculture sites were estimated to have already undergone an increase in water temperature of ~1 °C since the 1970s, coinciding with an average air temperature increase of the same magnitude. During the study period 2017–2022, the 30-year moving average of air temperature in south-western Germany has increased by a further 0.2 °C. Given the current rate of global warming and climate policies and pledges, the intermediate scenarios SSP245 and SSP370 are probably the best indicators of climate in upcoming decades (Hausfather and Peters, 2020; Raftery et al., 2017; Sherwood et al., 2020).

Under these scenarios, the extent to which study site water temperatures are predicted to further increase varies. Sites A, B, and D are projected to experience negligible to moderate warming. As long as groundwater remains available [not guaranteed (Riedel and Weber, 2020)], water temperature will remain within the range for rearing salmonids, with possible beneficial warming (Elliott, 1976). At sites C and E, by contrast, water temperatures are likely to rise by 2 °C in summer, exceeding the optimal range for cold-water aquaculture. The environmental niche model indicates that 37–77 % of current cold-water aquaculture facilities in southern Germany are likely to be located in areas of suboptimal climate conditions by the end of the century. This does not necessarily imply that cold-water aquaculture will be impossible at these sites, but clearly indicates incompatibility with business-as-usual.

3.8. Precipitation-related risks

Strong rain events resulted in changes in water temperatures in two study sites with the strongest effect at study site B. At this site, short-term increases in water temperature (>1 °C within 30 min in summer) were consistently preceded by strong precipitation occurring roughly 3 h prior. In one case, an increase of water temperature of 5 °C in an hour was recorded. An explanation could be the broad extent of impervious surfaces at the drainage area of B in contrast to the other sites. In a heavy rainfall event, this can lead to high accumulations of warmed run-off water. Warmed water entering the headwater stream that feeds the facility at site B abruptly increases water temperature in the rearing system. Increased frequency and intensity of strong rain events also carries the risk of flooding of the farm with fatal consequences for the fish (Wang et al., 2022).

At the other extreme, drought (*i.e.* low precipitation and/or increased evaporation) is also likely to negatively impact rearing conditions at the study sites, as evidenced by the ARIMA analysis. Low precipitation will result in low discharge and consequently lower flow rate at the facilities. Under this condition air temperature will have a greater effect on water temperature. Drought conditions, with reduced water supply, induces additional heat stress close to the critical thermal maximum for the salmonid species in the rearing system, especially in summer when air temperature may already be critically high. Flow rates lower than normal could also increase the concentration of suspended solids and toxic metabolic end products produced by the fish stock, since the water exchange rate is reduced, adding another layer of stress to the system (Becke et al., 2019).

A factor difficult to capture in the present risk assessment is how projected changes in precipitation affect long-term water availability for aquaculture facilities. Seasonal shifts in precipitation can diminish streamflow in summer, reducing water availability for facilities that are fed by surface waters. Sites fed by groundwater are likely to be more resilient, although availability of groundwater may be affected (Changnon et al., 1988). Groundwater levels show wide local variation, but that of most aquifers in Germany have declined during recent drought years (https://github.com/correctiv/grundwasser-data, accessed February 2023).

3.9. Synthesis and impact of climate change risks

Climate change has ramifications at short-term weather extremes creating temporary disruptions in water temperature. Additionally, long-term warming may increase vulnerability to summer temperature

peaks and may eventually push conditions in currently operating facilities beyond the upper thermal limits for salmonid production. The short and long term scales are interrelated, as a warming atmosphere leads to a steady increase in the frequency and intensity of weather extremes, droughts, heat waves, and heavy rainfall events (Masson-Delmotte et al., 2021).

Extreme short-term warming is of particular concern for salmonid welfare, since acute thermal stress and resulting increase in metabolism will elevate respiration rate (Johnston and Dunn, 1987). According to Wedemeyer (1996), respiration rate of stressed (active) salmonids can be eight times that of resting fish (Wedemeyer, 1996). Aeration systems may be unable to cope with such a rapid increase of oxygen demand, especially since higher temperatures reduce capacity for holding dissolved oxygen (Rounds et al., 2013). Consequently, oxygen levels could quickly drop below the recommended minimum for salmonids of 6 mg/L (Ellis et al., 2002). Additionally, the increased metabolism may boost excretion of substances like NH_3 and CO_2 to toxic levels (Nakada et al., 2007; Wedemeyer, 1997).

A temperature peak coinciding with low water levels, as is expected during drought in summer, worsens the situation. With a constant biomass in the rearing system, concentrations may rapidly approach critical levels (Zhao et al., 2018). For example, with a water inflow reduction of 50 %, NH_3 and CO_2 concentration are calculated to double, resulting in an increase of CO_2 from 20 mg/L to 40 mg/L (Formula/Table TS6). Concentrations of $CO_2 > 30$ mg/L can inhibit fish capacity to excrete CO_2 into the water, leading to accumulation in the blood to toxic levels, potentially resulting in lower growth and increased mortality (Ebeling and Timmons, 2010; Good et al., 2010; Hafs et al., 2012; Randall and Tsui, 2002; Schreckenbach, 2002). Even at ammonia concentrations below 0.05 mg/L, the level considered hazardous for salmonids, reduction in fresh water intake can lead to excess concentration that may cause adverse health effects by inhibiting the ability to excrete ammonia (Ebeling and Timmons, 2010; Randall and Tsui, 2002).

Another concern are climate change driven diseases. With low water quality and temperatures exceeding the optimal range, pathogen load may increase and disease resistance may be compromised (Alfonso et al., 2021). A prime example is proliferative kidney disease (PKD) in young salmonids. The causative agent of PKD, the myxozoan parasite *Tetracapsuloides bryosalmonae*, exhibits a complex lifecycle reliant on bryozoans and salmonids (Ros et al., 2022). The parasite is widespread in northern Europe and North America where it grows and produces spores in waters above 10 °C (Tops et al., 2009). Its primary host, bryozoans, can introduce the parasite into aquaculture systems. Infection of salmonids does not result in disease and mortality at water temperatures under 15 °C (Bettge et al., 2009). The parasite must be kept out of systems in warmer facilities to prevent significant mortality (Clifton-Hadley et al., 1986; Feist, 1993).

3.10. Climate change adaption and mitigation

Climate change is likely to result in water temperature dynamics that are outside the range of historic salmonid culture. Managers must prepare for projected conditions by considering currently available methods and innovations to establish resilience in the face of warming water and extreme weather events.

This study found evidence that shading of a facility contributes to cooling roughly equal to the projected temperature increase. This is in line with ecological studies reporting cooler water in areas shaded by riparian vegetation and forests (Bachiller-Jareno et al., 2019; Beschta, 1997; Garner et al., 2017; Rutherford et al., 1997; Spittlehouse et al., 2004). Kalny et al. (2017) observed a difference of 4.2 °C in daily maximum temperature of shaded and unshaded areas of the River Pinka in Austria. Depending on intensity and temporal scale, changes in water temperature can exert both positive and negative effects on aquaculture. The upper limit of lethality is considered to be 20 to 30 °C, which causes acute thermal shock for most salmonid species. However, if water temperature is slowly increased, salmonids can adapt to temperatures above their upper incipient lethal temperature(Jonsson, 2023). While study site D, which is completely roofed, does not heat up even on hot sunny days, the unroofed study site C shows intense warming during the day. Artificial shading provides protection from avian predators (Curtis et al., 1996), and the surface can be used for photovoltaic systems, reported to reduce the environmental impact of an aquaculture facility by >50 % (Brinker, 2019; Wind et al., 2022). The renewable energy generated can be used to offset aeration costs, and facilities could set up partial recirculation systems by treating and returning wastewater to the rearing system to compensate for reduced water supply (Sindilariu, 2007). This approach will help to prevent excessive concentrations of pollutants when available water is reduced, or fish metabolism increases due to elevated water temperatures. Combined with optimized feed quality and solids removal, pollutants in the water can be significantly reduced (Schumann and Brinker, 2020; Sindilariu, 2007). As Summerfelt and colleagues have shown, temporary recirculation is conducive to higher production than can be obtained by a serial reuse system (Summerfelt et al., 2009; Vinci et al., 2004). With respect to fluctuations in water availability, design of a filter system should consider the limited space in most fish culture facilities and additional operating costs of the filter system.

The adaption measures outlined above also address the risk of climate change mediated disease by keeping rearing conditions within optimal parameters. With respect to PKD, a system has been developed in the UK in which juvenile trout are briefly exposed to the parasite and subsequently kept in water <15 °C (Kinkelin and Loriot, 2001). At such temperatures, the fish will acquire resistance to the parasite, protecting them in warmer rearing water (Ros et al., 2022).

4. Conclusions

The climate crisis holds significant challenges for temperate land-based cold-water aquaculture. Foresight is crucial to continue the long history of professional salmonid farming within the 21st century, especially regarding the limited room for temperature adaptation in the commercial species. Shaded raceways, more efficient water use, and disease management are key actions to increase climate resilience. The boldest solution to climate and geographic independence of the sector would be to replace traditional land-based freshwater systems with recirculating aquaculture systems. However, while it is a viable option under certain scenarios, on a large scale such a solution would come at significant economic, energy, and ecological costs, rendering it incompatible with social, sustainability, and climate mitigation goals. Therefore, it is only with successful climate change adaption that the sector may develop as envisioned in the CERES report, which forecasts salmonid aquaculture to increase and to constitute important and environmental friendly food production in the future (Peck et al., 2020).

Significance statement

Aquaculture plays an increasingly important role in the sustainable production of protein rich food. Facilities that produce highly valued salmonids depend on ample clean cold water, a prerequisite potentially threatened by the climate crisis. Based on niche modelling and an extensive temperature dataset from five fish-rearing facilities, this study predicts the effects of ongoing climate change on salmonid farming. The results stress the urgent need to establish climate resilience and provides empirical evidence for the effectiveness of direct mitigation measures.

Consent for publication

Authors have agreed to submit it in its current form for consideration for publication in the Journal.

Ethics approval and consent to participate

Not applicable.

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CRediT authorship contribution statement

Tamara Wind: Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Conceptualization. **Albert Ros:** Writing – original draft, Visualization, Formal analysis. **Christoph Chucholl:** Writing – original draft, Formal analysis. **Samuel Roch:** Visualization. **Mark Schumann:** Writing – review & editing, Validation, Conceptualization. **Carsten Schulz:** Writing – review & editing, Validation, Supervision. **Alexander Brinker:** Writing – review & editing, Supervision, Formal analysis, Conceptualization.

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.

Data availability

The data that support the findings of this study are openly available in hydroshare.org at https://www.hydroshare.org/resource/cbf4e32a14a84761961662aaf4fc00aa/. Cite as: Wind, T., A. Ros (2023). Inland freshwater aquaculture in a warming world - data, HydroShare, http://www.hydroshare.org/resource/cbf4e32a14a84761961662aaf4fc00aa

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Appendix A. Supplementary data

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