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RESEARCH ARTICLE

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# Climate change will render size-selective harvest of cold-water fish species unsustainable in Mediterranean freshwaters

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## Abstract

1. Climate change is impacting the composition and functioning of virtually every ecosystem on Earth, and disrupting the productivity of exploited ones. Species are rapidly adjusting to their changing environments through evolutionary and/or plastic phenotypic changes in behavioural, physiological, phenological and life-history traits. Size-selective harvest produces severe demographic impacts on exploited populations and induces individual phenotypic changes in many of the same fitness-related traits as climate change and thus can impair local adaptation and acclimation. We addressed in the context of inland recreational fisheries two interrelated questions: (1) Will fisheries-induced phenotypic changes operate at different rates and direction than those induced by climate change, and thus hinder local adaptation and acclimation, threatening population persistence?; (2) which harvest regulations most likely lead to overexploitation of populations under the new environmental conditions?
2. We used an eco-genetic individual-based model to simulate the consequences of size-selective fishing for a cold-water fish species brown trout *Salmo trutta* across a range of regulatory (defined by exploitation rate and size-based limits) and environmental scenarios (warming vs. concurrent warming and streamflow reduction) in a Mediterranean system. We ran 1,620 combinations of fishing and environmental scenarios and analysed results using artificial neural networks.
3. In our simulations, (a) climate change and size-selective fishing both led to a reduced, truncated population, with increased juvenile but decreased adult growth and earlier maturation at smaller size, but fisheries-induced changes were stronger than those produced by climate change; (b) their effects were additive or dampened but rarely synergistic and (c) phenotypic changes in fitness-related traits resulted from both evolutionary and plastic processes.
4. *Synthesis and applications*. Our model-based analyses highlight that any size-selective fishing regime would lead to the overexploitation of cold-water freshwater fish populations if climate warming is accompanied by streamflow reduction—as projected in Mediterranean fisheries. Even if we assumed no future streamflow regime changes, only a limited range of size-based harvest regulations may provide an acceptable balance between conservation and fishery objectives. Thus, recreational fisheries of cold-water fish in Mediterranean climates might be more

sustainably managed under climate change if conservation-oriented strategies based on harvest bans (e.g. catch-and-release fishing) were implemented.

**KEYWORDS**

artificial neural networks, climate change, eco-evolutionary dynamics, fisheries-induced evolution, harvest regulations, individual-based model, phenotypic plasticity, size-selective harvest

## 1 | INTRODUCTION

Climate change is a main driver of the massive vertebrate population declines and extinctions currently observed worldwide (Ceballos et al., 2020), which has led to rapid change in assemblages (Blowes et al., 2019). Nevertheless, phenotypic responses to changing environmental conditions through plastic and/or evolutionary pathways are mitigating to some extent population fitness losses (Crozier & Hutchings, 2014; Scheffers et al., 2016). Local adaptation and acclimation appear especially critical for the persistence of freshwater fish, which live in systems where migration is restricted and where altitudinal redistributions commonly lag behind climatic changes, especially in warm areas with strong human pressure (Lenoir et al., 2020). Local human activities often compound challenges for sensitive taxa by exerting a strong selection pressure that operates on many of the same traits as climate change and thus have the potential to hinder local adaptation.

Commercial and recreational harvest is such a well-studied example in wild animal populations (Allendorf et al., 2008; Kuparinen & Festa-Bianchet, 2017). In particular, intensive and size-selective fishing (SSF) not only truncates the population structure and increases fluctuations in its dynamics but also induces individual stoichiometric and phenotypic changes in fitness-related traits, which feed back to population trajectories and affect the ecological dynamics of entire ecosystems (Diaz Pauli & Sih, 2017; Evangelista et al., 2020; Kuparinen et al., 2016).

Inland recreational fisheries are a relevant and valuable component of regional, national and global fisheries (Arlinghaus et al., 2017), but rapid contemporary environmental change (EC) is increasing their vulnerability to overfishing and collapse (Embke et al., 2019). Similarly to commercial fisheries, inland recreational fishing typically targets large individuals with the highest fitness potential (Arlinghaus et al., 2010), so its demographic and structural impacts on populations resemble those of EC (Ayllón et al., 2019). EC is reducing surplus fish production available for recreational harvest in a non-reversible way, so strong exploitation intensities can lead to recruitment overfishing (i.e. depletion of the breeding stock to the point that recruitment is impaired) and thus to the collapse of the fishery (Arlinghaus et al., 2017). In addition, modelling and empirical studies show that recreational fishing can also induce evolutionary changes of behavioural (Klefoth et al., 2017; Martorell-Barceló et al., 2018; Tillotson & Quinn, 2018; Uusi-Heikkilä et al., 2015), metabolic (Hessenauer et al., 2015) and life-history traits (Arlinghaus et al., 2009; Ayllón et al., 2018; Edeline et al., 2007; Matsumura et al., 2011; Thériault et al., 2008; Uusi-Heikkilä et al., 2015). If fisheries-induced trait selection opposes the direction of trait selection by EC, then local adaptation will be limited and surplus production will be reduced even further, threatening the sustainability of the fishery.

Some of the observed or predicted changes induced by SSF are not in line with those resulting from projected EC. For example, while increased temperature and decreased flow would lead to earlier maturation and decreased individual growth rates (Ayllón et al., 2019; Crozier & Hutchings, 2014), the effect of fishing depends on the local harvest regime which could favour evolution of either late (Poos et al., 2011) or early maturation (e.g. Ayllón et al., 2018; Matsumura et al., 2011; Uusi-Heikkilä et al., 2015), and either fast or slow juvenile growth rate (e.g. Dunlop et al., 2009; Matsumura et al., 2011), or even absence of selection on juvenile growth (e.g. Ayllón et al., 2018; Uusi-Heikkilä et al., 2015).

Phenotypic trait changes can cumulatively have a strong effect on average demographic rates and impair recovery potential of exploited populations after harvest has ceased, especially when genetic changes are involved (Piou et al., 2015; Uusi-Heikkilä et al., 2015). However, it is a challenging task to separate the genetic component of fisheries-induced trait changes from both plastic responses to environmental drivers and density-dependent feedbacks resulting from density reduction and thus relaxed competition (Kuparinen & Festa-Bianchet, 2017). For example, growth rate is a trait partly under genetic control and thus is subject to fisheries-induced evolution but it is also influenced by environmental conditions such as temperature and by density dependence, so those effects are difficult to separate and quantify from field data (Enberg et al., 2012). Similar challenges have arisen to conclusively demonstrate genetic adaptation to EC in the wild (Crozier & Hutchings, 2014; Merilä & Hendry, 2014).

We address here two interrelated questions affecting both conservation and management of exploited populations: (1) Will fisheries-induced phenotypic changes operate at different rates and direction than those induced by climate change, and thus hinder local adaptation and acclimation to the new environmental conditions, and threaten population persistence? (2) Which fishing regulations and exploitation intensities are most likely to lead to overexploitation of the population under the new environmental conditions?

To answer these questions, we used a structurally realistic eco-genetic individual-based model that accounts for adaptive behaviour, density-dependent processes, phenotypic plasticity and micro-evolution of life-history traits, and incorporates a fishing module that implements dynamic angling mortality and cryptic mortality sources such as illegal harvest and hooking mortality (inSTREAM-Gen; Ayllón et al., 2016, 2018). To assess the effects of angling harvest on a species vulnerable to EC in a realistic context, we simulated a stream-resident brown trout *Salmo trutta* L. mountain fishery at the warmest edge of the species distribution as our experimental system.

To address our research question (1), we assessed the numerical and structural population impacts and related phenotypic effects on size and reproductive traits of SSF across a range of regulatory (defined by exploitation intensity, size-based limits and allowed fishing gear types) and EC scenarios (warming alone, and warming concurrent with flow reduction), which were compared to a baseline situation without fishing or any environmental changes. Specifically, we wanted to determine (a) whether the predicted rates of individual responses to EC and SSF differ in strength and direction, and (b) the extent to which these responses can be attributed to plastic or evolutionary processes. To address our research question (2), we identified the fishing regulations leading to recruitment overfishing under each EC scenario. Here, we were interested in understanding whether phenotypic responses were rapid and strong enough to offset the demographic impacts exerted by concurrent SSF and EC, and thus prevent overfishing.

## 2 | MATERIALS AND METHODS

### 2.1 | Model system

We parameterized inSTREAM-Gen using population and fishing data from a typical brown trout fishery in Mediterranean mountain rivers, in the Aragón River basin in Northern Spain (see Appendix S1 and S2 in Supporting Information). Brown trout is a cold-water species, whose stream-resident populations in Southern Europe are mainly restricted to headwaters, where the cooler environment mitigates the harsh, warm climate. In recent decades, climate change has driven declines in population abundance and harvest rates in the lower reaches of the study basin, wherein climate envelope models have predicted the loss of more than 90% of current suitable thermal habitat for brown trout by 2100 (Almodóvar et al., 2012). Our modelled population typically starts to reproduce in the third year of life (age-2), the reproductive season being November–December with emergence in March–April. The period with most rapid growth goes from April through September, mostly coinciding with the highest temperatures but lowest flows.

### 2.2 | Model description

We provide in Appendix S1 a complete model description following the ODD protocol (Overview, Design concepts and Details; Grimm et al., 2020), a widely used standard documentation format for describing IBMs. The following summary focuses on parts relevant to this application.

InSTREAM-Gen simulates the complete trout life cycle using a daily time step, with streamflow and water temperature as environmental drivers. The model describes explicitly one stream reach, which is divided into cells that are characterized by their physical habitat, and their production rate of drift and benthic food. On each simulated day, the reach's environmental conditions are updated and the flow-dependent variables of individual cells are calculated. Afterwards, individual trout perform three actions:

1. All trout select a cell for feeding following a size-based dominance hierarchy, as commonly observed in stream-resident salmonids (e.g. Hughes, 1992). Resources (food, shelter and cover) used by a trout cannot be used by smaller individuals. Trout move to the available cell, within a radius that increases with body length, that maximizes short-term fitness, which is a function of the cell's mortality risk and growth potential (Railsback et al., 1999).
2. Trout feed and then grow; growth is modelled as the difference between gross energy intake from feeding and the respiration costs experienced in the cell. Drift food intake increases with the concentration of drifting prey and fish length (which increases swimming capacity), and varies nonlinearly with velocity (higher velocity carries more prey past but decreases capture success). Search food intake (benthic foraging) increases linearly with benthic food production and decreases linearly with water velocity. Respiration is modelled as the energetic costs of metabolism and swimming, including a standard respiration that increases with fish size and temperature, and an activity respiration that increases with swimming speed.
3. Each trout face six natural sources of mortality, the most important of which are starvation, predation by terrestrial animals and aquatic predation.

The next actions take place daily only during specific seasons:

4. Trout become mature when their length reaches their maturity size threshold, which is a sex-specific evolving trait. During the reproductive season, spawning females create a redd whose eggs are fertilized by the largest available mature male plus a random number of smaller subordinate males. The number of eggs is a power function of female length and also varies inversely with egg size.
5. Redds are subject to egg mortality due to superimposition, and extreme temperatures and flow events. Surviving eggs develop at a rate that increases nonlinearly with temperature.
6. When eggs are fully developed, they ‘emerge’ as new free-swimming trout and the two heritable traits (length at emergence and maturity size threshold) are transmitted. Each new trout inherits its genetic traits from the mother and one father randomly chosen from the males that fertilized the redd, with equal probability of fertilization across males. The phenotype of an individual is modelled as the sum of an inherited additive genetic effect (genotypic value) and a non-heritable environmental effect; these inheritance rules are based on the infinitesimal model of quantitative genetics (Lynch & Walsh, 1998). The genetic component of an evolving trait of each new trout is drawn from a normal distribution centred on the arithmetic mean of the two parental

values; its variance is independent of the parental trait values and equal to half the total additive genetic variance for the trait at the population level plus the variance potentially introduced by mutation.

In inSTREAM-Gen, the demographic and genetic trajectories of trout populations emerge from the growth, survival and reproduction of individual fish, processes driven by complex interactions among environmental conditions, heterogeneous physical habitat, competition for food and habitat, and adaptive behaviour. Thus, plastic responses in growth rates, and reproductive (e.g. age and size at maturity) and phenological (e.g. spawn or emergence time) traits can emerge from natural and anthropogenic changes in the environmental and ecological conditions experienced by the fish. Likewise, density-dependent changes in individual growth trajectories can emerge when natural mortality patterns, and thus intraspecific competition regimes, are altered. Since the model tracks the phenotypic value of all life-history traits and the genotypic value of those heritable at the individual level, the underlying nature of life-history change (genetic, plastic or both) can be traced.

## 2.3 | Fishing module

The underlying assumptions, technical implementation and parameterization of the fishing module are detailed in Appendix S2. The fishing module consists of three components: fishing pressure, capture rate and survival. Fishing pressure reflects the intensity of fishing in the reach and varies each simulated year as a function of the harvestable stock (number of trout that can be legally harvested during the angling season) and the exploitation rate (fraction of the harvestable stock that is harvested).

Capture rate is the mean number of times a fish is captured per day, and depends only on fishing pressure and fish length (Figure S1 in Appendix S2). Survival depends on how many times a simulated trout is captured, which is a function of capture rate, and whether it is harvested or released each time hooked, which depends on whether its length is within the legal limits set by parameters MinLL and MaxLL. The model assumes that voluntary release of caught legal-sized fish is allowed (40% in this study; Table S2 in Appendix S2). Hooking mortality is an additional mortality source, as the model assumes that a fraction of caught and released trout die of hooking. We also assumed that a fraction (5% in this study; Table S2) of the caught fish of non-legal size is illegally kept by anglers.

## 2.4 | Simulation scenarios

### 2.4.1 | Environmental scenarios

We simulated the trajectory of the modelled population between 1993 and 2100 under three environmental scenarios representing increasing levels of environmental change:

*No environmental change*
We modelled a baseline scenario that extends the historical temperature and flow regimes without environmental change, keeping only the historic range of environmental stochasticity. We used the data recorded at the closest gauging and meteorological stations to generate the streamflow and air temperature time series for 1993–2011. Time series for 2012–2100 were projected following the methods described in Ayllón et al. (2016). Projected air temperatures were translated into water temperatures using a regression model specifically developed for the Aragón River basin (see Ayllón et al., 2016).

*Climate warming*
This scenario represents temperature increases due to climate warming but not changes in flow, so we used the same flow time series developed for the no-environmental-change scenario above. We used the future air temperature projection corresponding to the Representative Concentration Pathway RCP6 for the closest meteorological station developed by the State Meteorological Agency (AEMET) to generate the water temperature time series.

*Climate warming and flow change*
This scenario represents temperature warming and streamflow reduction. We used the same water temperature times series described for the climate-warming scenario. We built on the streamflow projections of López-Moreno et al. (2014) for the River Aragón basin for 2021–2050, based on projected temperature and precipitation patterns under the A1B scenario and the expected evolution of land cover (see López-Moreno et al., 2014 for details). Thus, we modified daily streamflow from the no-environmental-change scenario following methods described in Ayllón et al. (2016).

### 2.4.2 | Fishing scenarios

Parameterization of the fishing module is described in Appendix S2. The modelled fishery includes only wild brown trout and is not stocked. It is open-regulated and has been historically managed using both input controls (licensing and fees, closed seasons, and method, gear and effort restrictions) and output controls (minimum-length limit and daily bag limit regulations). Voluntary catch and release is allowed and proportion of released fish is likely to be high (see Appendix S2). The fishing season is April through September.

To assess fishing-induced effects, we allowed the model population to evolve between 1993 and 2100 under 180 different combinations of exploitation rate and minimum- and maximum-length limits for each of three values of hooking mortality rate tested, so we designed a grand total of 540 fishing scenarios. Each fishing scenario was run under every environmental scenario, resulting in 1,620 different combinations of fishing and environmental scenarios. Finally, we ran one baseline scenario without fishing for each environmental scenario. We executed six replicates of each simulation scenario

(9,738 model runs in total). The fishing scenarios are thus cross-combinations of four parameters:

**Exploitation rate (ExpR)** is the percentage of the annual harvestable stock (i.e. trout of a size within legal limits) that is actually harvested (i.e. caught and kept by anglers). We simulated five levels of ExpR: 5%, 20%, 35%, 50% and 65%. Actual ExpR at the modelled fishery has been historically below 20%.

**Hooking mortality rate (Hm)** is the fraction of caught fish that die after being released. We simulated three values of Hm: 2%, 7.4% and 20%. They are based on values reported by Hühn and Arlinghaus (2011): 2% is the average value reported for brown trout fished with artificial bait, 7.4% is the average value reported for brown trout, including both artificial and live bait, and 20%, a very high value. Actual data for Hm do not exist in our modelled fishery, but because of the allowed bait (both live and artificial) and hook type and size, it should be close to our simulated intermediate value.

**Minimum-length limit (MinLL)** is the lower bound of the length range in which fish are legal to keep (cm). We simulated six levels: 0, 17, 18, 19, 20 and 21 cm. The 0-cm level is equivalent to no lower length limit. The actual MinLL at the modelled fishery has shifted around 19–20 cm over the last 25 years. The smallest value of the tested range approximates the population's average maturity-length threshold at initialization (16.5 cm), whereas the largest implies that no immature fish could be legally harvested under this regulation (Table S3 in Appendix S2).

**Maximum-length limit (MaxLL)** is the upper bound of the legal length range (cm). Six levels were used: 25, 27, 29, 31, 33 and 40 cm. Since the maximum trout length ever recorded in the fishery was 38 cm, the 40-cm level is equivalent to no upper length limit. Tested MaxLL values affect only age-3 and older trout, the lowest level (25 cm) preventing 40% of that age class from being legal to harvest (Table S3).

The combination of length-limit parameters results in three alternative fishing regulations: (a) a minimum-length limit regulation (when MinLL > 0 and MaxLL = 40 cm), (b) a maximum-length limit regulation (when MinLL = 0 and MaxLL < 40 cm) and (c) harvest-slot regulation (when MinLL > 0 and MaxLL < 40 cm). The combination of MinLL = 0 and MaxLL = 40 cm represents a lack of regulation.

## 2.5 | Model outputs

In every replicate, we recorded the density, biomass and mean individual length of four age classes (0, 1, 2 and 3+) every simulated year at September 1st. The size structure of the population was measured as the adult (age-2+ trout) to juvenile (age-0 and 1 trout) biomass ratio. We also recorded at the end of the spawning season the total fecundity of spawners and the mean length, mean genotypic values of the maturity-length threshold and length at emergence, and age at maturity of every individual spawner. Finally, we used two metrics to assess whether the modelled population experienced recruitment overfishing: (a) the annual spawning potential ratio (SPR), which was computed as the population fecundity under the fishing scenario relative to the unexploited situation (baseline scenarios; Arlinghaus et al., 2010); SPR is a widely used stock assessment metric to measure the impact of fishing on the potential productivity of a stock (Goodyear, 1993), values below 0.35 indicating recruitment overfishing (Arlinghaus et al., 2010). (b) The coefficient of variation (CV) in annual recruitment (measured as the density of age-0 trout at September 1st), as overfishing produces strong recruitment variability (Hsieh et al., 2006).

## 2.6 | Data analysis

### 2.6.1 | Artificial neural network

We used deep learning techniques to analyse simulation results by means of the H2O R package version 3.26.0.3 (LeDell et al., 2019). Specifically, we used multi-layer feed-forward artificial neural networks (ANNs) trained with stochastic gradient descent using back-propagation (see full methods and parameterization of ANNs in Appendix S3) to predict the mean value, over the last 15 simulated years (2086–2100), of the 14 selected model outputs as a function of two environmental parameters (rate of change in water temperature and flow) and four fishing parameters (Hm, ExpR, MinLL and MaxLL). For the analysis, we used the ratio of model outputs under the simulated scenarios to the baseline scenario (no fishing and no environmental change).

We optimized each ANN by selecting the network architecture (number of hidden layers and neurons within them) and activation function that provided the highest prediction accuracy (Appendix S3). Before training, we randomly split our dataset into training (60% of data), validation (20%) and test (20%) sets. The accuracy of each resulting model was computed by applying the ANN trained with the training set to the validation set. The optimal ANN was the one with the lowest mean squared error (*MSE*). Finally, we validated the optimized ANNs with the second independent testing set, which was not used for either training or optimizing the parameters of the network. We assessed model performance on the testing data based on the *MSE* and $R^2$ values. Finally, the relative importance of predictor variables was calculated using the Gedeon method. Analyses were run with the R software v. 3.6.1 (R Core Team, 2019).

### 2.6.2 | Type of interaction between environmental change and fishing

We analysed the type of effects on the 14 selected model outputs resulting from the combination of EC and SSF scenarios. We used response ratios (RRs) as effect-size metrics, which were expressed as percent difference from baseline conditions (no EC and no SSF). We calculated for each separate factor (EC and SSF) and for their additive effects the 95% confidence limits (CL) of the respective RRs following Darling and Côté (2008).

Then, we compared the observed mean RR from the combined factors (RRcomb) to the expected additive response ratio (RRadd): (a) if RRcomb overlapped with the predicted additive 95% CL, the effect was classified as *additive* (i.e. combined effects equalled the sum of separate effects); (b) if RRcomb fell above the 95% CL of the RRadd (being RRadd positive) or below the 95% CL of the RRadd (being RRadd negative), the effect was considered *synergistic* (combined effects exceeded the sum of separate effects); (c) if RRcomb fell below the 95% CL of the RRadd (being RRadd positive) or above the 95% CL of the RRadd (being RRadd negative), the effect was considered *dampened* (combined effects were less than separate effects) and (d) the effect was considered *antagonistic* when the combined effects and the sum of separate effects had opposite directions of change and the 95% CLs did not overlap.

## 3 | RESULTS

### 3.1 | Performance of trained ANNs and predictor variable importance

The optimal network architecture varied across ANNs, but they all have at least two hidden layers and performed better when using the ReLU activation function (Table 1). All trained networks showed a high performance ($R^2 > 0.75$) on the validation and test sets, especially those fitted to model outputs measured at the population level ($R^2$ close to 1), except for the network for mean length of age-2 trout (Table 1). *MSE* obtained on the test data were very similar to those obtained on the training data (Table 1), indicating a good generalization of the trained ANNs (i.e. they were not overfitted). Exploitation rate (ExpR) and minimum-length limit (MinLL) were the input variables with the largest contribution to network predictions, dominating over the environmental variables, whereas the contribution of the maximum-length limit (MaxLL) and the hooking mortality rate (Hm) was low compared to the other predictors (Table 1). Since Hm appears to be less influential on model outputs than the other parameters, we focused our subsequent analyses on ANN predictions setting Hm to 2%. The effects of Hm were apparent only at very high values (20%) concurrent with high ExpR, leading in general to increased population truncation and thus decreased spawning potential ratio (SPR), as well as to accelerated density and biomass decline under maximum-length limit regulations.

### 3.2 | Impacts on population abundance and age structure

Population density and biomass decreased under scenarios of environmental change (EC; Figures S2 and S3 in Appendix S4); since mortality was higher in large old trout, there was a strong decrease in the adult-to-juvenile biomass ratio (Figure 1). Likewise, size-selective fishing (SSF) reduced population density, biomass and adult-to-juvenile biomass. The negative impact increased quickly with increasing ExpR and decreasing MinLL, and moderately with increasing MaxLL (Figure 1; Figures S2 and S3). The impact was stronger on biomass than on density. Small MinLLs and high ExpR led to an extreme truncation of the population, with age-3+ trout disappearing (Figure 1). SSF impacted population structure more strongly than EC, except

**TABLE 1** Optimal architecture of trained artificial neural networks (number of neurons for each of up to three hidden layers), model performance (mean squared error and $R^2$) on the training and test sets, and relative importance (%) of environmental (temperature and flow) and fishing parameters (hooking mortality, exploitation rate, and minimum and maximum-length limits) for each model output

| Metric | Architec. | Train *MSE* | Train $R^2$ | Test *MSE* | Test $R^2$ | Temp | Flow | Hooking | ExpR | MinLL | MaxLL |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Life history | | | | | | | | | | | |
| Gen-Lemergence | 7–6–4 | 0.00078 | 0.85 | 0.00080 | 0.83 | 16.2 | 22.6 | 7.3 | 25.4 | 20.4 | 8.2 |
| Length-0 | 7–7–3 | 0.00042 | 0.84 | 0.00039 | 0.83 | 21.0 | 18.2 | 5.1 | 26.6 | 24.7 | 4.5 |
| Length-1 | 4–4–0 | 0.00045 | 0.94 | 0.00046 | 0.93 | 7.2 | 19.7 | 3.2 | 47.0 | 22.4 | 0.5 |
| Length-2 | 7–5–5 | 0.00062 | 0.49 | 0.00055 | 0.51 | 23.4 | 16.6 | 5.5 | 28.9 | 23.9 | 1.7 |
| Length-3+ | 5–4–3 | 0.00107 | 0.75 | 0.00097 | 0.78 | 13.4 | 15.5 | 2.1 | 27.5 | 39.1 | 2.4 |
| Gen-Lmaturity | 6–5–0 | 0.00027 | 0.89 | 0.00027 | 0.89 | 9.4 | 7.7 | 2.7 | 40.2 | 38.7 | 1.3 |
| Age-maturity | 6–6–4 | 0.00094 | 0.96 | 0.00091 | 0.96 | 10.1 | 18.7 | 2.1 | 37.3 | 30.7 | 1.1 |
| Spawn-length | 6–5–3 | 0.00029 | 0.95 | 0.00031 | 0.95 | 18.8 | 13.6 | 2.0 | 31.5 | 32.8 | 1.3 |
| Population | | | | | | | | | | | |
| Density | 6–5–5 | 0.00078 | 0.99 | 0.00086 | 0.98 | 21.1 | 26.1 | 3.0 | 21.9 | 26.6 | 1.3 |
| Biomass | 7–6–0 | 0.00022 | 1.00 | 0.00023 | 1.00 | 16.8 | 17.6 | 2.1 | 39.1 | 23.2 | 1.2 |
| Structure | 6–6–0 | 0.00090 | 0.99 | 0.00089 | 0.99 | 9.0 | 17.1 | 1.8 | 44.7 | 26.5 | 0.9 |
| Fecundity-3+ | 6–6–5 | 0.00102 | 0.99 | 0.00097 | 0.99 | 12.5 | 14.0 | 2.1 | 36.4 | 30.4 | 4.6 |
| SPR | 5–5–4 | 0.00241 | 0.96 | 0.00237 | 0.96 | 17.6 | 27.4 | 2.1 | 34.1 | 17.9 | 0.9 |
| CV-recruits | 7–5–4 | 0.00544 | 0.95 | 0.00594 | 0.95 | 11.5 | 16.8 | 5.6 | 27.8 | 34.4 | 3.9 |

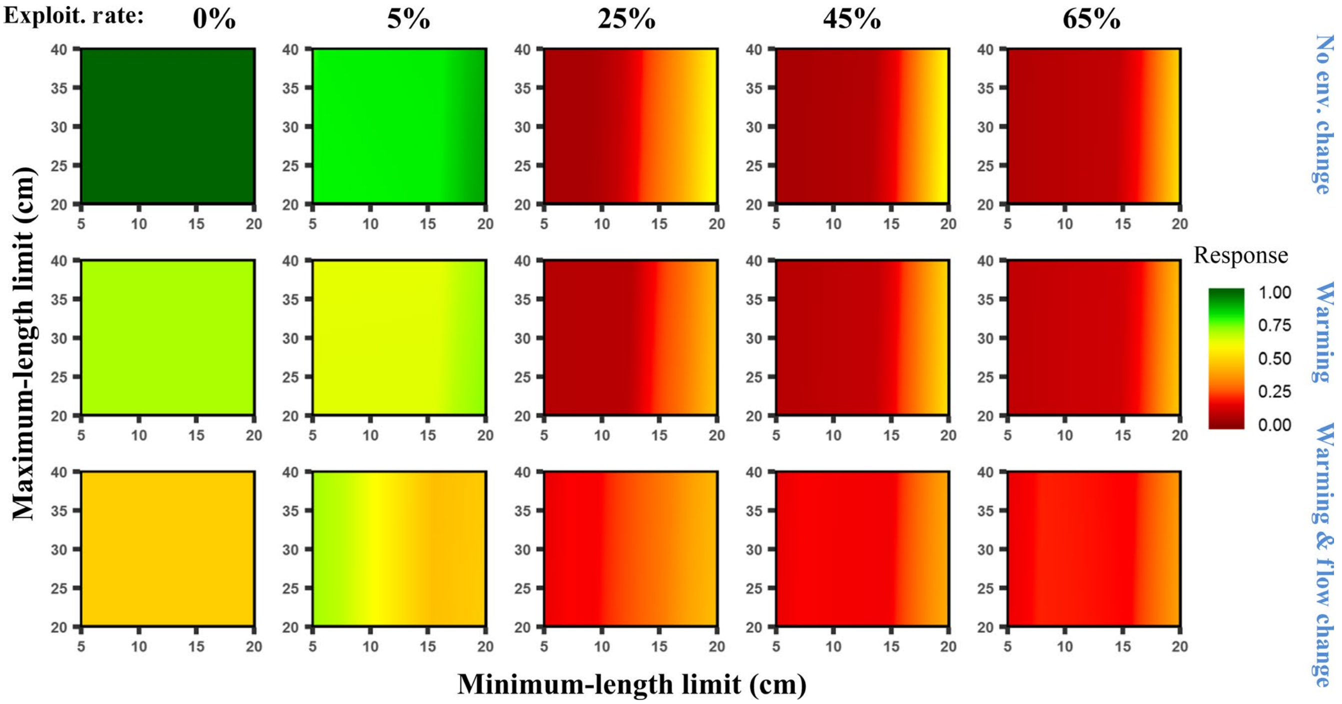

**FIGURE 1** Adult-to-juvenile biomass ratio under different fishing regulations and environmental scenarios. The hooking mortality rate was set to 2%. Colour scale on the right indicates the mean value over the last 15 simulated years (2086–2100) of six simulation replicates expressed as the ratio between the tested and the baseline scenario (mean value of tested scenario/mean value of baseline scenario). Baseline refers to the scenario without fishing and no environmental change [Colour figure can be viewed at wileyonlinelibrary.com]

when ExpR was very low or MinLL very large (Figure 1). Conversely, density and biomass reductions were stronger under EC than under SSF, except when high ExpR and small MinLL concurred (Figures S2 and S3). The combined effects of SSF and EC on density were rather additive (Appendix S5). By contrast, we mostly observed dampened effects on biomass and adult-to-juvenile biomass ratio, that is, the sum of the separated effect of each factor was significantly higher than their combined effect, at intermediate and high values of ExpR (Appendix S5).

### 3.3 | Phenotypic changes in body size and reproductive traits

Mean length of age-0 to 2 trout increased under EC scenarios (Figures S4–S6 in Appendix S4), but length of age-3 + trout markedly decreased (Figure S7 in Appendix S4). SSF produced the same patterns, the effect being stronger with increasing ExpR and decreasing MinLL. Decreasing the MaxLL ameliorated the impact of SSF on length of oldest trout (Figure S7). The combined effects of SSF and ECC on mean length of age-0 trout were rather additive while the combined effects on length of older trout were typically dampened at high ExpR (Appendix S5).

Regarding reproductive traits, age at maturity and mean length of spawners decreased under EC scenarios (Figure 2; Figure S8 in Appendix S4). Likewise, both traits decreased very rapidly with decreasing MinLL and increasing ExpR and slightly with increasing MaxLL (Figure 2; Figure S8). The combined effects of SSF and ECC on both traits were additive at low ExpR but dampened at high ExpR values and small MinLL (Appendix S5).

### 3.4 | Genetic basis of phenotypic changes

The Genotypic value of length at emergence diminished moderately under EC scenarios but experienced a strong decrease at very small values of MinLL and high ExpR under SSF scenarios (Figure 3). Decreasing MaxLL ameliorated such response. The combined effects of both factors were mostly additive (Appendix S5).

The Genotypic value of the maturity length threshold diminished moderately under EC scenarios, but decreased very rapidly with decreasing MinLL and increasing ExpR under SSF scenarios (Figure 4). The combined effects of both factors were additive at low levels of ExpR but dampened at intermediate and high values (Appendix S5).

### 3.5 | Overfishing

Spawning potential ratio (SPR) decreased under EC scenarios, leading to overfishing (SPR < 0.35) under the warming-and-flow-change scenario (Figure 5). SSF also produced a strong decrease in SPR, the impact being stronger with decreasing MinLL and increasing ExpR, leading to overfishing under the most aggressive fishing scenarios (Figure 5). At high levels of ExpR, the total fecundity of age-3 and older trout decreased towards zero, irrespective of the length limits

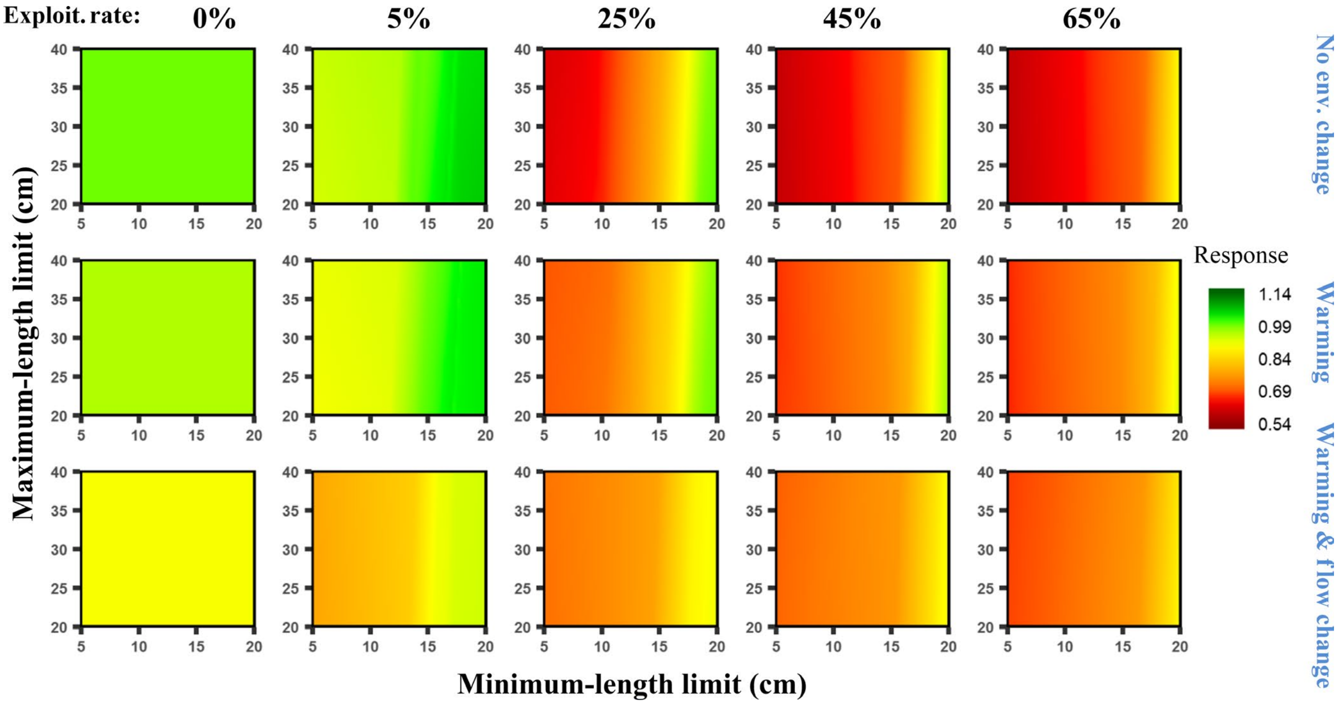

FIGURE 2 Age at maturity under different fishing regulations and environmental scenarios. Methods and formats are the same as for Figure 1 [Colour figure can be viewed at wileyonlinelibrary.com]

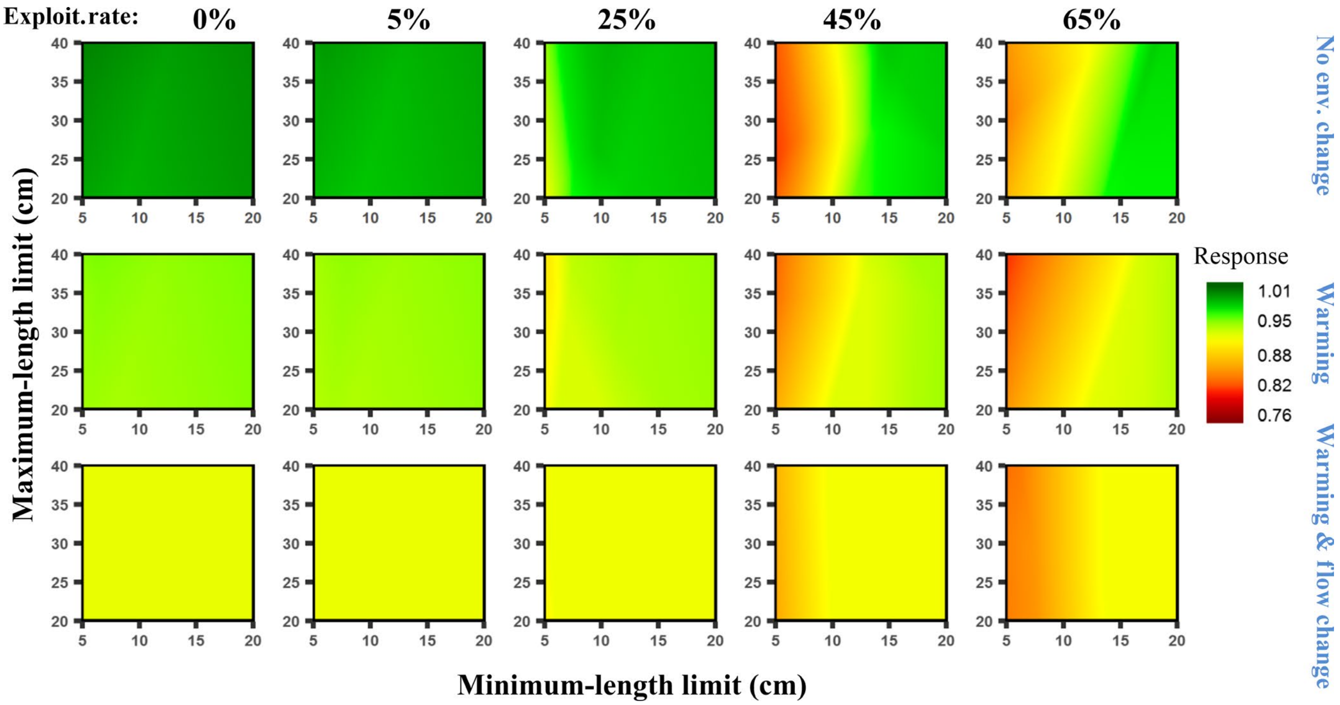

FIGURE 3 Genotypic value of length at emergence under different fishing regulations and environmental scenarios. Methods and formats are the same as for Figure 1 [Colour figure can be viewed at wileyonlinelibrary.com]

(Figure S9 in Appendix S4). Nevertheless, at low or intermediate ExpR decreasing MaxLL had a positive effect on old trout fecundity (Figure S9). The combined effects of SSF and EC on SPR were additive at low levels of ExpR but dampened at intermediate and high values (Appendix S5).

The coefficient of variation of recruitment increased under EC (Figure S10 in Appendix S4). SSF also produced increased variability in recruitment, which rapidly increased with decreasing MinLL, and increasing ExpR and MaxLL, leading to values indicative of overfishing under the most aggressive fishing scenarios (Figure S10). Indeed,

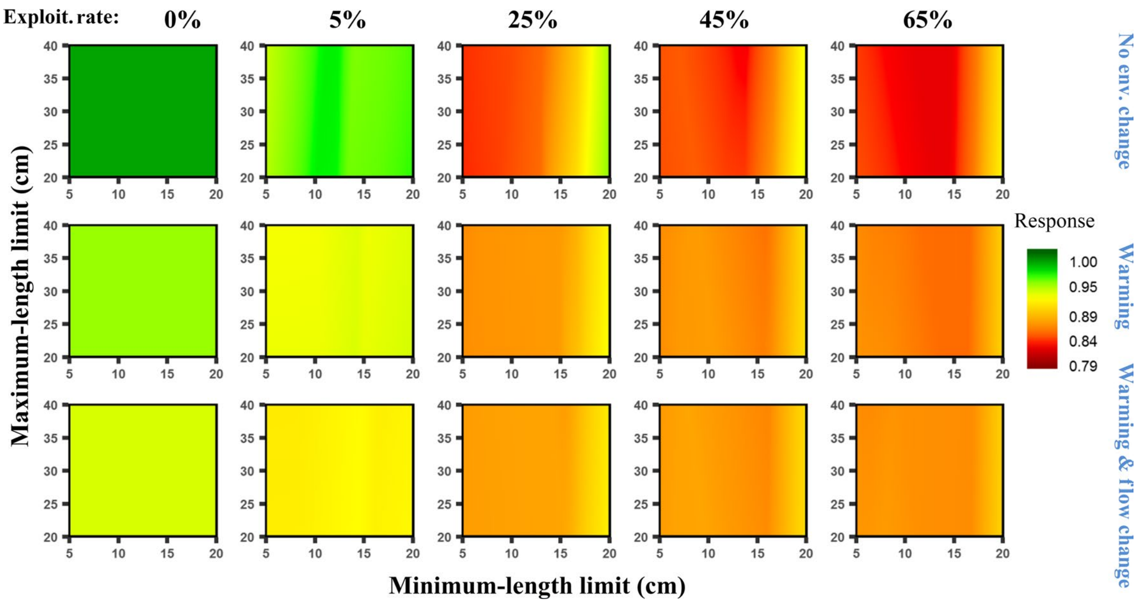

**FIGURE 4** Genotypic value of the maturity length threshold under different fishing regulations and environmental scenarios. Methods and formats are the same as for Figure 1 [Colour figure can be viewed at wileyonlinelibrary.com]

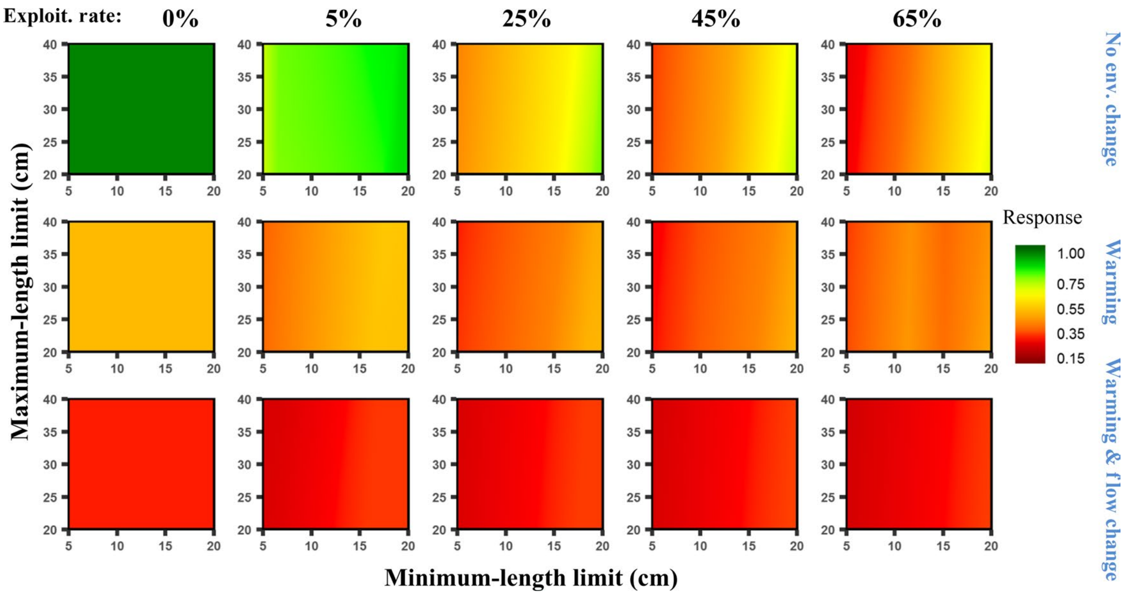

**FIGURE 5** Spawning potential ratio under different fishing regulations and environmental scenarios. Methods and formats are the same as for Figure 1 [Colour figure can be viewed at wileyonlinelibrary.com]

when MinLL was very small, the effects of SSF and EC were synergistic (Appendix S5).

## 4 | DISCUSSION

### 4.1 | Population-level consequences of environmental change and fishing

Our simulated changes in environmental conditions produced a stronger reduction in population abundance than SSF except under scenarios of concurrent intense exploitation and liberal harvest regulations. In contrast, while both stressors markedly truncated the simulated population, the impact of SSF on population structure was much stronger, as the oldest, largest individuals were extirpated when exploitation rate was very high or the minimum-length limit (MinLL) very small. Interestingly, since fishing-induced phenotypic responses of individuals were stronger, the decline in population fecundity was more severe under scenarios of EC alone.

The combined effects of both stressors on population numbers, structure and fecundity were additive or dampened, but rarely synergistic (only the implementation of a maximum-length limit regulation under EC produced a synergistic increased in recruitment variability). This result is line with the (sometimes unexpected) observation that synergistic population-level responses to multiple stressors are rather the exception than the norm (Côté et al., 2016; Darling & Côté, 2008). The predicted dampened interactions are likely due to relaxed competition; harvesting a fraction of the population frees up some of the very few safe and productive places to feed, so the remaining fish are more resistant to the negative impacts of increased metabolic costs and decreased energy inputs linked to elevated temperature and reduced flow (Ayllón et al., 2019). In any case, SSF under a context of EC, even at moderate exploitation rates, would lead to a juvenescent, reduced population with lower average body size (Figure 6: changes in age and size population structure).

### 4.2 | Strength and direction of individual phenotypic responses

In our simulations, increasing the rate of environmental change, increasing exploitation intensity and decreasing MinLL all resulted in earlier maturation at smaller size (Figure 6: mortality-mediated links between environmental drivers or fishing parameters and reproductive traits). This pattern is in line with previous empirical and theoretical research on the changes in maturation schedules in fish populations subject to commercial or recreational harvest (Dunlop et al., 2009; Edeline et al., 2007; Matsumura et al., 2011; Piou et al., 2015; Uusi-Heikkilä et al., 2015). It is also in agreement with observed phenotypic responses to climate change in fish (Audzijonyte et al., 2016; Crozier & Hutchings, 2014).

We observed divergent responses to EC and SSF in length at emergence, though. Harsher environmental conditions (weakly) selected for smaller size at emergence but fishing only produced evolutionary changes (towards smaller size at emergence) when MinLL was very small (i.e. when a maximum-length limit regulation is implemented).

Evolutionary downsizing of size at emergence under warming is consistent with metabolic theory. While being large at emergence provides marked benefits for growth and survival, and ultimately

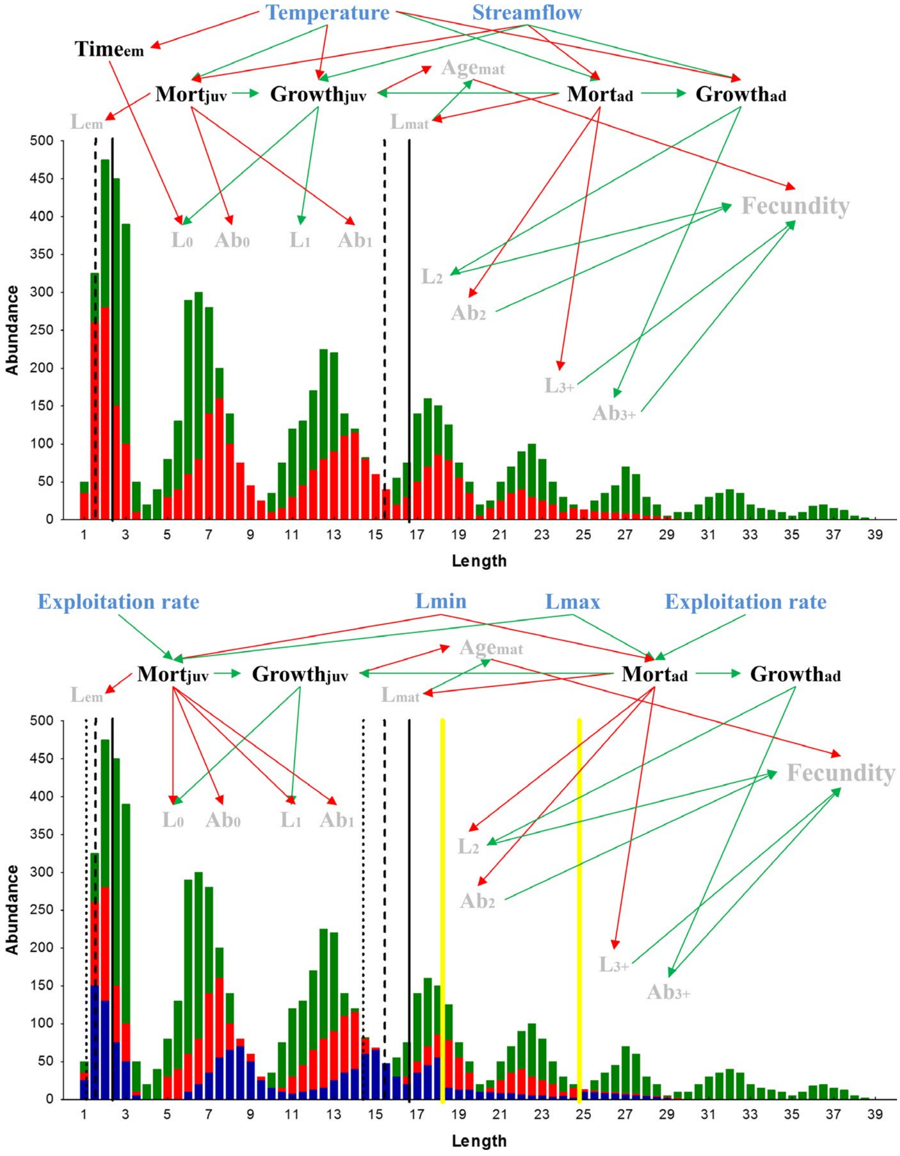

**FIGURE 6** Schematic summary of simulation results, including changes in age and size structure of the simulated population caused by environmental change (EC; top graph) and concurrent EC and size-selective fishing (EC + SSF; bottom graph). Green bars represent the population structure under the baseline scenario (no EC and no SSF), red bars the structure under an EC scenario and blue bars the structure under the EC + SSF scenario. Arrows represent the effects of environmental drivers (top panel) and fishing parameters (bottom panel; both in blue colour) on biological processes (emergence, growth and mortality; black colour) that mediate changes in phenotypic (length-at-age and age-at-maturity) and genotypic (length-at-emergence [Lem] and maturity length threshold [Lmat]) values of life-history traits and in population-level metrics (age-class abundance and total fecundity; grey colour). Green arrows indicate positive relationships and red arrows negative relationships. The vertical black lines represent the genotypic value of heritable traits (Lem and Lmat) under the baseline scenario (solid line), EC (dashed line) and EC + SSF (dotted line). Vertical yellow lines represent the minimum (MinLL) and maximum (MaxLL) length limits

for fitness (Barneche et al., 2018), getting large requires energy that induces costs associated with growth. Assuming constant food production, at temperatures over a species' growth optimum, growth efficiency decreases because metabolic costs increase faster than energy intake rates, and this negative effect of temperature is stronger as body size increases (Ohlberger, 2013). Consequently, elevated temperatures might initially lead to faster juvenile growth and decreased adult size-at-age (juveniles of ectotherms have higher temperature optima than adults; Ohlberger, 2013), but at temperatures over the juvenile growth optima, individuals with smaller size at emergence would be favoured. This situation is worsened when warming concurs with streamflow reduction because food availability, and thus intake rates, decline markedly (Ayllón et al., 2019). Decreased intake rate results from strong reductions in wetted area as well as in water velocity and depth at very low flows, which reduce both food production and transport. There is evidence that selection for smaller body size at maturity leads to selection for slower growth (Monnet et al., 2020), which is consistent with the results of our simulations of EC scenarios.

Since in our model a large size at emergence typically results in higher juvenile growth because of the assumed size-based feeding hierarchy, we expected phenotypes with larger size at emergence to be selected under high exploitation rate and a MinLL well below the maturity size (as predicted in Dunlop et al., 2009, for example). However, our simulations predicted evolution towards smaller size at emergence when MinLL was very small (i.e. under a maximum-length limit regulation). Our results suggest that if capture probability increases with fish length (as it typically does in recreational angling; e.g. Post et al., 2003), it is counterproductive to be ‘too large’ ‘too soon’ when the MinLL is set well below the maturity size. Our and previous modelling studies (reviewed by Enberg et al., 2012) suggest that evolution of either faster or slower growth will depend on the species ecology, vulnerability of individuals to fishing and local harvesting patterns.

In our modelled population, fishing-induced changes in body size and reproductive traits were much more rapid than those resulting from changes in environmental conditions. This result echoes findings from Darimont et al. (2009), who showed that phenotypic changes in harvested systems are much more rapid than changes in both natural and other anthropogenic contexts. Thus, detrimental fishing-induced phenotypic changes could be mitigated more effectively via harvest regulations than via mitigation of environmental changes. The combined effects of EC and SSF on size and reproductive phenotypic traits were either additive or dampened but not synergistic, with dampened responses emerging from scenarios in which combined effects on mortality were also dampened by relaxed competition at low densities.

## 4.3 | Evolutionary versus phenotypically plastic responses

We predicted increased juvenile body size under EC and SSF, whether both stressors act separately or in combination. Since our simulations showed no selection or selection for smaller size at emergence, observed patterns in juvenile body size are caused by plastic responses (Figure 6: arrows pointing to juvenile growth and size-at-age). Daily growth rates of juveniles and adults are predicted to decrease under the temperature and flow change scenarios simulated in our study (Figure S11 in Appendix S4). Nevertheless, Ayllón et al. (2019) showed that despite climate-driven reductions in daily growth rates, plastic changes towards earlier emergence can lead to larger size-at-age of age-0 trout due to a longer growing season. In addition, the predicted decline in population density would positively feed back on growth (Figure S11). Rapid responses in juvenile growth or size-at-age to changes in density induced by SSF (Audzijonyte et al., 2016; Enberg et al., 2012) or EC (Audzijonyte et al., 2016; Crozier & Hutchings, 2014; Ohlberger, 2013) are well documented in fish.

Our simulations also predicted earlier maturation at smaller size under EC and SSF, whether both stressors act separately or in combination. This pattern resulted from the combination of evolution towards smaller maturation size threshold and plastic processes leading to increased juvenile body size (Figure 6: arrows pointing to Agemat). Age at maturation is known to have both genetic and plastic components in fish and our predicted patterns are consistent with empirical observations and model predictions under warming conditions (Audzijonyte et al., 2016; Crozier & Hutchings, 2014; Ohlberger, 2013) and SSF (Audzijonyte et al., 2016; Eikeset et al., 2016; Enberg et al., 2012; Uusi-Heikkilä et al., 2015).

## 4.4 | Implications for fishery management in an environmental change context

Despite all the rapid phenotypic changes described above, the predicted decline in adult density and mean size of spawners produced a reduction in SPR and an increase in recruitment variability in our modelled population. Under conditions of concurrent warming and streamflow reduction, any consumptive fishing regimen would lead to the overexploitation of the population, irrespective of the exploitation intensity and the size-selectivity of the fishery.

We also predicted that implementing a maximum-length limit regulation would lead to recruitment overfishing even at moderate exploitation rates and even if streamflow does not change. While the implementation of a minimum-length limit regulation with a relatively small MinLL (e.g. 17 cm) and an intermediate exploitation rate could reconcile conflicting fishery and conservation objectives, it would lead to the reproductive stock comprising mostly young individuals (Figure 6: changes in age structure in bottom graph). Old, large, fecund females have a disproportionally large contribution to population productivity, stability and resilience through maternal effects, so their removal can lead to increased recruitment variability and unstable population dynamics (Hixon et al., 2014). Harvest-slot limits help protect old, large female spawners while maintaining fishery benefits (Ahrens et al., 2020; Arlinghaus et al., 2010; Gwinn et al., 2015). In our modelled fishery, implementing a harvest-slot regulation with a small MaxLL increased total fecundity of age-3+ trout, but the effect was relatively weak because warming tended to decrease the density and size-at-age of that age class (Figure 6: compare the benefits of implementing an Lmax between scenarios with and without climate change).

Therefore, our modelling study suggests that under conditions of concurrent warming and flow reduction—as projected in Mediterranean fisheries—recreational harvest of cold-water freshwater fish species would not be sustainable. Even if we assumed just a warming environment and not hydrological change, only a very limited range of harvest regulations could provide an acceptable balance between conservation and fishery objectives. Since elevated temperatures or decreasing flows result in strong reduction of the stream's carrying capacity, especially for adult fish, stocking is unlikely to increase stock abundance or fishery yield; stocking for fishery enhancement can be a useful management measure only when the adult stock is below its carrying capacity due to recruitment bottlenecks (Arlinghaus et al., 2016). Nevertheless, stocking might still increase the quality of fishing if management considers a put-and-take fishery.

If the goal is to maintain consumptive fishing, then enhancement measures should rather focus on increasing suitable thermal and physical habitat. Ayllón et al. (2019) showed that hydrological change is the most critical dimension of climate change for stream trout, so the flow regime needs to be carefully managed (e.g. through setting adequate environmental flows) to maintain physical habitat structure and diversity in the fishery (Arlinghaus et al., 2016). There are also a wide range of restoration options to ameliorate thermal stresses on cold-water freshwater fish, including minimization of summer water withdrawal, increasing shade from riparian vegetation, facilitating water exchange between the river channel and cooler hyporheic flows or excavating deep pools to access cool ground water (Isaak et al., 2018).

Alternatively, harvest bans via total catch-and-release (C&R) policies are growing as a conservation strategy to increase sustainability of recreational fisheries (Arlinghaus et al., 2007). The benefits of C&R fishing can be undermined if hooking mortality is too high, so fishing practises (voluntary or via regulation) that maximize post-release survival are critical. Importantly, hooking mortality increases markedly with water temperature (Arlinghaus et al., 2007), so the effectiveness of C&R policies can be strongly reduced under climate change if not accompanied by measures to ameliorate thermal stress on fished populations.

Still, our model is a simplified representation of a real fishery. We did not account for temperature dependence of hooking mortality, nor for potentially important (but poorly understood) processes driving effort dynamics like inverse density-dependent catchability or changes in vulnerability due to learned hook avoidance or behavioural adaptation, nor for other complex interactions and feedbacks between fisher behaviour and ecological processes (see review by Arlinghaus et al., 2017). More empirical and modelling studies are needed to assess the consequences of ongoing environmental change for the sustainability of inland fisheries in the coming decades.

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## AUTHORS' CONTRIBUTIONS

D.A., A.A. and G.G.N. conceived the ideas; All authors collected the essential field data; D.A. designed the methodology, performed the simulation experiments, analysed the data, and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## DATA AVAILABILITY STATEMENT

Model code, input files and output data available via the Figshare Repository https://doi.org/10.6084/m9.figshare.13280459.v1 (Ayllón et al., 2020).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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