Optimal harvest regulations under conflicting tradeoffs between conservation and recreational fishery objectives

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Abstract

Length-based harvest regulations alter the fishing-induced demographic and evolutionary trajectories of exploited stocks and thus shape the existing tradeoffs among fishery and conservation objectives. We used a structurally realistic eco-genetic individual-based harvest model that implements dynamic angling mortality and cryptic mortality sources (illegal harvest and hooking mortality). We (1) analyzed the effects of alternative length-based harvest regulations under scenarios involving different combinations of exploitation intensity and hooking mortality on a suite of indicators of fishery performance and conservation status of a freshwater fish stock, and (2) determined the regulations that optimize the tradeoff among selected indicators under different management strategies, and fishery and conservation objectives. Fishing scenarios under a maximum-length limit regulation maximized harvest yield but led always to recruitment overfishing, irrespective of the exploitation and hooking mortality rates simulated. Fishing scenarios under a harvest slot limits regulation (HS) were best at maintaining a high status of old, large, fecund fish and a more natural age-structure with higher biomass and reproductive potential, performing increasingly better than minimum-length limit (MLL) regulations with decreasing hooking mortality. Both regulation types were effective at preventing overexploitation and only under scenarios with low restrictiveness and high exploitation intensity and hooking mortality was the stock at risk of recruitment overfishing. MLLs outperformed HS regulations in terms of fishery performance, consistently presenting greater harvest yield and efficiency, and size of harvested fish. High rates of hooking mortality rendered HS regulations less effective than assumed, so they were always outperformed by MLLs irrespective of the management strategy and objectives. When hooking mortality was low, HSs constituted the optimal regulation type in most cases except when high fishery performance was favoured over conservation objectives or harvest of large fish was regarded as critically important.

Keywords: recreational fishery, harvest regulation, length-based limits, eco-genetic modeling, brown trout

1. Introduction

Recreational fisheries represent the dominant sector targeting wild freshwater fish stocks in industrialised countries and are becoming also an important social and economic resource in many transitional economies (Arlinghaus et al. 2017, Brownscombe et al. 2019). On the one hand, recreational fishing has high socio-economic and socio-cultural importance and is a major cultural service provided by aquatic ecosystems (Lynch et al. 2016, Arlinghaus et al. 2017). On the other hand, there is increasing evidence that recreational fishing can substantially affect not only the demography (Almodóvar et al. 2002, Almodóvar and Nicola 2004) but also the evolutionary trajectories of exploited fish stocks (Fenberg and Roy 2008, Arlinghaus et al. 2017, Díaz Pauli and Sih 2017, Ayllón et al. 2018), which intensifies fisheries declines and inhibits population recovery. Therefore, diligent management is necessary to maintain sustainable recreational fisheries that balance socio-economic benefits with conservation goals (Brownscombe et al. 2019).

The recreational fishery manager must reconcile often conflicting conservation and socio-economic goals, so for this purpose, different types of regulations of harvest and landings can be implemented in the fishery (reviewed in Arlinghaus et al. 2016). Regulations can be either input (effort) or output (harvest) controls (see Arlinghaus et al. 2016 for examples of either types). Length-based harvest regulations and limits are one of the most common output control measures, and are typically used to limit fishing mortality or manipulate population structure. However, the choice of the size limit type can lead to very different population trajectories and thus to different tradeoffs between conservation and fishery objectives (García-Asorey et al. 2011, Gwinn et al. 2015).

The optimal length-based harvest regulation for a particular stock depends on the management objectives, the demographic conditions of the stock and the intensity of the exploitation (Arlinghaus et al. 2016). The most common length-based harvest regulation is a minimum-length limit (MLL), where only fish larger than a threshold can be harvested, and thus is set to protect small, immature fish and consequently prevent growth overfishing (i.e., depletion of the young part of the stock before they have reached their full growth potential). While biomass yield is typically maximized by implementing a MLL, when fishing effort is too intensive, a MLL can lead to a severe truncation of the population's size-structure (Arlinghaus et al. 2010, Pierce 2010) and, in extreme cases, to recruitment overfishing (i.e., depletion of the reproductive part of the stock to the point that recruitment is impaired) (Sánchez-Hernández et al. 2016). In contrast to MLL regulations, under a maximum-length limit regulation (MXLL) only fish smaller than a threshold can be harvested, and thus is set to protect large, mature fish, while reducing abundance and competition among small fish, leading to improved population size structure (Pierce 2010). Harvest slot limits regulation (HS) implies a combination of minimum- and maximum-length limits, so that only fish within those limits are harvested, and is used to protect both young, immature fish and large, fecund spawners. Modelling studies indicate that size-balanced harvest targeted at protecting old, large fish improve population abundance, structure and resilience (Arlinghaus et al. 2010, Law and Plank 2018). Further, although HS regulations have been traditionally assumed to be inferior to MLL regulations in terms of fishery performance, Gwinn et al. (2015) showed that HS regulations are likely more effective at simultaneously reaching multiple fishery and conservation objectives with little impact on angler satisfaction for a wide range of species' life-history types..

However, length-based harvest regulations are effective only if fished fish that are not within the legal size ranges survive the release event to either reproduce or be harvested at a larger size in the future (Coggins et al. 2007, Pine et al. 2008, Johnston et al. 2015). Increased hooking mortality of fish that are released by anglers can put stocks of species with low compensatory abilities at risk of recruitment overfishing, and result in reductions in fishery yield, harvesting efficiency and losses in angling quality (Johnston et al. 2015). In addition, noncompliance with length-based harvest regulations can be very high in recreational fisheries, and has the potential to accelerate the decline of vulnerable species and lead to the collapse of already depleted stocks (Post 2013, Johnston et al. 2015). Therefore, hooking mortality and regulation noncompliance strongly affect the efficacy of length-based harvest regulations to optimize the tradeoff between conservation of the stock and performance of the fishery.

The overall objective of the study was to explore the effects of size-selective harvest implemented through different types of length-based regulations (minimum, maximum, and harvest-slot length limits), that differ in their restrictiveness and intensity of exploitation, under varying levels of hooking mortality on both demographics of the fish stock and fishery metrics. A further (or additional) goal was to determine the optimum harvest strategies that harmonize several indicators of fishery performance and stock status under competing exploitation and conservation goals. To predict the coupled ecological and evolutionary outcomes of alternative management strategies, we used a structurally realistic eco-genetic individual-based model that accounts for density-dependent processes, phenotypic plasticity, and micro-evolution of life-history traits (inSTREAM-Gen; Ayllón et al. 2016). We used a version of inSTREAM-Gen which includes a fishing module that implements dynamic angling mortality, and cryptic mortality sources (illegal harvest and hooking mortality) (Ayllón et al. 2018).

2. Materials and methods

2.1. Model description

InSTREAM-Gen was implemented in the freely available software platform NetLogo 5.0.4 (Wilensky 1999) and is extensively described in Ayllón et al. (2016) and in the TRACE document (Grimm et al. 2014) provided as supplementary material to Ayllón et al. (2016). The model and its documentation are freely available online (https://github.com/DanielAyllon/inSTREAM-Gen-Fishing-version). The ecological structure of the model builds on inSTREAM (version 4.2; Railsback et al. 2009), to which inSTREAM-Gen added an inheritance model to allow for the genetic transmission of two fitness-related traits that are independent of each other: size at emergence (the length of new fish produced in the model as they hatch from eggs) and maturity size threshold (minimum length for spawning). We summarize below only the main features of the model, since a detailed model description that follows the ODD (Overview, Design concepts, Details) protocol for describing individual-based models (Grimm et al. 2006, 2010) is provided in Appendix A.

InSTREAM-Gen is spatially explicit and models a stream reach as a grid of cells that represent patches of relatively homogeneous habitat, and are characterized by both dynamic flow-dependent (e.g., food production) and static (structural elements) variables. The model simulates the complete trout life cycle using a daily time step, with stream flow and water temperature as the driving environmental variables. On each simulated day, environmental and habitat conditions are updated, and then trout individuals perform four processes. (1) Trout select the habitat that maximizes short-term fitness following a size-based dominance hierarchy by which larger trout have first choice. (2) Trout feed and grow according to standard bioenergetics. (3) Trout face six natural sources of mortality, which are modelled as daily survival probabilities that depend on the fish state and habitat and environmental conditions. In addition, trout are subject to mortality by angling during the fishing season. (4) During the spawning season, mature females spawn when environmental conditions are favourable, creating a redd whose eggs are fertilized by the largest available male spawner and a random number of subordinate spawners. The number of laid eggs increases exponentially with female length and is traded off with egg size to mimic observed patterns in real trout populations (see Jonsson and Jonsson 2011). Given that in our model size at emergence is an inherited trait, females with a larger genetic value of the trait produce larger but fewer eggs than females with average genetic values.

Redds are modelled as individual agents that store the genetic information of the mother and all fathers. Redds are subject to five separate sources of egg mortality, and surviving eggs develop at a rate that depends on temperature. When they are fully developed, new trout emerge and the heritable traits are transmitted. Each new trout inherits its genetic traits from the mother and one father randomly selected from the males that contributed to the redd. The phenotype of an individual is modelled as the sum of an inherited additive genetic effect (genotypic value) and a non-heritable environmental effect. The inheritance rules are based on the infinitesimal model of quantitative genetics (Lynch and Walsh 1998).

2.2. Fishing module

The fishing mortality component builds on models implemented in inSTREAM-SD (Railsback et al. 2013). The assumptions and technical implementation of the module is fully described in Appendix B and parameter values and sources are provided in Appendix C. The fishing module consists of three elements: fishing pressure, capture rate, and survival. Fishing pressure is a model input that reflects the intensity of fishing in the reach (person-hours per day). Capture rate is the mean number of times a fish is captured per day, and depends only on fishing pressure and fish length (capture probability being lower for smaller fish; see Figure B1 in Appendix B). Therefore, the risk to an individual trout of being hooked is a function of fishing pressure but not directly of trout abundance (although abundance has an indirect effect on risk per trout via the fishing pressure; Appendix B). 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.

The simulated fishing regulation defines whether a hooked fish is harvested or released. Under the MLL regulation, anglers can keep every caught fish larger than a fixed length threshold. Under the MXLL regulation, anglers can keep every caught fish smaller than a fixed length threshold. Under the HS regulation, anglers can keep all fish with a size within the harvestable slot. The model assumes that voluntary release of caught legal-sized fish is allowed, so a fraction (40% in this study; estimated via calibration, see Appendix C) of the hooked fish of legal size are released by anglers.

Hooking mortality is modelled as a separate mortality source, but it is related to angling mortality because the model assumes that a fraction of caught and released trout die of hooking. We tested three different rates of hooking mortality based on values reported by Hühn and Arlinghaus (2011): 2% (average value reported for brown trout fished with artificial bait), 7.4% (average value reported for brown trout, including both artificial and live bait), and 20%, a high value, half-way the average value (12.1±6.7%) reported for brown trout fished with live bait and the average value (27%) reported for salmonids with the same bait type. We implemented noncompliance mortality from illegal harvest by assuming that a fraction (5% in this study; estimated via calibration, see Appendix C) of the fish of non-legal size was illegally kept by anglers.

2.3. Simulation scenarios

We used data from a brown trout *Salmo trutta* fishery in northern Spain (Appendix C). The time series (1993-2100) for environmental and hydraulic conditions were the same for all tested scenarios and were generated following the methodology described in Ayllón et al. (2016). That is, the water temperature and flow time series for 1993-2011 were based on the historical records collected by the meteorological and gauging station located in the study basin, while the 2012-2100 time series were projected to mimic the historical patterns of occurrence of environmental flow events (extreme low flows, low flows, small and large floods). To evaluate effects of fishing, we simulated the model population under 180 different fishing scenarios for each value of hooking mortality rate (Hm) tested (2, 7.4 and 20%), so we designed a grand total of 540 simulation scenarios. The fishing scenarios are cross-combinations of three angling parameters: exploitation rate, and minimum and maximum length limits.

Exploitation rate (ExpR) is the percentage of the yearly harvestable stock (i.e., trout of a size within legal limits) that is actually harvested (i.e., hooked and kept by anglers). We simulated five levels of ExpR: 5, 20, 35, 50 and 65%. Fishing pressure (expressed as angler-hours per km and day) in our model is then a linear function of the harvestable stock (number of trout that can be legally harvested during the angling season), the exploitation rate, the angling efficiency (parameter defining the number of angler-hours necessary to catch and keep a trout) and the length of the modelled reach (in km) and the angling season (in days). Harvestable stock is estimated as the sum of the trout that have a legal size at the beginning of the angling season plus the trout that would reach legal size during the angling season. To estimate the latter, all trout project their growth over the whole season from the conditions experienced at the beginning of the season; if the projected size is greater than the minimum length limit, then the trout is considered within the harvestable stock. Since the exploitation rate is fixed but the harvestable stock varies from year to year, fishing pressure is thus a dynamic variable.

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 minimum-length limit at the simulated fishery has been typically set to 19 cm over the last 25 years, so we chose this value as the central value of the tested range; the lower value of the tested range was set to 17 cm, which approximately equals the population's average maturity-length threshold (minimum length for spawning) at initialization (16.7 cm); the upper limit of the tested range was set to 21 cm so that no immature fish could be legally harvested under this regulation. The historical length and age distributions observed at our modelled reach (see Appendix C) lets us estimate the harvestable stock at initialization of model runs. Under the most restrictive regulation (MinLL=21 cm), the harvestable stock consists only of age-3 and older individuals (Table 1). When the MinLL is increasingly smaller, the number of age-2 trout fish within the harvestable stock increases. If MinLL is reduced down to 17 cm, then almost 75% of age-2 trout are of legal size. When MinLL is set to 0, then all fish below the MaxLL are harvestable (note that the probability of capture is close to zero for fish below 7 cm; Figure S2-1 in Appendix B).

Maximum-length limit (MaxLL) is the upper bound of the legal length range (cm). Six levels were used: 25, 27, 29, 31, 33 and 100 cm. The 100-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 1).

2.4. Model outputs

We executed six replicates of each fishing scenario. In every replicate, the model records each simulated year the density and biomass of four age classes (0, 1, 2, and 3 and older trout) at the end of the summer. We also recorded the density, mean length and fecundity of spawners broken out by age classes at the end of the spawning season. We analyzed the effects of fishing scenarios on three indicators of the stock conservation status: total population biomass, the ratio of adult to juvenile biomass, to represent age and size truncation, and the spawning potential ratio (SPR), to evaluate the reduction in potential reproductive output caused by fishing; SPR was estimated as the ratio of the potential fecundity per recruit under the fishing scenario relative to the unexploited situation (Goodyear 1993). We additionally analyzed the effects of fishing scenarios on metrics that characterize the status of the oldest and largest individuals of the population (age-3 and older), including their density, biomass and total fecundity, and the proportion that their fecundity represent from population's total.

Regarding the fishery metrics, the model recorded each simulated year the number and biomass of fish killed by angling and hooking at the end of the fishing season, as well as their mean individual weight. These metrics were recorded broken out by age classes. We estimated the contribution of each age class (%) to total harvest biomass and total biomass of trout killed by hooking. We also calculated the harvesting efficiency, i.e. the ratio of harvest biomass to total biomass loss due to fishing (harvested fish plus fish killed by hooking after release), as well as the catch per unit effort.

2.5. Data analyses

First, we assessed the effect of each angling parameter (ExpR, MinLL, MaxLL and Hm) on the mean value of all conservation status and fishery outputs over the last 15 simulated years

(2086-2100). To do this, we performed linear regressions, including the four angling parameters as independent factors and accounting also for their interaction (540 combinations overall), and analyzed both the direction of the effect and its magnitude. For the latter, we decomposed the percentage of variance explained by each angling parameter using the *relaimpo* package v2.2-2 for R (Groemping and Matthias 2015).

Second, we determined the optimal regulation (or set of optimal regulations), defined as the combination of minimum and maximum length limits and exploitation rate that optimizes the tradeoff between conservation and fishery objectives under each tested hooking mortality rate, using multi-objective optimization (MOO) techniques. MOO is the process of optimizing systematically and simultaneously a collection of objective functions. A solution for a MOO problem is called Pareto optimal if there is no other solution that improves in value any objective function without detriment to at least one other function. The set of Pareto optimal solutions is called the Pareto set and for a given Pareto set, the corresponding objective function values in the objective space are called the Pareto front (Konak et al. 2006). We estimated the Pareto set and corresponding Pareto front that maximizes (1) three fishery objectives (total harvest yield, mean weight of harvested fish and harvesting efficiency) subject to constraints on three conservation objectives (total population biomass, the ratio of adult to juvenile biomass, and the total fecundity of age-3 or older fish) –i.e. a conservation-based management scenario–, and (2) the three conservation objectives subject to constraints on to the three fishery objectives –i.e. an exploitation-based management scenario–. We used the regression models fitted in the first analysis as the mathematical functions to be maximized (Appendix D). We performed these analyses under increasing levels of constraint by the conservation/fishery objectives. To do this, fishery and conservation objective functions were constrained to have a value equal or higher than a management goal. We set tested management goals as the value of all nine deciles of the distribution of each metric across all simulation scenarios, restricted to MLL and HS regulations (150 scenarios under each hooking mortality rate). We did not take into account simulation outputs from the 30 scenarios representing a MXLL regulation because they could introduce a large bias into the analysis, as they resulted in very high values for the fishery metrics but extremely low values for the conservation metrics (see Results section), and thus are not sustainable.

We solved the MOO problems by means of the NSGA-II genetic algorithm (Deb et al. 2002) implemented in the *mco* package v1.0-15.1 for R (Mersmann et al. 2014). In MOO genetic algorithms, each solution in the solution space is a chromosome, a population is a collection of chromosomes, and a generation is an algorithmic iteration (Konak et al. 2006). The NSGA-II algorithm optimizes a multidimensional function by successive sampling of the search space; each population is obtained by creating so called offspring search points from the best individuals in the previous population, which are calculated by non-dominated sorting breaking ties using the crowding distance. We set the number of generations to 150 and the population size to 1000. All statistical analyses were performed with the R software v. 3.3.3 (R Core Team 2017).

3. Results

3.1. Effects of length limits

MinLL was the fishing parameter that exerted the strongest effect on most tested metrics but had little influence on the main metrics related to hooking mortality, such as biomass loss, mean weight of fish dead by hooking and harvesting efficiency (Table 2). Increasing MinLL decreased the catch-per-unit-effort (CPUE) and the harvest yield but increased the mean size of harvested fish because the proportion of age-3 and older fish harvested increased while the proportion of the other age classes was reduced (Table 2, Figure 1). After controlling for the effects of the hooking mortality rate, increasing MinLL decreased the biomass loss by hooking mortality and the proportion of age-1 trout killed by this mortality source while increased the proportion of age-2 and older trout killed, and thus the mean size of fish killed by hooking. MinLL had a negative relationship with harvesting efficiency. MinLL had a positive effect on all conservation metrics, thus a larger MinLL resulted in higher population biomass, adult to juvenile biomass ratio (.i.e, lower truncation of the population), SPR and conservation status of age-3 and older trout (Table 2, Figure 2).

Implementing a MaxLL had a significant but weak effect on all metrics, except on biomass loss by hooking mortality, with which no significant relation was detected (Table 2). Increasing MaxLL (i.e., decreasing the proportion of the largest fish that are protected from harvest) increased the CPUE and the harvest yield and the proportion of age-3 and older trout harvested and thus mean size of harvested fish (Table 2, Figure 1). In contrast, increasing MaxLL increased the proportion of age-1 and 2 trout killed by hooking while decreased the proportion of older trout killed and thus the mean size of fish killed by hooking mortality. MaxLL had thus a positive effect on harvesting efficiency. The effect of MaxLL on conservation metrics was opposite to that of MinLL, so increasing MaxLL decreased the population biomass, adult to juvenile biomass ratio (increased truncation of the population), SPR and conservation status of age-3 and oldest trout (Table 2, Figure 2).

3.2. Effects of exploitation rate

The effect of ExpR on fishery and conservation metrics was opposite that of MinLL (Table 2, Figures 1 and 2): increasing ExpR decreased all conservation metrics, CPUE, harvesting efficiency, the proportion of age-3 and older trout harvested and killed by hooking and thus mean size of fish harvested and killed by hooking, while increased harvest yield and the proportion of trout younger than age-3 trout harvested and killed by hooking.

3.3. Interactive effects between length limits

The effect of the interaction between the minimum and maximum length limits was significant on most fishery and conservation metrics, being the effect however weak (Table 2). The positive effect of decreasing MaxLL (making the regulation more restrictive) on conservation metrics increased with increasing MinLL, so that at a fixed ExpR, maximum values of conservation metrics were attained under the most restrictive regulations (Figure 2). The benefits of implementing a HS regulation over a MLL regulation, in terms of conservation, increased in general with increasing ExpR (Figure 3). Likewise, the positive effects of increasing MaxLL (making the regulation less restrictive) on CPUE, harvest yield and size of harvested fish increased with increasing MinLL (Figure 1).

3.4. Interactive effects of exploitation rate and length limits

We detected significant interactive effects of MinLL and ExpR on all metrics, but only in a few cases were the effects really strong (Table 2). In most of the cases, the interaction of both factors amplified their separate effects (i.e., their effects were synergistic). In consequence, effects on studied metrics were strongest under the most aggressive fishing scenarios (high ExpR and small MinLL) and were exacerbated by increasing levels of hooking mortality rate (Figures 1 and2). In fact, the population went extinct when ExpR was set to 65% under a MXLL regulation (i.e., MinLL=0 cm), irrespective of the maximum-length limit simulated, when Hm was 20% (Figure 2). The strongest effects of the interaction between both parameters were on CPUE, harvest yield, and proportion of age-2 trout harvested and dead by hooking, since decreasing the MinLL to 0 cm (.i.e, implementing a MXLL regulation) reversed the direction of the effect of ExpR on those two latter fishery metrics under MLL and HS regulations (Figures 1 and2).

The interaction between ExpR and MaxLL had significant, but weaker, effects on roughly the same metrics as the interaction between MinLL and MaxLL had (Table 2). However, it had no effects on metrics related with hooking mortality. The positive effects of decreasing MaxLL on conservation metrics were stronger at higher exploitation rates (Figures 2 and 3).

3.5. Hooking mortality rate

Logically, hooking mortality rate (Hm) was the main predictor of total biomass loss by hooking, mean weight of fish dead by hooking and harvesting efficiency (Table 2). It had a significant but lower effect on the rest of studied metrics. Increasing Hm decreased all conservation metrics as well as CPUE, total yield and mean weight of harvested fish (Table 2).

Regarding its interactions with the rest of angling parameters (see Table 2), Hm intensified the negative effects of increasing ExpR on all conservation metrics, CPUE and mean weight of harvested fish, but the positive effect of increasing ExpR on total yield diminished with increasing levels of Hm. Hm also intensified the negative effects of decreasing MinLL on all conservation metrics, while the negative effects of increasing Hm on CPUE and total yield and the positive effects on biomass loss by hooking were stronger at smaller MinLL (especially when MinLL = 0 cm, i.e. under a MXLL regulation). The interaction between MinLL and Hm had its strongest effects on mean weight of fish dead by hooking since the value of Hm reversed the relationship between the fishery metric and the angling parameter (positive when Hm was 2 or 7.4% but negative when it was 20%). Increasing Hm also amplified the interactive effects of ExpR and MinLL described in Section 3.4. Finally, the interaction between Hm and MaxLL was non-significant in almost all studied metrics.

3.6. Optimal harvest regulation

In simulations performed with a very high Hm (20%), all fishing scenarios under a maximum-length limit (MXLL) regulation were not sustainable (Figure 4): under the lowest ExpR (5%) population biomass was over the median value of all simulated scenarios but the population was highly truncated and thus the SPR was very low; increasing the ExpR decreased all conservation metrics, to the point that the population went extinct when ExpR was maximum (65%). Fishing scenarios under a MXLL regulation yielded the maximum harvest, which was however comprised of trout of small size (Figure 4). Fishing scenarios under a harvest-slot (HS) regulation had slightly higher values in conservation metrics than those under a minimum-length limit (MLL) regulation; in contrast, harvesting efficiency and mean size of harvested fish were higher in fishing scenarios under a MLL regulation (Figure 4). When Hm was reduced down to 2%, fishing scenarios under a MXLL regulation were still not sustainable because SPR was below 0.35 (an indication of overexploitation) in all scenarios (Figure 1). Fishery metrics kept performing better under a MLL regulation compared to HS under most fishing scenarios, but HS regulations outperformed MLL regulations regarding conservation metrics, being the difference in performance especially high in those metrics describing the status of the oldest and largest fish (Figures 3 and 4).

As a result, multi-objective optimization analyses showed that under high levels of hooking mortality (20%), MLL regulations optimized always the tradeoff between conservation and fishery metrics irrespective of the management strategy (exploitation-based or conservation-based) and management objective (level of performance in the conservation or fishery metrics) set (Figure 5).

At low levels of hooking mortality (2%), MLL regulations outperformed HS regulations in an exploitation-based management strategy context only when the required level of performance in the fishery metrics was very high (i.e., management strongly focused on exploitation), while HS were the optimal regulations otherwise (Figure 5). Maximization of fishery objectives subject to constraints in conservation objectives (conservation-based management) could be achieved by implementing either a MLL or a HS regulation when Hm is low (Figure 5). This happened because (1) harvest yield and harvesting efficiency are traded off with size of harvested fish, while conservation metrics covaried in the same direction (Figure 4), and (2) conservation metrics had higher values under HS regulations than under MLL regulations at any combination of MinLL and ExpR (Figure 3). Therefore, reaching a given management objective (level of performance in the conservation metrics) involved MLL regulations implementing larger MinLLs and lower ExpRs than those implemented under a HS regulation type, which resulted in lower yield and harvesting efficiency but larger size of harvested fish in the former regulation type. So the optimal harvest regulation type (MLL vs. HS) would depend on which fishery metrics are to be maximized, either yield and harvesting efficiency (maximized by HS) or size of harvested fish (MLL).

4. Discussion

In this study we compared the effectiveness of three length-based harvest regulation types implementing different levels of restrictiveness, under scenarios of varying exploitation intensity and hooking mortality, for optimizing fishery goals while maintaining the abundance, age structure and reproductive potential of the stock within sustainable levels. In our simulations, irrespective of the hooking mortality rate simulated, fishing scenarios under a maximum-length limit (MXLL) regulation maximized harvest yield and catch-per-unit-effort but greatly reduced mean size of harvested fish, which was moreover remarkably lower than the size of fish killed by hooking; harvesting was also less efficient compared to the other regulation types when hooking mortality was high (20%). In addition, all fishing scenarios under a MXLL regulation led to values of spawning potential ratio (SPR) that indicate recruitment overfishing (SPR<0.35; Mace 1994) and even to the extinction of the stock when exploitation rate (65%) and hooking mortality (20%) were very high. The number, size and fecundity of simulated spawners were strongly reduced under MXLL regulations at all hooking mortality rates tested. A MXLL would be viable in our modelled population only under upper limits much smaller than those tested in this study and very low exploitation rates. MXLL regulations are set to protect the largest and thus most fecund fish in the stock, which would theoretically reduce the strength of fishing-induced selection pressures (Baskett et al. 2005, Williams and Shertzer 2005), or increase individual growth and thus production by reducing the numbers of overabundant young age classes (Arlinghaus et al. 2016). However, we did not detect such mitigation effects.

In our model, the implementation of an upper limit was thus effective to maintain the conservation objectives for the stock only when combined with a minimum-length limit. In fact, conservation metrics were maximized in fishing scenarios under a harvest slot limits regulation (HS), although they performed just slightly better than scenarios under a minimum-length limit (MLL) regulation when the hooking mortality was high. Both HS and MLL performed similar and were good at maintaining population biomass and structure within the natural ranges without harvest when the exploitation rate was low and the MinLL was large. In contrast, under the most aggressive fishing scenarios (very high exploitation rate and small MinLL) combined with a high hooking mortality, the population got severely truncated and SPR decreased to values close to 0.35 under both harvest regulations. Only under these scenarios the stock was put on risk of overfishing though thanks to plastic and evolutionary responses that buffered the impacts of intensive fishing and liberal restrictions (see Ayllón et al. 2018). This is in line with previous studies (e.g., Arlinghaus et al. 2010) showing that increasing the MinLL, even under high fishing effort, precludes overfishing and improves the size structure of the exploited population. In our simulations, increasing exploitation intensity worsens all conservation metrics irrespective of the harvest length limits, as described in the literature (e.g., Arlinghaus et al. 2010, García-Asorey et al. 2011).

Similar to our findings for trout, the model of Arlinghaus et al. (2010) for pike *Esox lucius* did not suggest a considerable advantage of implementing HSs over MinLL regulations when the management goal is to conserve stock biomass or its reproductive potential (in terms of SPR). Likewise, Gwinn et al. (2015) found that both regulation types were similarly effective at conserving the spawning stock (SPR) across a wide range of management objectives and species life-history strategies, although, like in our case, SPR levels are maintained through a larger proportion of eggs from younger spawners in MLLs. However, if the goal of harvest regulations in pike stocks was to maintain high abundance of large fish in the stock and manage size structure, HSs outperformed MLLs (Arlinghaus et al. 2010). Similarly, simulations from García-Asorey et al. (2011) indicated that for a given harvest yield, MLLs were best at maintaining larger steelhead trout *Oncorhynchus mykiss* stocks but HSs were best at preserving large trout. Our results are in agreement with such findings; for a given exploitation intensity and MinLL, a HS regulation resulted in markedly higher density, biomass and fecundity of old, large fish and thus in a more balanced population structure compared to a MLL, and the benefits of HSs were increasingly larger with decreasing hooking mortality. Increasing exploitation intensity or decreasing MinLL raises the fishing effort and thus the capture rate of the simulated largest trout (capture probably increases with body size in our model). Hence without the implementation of a maximum-length limit, the oldest and largest trout were entirely removed from the stock under such simulation scenarios, which implied a strong truncation of the population and only increasingly younger and smaller spawners –because of selection for lower maturation size thresholds (Ayllón et al. 2018)– were left. Old, large, fecund female fish have a disproportionally larger contribution to stock productivity, stability and resilience than smaller females because of maternal effects (Hixon et al. 2014). Hence from a conservation perspective, HSs were superior to MLLs even under scenarios of high hooking mortality.

In our simulations, mean size of harvested fish was smaller under HS regulations compared to MLLs, harvest yield and catch-per-unit-effort were similar and, unexpectedly, harvesting efficiency was also similar when hooking mortality was low but lower under HS regulations when it was high. There is no clear pattern in the literature regarding which harvest regulation should produce higher biomass yield; while Matsumura et al. (2011) predicted a decrease in biomass yield of pike under MLLs compared to HSs, simulations from Gwinn et al. (2015) suggested that MLLs were more effective at maximizing biomass yield for a wide range of species irrespective of management objective and exploitation rate.

On the other hand, the consensus view is that HSs outperforms MLLs in terms of harvesting efficiency (Arlinghaus et al. 2010, Matsumura et al. 2011, Gwinn et al. 2015), but our simulations indicated that it actually depended on the hooking mortality rate. In our modelled fishery, the efficiency of age-3 and older trout harvest greatly decreased under HSs when the hooking mortality rate was high, especially under the most restrictive scenarios (larger MinLLs), because the reduction in harvest was not paralleled by a reduction in biomass losses due to hooking mortality; this latter was even up to 75% higher under the scenarios with the highest exploitation rates (and thus fishing effort) because most released fish died after repeated catch-and-release events. This is also the reason why implementing HSs did not provide a substantial advantage compared to MLLs regarding conservation indicators when the hooking mortality rate was high. Note here that our model does not account for the consequences of repeated catch and release on fish intrinsic vulnerability to angling due to learned hook avoidance (e.g., Askey et al. 2006), which could alter capture rates and thus hooking mortality rates. In addition, regulation noncompliance added an extra mortality pressure that targets also preferentially at the individuals experiencing higher capture rates, i.e. the largest ones. Implementation of either HS or MLL regulations resulted in similar harvesting efficiency when the hooking mortality rate was low, irrespective of the exploitation rate simulated.

Our results are thus in line with previous research. According to Gwinn et al. (2015), HSs are superior to MLLs in increasing harvesting efficiency, reducing overexploitation risk and conserving a more natural population structure only when hooking mortality is low. Likewise, Coggins et al. (2007) showed that postrelease mortality rates above 20% substantially impacted fishery objectives, reducing fishery yield and harvesting efficiency. Regarding conservation goals, previous studies have found that under high rates of postrelease mortality neither MLL nor HS regulations are effective at sustaining breeder biomass and preventing recruitment overfishing under high exploitation intensity, especially in species with low compensatory abilities (Coggins et al. 2007, Pine et al. 2008, Gwinn et al. 2015, Johnston et al. 2015). In our modelled stock, the fishing-induced plastic and evolutionary responses prevented the population from recruitment overfishing even under the most aggressive fishing scenarios at the highest mortality rate simulated (20%). Hence in agreement with simulation results from Johnston et al. (2015), the combined mortality from hooking mortality and regulation noncompliance must be over 25% so that size-based harvest regulations cannot avert overfishing in resilient species like brown trout.

In consequence, under high rates of hooking mortality (20%), MLLs provided a more optimal compromise between fishery performance and stock status than HSs irrespective of the management strategy implemented (exploitation-based or conservation-based) and target fishery or conservation objectives (level of performance of metrics). By contrast, when hooking mortality was low (2%), MLL regulations outperformed HS regulations in harmonizing conflicting fishery and conservation metrics under an exploitation-based strategy only when management objectives were markedly targeted at maximizing fishery performance; HS regulations were superior otherwise. Finally, in a conservation-based management context, both length-based regulation types provided optimal tradeoffs at any conservation threshold simulated except when a very high performance in conservation metrics was the priority. The optimal regulation type depended then on a catch- (harvest yield) vs. non-catch-related (size of harvested fish) fishery attributes choice. Note however that optimal MLL regulations must be linked in this case to low levels of exploitation rate and thus to the implementation of input controls to reduce fishing effort.

5. Conclusions

Regulations based on maximum-length limits were not sustainable in our modelled fishery, since they led to recruitment overfishing irrespective of the exploitation and hooking mortality rates simulated. Minimum-length limit regulations were superior to harvest slot regulations regarding fishery performance, especially when simulated hooking mortality was high. By contrast, harvest slot limits regulations were best at maintaining a more natural age and size-distribution, and higher biomass and fecundity of large trout and thus population reproductive potential, although they performed just slightly better than minimum-length limit regulations when hooking mortality was high..Our simulations thus suggest that high rates of hooking mortality and illegal harvest reduce the efficiency of harvest slot limits, and under such circumstances minimum-length limit regulations always provide a better tradeoff between conservation and fishery objectives. When harvesting is highly inefficient, management actions must simultaneously target at reducing fishing effort, controlling illegal harvest and increasing postrelease survival before slot limits regulations are implemented. If hooking mortality is under control, minimum-length limits constitute the optimal regulation type only when high fishery performance is favoured or harvest rather than capture of large fish is considered critically important by anglers.

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Tables

Table 1. Percentage of individuals of each age class that are included in the harvestable stock for each length limit scenario at the beginning of the simulation period (1993-2004). Age-1 individuals are included in the harvestable stock only when a maximum-length limit regulation (MXLL; Lmin = 0 cm) is implemented, in which case all individuals are harvestable.

Age class	**Age 2**						**Age 3 & older**					
Lmin / Lmax	**25**	**27**	**29**	**31**	**33**	**100**	**25**	**27**	**29**	**31**	**33**	**100**
0	100	100	100	100	100	100	71.6	80.7	88.1	93.3	97.2	100
17	72.6	72.6	72.6	72.6	72.6	72.6	71.6	80.7	88.1	93.3	97.2	100
18	45.2	45.2	45.2	45.2	45.2	45.2	71.6	80.7	88.1	93.3	97.2	100
19	20.1	20.1	20.1	20.1	20.1	20.1	71.6	80.7	88.1	93.3	97.2	100
20	5.8	5.8	5.8	5.8	5.8	5.8	71.6	80.7	88.1	93.3	97.2	100
21	0	0	0	0	0	0	60.3	69.4	76.8	82	85.9	88.7

Table 2. Effects of angling parameters –minimum (Mn) and maximum (Mx) length limits, exploitation rate (Er) and hooking mortality rate (Hm)– and their interactions on population conservation and fishery metrics. Symbols show the direction (+ increase, - decrease) and significance of the effect (n.s. non-significant, * *P*<0.05, ** *P*<0.01, *** *P*<0.001) as well as its magnitude (percentage of variance explained).

Pattern	**Mx**	**Mn**	**Er**	**Hm**	**Mx:Mn**	**Mx:Er**	**Mn:Er**	**Mx:Hm**	**Mn:Hm**	**Er:Hm**	**Mn:Er:hm**
Conservation metrics											
Biomass total	(-)*** [0.1]	(+)*** [78.8]	(-)*** [15.7]	(-)*** [0.8]	*** [0.1]	*** [0.1]	*** [4.0]	n.s.	*** [0.1]	*** [0.2]	*** [0.2]
Ratio adults to juveniles	(-)*** [0.3]	(+)*** [60.8]	(-)*** [31.7]	(-)*** [1.3]	*** [0.1]	*** [0.1]	*** [5.3]	*** [0.1]	*** [0.2]	*** [0.2]	*** [0.1]
Spawning potential ratio	(-)*** [0.2]	(+)*** [67.4]	(-)*** [28.1]	(-)*** [1.6]	*** [0.1]	** [0.1]	*** [2.0]	** [0.1]	*** 0.1]	*** [0.2]	*** [0.2]
Fecundity fish age-3	(-)*** [0.7]	(+)*** [40.7]	(-)*** [47.5]	(-)*** [1.4]	*** [0.2]	*** [0.1]	*** [8.8]	*** [0.1]	*** [0.3]	*** [0.1]	*** [0.2]
Fishery metrics											
Catch-per-unit-effort	(+)*** [0.8]	(-)*** [26.7]	(-)*** [32.4]	(-)*** [1.4]	*** [0.2]	*** [0.2]	*** [34.2]	n.s.	*** [1.0]	*** [0.9]	*** [2.2]
Total harvested biomass	(+)*** [0.8]	(-)*** [55.0]	(+)*** [17.5]	(-)*** [1.8]	*** [0.1]	*** [0.1]	*** [22.5]	n.s.	*** [0.4]	*** [1.0]	*** [0.8]
Proportion Harvested age-1	(-)* [0.1]	(-)*** [93.4]	(+)*** [2.6]	(+)*** [0.1]	n.s.	n.s.	*** [2.5]	n.s.	*** [1.0]	*** [0.1]	*** [0.5]
Proportion Harvested age-2	(-)*** [1.2]	(-)*** [66.6]	(+)*** [10.5]	(+)*** [0.3]	*** [0.3]	*** [0.2]	*** [19.6]	n.s.	*** [0.7]	*** [0.1]	*** [0.3]
Proportion Harvested age-3	(+)*** [0.6]	(+)*** [80.7]	(-)*** [14.6]	(-)*** [0.7]	*** [0.1]	*** [0.1]	*** [2.9]	n.s.	*** [0.1]	*** [0.1]	*** [0.1]
Biomass loss by hooking	n.s.	(-)*** [8.5]	(+)*** [6.0]	(+)*** [49.2]	** [0.1]	n.s.	*** [7.8]	n.s.	*** [16.4]	*** [3.2]	*** [8.8]
Proportion Hooking age-1	(+)*** [0.2]	(-)*** [80.6]	(+)*** [10.5]	(+)*** [3.6]	*** [0.1]	n.s.	*** [3.1]	n.s.	*** [0.4]	*** [0.1]	*** [1.4]
Proportion Hooking age-2	(+)*** [1.6]	(+)*** [71.0]	(+)*** [2.3]	(-)*** [3.1]	* [0.5]	n.s.	*** [14.0]	** [0.3]	*** [2.8]	*** [0.4]	*** [3.9]
Proportion Hooking age-3	(-)*** [2.2]	(+)*** [52.3]	(-)*** [33.1]	(-)*** [3.1]	*** [0.6]	n.s.	*** [6.0]	** [0.2]	*** [0.3]	* [0.1]	*** [1.9]
Harvesting efficiency	(+)*** [1.0]	(-)*** [2.0]	(-)*** [0.8]	(-)*** [92.3]	*** [0.5]	*** [0.2]	*** [0.2]	*** [0.1]	*** [2.1]	*** [0.4]	*** [0.4]
Mean weight harvested fish	(+)*** [2.0]	(+)*** [85.1]	(-)*** [9.8]	(-)*** [0.1]	*** [1.0]	*** [0.7]	*** [0.7]	n.s.	*** [0.4]	n.s.	n.s.
Mean weight hooked fish	(-)*** [1.4]	(+)*** [12.3]	(-)*** [16.6]	(+)*** [19.9]	*** [0.7]	n.s.	*** [1.5]	n.s.	*** [44.2]	* [0.2]	*** [2.7]

+++ The interaction terms Mx:Mn:Hm and Mx:Er:Hm did not have significant effects on any output except on harvesting efficiency (*P*<0.01), contributing in both cases to 0.1% of the total explained variance.

Figure captions

Figure 1. Effect of exploitation rate, and minimum (MinLL) and maximum-length (MaxLL) limits on five fishery metrics at final simulation time under three harvest regulations – Minimum-length limit regulation (MLL: maximum-length limit of 100 cm), Maximum-length limit regulation (MXLL: minimum-length limit of 0 cm), and Harvest slot regulation (HS: maximum-length limit of 25 cm) – and two hooking mortality rates (2% vs. 20%). Colour scales on the right of each graph indicate mean values (biomass in kg ha^{-1}, individual fish weights in g, and harvest efficiency in %) over the last 15 simulated years, 2086-2100. Note that the range of values of fishery metrics varies across harvest regulations and simulated hooking mortality rates.

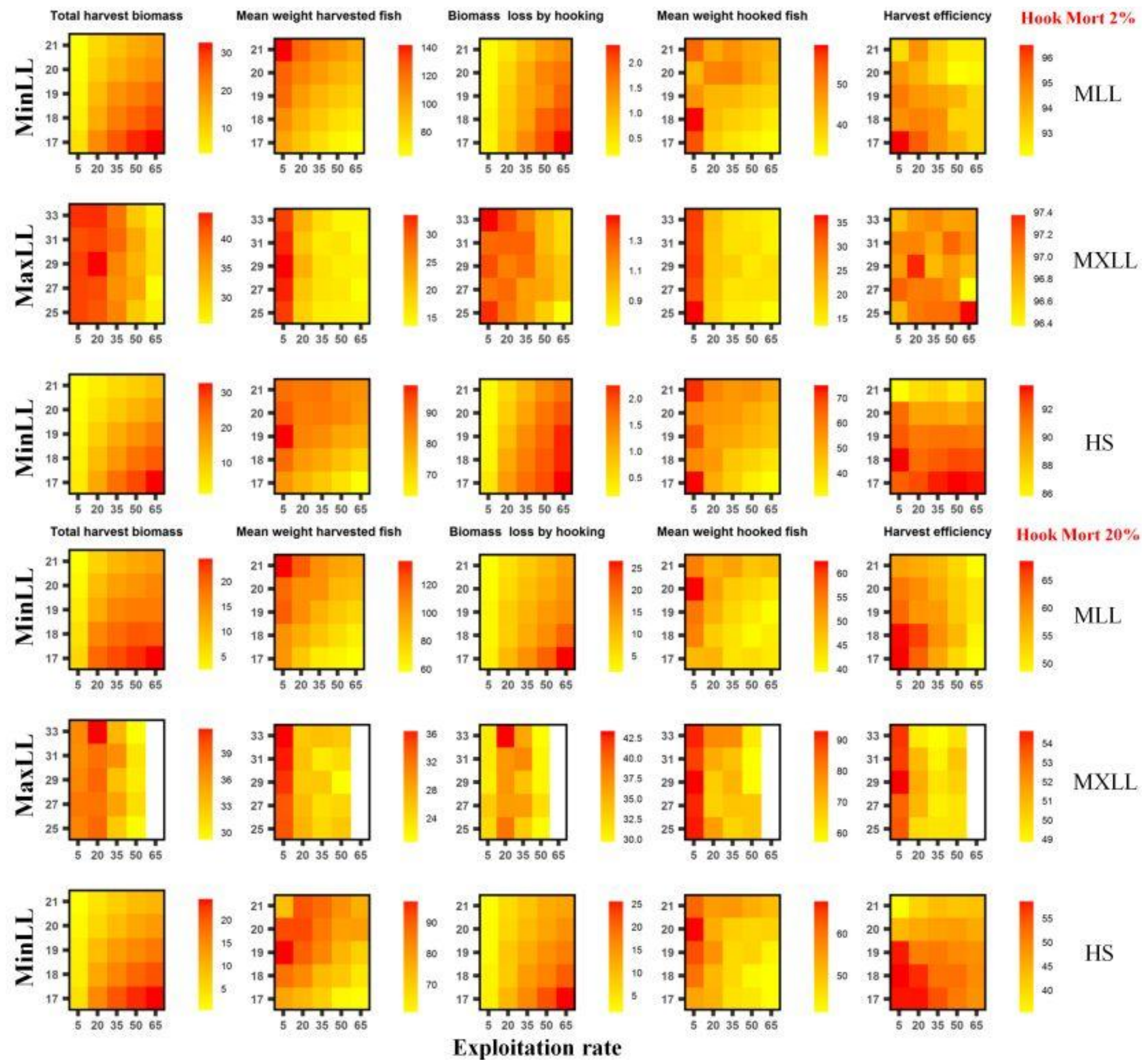
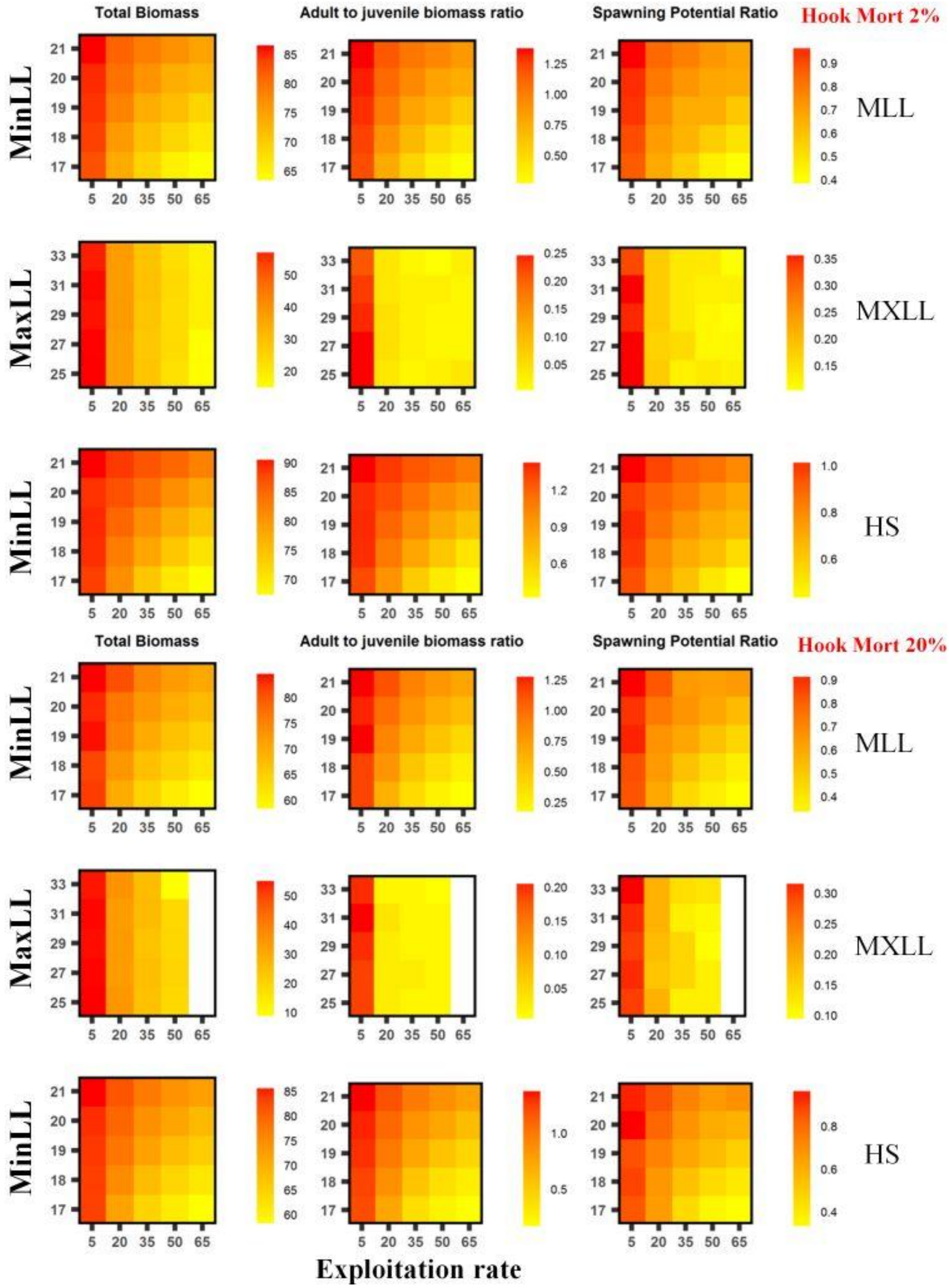

Total harvest biomass
Mean weight harvested fish
Biomass loss by hooking
Mean weight hooked fish
Harvest efficiency
Hook Mort 2%
MinLL
MaxLL
MinLL
MLL
MXLL
HS
Total harvest biomass
Mean weight harvested fish
Biomass loss by hooking
Mean weight hooked fish
Harvest efficiency
Hook Mort 20%
MinLL
MaxLL
MinLL
MLL
MXLL
HS
Exploitation rate

Figure 2. Effect of exploitation rate, and minimum (MinLL) and maximum-length (MaxLL) limits on three conservation metrics at final simulation time under three harvest regulations – Minimum-length limit regulation (MLL: maximum-length limit of 100 cm), Maximum-length limit regulation (MXLL: minimum-length limit of 0 cm), and Harvest slot regulation (HS: maximum-length limit of 25 cm) – and two hooking mortality rates (2% vs. 20%). Colour scales on the right of each graph indicate mean values (biomass in kg ha^{-1}, adult to juvenile biomass ratio and Spawning Potential Ratio are unitless) over the last 15 simulated years, 2086-2100. Note that the range of values of conservation metrics varies across harvest regulations and simulated hooking mortality rates.



Total Biomass
Adult to juvenile biomass ratio
Spawning Potential Ratio
Hook Mort 2%
MinLL
MaxLL
MinLL
MLL
MXLL
HS
Total Biomass
Adult to juvenile biomass ratio
Spawning Potential Ratio
Hook Mort 20%
MinLL
MaxLL
MinLL
MLL
MXLL
HS
Exploitation rate

Figure 3. Difference in mean values over the last 15 simulated years (2086-2100) of six conservation metrics between simulations performed under a harvest slot (HS; maximum-length limit of 25 cm) and a minimum-length limit regulation (MLL) at different values of exploitation rate, minimum-length limit and hooking mortality rate. It is expressed as the percentage change: [(mean HS - mean MLL)/mean MLL] x 100.

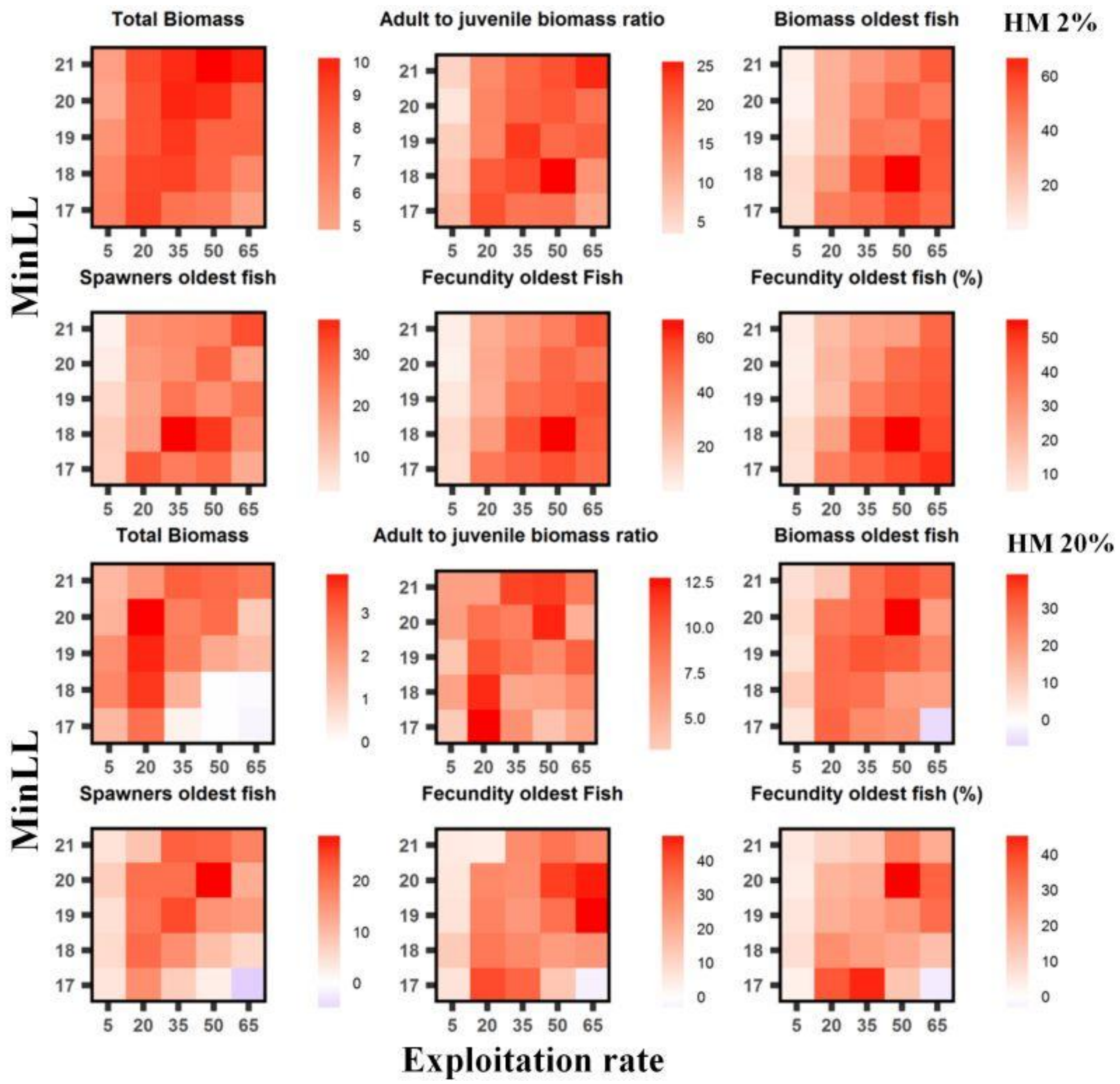


Figure 4. Change in mean values over the last 15 simulated years, 2086-2100, from six fishery and conservation indicators across a normalized range in indicator level (0, 25, 50 ,75, 100%) for alternative fishing scenarios under Minimum-length (MLL) and Maximum-length (MXLL) limit, and Harvest slot (HS) regulations. The axis attributed to each indicator, specified in the central graph, is the same across graphs. The colour palette red-blue-green indicates increasing restrictiveness in the fishing scenario: minimum-length limit of 17, 19 and 21 cm under MLL, maximum-length limit of 33, 29 and 25 cm under MXLL, and combination of minimum and maximum-length limits of 17-25, 19-25 and 21-25 cm under HS. The combination of width and type of line indicates the exploitation rate of the fishing scenario: thin-solid, thin-dashed and thick-solid are 5, 35 and 65% respectively.

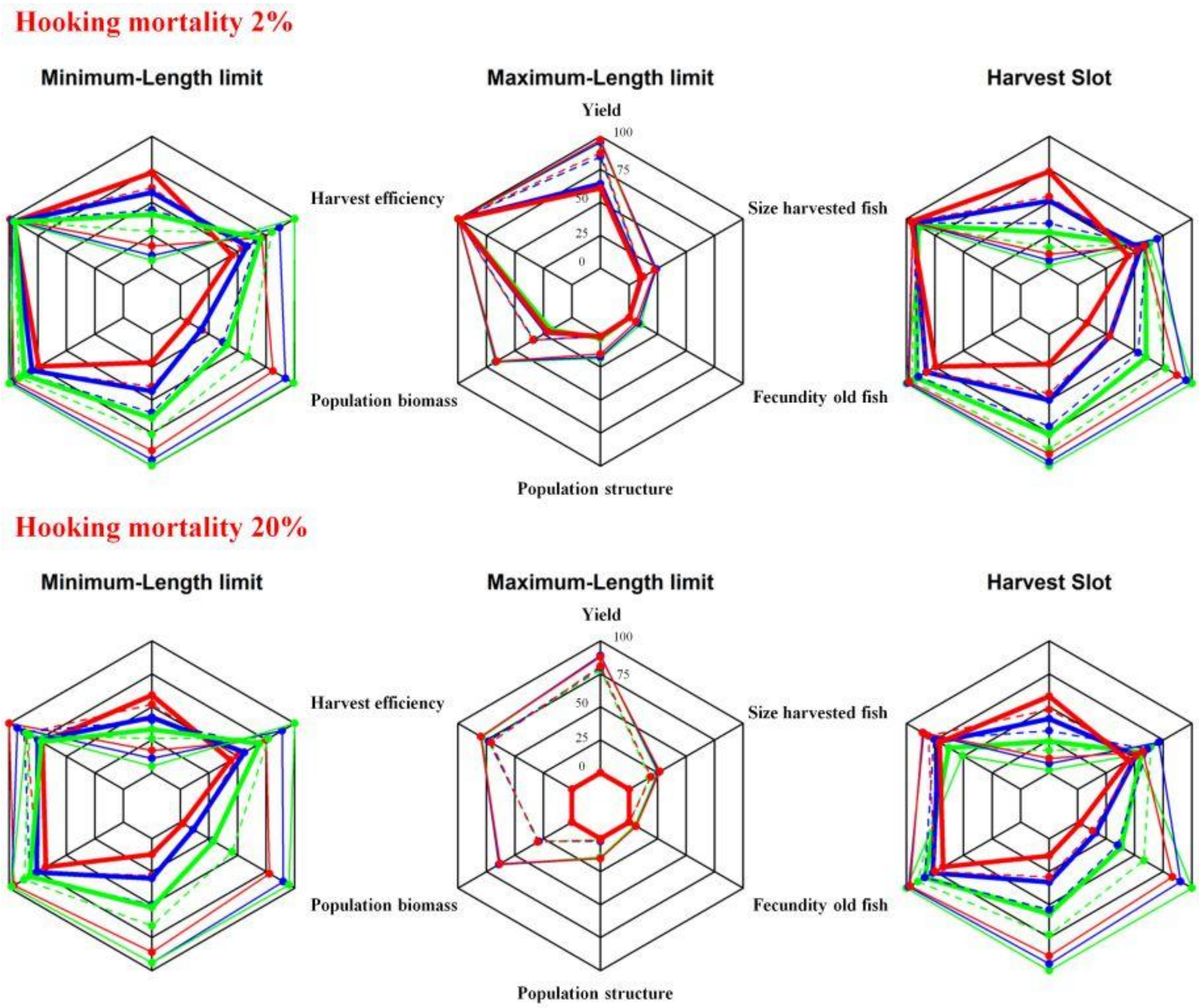


Figure 5. Minimum (grey line) and maximum (black line) values of the Pareto optimal range of maximum-length limit for two multi-objective optimization analyses: 1) maximization of conservation metrics (population biomass, ratio of adult to juvenile biomass and total fecundity of oldest fish) constrained to meet increasing thresholds for performance in fishery metrics (yield, harvesting efficiency and mean weight of harvested fish), measured as the percentile of the maximum possible value of each metric; 2) maximization of fishery metrics constrained to meet increasing thresholds for performance in conservation metrics. It indicates the optimal length-based harvest regulation (minimum-length limit vs. harvest slot) under competing fishery and conservation objectives. Plots in the left side are the solutions for simulations performed with a hooking mortality rate (Hm) of 2%, while plots in the right side are those for an Hm of 20%.