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How ecological processes shape the outcomes of stock enhancement and harvest regulations in recreational fisheries

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ABSTRACT

Fish stocking and harvest regulations are frequently used to maintain or enhance freshwater recreational fisheries and contribute to fish conservation. However, their relative effectiveness has rarely been systematically evaluated using quantitative models that account for key size- and density-dependent ecological processes, and adaptive responses of anglers. We present a new integrated model of freshwater recreational fisheries where the population dynamics of two model species affect the effort dynamics of recreational anglers. With this model we examined how stocking various fish densities and sizes (fry, fingerlings, and adults) performed relative to minimum-length limits using a variety of biological, social and economic performance measures, while evaluating trade-offs. Four key findings are highlighted. First, stocking often augmented the exploited fish population, but size- and density-dependent bottlenecks limited the number of fry and fingerlings surviving to a catchable size in self-sustaining populations. The greatest enhancement of the catchable fish population occurred when large fish that escaped early bottlenecks were stocked, but this came at the cost of wild-stock replacement, thereby demonstrating a fundamental trade-off between fisheries benefits and conservation. Second, the relative performance of stocking naturally reproducing populations was largely independent of habitat quality and was generally low. Third, stocking was only economically advisable when natural reproduction was impaired or absent, stocking rates were low, and enough anglers benefitted from stocking to offset the associated costs. Fourth, in self-sustaining fish populations, minimum-length limits generally outperformed stocking when judged against a range of biological, social and economic objectives. By contrast, stocking in culture-based fisheries often generated substantial benefits. Collectively, our study demonstrates that size- and density-dependent processes, and broadly the degree of natural recruitment, drive the biological, social
and economic outcomes of popular management actions in recreational fisheries. To evaluate these outcomes and the resulting trade-offs, integrated fisheries-management models that explicitly consider the feedbacks among ecological and social processes are needed.

**KEYWORDS** density-dependence, size-dependent mortality, harvest regulations, fish stock enhancement, human dimensions, recreational fishing, northern pike (*Esox lucius*), common carp (*Cyprinus carpio*).
INTRODUCTION

Many inland fish populations are under threat due to anthropogenic impacts on habitat quality and quantity, climate change, the stocking and spread of non-native fishes and genotypes and resulting changes in genetic diversity, and overharvest (Dudgeon et al. 2006, Laikre et al. 2010, Cooke et al. 2016). Recreational fishers are the dominant users of inland fish stocks in industrialized countries (Arlinghaus et al. 2002, FAO 2012), and their activities and expenditures are fundamentally important drivers for fish conservation and fisheries-management activities (Arlinghaus 2006, Tufts et al. 2015). Collectively, recreational fishers can exert substantial harvesting pressures on fish populations (Post et al. 2002, Cooke and Cowx 2006, Lewin et al. 2006). Managers tend to respond to impacts on recreational fisheries using three general strategies (Arlinghaus et al. 2016): i) implementing input and output regulations that control fishing effort (input) or regulate which sizes and how many fish are harvested (output), ii) improving and restoring habitat, or iii) engaging in stocking-based enhancements. Among these, harvest regulations and stocking are the most widespread due to tradition and ease of implementation (van Poorten et al. 2011, Arlinghaus et al. 2016, Sass et al. 2017).

To manage fish stocking sustainably, it is important to understand when to engage in a specific action and when to use alternatives (Lorenzen 2014, Arlinghaus et al. 2016, Arlinghaus et al. 2017). Although stocking can help fish stocks recover and enhance fisheries use and catch (Lorenzen et al. 2012, Amoroso et al. 2017), the practice can also contribute to the decline of wild fish populations by elevating competition or predation, fostering disease outbreaks, promoting mixing of wild populations with domesticated, hatchery-reared fishes (Laikre et al. 2010, van Poorten et al. 2011, Lorenzen et al. 2012), and potentially increasing fishing pressure on wild stocks (Baer et al. 2007). The ability of stocking to maintain or boost fisheries catches
beyond levels achievable by wild populations may correlate with a decline in environmental 
quality that constrains natural recruitment, thereby freeing “niches” for hatchery fish (Rogers et 
al. 2010, Ziegler et al. 2017). However, stocking hatchery fish may further burden an already 
dwindling wild stock (Laikre et al. 2010, van Poorten et al. 2011, Cochran-Biederman et al. 
2015), creating a fundamental trade-off between wild fish conservation and maintaining or 
enhancing fisheries through (successful) stocking (Lorenzen 2005, Camp et al. 2017, Amoroso et 
al. 2017). In light of key feedbacks among the ecological and social components of a fishery 
(Camp et al. 2014, Lorenzen 2014, Arlinghaus et al. 2016), navigating this trade-off demands 
careful analysis of how the outcomes from stocking vary with ecological conditions (e.g., 
whether a stock is self-sustaining or not) and properties of the management intervention (e.g., 
size and density of stocked fishes, fitness of hatchery fish in the wild). Such an analysis using an 
integrated social-ecological model of recreational fisheries that incorporates a mechanistic model 
of angler behavior and a realistic ecological representation of a stock-enhanced fishery regulated 
by multiple size- and density-dependent ecological processes has so far not been completed.

An alternative management response common in freshwater recreational-fisheries management 
is the implementation of harvest regulations (Arlinghaus et al. 2016). Harvest regulations are 
used to limit fishing mortality, manage size structure, and distribute harvest more equally among 
anglers (Radomski et al. 2001). However, constraints on an individual’s ability to harvest fish 
can have high social costs for angler groups most affected by the regulations (Beard et al. 2003, 
Johnston et al. 2011, Haglund et al. 2016). Thus, implementing restrictive harvest controls is 
rarely preferred by anglers over stocking or the control of perceived or real competitors (e.g., 
commercial fishers, fish-eating birds, Arlinghaus and Mehner 2003a, Dorow and Arlinghaus 
2012). An analysis of fish-angler interactions that integrates ecological and social dimensions
and considers dynamic angler responses is needed to outline the ecological and socio-economic conditions that favor one management approach (e.g., harvest restrictions) over another (e.g., stocking) (Arlinghaus et al. 2017).

A range of fish stocking models incorporating key ecological mechanisms, such as density- and size-dependent mortality, are available to examine the ecological conditions constraining the additive potentials of fish stocking (e.g., Lorenzen 2005, Rogers et al. 2010, Askey et al. 2013, Camp et al. 2014). However, few of these models have explicitly considered multi-attribute decision making by anglers. Both strategic and tactical recreational-fisheries models should consider anglers’ preferences and behavioral responses to policy interventions (Johnston et al. 2010), because they can strongly influence social (e.g., effort directed at a given site) and ecological (e.g., fish abundance or catch rate) outcomes (Arlinghaus et al. 2017). Mechanistic choice models based on economic random utility theory can be used to extrapolate complex, human behavioral responses (Fenichel et al. 2013a), but no stocking model using a rigorous choice-based representation of angler behavior exists. Considering both the ecological and social dimensions of fisheries will likely affect management trade-offs, and the costs and benefits of particular management actions. Moreover, judging the performance of any management action will depend on the performance measure used, and ultimately on the underlying normative framework and objectives (e.g., conservation, fisheries quality, economic benefits) upon which the measures are based (Fenichel et al. 2013b, Camp et al. 2017).

Management actions such as harvest regulations and stocking will likely not be equally effective at achieving various objectives, because they differentially affect fish populations and anglers. The outcomes of stocking will be governed by a range of ecological processes that determine how hatchery reared fish interact with their wild conspecifics (Lorenzen 2014). Most fish
populations are regulated by density-dependent compensatory mortality in the early juvenile stage (Lorenzen 2005). Another key regulatory process is size-dependent mortality coupled with density-dependent growth in later life stages (Lorenzen 2005). Size- and density-dependent ecological processes are relevant for the success of minimum-length limits because they will determine if fishing mortality is being affected (FAO 2012). These processes are also important for determining stocking success, because they influence whether or not stocked fish can circumvent factors limiting the wild population (Lorenzen 2005, Rogers et al. 2010, Camp et al. 2014). In addition, limited recruitment or productivity due to poor habitat quality, compensatory changes in growth or survival of fish populations, and a lack of local adaptation of stocked fishes to the wild can limit the ability of hatchery-reared fish to survive and reproduce (Cowx 1994, Lorenzen et al. 2012, Cochran-Biederman et al. 2015). The situation is somewhat different in non-naturally reproducing populations where stocked fish will not face intraspecific competition with wild conspecifics.

We hypothesize that stocking should generate large social and economic benefits when natural reproduction is lacking, while harvest regulations shall socio-economically outperform most stocking events in self-sustaining stocks. We also hypothesize that stocking will be most effective when large, recruited fishes are stocked that are no longer affected by compensatory juvenile mortality (Lorenzen 2005), but that such stocking in naturally-reproducing populations will create a fundamental trade-off between conservation and fisheries benefits (Amoroso et al. 2017, Camp et al. 2017). We test these hypotheses using a fully integrated model of fish-angler interactions with explicit angler behavioral feedback grounded in economic utility theory. We use this model to systematically explore how the contrasting ecology of two freshwater fishes, naturally-reproducing and non-reproducing, shape the ecological, conservation and
socioeconomic outcomes of both stocking and a commonly applied harvest regulation, the minimum-length limit (MLL). In the model, angler behavior is described mechanistically as a function of multiple attributes of the fishing experience using results from an empirically grounded stated preference model of anglers (Arlinghaus et al. 2014). The ecological sub-model is calibrated to represent two prototypical freshwater fish populations, naturally-reproducing northern pike (Esox lucius) that recruits to the fishery and common carp (Cyprinus carpio) that does not naturally recruit to the fishery (referred to as non-reproducing). Pike was chosen because it is a popular target species among anglers that is commonly stocked in both North America (Paukert et al. 2001, Margenau et al. 2008) and Europe (Wedekind et al. 2001, Arlinghaus and Mehner 2004, Hühn et al. 2014). Both stock enhancement (stocking into wild populations) and culture-based stocking (into systems in which natural reproduction is absent) can occur (Lorenzen et al. 2012). Despite carp being considered a pest in North America, Australia and some parts of Europe (e.g. Spain), carp was chosen because of its importance as a culture-based, harvest-oriented inland fishery in central Europe (Wedekind et al. 2001, Arlinghaus and Mehner 2003b, Vilizzi et al. 2015). In central Europe, carp populations depend almost entirely on stocking, because, while they regularly spawn, they rarely recruit to the population successfully in the wild (Kottelat and Freyhof 2007). Hypotheses for why this occurs include; unsuitable temperatures and flow for spawning, and competition or predation from native cyprinids that usually spawn substantially earlier than carp (Kottelat and Freyhof 2007, Bajer and Sorensen 2010). In the model we also considered recruitment-limited pike populations, such as might occur in response to the loss of vegetated habitat (Casselman and Lewis 1996), thereby studying the full range of possibilities as to how the degree of natural recruitment affects stock enhancement outcomes relative to harvest regulations. Our simulation exercise was meant
to produce strategic insights into the trade-offs inherent in common fisheries management actions in light of ecological constraints, rather than to generate tactical insights informing management of a particular fishery.

METHODS

The potential effects of stocking and harvest regulations, specifically minimum-length limits (MLLs) on biological, social, and economic outcomes were investigated using an integrated bioeconomic recreational-fisheries model adapted from earlier work (Johnston et al. 2010, 2013). The model included three main components: 1) a deterministic age- and size-structured biological sub-model to describe the fish population dynamics, 2) a social sub-model to describe angler effort dynamics, and 3) a management component, which allowed for different MLLs, stocking sizes and stocking densities to be investigated (Figure 1). We used the model to evaluate how well stocking different sizes of fish – fry, fingerlings, and adults (Appendix S1: Figures S1 and S2) – at a variety of stocking densities performed relative to various MLLs in terms of achieving biological, social, and economic management objectives, and the trade-offs involved, for a single-lake fishery. This evaluation was done for naturally-reproducing northern pike, representing a stock enhancement scenario, and for non-reproducing common carp, representing a culture-based stocking scenario. Six performance measures covering a range of commonly used ecological, social and economic objectives were evaluated. In addition, the age structure and composition (wild vs. hatchery origin fish) of the fish population was examined for some simulations as a further conservation objective. The simulations were run until the population reached an equilibrium prior to the commencement of fishing or implementation of management policies and then run for additional time until the model reached a new equilibrium after the changes were introduced. In the stocking scenarios, stocking occurred annually at the
beginning of each year. Information from an interdisciplinary study on fish stocking and anglers in Lower Saxony, Germany (www.besatz-fisch.de), was used to inform the biological and social sub-models (Arlinghaus et al. 2014, Hühn et al. 2014, Arlinghaus et al. 2015). Model equations can be found in Table 1 and parameter values in Appendix S1: Table S1. Software based on the model presented here is freely available at http://www.ifishman.de/en/practioner/software/ in English or German, which can be used to reproduce the results presented here and run simulations for a range of other freshwater species.

_Biological sub-model_

The biological sub-model included the following key ecological processes: density-dependent growth, reproduction, and density- and size-dependent survival during the early life stage (age-0 fish) and later life stages. These processes are essential to properly represent the ecological changes induced by the density increase through stocking (Lorenzen 2005). A bi-phasic model developed by Lester et al. (2004) was used to describe somatic growth. This model assumed that the annual growth in length of immature fish was linear and dependent on biomass density to represent density-dependent growth (Table 1, eqn. 2a-2b), while mature fish only realized a proportion of the annual growth potential (Table 1, eqn. 2c) due to the diversion of resources to reproduction. Thus, post-maturation growth was also density dependent. To create a more realistic size distribution and simulate the cumulative effects of differential size-dependent mortality (Walters and Martell 2004), 11 size classes (i.e., growth trajectories) within an age class were modelled. For simplicity, stocked and wild fish were assumed to have the same growth rates, but relative survival and reproductive fitness could differ (see below). Maturation was assumed to be size and age dependent as is typical in fish (Table 1, eqn. 3a). Reproduction was a linear function of female mass (Walters and Martell 2004) (Table 1, eqn. 3b), and the
potential for differential relative reproductive success between hatchery and wild fish (Lorenzen 2005) was explicitly included in the model (Table 1, eqn. 3b, \( \rho \), Appendix S1: Table S1). In the case of carp, natural reproduction was assumed to be zero, and in the pike simulations we assumed various scenarios for the degree of natural recruitment to represent healthy and disturbed ecosystems.

Differing from earlier applications (Johnston et al. 2010, 2013, Johnston et al. 2015), the survival of larvae to age-1 was assumed to be size and density-dependent (Table 1, eqns. 4a-f and 5a-d) to better represent the outcomes of stock enhancement using hatchery reared fry or juveniles (Lorenzen 2005). To that end, we modified and implemented a method pioneered by Lorenzen (2005), where recruitment to age-1 was “unpacked” so that pre- and post-stocking survival of age-0 fish (fry or fingerlings) were described independently, allowing all fish to experience density-dependent and size-dependent mortality - two processes which are commonly experienced by fishes in this early life stage (Lorenzen 1996, 2005, Hazlerigg et al. 2012). We modified the methods of Lorenzen (2005) by representing a Ricker-type stock-recruitment model rather than a Beverton-Holt stock-recruit relationships, because a Ricker recruitment model has been used to describe the early survival for pike (Edeline et al. 2008) and carp (Brown and Walker 2004, based on data presented in Koehn et al. 2000) (see Appendix S1 for derivation). In the pre-stocking phase (Table 1, eqns. 4a-f), wild and hatchery origin larvae (i.e., offspring of stocked fish) underwent the same density-dependent survival bottleneck. During this phase it was possible for a proportion of hatchery larvae to transition to wild strain fish due to natural selection similar to Lorenzen (2005) (Table 1, eqn. 4f, \( h^2 \), Appendix S1: Table S1). The potential for differential survival of age-0 hatchery fish relative to age-0 wild fish was also included in the model (Table 1, eqn. 4f, \( \gamma \), Appendix S1: Table S1), because empirical data has
shown stocked fishes often have lower relative survival fitness (Lorenzen 2006, Lorenzen et al. 2012, Hühn et al. 2014). In the post-stocking phase (Table 1, eqns. 5a-d), the age-0 fish that survived the pre-stocking phase as well as age-0 fish stocked that year (fry or fingerlings) experienced further density-dependent survival, but at a reduced intensity because fish were larger and, thus, were less vulnerable to size-dependent mortality than smaller fish (Lorenzen 2005). Consequently, in our model, stocked fingerlings experienced lower natural mortality than smaller fry. Similar to Coggins et al. (2007), fish surviving to age-1 were allocated to a growth trajectory assuming a normal distribution. Although carp did not reproduce, stocked fry or fingerlings were still assumed to experience size- and density-dependent mortality.

Natural mortality rates of age-1 and older fish were also assumed to be size- and density-dependent using an empirical relationship presented by Lorenzen (1996, 2000) (Table 1, eqn. 6b). To introduce density-dependence in survival, we assumed that the allometric exponent of size-dependent mortality relationship changed with density (Table 1, eqn. 6d), but that the mortality rate of very large fish changed very little with density (see Appendix S1 for derivation). Thus, changes in density had a greater impact on the natural mortality rate of small fish compared to larger fish, agreeing with empirical studies and population dynamical theory of stock enhancements (Lorenzen 2005). Incorporating size- and density-dependence into post-recruitment survival allowed for increased mortality of small fish from predation by, and competition with, larger fish, including fish stocked at larger sizes and older ages than age-0. Model predictions in the absence of density-dependent survival of age-1 and older fish was explored in the supplementary material (Appendix S1: Figures S6, S7, and S8). In scenarios in which older fish (> age-0) were stocked, fish were added to the abundance of surviving hatchery origin fish in the appropriate age category and allocated normally among the growth trajectories.
The possibility of differential survival of fish of hatchery origin relative to wild fish beyond the first year of life was also explicitly included in the model (Table 1, eqn. 6a, Appendix S1: Table S1).

To account for the size-dependent processes inherent to fishing mortality, a sigmoidal vulnerability curve was used to determine vulnerability of fish to capture (Table 1, eqns. 6f-g, Appendix S1: Figure S1), as is typical in recreational fisheries models (Post et al. 2003, Arlinghaus et al. 2009, Allen et al. 2013). MLLs were used to determine which fish were legally harvestable (Table 1, eqn. 6i). No bag limit was assumed; thus, all fish of legal size were harvested. To account for illegal harvest (Sullivan 2002, Johnston et al. 2015), a percentage of undersized fish were also harvested (Table 1, eqn. 6i). Undersized fish that were released experienced hooking mortality (Table 1, eqn. 6j) – an important process in recreational fisheries (Post et al. 2003, Coggins et al. 2007, Johnston et al. 2015).

Social sub-model

In the social sub-model, annual angling effort was determined by the fishery quality of past fishing experiences (Table 1, eqn. 7d), and constrained by available fishing time in line with empirical data (Table 1, eqn. 7d, $d_{\text{max}}$, Appendix S1: Table S1). Note that our use of the term fishing quality encompasses all dimensions that affect the angler utility, including: expected catch rate, average size of fish caught, catch rate of trophy fish (as per Arlinghaus et al. 2014, fish larger than a threshold size, $L_T$, Appendix S1: Table S1), the number of other anglers seen while fishing (a measure of crowding), MLL (which measure preferences for retention of fish for own consumption), license fees to fish within the water, preference for target species, stocking frequency (an independent effect of knowing that a fishery is stocked), and the composition of
the catch (percent wild fish in the catch). Following random utility theory, the benefits anglers
derived from each fishery attribute, called part-worth utilities (Appendix S1: Figure S3), were
summed to determine the overall utility gained from fishing (Table 1, eqn. 7a) (Hunt et al. 2011,
Fenichel et al. 2013a). Using the utility model, anglers responded dynamically to changes in the
perceived quality of the fishery over time. The probability of fishing was determined primarily
by the utility experienced in the previous year (Table 1, eqn. 7a-b), but a fishing-behavior
persistence term (Table 1, eqn. 7c, $\varphi$, Appendix S1: Table S1) accounted for the fact that
previous experiences and fishing habits also influence anglers’ fishing decisions (Adamowicz
1994) by including previous experiences at a discounted rate.

The theoretical utility-based sub-model of angler behavior was informed empirically by results
from a stated discrete-choice experiment conducted on German anglers in Lower Saxony
(Arlinghaus et al. 2014). This choice experiment exposed anglers to stocking-related attributes as
well as a large range of catch rates, thereby allowing the (dis)utility of very low catches near zero
to be explicitly estimated. For application in the present study, the parameter values for angler
preferences ($u_i - u_{i0}$, Appendix S1: Table S1) differ somewhat from those reported by
Arlinghaus et al. (2014). The choice model data were reanalyzed assuming that the part-worth
utility function of MLL (Table 1, eqn 9f) was quadratic rather than linear, because the quadratic
form best described the data for pike and carp (Arlinghaus et al. unpublished data). Arlinghaus et
al. (2014) found that the two stocking attributes did not have a significant influence on angler
utility. Thus, we assumed that anglers did not know that pike were stocked and were unable to
identify hatchery versus wild origin pike, which is likely. By contrast, for carp we assumed that
anglers were aware that carp were stocked and of hatchery origin, because these are culture-
based fisheries. The parameters from the choice model were species-specific, but for simplicity
represented the average angler as estimated by Arlinghaus et al. (2014). Hence, angler behavior
differed based on the species targeted, but all anglers were assumed to behave the same when
fishing for the same species. An exploration of angler heterogeneity is reserved for future work.

While the choice model allowed for variation in license cost $\epsilon_\text{l}$, daily bag limit $DBL$,
preference for target species, and stocking frequency, these aspects were not investigated in this
study. Thus, levels of these attributes were held constant (Appendix S1: Table S1). Our model
was designed to represent a single-lake fishery, such as those run by angling clubs in central
Europe. Managers of such fisheries have control over input and output regulations, as well as
over what size and density of fish stocked, without involvement of public agencies as is typical
for central Europe (Daedlow et al. 2011).

Range of MLLs, stocking strategies, and performance measures examined

In the model scenarios, MLLs ranged from zero to mandatory total catch-and-release (i.e., the
maximum size fish could achieve, $0 - L_{\text{max}}$, Appendix S1: Table S1). The size of fish stocked and
the range of stocking densities explored reflected information from a survey of over 2000
angling clubs (61% response rate) throughout Germany (Arlinghaus et al. 2015). Accordingly, in
the pike scenarios, fry, fingerlings and adults were assumed to be about 2 cm, 20 cm, and age-2
(35-40 cm), respectively, and in the carp scenarios about 4 cm, 15 cm, and age-2 (40 cm),
respectively ($L_x$, Appendix S1: Table S1). These sizes were commonly reported in the datasets.

For pike, the range of stocking densities of all three stocking sizes initially modelled were chosen
to reflect the range in annual stocking expenditures reported by angling clubs across Germany,
i.e., a mean of 50 € ha$^{-1}$ yr$^{-1}$ for pike (range 3–154 € ha$^{-1}$ yr$^{-1}$, 5th and 95th percentile
respectively). Thus, the range of stocking densities for each of the three size classes we tested (
$J_b$, for fry and fingerlings, $N_s$, for adults, Appendix S1: Table S1) resulted in the associated range in stocking costs being identical across size classes (Table 2), thereby allowing a direct comparison of the effect of varying stocking sizes for the same monetary investment. For carp, the expenditure range reported by German angling clubs was much greater (mean 210 € ha$^{-1}$ yr$^{-1}$, range 7–710 € ha$^{-1}$ yr$^{-1}$, 5th and 95th percentile respectively). For comparative purposes we investigated stocking expenditures in a similar range to pike (0, 5, and 100 € ha$^{-1}$ yr$^{-1}$) instead for carp (Table 2), translated into numerical stocking abundance. Average angler density in Germany and in the five study clubs involved in our stocking project, measured as the number of anglers licensed to fish a given area of water, was approximately 5 licensed anglers ha$^{-1}$, ranging from about 1 to 10 licensed anglers (ha$^{-1}$). Thus, as a surrogate for latent fishing pressure, we used these three angler densities in our model simulations but allowed realized fishing pressure to vary in response to changes in fishing quality following the utility model.

We considered six main performance measures for each of the policies we examined. Two measures related to biological objectives: 1) augmentation (i.e., increased density) of the overall population, and 2) the density of fish fully vulnerable to the fishery, assumed to be those surviving until their third birthday (age-2 and older fish at the end of the year) (Figure S1). In addition, the age structure and composition (wild vs. hatchery origin fish) of the fish population was examined for some simulations as a further conservation objective. Two measures addressed social objectives: 3) the average catch rate, which is often used as a surrogate of angler well-being (Cox et al. 2003), and contrasted it with 4) a more integrated measure of average angler welfare (benefit), net willingness-to-pay (WTP) (Table 1, eqn 8a). Net WTP is a measure which quantifies the change in satisfaction (inclusive value) relative to the status quo expressed in monetary terms (Edwards 1991, Cole and Ward 1994, Loomis and Fix 1999). As status quo, we
used the unstocked and unregulated (no MLL) scenario. To address economic considerations, we calculated 5) the per capita costs associated with stocked fish surviving until they were fully vulnerable to the fishery (i.e., their third birthday, Table 1, eqn 8e), as well as 6) an integrative measure of the net economic benefit (aggregated angler welfare minus costs, Table 1, eqn 8e). Net economic benefit was measured as aggregated social welfare, the sum of individual angler welfare (WTP) across all licensed anglers, minus the financial cost of stocking. Stocking costs were determined based on empirical fish size-cost relationships estimated from Germany (Appendix S1: Figure S2). We used these metrics to evaluate and implicitly rank policy outcomes. Additionally, we examined the size structure and composition (wild vs. hatchery origin) of the fish population in some scenarios to evaluate size/age truncation effects from fishing and replacement of wild fish by hatchery origin fish as a further commonly applied conservation objective (Rogers et al. 2010, Camp et al. 2017).

Outline of analyses

In scenario 1 (Table 2), we evaluated how well annually stocking of various sizes of fish – fry, fingerlings and adults – at a range of realistic densities preformed relative to the use of a range of MLLs in relation to the six performance measures outlined above. This was done for pike, and latent fishing pressure was assumed to be moderate at 5 licensed anglers ha\(^{-1}\).

Variations on the base scenario 1 (Table 2) were then used to investigate the sensitivity of outcomes to some of the model assumptions. In scenario 2 (Table 2), we compared naturally-reproducing pike and non-reproducing carp, when stocking expenditures were the same for both species. We evaluated results at low (1 licenses ha\(^{-1}\)) and high (10 licenses ha\(^{-1}\)) latent fishing
pressure, and when the range in stocking densities reflected low (5 € ha$^{-1}$) to moderate (100 € ha$^{-1}$) stocking costs for both species.

In scenarios 3 and 4, for pike only, we examined how sensitive the model predictions were to modifications of some of the key model assumptions. In these scenarios (Table 2), we examined results for low and moderate stocking densities (5 € ha$^{-1}$ to 100 € ha$^{-1}$, respectively) and moderate latent fishing pressure (5 licenses ha$^{-1}$). Four biological assumptions were examined in two sets of scenarios. 1) In scenarios 3A and 3B (Table 2), we tested the hypothesis that stock enhancement may be more beneficial in habitats where natural reproduction is impaired (Rogers et al. 2010). We examined two cases; one where the productivity parameter ($\alpha$, Appendix S1: Table S1) in the stock-recruitment relationship related to the slope near the origin was reduced by half (Table 2, scenario 3A), and a second where the strength of density-dependence ($\beta$, Appendix S1: Table S1) in the stock-recruitment relationship was doubled (Table 2, scenario 3B), resulting in greater inter-specific competition effectively reducing habitat capacity. In both cases, maximum recruitment was reduced. 2) We examined two scenarios, one in which stocked fish had reduced fitness (Table 2, scenario 4A), and a second in which stocked fish had reduced fitness but whose offspring evolved to wild-type fish in the F1 generation (Table 2, scenario 4B). In both scenarios 4A and 4B (Table 2), hatchery origin fish had reduced reproductive success, and reduced survival in both the juvenile and adult stages (relative survival of stocked age-0 fish was 50%, of stocked adults was 90%, and relative reproductive success was 56% compared to wild fish) following empirical data (Hühn et al. 2014). In scenario 4B (Table 2), we relaxed the base assumption that larvae produced by spawners of hatchery origin retained a hatchery origin phenotype (Table 1 eqn. 4f, $h^2 = 0$), and tested the opposite extreme where all larvae produced by hatchery origin spawners transitioned to wild type due to natural selection (Table 1 eqn. 4f,
h² = 1) (Lorenzen 2005). These scenarios were not examined for carp because it is unrealistic to assume wild recruitment of this species in central and northern Europe.

RESULTS

Outcomes of stocking vs. harvest regulations (MLLs) for pike

From a biological and conservation perspective, in the base scenario (Table 2, scenario 1) where hatchery and wild pike were assumed to have equal fitness, increasing MLLs generally increased total pike density and the density of vulnerable pike, although this pattern was less evident for total pike density when fingerlings were stocked (Figure 2). Density increased rapidly around an MLL of 40 cm as MLLs began to protect the age-2 cohort from harvest (Appendix S1: Figure S4). Total pike densities increased with increased stocking density for all sizes stocked, particularly when MLLs were low (< 40 cm) and the pike population was overfished at a latent license density of 5 angling licenses ha⁻¹ in the absence of stocking. Total densities were highest when fingerlings were stocked and lowest when fry were stocked, and stocking pike fry had minimal effects on total pike density at all MLLs > 40 cm (Figure 2, left column). By contrast, adult stocking resulted in the greatest increases in vulnerable pike density (i.e., catchable size), whereas stocking fry and fingerlings had very little effect on this metric (Figure 2, second column). Any benefits of stocking to pike density, however, came at the cost of severe wild stock replacement by hatchery origin fish (Figure 3). Even at low annual stocking densities, stocked fingerlings and adults at equilibrium replaced most of the wild fish. Replacement of wild stocks was less severe when fry were stocked at low densities and MLLs were high, but was a concern at high fry stocking densities, despite the lack of additive effects on the overall pike stock. Replacement was less severe at high MLLs, particularly for fry, suggesting that they improve the
buffering capacity of wild populations against invasion by hatchery phenotypes by reducing
fishing mortality of adults.

From a social perspective of the fishing quality, stocking pike had positive impacts on average
catch rates, but the catch-rate effects were much more pronounced and dependent on stocking
density when adult pike were stocked relative to fry and fingerlings (Figure 2, third column). MLLs did not influence catch rates as much when fry and fingerlings were stocked as they did
when adults were stocked. Yet, despite the potential for large increases in pike catch rates due to
stocking (particularly the stocking of immediately catchable adults), the average benefit to an
angler (measured by average net WTP) was largely uninfluenced by stocking pike of any size or
density (Figure 2, fourth column), although net WTP was generally slightly higher when adults
were stocked. MLLs had a stronger effect on net WTP than stocking, with the benefits initially
increasing and then decreasing with increasing MLLs. These findings revealed that intermediate
MLLs maximized angler well-being.

From an economic perspective, high stocking densities generally increased the per capita costs
associated with stocked pike surviving to be fully vulnerable to the fishery (Figure 2, fifth
column). By this metric, adult stocking was the most cost effective, followed by fingerlings. Fry
were the least cost effective. Survivor costs were generally highest when MLLs were low (< 40
cm) but decreased rapidly when MLLs reached 40 cm and protected fish from harvest, and then
slowly increased as MLLs increased further as density-dependent processes became more
important. Importantly, however, the net economic benefits of stocking were negative for most
stocking strategies evaluated (10–154 € ha\(^{-1}\) yr\(^{-1}\)) when fishing pressure was moderate (5 licenses
ha\(^{-1}\)) (Figure 2, right column). Only very low stocking densities (<10 € ha\(^{-1}\) yr\(^{-1}\)), resulted in a
positive net benefit. When stocking was absent, use of MLLs up to about 110 cm produced a
positive net economic benefit (peaking at 8.8 € ha\(^{-1}\) yr\(^{-1}\) at an MLL of ~60 cm) at intermediate fishing pressures.

Stocking outcomes in reproducing (pike) versus non-reproducing (carp) populations

A direct comparison of the outcomes for reproducing pike and non-reproducing carp with the same stocking expenditures (0, 5 or 100 € ha\(^{-1}\)) under low and high latent fishing pressure (1 angler ha\(^{-1}\) or 10 anglers ha\(^{-1}\), Table 2 scenarios 2A and 2B) revealed several similarities to results above, but also important differences in the relative effects of stocking compared to MLLs. Similar to pike, stocking carp enhanced total carp density and the density of vulnerable carp (Figure 4), with higher stocking densities having larger effects. Like pike, stocking carp fingerlings produced the highest total densities of carp. Stocking adults generally produced higher densities of vulnerable carp and higher catch rates than stocking of either fry or fingerlings (Figure 4), except under high latent fishing pressure (10 anglers ha\(^{-1}\)) and low MLLs (< 50 cm). Unlike pike, where stocking pike at low densities into a self-sustaining population (i.e., under low latent fishing pressure, 1 angler ha\(^{-1}\), or when MLLs > 50 cm protected adults from harvest) had little impact on the fish density, the density of vulnerable fish, and catch rates, stocking carp of any size was always beneficial and much less influenced by MLLs compared to the pike scenarios (Figure 4). Even stocking fry improved carp density, vulnerable carp density, and catch rates, whereas stocking pike fry only had an effect when the pike population was heavily exploited (i.e., high latent fishing pressure of 10 anglers ha\(^{-1}\), and low MLLs < 40 cm), and only enhanced total pike density having little impact on vulnerable pike density or catch rates (Figure 4).
Similar to pike, MLLs were more important for determining net WTP in carp than variation in stocking size or number (Figure 4). However, stocking carp increased net WTP more than stocking pike did, and unlike pike where stocking only performed better than MLLs at high fishing pressure and low MLLs, stocking carp always resulted in a highly positive net WTP that was much greater than the use of MLLs alone (Figure 4). Carp net WTP was also much less influenced by latent fishing pressure than the pike’s net WTP.

The per capita costs of fish surviving to a vulnerable age were much lower for carp than pike, but as in the case of pike the costs tended to be lowest when MLLs were around 40 cm and increased with stocking density (Figure 4). Also, similar to pike, carp fry were least cost-effective to stock. However, unlike pike, the most cost-effective stocking size for carp was context-dependent. Low densities of carp fingerlings were generally most cost-effective, but as stocking densities increased, adult carp became more cost-effective than fingerlings in most cases (Figure 4).

Finally, like pike, the net economic benefit of stocking carp was not strongly influenced by the size of fish stocked, with adults and fingerlings performing slightly better than fry (Figure 4). However, unlike pike, stocking carp was much more likely to result in a positive net benefit, occurring at lower latent fishing pressures, under a broader range of stocking densities, and being of higher magnitude (Figure 5). It should be noted, at higher latent effort, even pike stocking resulted in a positive net benefit. Moreover, the net economic benefit from stocking carp was more likely to exceed the net benefit from the use of MLLs alone; something which only occurred for pike at low MLLs when latent fishing pressure was high. Thus, overall stocking of carp outperformed stocking of pike economically and socially.

*The ecological constraints on stocking wild fish populations*
The model outcomes were generally robust to some key assumptions made about ecological constraints on the production of wild pike. Changes in population productivity and habitat capacity (Table 2, scenarios 3A and 3B), as expected, reduced total pike density and vulnerable pike density in both the unstocked and stocked scenarios (Figure 5). Despite these differences, the patterns in terms of the performance of stocking were generally qualitatively similar to the unaltered scenario, i.e., reduced habitat quality did not improve the prospects of stocking generating additive effects on the pike stock and fishing quality. One exception involved stocking pike fingerlings at high density when habitat capacity was poor. In this case, total pike density declined with increasing MLLs rather than staying relatively static in the unaltered case (Figure 5). Reduced habitat capacity and productivity also reduced catch rates, but the effects on catch rates were less severe (Figure 5). That said, reductions in baseline catch rates in the unstocked and unregulated scenario due to reduced productivity were orders of magnitude smaller than the baseline and diminished habitat capacity scenarios (e.g., at 5 licenses ha\(^{-1}\), and no MLL or stocking; 1.9 \(10^6\) pike d\(^{-1}\), for baseline and poor habitat capacity, 2.8 \(10^{13}\) pike d\(^{-1}\), for low productivity scenario). As a result, changes in habitat capacity had no discernable effect on net WTP, but reduced productivity resulted in much higher net WTP under all stocked and unstocked scenarios (Figure 5). Reductions in habitat capacity and productivity increased the per capita costs of stocked fry and fingerlings surviving to a vulnerable age, particularly when they were stocked at high stocking densities (Figure 5). Similar to net WTP, changes in habitat capacity had little impact on the net economic benefits of pike stocking, while reduced productivity increased net benefit in all scenarios. However, this effect was not enough to exceed the benefit of using moderate to high MLLs alone in the management of pike in a habitat-constrained fishery (Figure 5).
Stocked pike, like many other fishes, are known to suffer from lower fitness relative to wild fishes, so we also examined this key assumption for systematic effects (Table 2, scenarios 4A and 4B). The realistic assumption that stocked fish had generally lower fitness (i.e., lower reproductive success, and lower survival) than similarly-sized wild conspecifics caused reductions in total pike density, vulnerable density, and catch rates relative to the scenario of equal fitness. Reductions were most pronounced when fingerlings were stocked and least pronounced when adults were stocked (Figure 5). Lowered fitness of stocked fish increased the per capita costs of stocked fry and, to a lesser extent, the number stocked fingerlings surviving to vulnerable sizes, but had little influence on net WTP or net economic benefit of pike stocking. Simulating strong natural selection by introducing a heritability of one (i.e., 100% transition of hatchery spawned fish to wild origin, Table 2, scenario 4B) reversed some of the effects on total fish density that low fitness introduced but had little influence on other output measures (Figure 5). Thus, the results presented were robust to these model sensitivities.

**DISCUSSION**

Our model integrated a size-structured fish population model (which included multiple size- and density-dependent feedbacks) with a mechanistic sub-model of adaptive angler behavior. Through key size- and density-dependent ecological processes we explicitly accounted for the compensatory response of the fish population and how they respond to the change in density induced by stocking or harvesting. The coupled social-ecological model thus allowed the systematic study of how ecological processes drive the biological, social and economic outcome of commonly applied management interventions in recreational-fisheries management. We show that the expected benefits of stocking versus managing the fishery solely with harvest regulations vary greatly depending on the ecological condition of the population being supplemented along a
gradient of reproducing and self-sustaining to non-reproducing. The evaluation of outcomes also varies strongly with the metric that is used to judge performance, identifying some key trade-offs, e.g., among conservation and fisheries benefits in the case of stock enhancements in naturally self-sustaining populations. Both hypotheses initially stated were supported. First, stocking promises to have additive ecological and large social effects when natural reproduction of the target species is lacking or when fish large enough to have escaped strong juvenile mortality compensation are stocked in self-sustaining populations. However, in the latter case this comes at the costs of replacement of wild fish by hatchery fish over time, creating a fundamental trade-off among successful stock enhancement and wild fish conservation (*sensu* Rogers et al. 2010, Amoroso et al. 2017, Camp et al. 2017). Second, harvest regulations socially and economically outperform stocking measures when managing naturally reproducing populations.

*Conservation and catch outcomes*

Our results underscore the importance of ecological processes for determining the outcomes of common recreational-fisheries management actions. Like other studies (e.g., Lorenzen 2005, Camp et al. 2014), we found density-dependent growth and size- and density-dependent mortality responses of fish populations constrained the contribution of stocking to the exploited population and limited the catch rates that anglers could enjoy. For example, stocking fry into a self-sustaining population (e.g., pike at low latent effort or high MLLs where the stock was not overfished) produced no additive effects to the vulnerable population and to catch rates relative to the use of MLLs alone. These model predictions agree well with empirical findings for stock-enhanced pike and other species (e.g., Li et al. 1996, Skov et al. 2011, Hühn et al. 2014), and findings of previous stocking models (e.g., Lorenzen 2005, Camp et al. 2014). Stocked
fingerlings that escaped more of the early mortality bottleneck, on the other hand, were predicted to augment the overall population beyond levels achieved by MLLs alone, particularly when hatchery fish had a high relative fitness. However, in naturally reproducing populations high size-dependent natural mortality rates of stocked fingerlings resulted in only minimal increases in the densities of fish vulnerable to capture, while the largest additive effects on vulnerable density and thus catch rates were predicted from the stocking of large, recruited fishes in such situations. These findings are consistent with empirical results for a range of species (e.g., Li et al. 1996, Baer and Brinker 2008) and theoretical studies (e.g., Rogers et al. 2010, Garlock et al. 2017). Our findings are also consistent with a recent pike stocking experiment that found that stocking age-0 fingerlings enhanced stocks one year later (age-1), but the additive effect was no longer present in the age-2 cohort when the fish became vulnerable to the fishery and size-dependent mortality had regulated the cohort’s abundance back to carrying capacity (Arlinghaus et al. 2015, Guillerault et al. 2018). The reason for the superior performance of large-sized stocked fishes in naturally recruiting situations is that stocked adults experience much less natural mortality than fingerlings because of the allometry of the size-mortality relationship (Lorenzen 2000). At the same time, they may be large enough to be immediate vulnerable to capture by fishing gear (Lorenzen et al. 2012). The benefits from stocking large fish in both naturally reproducing and non-reproducing situations that we found in our model are generally consistent with other models (Askey et al. 2013, Camp et al. 2014, Garlock et al. 2017) and empirical studies (e.g., Wiley et al. 1993, Yule et al. 2000, Meyer et al. 2012). Our model supports the trend seen in some countries to stock increasingly larger fish including catchable fish in stock-enhancement efforts (Halverson 2008), which is likely a response to fry and small fingerlings rarely producing sustained outcomes for ecological reasons. However, the more
successful stock enhancement efforts in naturally reproducing stocks become, the more likely these efforts are to replace the wild stock component (Rogers et al. 2010, van Poorten et al. 2011), and potentially increase angling impacts by attracting increased fishing pressure (Baer et al. 2007), thereby creating a fundamental, trade-off among fisheries benefits and conservation (Camp et al. 2017, Amoroso et al. 2017).

Despite abundant ecological risks (e.g., Laikre et al. 2010, van Poorten et al. 2011), our findings and related work (Cowx 1994, Lorenzen et al. 2012, Sass et al. 2017) suggest stocking can, when properly conducted, play an important role in rehabilitating fisheries that are no longer self-sustaining or creating or maintaining fishing opportunities when local fishing pressures are high. Specifically, we found that stocking fish populations that were not self-sustaining (e.g., carp or heavily overexploited pike at low MLLs) was successful in establishing and enhancing the fisheries for the benefit of anglers and conservation. In these culture-based situations, stocking fish of small size also elevated catch rates, because otherwise the population would not persist. Interestingly, unlike the case in pike, we found that carp fingerlings contributed more to the vulnerable population than adults in two situations, 1) when stocking densities were low, and 2) when stocking densities were high, fishing pressure was high, and MLLs were low (overfished stocks). Ecological processes were important for determining stocking outcomes in these cases. In the first case, similar to what Lorenzen (1995) and Hunt et al. (2014) found, density-dependent processes resulted in a trade-off between the number of fish stocked and fish size, which had impacts on natural mortality rates. At low stocking densities, fingerling growth rates were fast and size- and density-dependent mortalities were reduced, resulting in more fingerlings surviving to the vulnerable stage. The reverse was the case at higher stocking densities, except when the catchable-sized adults experienced high fishing mortality rates under high fishing
pressure and liberal harvest limits, resulting in low residence times of stocked adults. Thus, the possible enhancement effects of different fish sizes are tightly coupled to the degree of natural recruitment, stocking rate, local harvesting pressure and the harvest regulations in place. Models such as ours (available at http://www.ifishman.de/en/practioner/software/) and others (Varkey et al. 2016, Garlock et al. 2017), can help to define species-specific expectations and inform management policies as to which life stage is likely to perform best, but adaptive stocking experiments are then needed to identify the most suitable stocking strategy for a given target species and system (Arlinghaus et al. 2017).

Ecological processes are also responsible for the prediction that the conservation benefits from stocking recruitment-limited populations may actually be slim. Recruitment limitations due to habitat bottlenecks are among the most often cited arguments (Cowx 1994) for so called compensatory stock-enhancement efforts in impaired populations (Lorenzen et al. 2012). However, we found that reductions in maximum habitat capacity for recruits and generally a reduced productivity did not render stocking relatively more beneficial to the population or the fishery, particularly when small sizes were used in stocking. Our results agree with a recent empirical study by Guillerault et al. (2018) who reported that the additive effects of pike stocking were largely independent of the quality of the habitat for the target species in lakes. Our findings contrast those of other studies (e.g., Rogers et al. 2010, Ziegler et al. 2017) who reported that stocking is increasingly beneficial when natural reproduction is impaired from habitat loss. However, even then the size-at-stocking is bound to determine stocking outcomes, and only sizes beyond recruitment bottlenecks are likely to perform well (Lorenzen 2005). Varying assumptions in related models and ours can explain the divergent study findings. For example, Rogers et al. (2010) assumed that habitat degradation only affected the wild-spawned fish and did not affect
the hatchery-released fish. By contrast, we assumed that all fish, including the offspring from
surviving stocked fish, were constrained by the conditions of the waterbody. Hence in our study,
even stocking adults, which elevate catch rates and increase spawning stock in the short-term,
will not produce long-term biological benefits by improving recruitment, but it will benefit
anglers by creating a put-and-take or a put-grow-and-take fishery. Similarly, Ziegler et al. (2017)
found that stocking larger individuals allowed fish to escape the high predation mortality when
predation refugia utilized by young-of-year walleye (*Sander vitreus*) was removed from lakes,
and Li et al. (1996) reported that fingerling stocking enhanced a walleye abundance index more
than fry stocking, but only in lakes where natural recruitment was essentially absent. Under
conditions of low habitat quality where natural recruitment is constrained, stocking is a bandage
solution used to increase abundance and improve catch rates, rather than addressing the
underlying problem (Sass et al. 2017). In such situations, habitat restoration promises to be the
only tool able to sustainably elevate the productivity and carrying capacity of a given ecosystem
for fish (Sass et al. 2017). Although our model did not explicitly allow habitat management to be
explored, changes to the parameters of the stock-recruitment relationship can be used to inform
how well this practice preforms compared to stocking or MLLs.

The realistic assumption of reduced fitness of stocked fish relative to wild conspecifics
(Lorenzen et al. 2012, Hühn et al. 2014, Arlinghaus et al. 2015) can further minimize the benefits
of stocking. For example, in a replicated pond study, Hühn et al. (2014) found that cultured
juvenile pike fry performed half as well in terms of growth and juvenile mortality when forced
into competition with wild recruits, but did as well as wild recruits when stocked in ponds with
no wild pike. Despite their lower fitness, however, some stocked fry established in the stock
enhancement treatments leading to the replacement of wild recruits rather than increasing the
year class abundance (Hühn et al. 2014). The circumvention of sexual selection during artificial breeding can also reduce reproductive fitness (Thériault et al. 2011). Given the lower fitness of hatchery fish, even those held for only brief periods in the hatchery (Araki et al. 2007, Thériault et al. 2011, Christie et al. 2014), establishment of hatchery fish in natural stocks can ultimately also lead to a reduced productivity of the fishery (Chilcote et al. 2011). We found that reducing the fitness of hatchery-origin fish reduced the benefits associated with stocking fry or fingerlings, in agreement with Lorenzen (2005) and Rogers et al. (2010), although if, as has been suggested (Lorenzen 2005), natural selection causes hatchery fish to evolve wild-type phenotypes this could partially compensate for the lower stocking success resulting from differential survival. Despite lower fitness, we found that releasing low fitness juvenile or adult pike in larger numbers could still produce fisheries benefits, simply due to numerical effects. The caveats include the possible replacement of the wild stock components by hatchery fish and a possible reduction in long-term sustainability.

Alternatively, hatchery fish could survive well to recapture but show low reproductive success relative to wild spawners (Lorenzen et al. 2012). If the phenotypes to be released survive well, but do reproduce effectively, stock enhancements could be of less conservation concern, while still delivering fisheries benefits. We did not examine this scenario in our model, nor did we evaluate other factors such as differential growth or catchability of hatchery and wild fish (Mezzera and Largiadèr 2001, Biro and Post 2008, Klefoth et al. 2012), and these processes will positively affect the fisheries performance of stocking programs by offering greater returns of hatchery fish that have higher catchability (Lorenzen et al. 2012). Moreover, the high catchability could reduce the residence times (time between stocking and recapture) of hatchery fish minimizing the risk of introgression (Mezzera and Largiadèr 2001, Baer et al. 2007).
Stocking triploids is an alternative to effectively avoid interbreeding of hatchery fish and wild fishes, thereby minimizing the impacts of wild stocks in the long term while providing fishing opportunities (Koenig et al. 2011, Lorenzen et al. 2012).

Social outcomes

From a social perspective, we found that stocking naturally reproducing pike populations had little effect on angler well-being as long as a threshold catch rate was achieved in the fishery. Socially, we found intermediate MLLs generally outperformed stock enhancements in naturally reproducing situations, but, in line with Rogers et al. (2010), stocking can benefit naturally reproducing fisheries that experience high fishing mortality. In the latter case, recruitment overfishing limited egg production, because not enough adults were surviving to reproduce. Thus, while stocking can be effective for managing heavily exploited populations, a more sustainable approach would be using restrictive harvest regulations, which can then be combined with put-growth-and take type of enhancements to satisfy angler demands (Arlinghaus et al. 2016).

Similar to other studies (e.g., Johnston et al. 2010, Camp et al. 2016), our results challenge a common assumption that angler utility (or satisfaction), is determined primarily or exclusively by angler catch rates (e.g., Carpenter et al. 1994, Post et al. 2003, Rogers et al. 2010). We found the success of stocking, as measured by net WTP, was not tightly correlated with catch rates, even when stocking created large differences in catch rates. Although catch rate was a highly significant attribute in the choice experiment used to inform angler behavior in our study (Arlinghaus et al. 2014), the lognormal form of the part-worth utility function for catch rate (Appendix S1: Figure S3) meant that the marginal gains in utility that came with increased catch
rates rapidly diminished as catch rates exceeded a certain minimally acceptable threshold.

Empirical studies have found similar relationships between catch and satisfaction (e.g., Patterson and Sullivan 2013, Beardmore et al. 2015, Hyman et al. 2016). In other words, anglers were very dissatisfied when catch rates were extremely low, but once catch rates were “good enough” (roughly 1 fish daily, Arlinghaus et al. 2014) they had little further impact on angler satisfaction. As a consequence, it has been found empirically that intermediate stocking rates attract the greatest fishing effort, because low stocking rates produce catch rates low enough to affect anglers’ behavior and high stocking rates reduce fish growth and affect anglers’ satisfaction with the size of fish caught, thereby attracting less fishing effort (Mee et al. 2016). We argue that a diminishing marginal return in utility from increasing catch rates is consistent with economic (Beardmore et al. 2015) and motivational theory (Finn and Loomis 2001), and is likely found in most recreational fisheries. That said, some anglers have been implied to have linear or accelerating preferences for catch rates (e.g., Varkey et al. 2016), such as those targeting high-catch-rate small-bodied cyprinid species in Germany (Beardmore et al. 2015). If such relationships exist, our model predictions may not hold.

The non-linear relationship between catch and utility explains, in part, why MLLs were much more important than the stocking strategy for determining angler well-being (and thus satisfaction) in naturally reproducing fish in our study. When MLLs were sufficiently high (>40 cm) to offer some protection to catchable fish, then catch rates were “good enough” using MLLs alone and any improvements to catch rates from stocking had minimal impacts on angler satisfaction and behavior. A second reason why MLLs impacted angler satisfaction was because harvest regulations also affect anglers directly through the perceived restrictions they might have on harvest. Other studies have confirmed that regulations can affect angler use (e.g., Beard et al.
2003, Johnston et al. 2011, Haglund et al. 2016). The quadratic (i.e., hump shape) form of the part-worth-utility relationship for MLLs (Appendix S1: Figure S3) implies that there is a balance between desires to conserve the fish resource and perceived ability to harvest (Johnston et al. 2010), thus, generally intermediate MLLs were preferred by the majority of anglers in our model.

While utilizing MLLs may represent a more sustainable approach to managing naturally reproducing populations, culture-based fisheries maintained by stocking can generate substantial social benefits that would not occur in the absence of stocking (Arlinghaus et al. 2016). We found that if fish reproduction was nonexistent (carp) or impaired (overexploited pike), then stocking positively influenced angler satisfaction, because without stocking catch rates were low enough to be a matter of concern. However, in such situations the differences among stocking strategies were not pronounced, because all stocking strategies resulted in catch rates that were “good enough”. Anglers often prefer stocking over other management measures, because it is relatively easy to implement, less restrictive, and generally perceived to help fish stocks and maintains catch rates (Arlinghaus and Mehner 2003a, Dorow et al. 2009, Garlock and Lorenzen 2017). Thus, stocking in culture-based fisheries can potentially be used to provide fishing opportunities that draw fishing pressure away from wild stocks or increase participation (Fayram et al. 2006, Baer et al. 2007, Mee et al. 2016). That said, there is a need to inform and maybe even “educate” anglers about which forms of stocking are beneficial and which are unlikely to generate additive effects (Fujitani et al. 2017). Otherwise, decision-makers will continue to experience strong pro-stocking social norms of anglers and be constantly challenged to re-invest license money back into the waters (Riepe et al. 2017), despite knowing that many of these stocking efforts will likely not benefit the fishery and challenge conservation objectives.
Economic outcomes

The effects of stocking on fish abundance, catch rates, and angler welfare ultimately affected the economic feasibility of stocking strategies relative to the management of fisheries based on the “cost-free” MLL. Stocking few fish was generally more cost effective than stocking high densities due to size- and density-dependent regulatory processes, and these processes were also important for determining which size of fish was most cost effective. Similar to other studies (Santucci Jr and Wahl 1993, Leber et al. 2005, Garlock et al. 2017), we found that fingerlings were more cost effective than fry, because fingerlings experienced less mortality from the early life-stage bottleneck than fry did. Likewise, in agreement with Wiley et al. (1993) we found that stocking catchable adults was generally more cost-effective than stocking sub-catchable fingerlings, because of the strong natural mortality (from size and density dependence) that fingerlings experienced prior to becoming vulnerable to the fishery. The faster fish reach vulnerable sizes, the more effective stocking will be, making fish growth rates an important predictor of stocking outcomes (Garlock et al. 2017). In addition, minimizing mortality of fish, particularly fry and fingerlings, using MLLs before they become fully vulnerable to the fishery, improved the cost-effectiveness of stocking, while more restrictive regulations reduced cost-effectiveness because fish were “lost” due to density-dependent mortality. The benefits of stocking larger fish, however, requires that there are sufficient survival benefits to offset the costs of producing larger fish. For example, in carp, low stocking densities minimized size-dependent mortality of fingerlings making them more cost effective than adults. Moreover, high mortality rates from fishing (high latent effort) for adults, which were fully vulnerable to harvest at the time of stocking, outweighed any benefits of size for determining natural mortality rates, until MLLs offered some protection. Our findings are similar to Diana and Wahl (2009) who
reported that stocking medium-sized largemouth bass (*Micropterus salmoides*) fingerlings was most cost-effective, because stocking larger fish did not provide additional survival benefits. Despite adults being generally more cost-effective, they require more space and long production periods making them expensive to produce even at low stocking densities. Monetary stocking costs may not be of great concern if only a few lakes close to urban areas are stocked to satisfy anglers (Cole and Ward 1994, Post and Parkinson 2012), or for angling clubs in Germany or elsewhere in central Europe that have few stocks to manage, high license income and little alternative uses for the income than stocking. But costs may be a problem for North American agencies charged with managing hundreds if not thousands of stocks among which they must allocate a limited budget (Cowley et al. 2003). In this context, our research suggests that low stocking rates of adults may be cost-effective in many situations, not only in put-and-take urban lakes. However, an evaluation of whether these fish can be produced in a cost-effective manner needs to be evaluated (Garlock et al. 2017), and any additional issues from domestication and long holding times in hatcheries that could reduce survival post-release need to be evaluated (Lorenzen et al. 2012).

In practice, management objectives often focus on improving fishing opportunities or maximizing license sales (Askey et al. 2013, Dabrowska et al. 2014, Hunt et al. 2017), rather than on individual angler satisfaction as we did, particularly if fisheries agencies depend on license income for funding. By contrast, local angling clubs under private fishing right systems in central Europe who are sufficiently funded likely focus more on angler satisfaction-objectives and not whether stocking or any other measures recruits new members to clubs. When we examined whether the socioeconomic benefits (social welfare) of stocking outweighed the financial costs of stocking (assuming financial costs of changing MLLs were zero) we found a
striking difference between the economic performance of stocking into naturally reproducing and non-reproducing populations. Moderate MLLs in the absence of stocking maximized the net economic benefit from fishing for pike, while the economic benefit of stocking pike rarely exceeded the use of MLLs alone. This is because MLLs were sufficient to preserve fishery benefits without the added costs from culturing fish. Stocking was only the economically best option when MLLs offered little protection to the pike population and recruitment overfishing was occurring under higher levels of latent fishing pressure. By contrast, we found it was economically advisable to create a culture-based fishery using carp, particularly when adults were stocked at low densities. Our results are in agreement with other stocking models (Lorenzen 2005, Rogers et al. 2010) that reported stocking was much more advisable in culture-based situations compared to stock-enhancement scenarios. Such information can inform the allocation of stocking resources within the landscape of lakes, with and without natural fish populations, to maximize the benefits the angling community receives while avoiding incurring unneeded costs (Cowley et al. 2003).

The reasons behind our findings relate to the two components that determined net economic benefit – net WTP and latent fishing effort. In this context, the definition of the status quo situation (unregulated and unstocked) used to calculate the net WTP was very important for the findings. When catch rates approached zero in the status quo scenario, as occurred when the population was heavily overexploited (pike) or lacked natural reproduction (carp), anglers were willing to pay much more to improve the situation because of the large disparity between the regulated/stocked scenarios and the status quo case. Whereas if catch rates in the status quo situation approached “good enough” in scenarios where the population was self-sustaining, then there was much less gained from the stock-enhanced scenario, because of the above-mentioned
nonlinear relationship between angler satisfaction and catch rates. The second important factor
determining the net economic benefit generated by a given policy was latent fishing effort,
because it determined the aggregated angler welfare (net WTP multiplied by latent effort) of a
given policy. When net per angler WTP was low, more anglers and lower stocking densities
were required to produce a positive net economic benefit for the fishery as a whole. Such a
situation was rare for pike, even at low stocking densities, unless latent angling pressure was
moderate to high. By contrast, stocking carp often produced a positive net economic benefit,
except when there were not sufficient anglers to benefit from the culture-based fishery. It should
be cautioned, however, that our results are largely the result of the nonlinear relationship
between catch rates and angler satisfaction. A greater sensitivity of angler utility and behavior to
catch rates not approaching zero, as has been assumed in other modelling exercises (e.g., Allen et
al. 2013, Camp et al. 2014), could change predictions about the net economic benefits and
success of stocking strategies.

In the face of financial constraints, our results are good news for managers facing tough
budgetary decisions. If one has a limited budget to allocate, our results suggest that creating
culture-based fisheries with a desired species, rather than stocking naturally reproducing
populations provides the best investment. In doing so, managers create more fishing
opportunities, greater benefits to anglers, and a better return on their investment. Stocking may
also have the added benefit of drawing fishing effort away from wild stocks, but only if
additional effort attracted to the system does not put additional pressure on wild stocks (Fayram
et al. 2006, Baer et al. 2007, Meyer et al. 2012). The recommendation to stock a nonnative
species such as carp also assumes that one is not concerned with the possible negative ecological
consequences of high carp biomasses (e.g., water quality impacts, habitat degradation,
competition with other species, etc. Matsuzaki et al. 2009, Weber and Brown 2009, Vilizzi et al. 2015). However, as carp do not regularly recruit in central Europe (Kottelat and Freyhof 2007), environmental impacts may be controlled in what effectively becomes a put-grow-and take fishery. Research has found that, if overall biomass is kept within limits (< 50 kg ha\(^{-1}\)), impacts on water quality (Mehner et al. 2004, Vilizzi et al. 2015) and aquatic ecosystems (Barthelmes and Brämick 2003) may be limited. Thus, if anglers follow economic principles and minimize costs when making stocking decisions, the low stocking intensities suggested from our research should minimize conflicts among conservation and fisheries objectives for this species.

Allocating stocking funds to carp does not mean a loss for pike anglers (or other naturally occurring species). Our study has a clear message: if fish populations are self-sustaining, we suggest that stocking is not economically advisable and will only rarely increase angler welfare. Managers can use MLLs or other forms of harvest controls, for example harvest slots (Gwinn et al. 2015), to achieve the same or greater benefits, without bearing the costs associated with stocking. However, overly restrictive MLLs may not be an option either, because harvest contributes substantially to angler welfare in many cultures (Arlinghaus et al. 2014). The use of harvest restrictions has the additional benefit of avoiding the possible negative ecological effects of stocking fish, such as replacement of the wild stock (Rogers et al. 2010, van Poorten et al. 2011, Camp et al. 2014), effects on genetic integrity, spread or disease, etc. (Cowx 1994, Araki et al. 2007, Lorenzen et al. 2012), as well as negative impacts of the welfare on other stakeholders (e.g., conservation lobby groups) that we did not account for in our model.

\textit{Limitations}
Our model has a number of limitations that are worth noting. In the biological sub-model, the impacts of stocking were strongly dependent on the strength of the size- and density-dependent compensatory responses at the different life stages. While we did observe effects from density-dependent mortality, we did not observe large declines in the number of fry or fingerlings surviving to age-1 at extremely high stocking densities as one might expect from a Ricker stock-recruitment relationship (Fayram et al. 2005), nor did we see overall densities reaching a maximum carrying capacity at high stocking densities for any fish size. This is a result of the stocking densities we investigated, and density-dependent mortality in age-1 and older fish. Thus, it is possible that our predicted outcomes from stocking are overly optimistic, because density-dependent feedbacks were not sufficiently strong. Moreover, our conclusions that stocking is generally not beneficial for naturally-reproducing pike and beneficial only in low densities for non-reproducing carp are unlikely to be affected by decreased mortality at higher stocking densities because catch had such little impact on angler utility. However, reduced natural mortality rates of small fish due to changes in the size- and density-dependent survival relationships could result in fingerlings being a more effective size to stock than adults. We did, however, find that our model predictions were robust to the assumption of density-dependent mortality of fish age-1 and older. Model predictions in the absence of density-dependent mortality for fish of age-1 and older were qualitatively similar (Appendix S1: Figures S6, S7, and S8). The only differences of note were that compared to stocking carp adults, stocking carp fingerlings did not produce higher vulnerable densities and catch rates or lower survivor costs under high latent effort. In addition, the inability of pike populations to compensate for the low density of predators in the system caused by heavy exploitation resulted in a greater range of
MLLs where populations were unsustainable and higher WTP, survivor costs, and net benefits, although the patterns were qualitatively the same as the density-dependent scenarios.

In terms of the social sub-model, we assumed that MLLs have no direct monetary cost. While this may be reasonable because the implementation framework is already in place, other associated costs, such as enforcement costs, were not included in our model. Our model was also based on a specific, mechanistic model of angler behavior. As discussed previously, the lognormal relationship between catch and utility had a strong influence on our results, and other functional forms in this relationship may alter the outcomes. An additional limitation of our model was that we made the simplifying assumption that all anglers had identical time-invariant preferences. In reality, preferences may shift over time (Hunt et al. 2011), and particularly assumptions about angler heterogeneity might affect model outcomes substantially (Johnston et al. 2010, 2013, Matsumura et al. 2017). Thus, further investigations using preferences from different angler populations composed of diverse angler types are needed to test the robustness of our findings.

Another aspect that our long-term equilibrium dynamics model did not consider was the temporal variability in the fishery. Seasonality and stochasticity are inherent characteristics of fisheries. Differences in catch can develop because anglers differ not only in their skill (Dorow et al. 2010, Ward et al. 2013) but also in when they go fishing (Hunt et al. 2007). Thus, after a stocking event, particularly of large fishes, there is the potential that those anglers who come first and spend more time fishing shortly after stocking will reap more benefits than anglers who arrive later. Changes in fish behavior can further inflate the disproportionate distribution of benefits, if stocked fish alter their behavior over time to become less vulnerable to fishing gear (e.g., van Poorten and Post 2005, Askey et al. 2006, Klefoth et al. 2013). However, any short-
term catch rate boosts from stocking would likely not affect social outcomes, because of the non-
linearity in the catch-utility relationship, but they could alter predictions about biological
enhancement.

Finally, the results we presented in our study relate to the benefits of stocking a single lake with
a single-species population. In reality, individual fisheries are embedded in the broader landscape
and therefore require broader management perspectives (Lester et al. 2003, Hunt et al. 2011, Mee
et al. 2016). It is important for managers to understand how changes in regulations will effect
target-species substitution and site substitution (Gentner and Sutton 2008, Sutton and Ditton
2005) in multi-species fisheries. Furthermore, stocking strategies that work locally may not be
the best regional solution (Askey et al. 2013, Varkey et al. 2016), and managers must figure out
how to allocate limited stocking resources optimally within the landscape (Cowley et al. 2003).
Hence, our work should be extended to broader spatial scales to investigate the optimal policy
mixes in a landscape of diverse fisheries and diverse angler populations.

Conclusions

One of the key findings from our study and related work (e.g., Askey et al. 2013, Camp et al.
2017, Garlock et al. 2017) is that the stocking strategies considered to be the most successful will
strongly depend on ecological processes of the managed species and the performance measure
used to judge management success. We found that the presence or absence of natural
reproduction, and the strength of size- and density-dependent processes regulating the
population, were key for determining whether stocking can produce additive effects and elevate
fishing quality or not. However, we also found that a move away from mere biological objectives
(increased abundance), to social (increased angler satisfaction) or economic objectives (return on
investment) can result in different conclusions about the most appropriate management strategy. For self-sustaining populations, from both conservation and economic perspectives, stocking is rarely beneficial, while it is necessary for culture-based fisheries.

A strength of our study was the ability to evaluate the outcomes of various management tools and strategies not only from a biological perspective, but also in terms of social benefits and economic feasibility by using a conceptually rigorous cost-benefit analysis. For naturally reproducing species, the additive effects promised by some forms of stocking do not necessarily translate into an increase in angler well-being, and the practice is often economically inefficient. In addition, stocking runs the strong risk of the pervasive replacement of wild fishes by stocked ones (van Poorten et al. 2011), and potentially increases mortality of wild fish if fishing pressure increases after stocking (Baer et al. 2007). By contrast, in non-reproducing species stocking has additive effects, increases angler satisfaction, and when conducted properly is economically advisable. These results highlight that a species’ reproductive ecology in combination with normative metrics creates important trade-offs. The key trade-off is generally between economic efficiency and conservation concerns (Camp et al. 2017), which often results in opposing recommendations about which is the “best” strategy. Yet, in some situations, for example stocking fish into severely depleted populations, stocking can create a win-win for both conservation and anglers’ interests, particularly when local broodstock are used and stocking is a temporary practice that is paired with habitat enhancement efforts. Similarly, using economic objectives to inform stocking decisions may bring about lower stocking densities that minimize conservation concerns (e.g. water quality and carp).

Our findings that stocking self-sustaining populations provided little benefit to angler welfare and rarely produced a positive return on investment, despite increased abundance, are
noteworthy because they contradict recommendations stemming from traditional metrics, such as population density or catch rate, often used to evaluate management success. Our results also challenge the common assumption that catch is the primary driver of angler utility and behavior, and underscores early insights by Cole and Ward (1994) that managing according to angler benefits is bound to lead to different results than managing fishing opportunities (i.e., catch or supply). Our study demonstrates the usefulness of using a social-ecological modelling framework, because only through an integrated model with a mechanistic description of behavior could we uncover these insights. While some studies have linked angler behavior to catch-related fishery quality (e.g., Rogers et al. 2010, Askey et al. 2013, Camp et al. 2014), our study differed from these because angler behavior was explicitly determined by numerous catch and non-catch related attributes and informed by the preferences of real anglers (Arlinghaus et al. 2014). A further benefit of using an integrated bioeconomic modelling framework is it forces managers to be transparent about their objectives and normative framework (Fenichel et al. 2013b). It is ultimately the tight interplay of ecology and the human dimensions that will determine the success of any management action.

**ACKNOWLEDGEMENTS**

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### TABLES

**Table 1.** Bioeconomic model equations. Parameter values and their sources for northern pike (*Esox lucius*) and common carp (*Cyprinus carpio*) are listed in Appendix S1: Table S1.

Derivations of some of the equations can be found in Appendix S1. PWU = part-worth utility.

<table>
<thead>
<tr>
<th>Equation</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Age-structured fish population</strong></td>
<td></td>
</tr>
<tr>
<td>$N_{ag}$</td>
<td>Density of fish within age class $a$ and growth trajectory</td>
</tr>
<tr>
<td>$L_{ag}$</td>
<td>Length of fish within age class $a$ and growth trajectory $g$</td>
</tr>
<tr>
<td><strong>1a</strong> $N_{total} = \sum_{a} \sum_{g} N_{ag}$</td>
<td>Total fish population density</td>
</tr>
<tr>
<td><strong>1b</strong> $B_{total} = \sum_{a} \sum_{g} N_{ag} W_{ag}$</td>
<td>Total fish biomass density</td>
</tr>
<tr>
<td><strong>1c</strong> $D_{E} = \sum_{a} \sum_{g} N_{ag} L_{ag}^{2}$</td>
<td>Total effective density</td>
</tr>
<tr>
<td><strong>Growth</strong></td>
<td></td>
</tr>
<tr>
<td><strong>2a</strong> $L_{ag,t+1} = L_{ag,t} + h_{g,j} P_{ag}$</td>
<td>Length of fish within age class $a$ and growth trajectory $g$ at time $t + 1$</td>
</tr>
<tr>
<td><strong>2b</strong> $h_{g,j} = h_{max} \frac{L_{ag}}{[1 + B_{total,t} / B_{1;2}]}$</td>
<td>Maximum annual growth of a fish within growth trajectory $g$, which was dependent on the total fish biomass density at the beginning of the year</td>
</tr>
<tr>
<td><strong>2c</strong> $P_{ag} = \begin{cases} 1 - \frac{G}{3+G} \left(1 + \frac{L_{ag}}{h_{g}} \right) &amp; \text{if mature} \ 1 &amp; \text{if immature} \end{cases}$</td>
<td>Proportion of the annual growth potential which a fish of age $a$ and growth trajectory $g$ allocates to growth</td>
</tr>
<tr>
<td><strong>2d</strong> $W_{ag} = wL_{ag}^{l}$</td>
<td>Mass of a fish of age $a$ and growth trajectory $g$</td>
</tr>
<tr>
<td><strong>Maturation and Reproduction</strong></td>
<td></td>
</tr>
<tr>
<td><strong>3a</strong> $L_{mat,a} = b_1 + b_2 a$</td>
<td>Threshold length a fish of age $a$ must achieve to mature ($L_{ag} &gt; L_{mat,a} = \text{mature}$)</td>
</tr>
</tbody>
</table>
### Mortality age-0 pre-stocking

- **4a** \( s_{1,t} = \alpha_1 e^{-\beta_1(N_{0w,t} + N_{0h,t})} \)  
  Survival of fish during the pre-stocking phase at time \( t \)

- **4b** \( \alpha_1 = \left( \frac{L_0}{L_s} \right)^{\frac{\lambda'}{\lambda_{\text{max}}}} \)  
  Maximum survival rate of larvae during the pre-stocking phase (see Appendix S1 for derivation)

- **4c** \( \beta_1 = \frac{\ln \frac{L_0}{L_s}}{\ln \frac{L_0}{L_{\text{rec}}}} \beta \)  
  Strength of the density-dependence during the pre-stocking phase (see Appendix S1 for derivation)

- **4d** \( M_1^* = h_{\text{max}} \frac{\ln \alpha}{\ln \frac{L_0}{L_{\text{rec}}}} \)  
  Natural mortality rate of an age-0 fish of 1 cm at zero density

- **4e** \( L_{\text{rec}} = L_0 + h_{\text{max}} \)  
  Maximum average length at recruitment

- **4f** \( J_{0w,t} = s_{1,t}(N_{0w,t} + h^2 N_{0h,t}) \)  
  Density of age-0 wild \( J_{0w,t} \) and hatchery \( J_{0h,t} \) origin fish surviving the pre-stocking phase at time \( t \)

### Mortality age-0 post-stocking

- **5a** \( s_{2,t} = \alpha_2 e^{-\beta_2(J_{0w,t} + J_{0h,t} + J_{0h,t})} \)  
  Survival of fish during the pre-stocking phase at time \( t \)

- **5b** \( \alpha_2 = \frac{\alpha}{\alpha_1} \)  
  Maximum survival rate of larvae during the post-stocking phase (see Appendix S1 for derivation)

- **5c** \( \beta_2 = \frac{\beta - \beta_1}{\alpha_1 e^{-\beta_1(N_{0w,t} + N_{0h,t})}} \)  
  Strength of the density-dependence during the post-stocking phase (see Appendix S1 for derivation)

- **5d** \( N_{1g_{0w,t+1}} = s_{2,t} \sigma_1 J_{0w,t} \)  
  Density of wild \( N_{1g_{0w,t+1}} \) and hatchery \( N_{1g_{0h,t+1}} \) origin fish of age \( a = 1 \) and growth trajectory \( g \) at time \( t+1 \)

### Stocking and Mortality age-1 and older fish

- **6a** \( N_{ag_{0h,t+1}} = \begin{cases} N_{ag_{0h,t}} + \sigma_1 N_{S_{0h,t}} & \text{if } a = a_S \\ N_{ag_{0h,t}} & \text{if } a \neq a_S \end{cases} \)  
  Density of hatchery origin fish after recruited fish were stocked

Density of wild \( N_{0w,t} \) and hatchery \( N_{0h,t} \) origin larvae produced by spawners at time \( t \). NOTE: \( N_{0w} \) and \( N_{0h} \) were assumed to be zero when modelling carp.
<table>
<thead>
<tr>
<th>Equation</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>$M_{ag,t} = M_{r,t_{max}} \left( \frac{L_{ag,t}}{L_{\text{max}}} \right)^{c_i}$</td>
<td>Instantaneous natural mortality rate of a fish of length $L_{ag}$ at time $t$</td>
</tr>
<tr>
<td>$M_{r,t_{max}} = \frac{h_{\text{max}}}{L_{\text{max}}}$</td>
<td>Reference instantaneous natural mortality rate at length $L_{\text{max}}$</td>
</tr>
<tr>
<td>$c_i = \frac{\ln[1 + (1 - \gamma)D_{rel,i}]}{\ln(M_{r,t_{max}})} - 1$</td>
<td>Allometric exponent of size-dependent mortality relationship at time $t$</td>
</tr>
<tr>
<td>$D_{rel,i} = \frac{D_{i}^2 - D_{\text{Equilb}}}{D_{\text{Equilb}}}$</td>
<td>Relative effective density at time $t$</td>
</tr>
<tr>
<td>$v_{ag,t} = \frac{1}{1 + \exp(-y(L_{ag,t} - L_{50}))}$</td>
<td>Proportion of fish of age $a$ and growth trajectory $g$ vulnerable to capture by anglers at time $t$</td>
</tr>
<tr>
<td>$L_{50} = zL_{\text{max}} + L_{\text{shift}}$</td>
<td>Size at 50% vulnerability to capture</td>
</tr>
<tr>
<td>$C_{ag,t} = qE_{I}v_{ag,t}$</td>
<td>Instantaneous catch rate of fish of age $a$ and growth trajectory $g$ at time $t$</td>
</tr>
<tr>
<td>$f_{H,ag} = \begin{cases} 1 &amp; \text{if } L_{ag} \geq MLL \ f_{n} &amp; \text{if } L_{ag} &lt; MLL \end{cases}$</td>
<td>Proportion of captured fish of age $a$ and growth trajectory $g$ harvested by anglers</td>
</tr>
<tr>
<td>$F_{ag,t} = f_{H,ag} C_{ag,t} + f_{n} C_{ag,t} (1 - f_{H,ag})$</td>
<td>Instantaneous fishing mortality rate of fish of age $a$ and growth trajectory $g$ at time $t$</td>
</tr>
<tr>
<td>$s_{agw,t} = e^{-(M_{ag,t} + F_{ag,t})}$, $s_{agh,t} = e^{-(M_{ag,t}/\gamma_i + F_{ag,t})}$</td>
<td>Survival of wild $s_{agw,t}$ and hatchery $s_{agh,t}$ origin fish of age $a$ and growth trajectory $g$</td>
</tr>
<tr>
<td>$N_{a+1,gw,t+1} = N_{agw,t} s_{agw,t}$, $N_{a+1,gh,t+1} = N_{agh,t} s_{agh,t}$</td>
<td>Density of wild $N_{a+1,gw,t+1}$ and hatchery $N_{a+1,gh,t+1}$ origin fish of age $a+1$ and growth trajectory $g$ at time $t + 1$</td>
</tr>
</tbody>
</table>

**Angler-effort dynamics**

<table>
<thead>
<tr>
<th>Equation</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>$U_{t} = U_{in} + U_{Spp} + U_{Cost}$, $U_{cp} + U_{T} + U_{l_{\text{max}}} + U_{A_{0}} + U_{MLL} + U_{DBL} + U_{Stock} + U_{Comp}$</td>
<td>Conditional indirect utility gained by an angler from choosing to fish (where $U_{in}$ is the basic utility gained from fishing, $U_{Spp}$ is the PWU of preferred species, $U_{Cost}$ is the PWU of annual license cost, $U_{A_{0}}$ is the PWU of average daily catch, $U_{T}$ is the PWU of average size of fish caught annually, $U_{l_{\text{max}}}$ is the PWU of trophy catch rate, $U_{Comp}$ is the PWU of anglers seen, $U_{MLL}$ is the PWU of</td>
</tr>
</tbody>
</table>
minimun-length limit $MLL$, $U_{DBL}$ is the PWU of daily bag limit $DBL$, $U_{Stock}$ is the PWU of stocking frequency, and $U_{Comp}$ is the PWU of catch composition).

<table>
<thead>
<tr>
<th>Equation</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>$p_{t,j} = \frac{\exp(\hat{U}<em>t)}{\exp(\hat{U}<em>t) + \exp(U</em>{out}) + \exp(U</em>{no})}$</td>
<td>Probability an angler chooses to fish, over the alternatives of not fishing or fishing elsewhere (where $\hat{U}<em>t$ applies to the previous year, $U</em>{no}$ is the utility gained from not fishing, and $U_{out}$ is the utility gained from fishing elsewhere)</td>
</tr>
<tr>
<td>$p_{F,j} = (1 - \varphi)p_{t,j} + \varphi\hat{p}_F$</td>
<td>Realized probability an angler of type $j$ fishes (where $\hat{p}_{Fj}$ applies to the previous year)</td>
</tr>
<tr>
<td>$E_t = p_{F,t}d_{max}A_L\Psi$</td>
<td>Total annual realized fishing effort density at time $t$</td>
</tr>
</tbody>
</table>

**Response variables**

<table>
<thead>
<tr>
<th>Expression</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>$WTP = \frac{U_{base} - U_{scenario}}{u_1}$</td>
<td>Willingness to pay</td>
</tr>
<tr>
<td>$W = A_LWTP$</td>
<td>Aggregated social welfare</td>
</tr>
<tr>
<td>$NB = W - \epsilon_S$</td>
<td>Net economic benefit</td>
</tr>
<tr>
<td>$\epsilon_S = \begin{cases} J_0\theta L_s^\lambda &amp; a_s = 0 \ N_s\theta L_s^\lambda &amp; a_s &gt; 0 \end{cases}$</td>
<td>Cost of stocking</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Expression</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\epsilon_{ind} = \begin{cases} \epsilon_S / J_0 &amp; a_s = 0 \ \epsilon_S / N_s \sum_{g=1}^{2} \sigma_{Ng}\sum_{a=a_g}^{2} &amp; a_s &gt; 0 \end{cases}$</td>
<td>Cost per stocked individual surviving from the time of stocking until the end of age 2</td>
</tr>
</tbody>
</table>

**Part-worth-utility (PWU) functions**

<table>
<thead>
<tr>
<th>PWU</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>$U_{ag} = u_1\epsilon_L$</td>
<td>PWU of annual license cost</td>
</tr>
<tr>
<td>$U_{\tau_0} = u_2 \log_{10} \overline{C}_D$</td>
<td>PWU of daily catch $\overline{C}_D$</td>
</tr>
<tr>
<td>$U_T = u_3 \log_{10} \left( \frac{T}{\overline{T}_{ref}} \right)$</td>
<td>PWU of average size of fish caught annually $\overline{T}$</td>
</tr>
<tr>
<td>$U_{l_{max}} = u_4l_{max}$</td>
<td>PWU of the catch rate $l_{max}$ of trophy-sized fish ($L_{ag} &gt; L_T$)</td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>9e</td>
<td>$U_{Ao} = u_5 \bar{A}_D$</td>
</tr>
<tr>
<td>9f</td>
<td>$U_{MLL} = u_6 MLL + u_7 MLL^2$</td>
</tr>
<tr>
<td>9g</td>
<td>$U_{DBL} = u_8 DBL$</td>
</tr>
<tr>
<td>9h</td>
<td>$U_{Stock} = u_9 I$</td>
</tr>
<tr>
<td>9i</td>
<td>$U_{Comp} = u_{10} \frac{C_{Dw}}{C_{Dtotal}}$</td>
</tr>
</tbody>
</table>
**Table 2.** Parameters used in model scenarios. Bold font indicates changes in the parameters relative to the base case, scenario 1.

Scenarios 2A and 2B compare pike and carp, scenarios 3A and 3B compare assumptions about productivity and habitat changes, and scenarios 4A and 4B compare assumptions about relative fitness and heritability.

<table>
<thead>
<tr>
<th>Variable</th>
<th>1 (Base)</th>
<th>2A</th>
<th>2B</th>
<th>3A</th>
<th>3B</th>
<th>4A</th>
<th>4B</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>Pike</td>
<td>Pike</td>
<td>Carp</td>
<td>Pike</td>
<td>Pike</td>
<td>Pike</td>
<td>Pike</td>
</tr>
<tr>
<td>Latent Fishing Pressure</td>
<td>Moderate</td>
<td>Low, High 1, 10 licenses ha⁻¹</td>
<td>Low, High 1, 10 licenses ha⁻¹</td>
<td>Moderate</td>
<td>Moderate</td>
<td>Moderate</td>
<td>Moderate</td>
</tr>
<tr>
<td>Stocking Expenditure</td>
<td>Observed</td>
<td>Fixed 0,5,100 € ha⁻¹</td>
<td>Fixed 0,5,100 € ha⁻¹</td>
<td>Fixed 0,5,100 € ha⁻¹</td>
<td>Fixed 0,5,100 € ha⁻¹</td>
<td>Fixed 0,5,100 € ha⁻¹</td>
<td>Fixed 0,5,100 € ha⁻¹</td>
</tr>
<tr>
<td>Habitat</td>
<td>Normal</td>
<td>Normal</td>
<td>Normal</td>
<td>Reduced α / 2</td>
<td>Reduced 2 * β</td>
<td>Normal</td>
<td>Normal</td>
</tr>
<tr>
<td>Relative Fitness</td>
<td>Equal</td>
<td>Equal</td>
<td>n.a.</td>
<td>Equal</td>
<td>Equal</td>
<td>Unequal</td>
<td>Unequal</td>
</tr>
<tr>
<td>Heritability</td>
<td>None</td>
<td>None</td>
<td>n.a.</td>
<td>None</td>
<td>None</td>
<td>None</td>
<td>100%</td>
</tr>
<tr>
<td>Utility from Stocking</td>
<td>Absent</td>
<td>Absent</td>
<td>Present</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
</tr>
<tr>
<td>Stocked Fish Recognition</td>
<td>Unidentified</td>
<td>Unidentified</td>
<td>Identified</td>
<td>Unidentified</td>
<td>Unidentified</td>
<td>Unidentified</td>
<td>Unidentified</td>
</tr>
</tbody>
</table>
**FIGURE CAPTIONS**

**Figure 1.** Schematic of modelled fishery components and their interactions (modified from Johnston et al. 2013).

**Figure 2.** The effects of stocking pike fry (2 cm), fingerlings (20 cm) and adults (age-2, 35-40 cm) at a range of densities across a range of minimum-length limits (MLLs) and a range of stocking densities (0 - $L_{\text{max}}$) calibrated to reflect the range of annual expenditures (0-154 € ha$^{-1}$) on pike stocking by angling-clubs in Germany (Table 2, scenario 1). Effects of stocking and MLLs on total fish density, density of vulnerable fish (age-2 and older fish at year end), catch rates, change in angler welfare (net willingness-to-pay, WTP) relative to the unregulated and unstocked case, per capita costs of stocked fish surviving to a vulnerable size (their third birthday), and net economic benefit, were evaluated. Latent fishing pressure was moderate (5 licenses ha$^{-1}$). Very close contour lines indicate rapid changes in the performance measure.

**Figure 3.** Age structure of a pike population under three different minimum-length limits (MLLs, no MLL, 48 cm, and 120 cm), when fry, fingerlings and adults were stocked at low (3 € ha$^{-1}$), or high (154 € ha$^{-1}$) densities, or not stocked at all. The abundance of fish older than age-6 were not presented for visual clarity. The percentages listed in the corner of each panel represent the percent of the population that is composed of wild-origin fish under low (tightly hashed bar) and high (coarsely hashed bar) stocking densities.

**Figure 4.** The effect of stocking pike and carp fry, fingerlings and adults at densities that represent annual stocking expenditures of 0, 5, and 100 € ha$^{-1}$ (Table 2, scenario 2). For pike, these expenditures corresponded to densities of 0, 159 and 3174 fry ha$^{-1}$ (2 cm), 0, 3 and 58 fingerlings ha$^{-1}$ (20 cm), and 0, 1 and 24 adults ha$^{-1}$ (age-2), respectively, and for carp to
densities of 0, 98 and 1967 fry ha\(^{-1}\) (4 cm), 0, 8 and 155 fingerlings ha\(^{-1}\) (15 cm) and 0, 1 and 23 adults ha\(^{-1}\) (40 cm), respectively. Effects of stocking and MLLs on total fish density, density of vulnerable fish (age-2 and older fish at year end), catch rates, change in angler welfare (net willingness-to-pay, WTP) relative to the status quo, per capita costs of stocked fish surviving to a fully vulnerable size (their third birthday), and net economic benefit, were evaluated under low and high latent fishing pressure (1 and 10 licenses ha\(^{-1}\), respectively). The grey areas indicate situations where the benefit to anglers was not greater than the status quo (no stocking and no MLL), or where there was no positive net economic benefit.

**Figure 5.** The sensitivity of pike model outcomes to changes in model assumptions, under annual stocking expenditures of 0, 5, and 100 € ha\(^{-1}\), and moderate latent fishing pressure, 5 licenses ha\(^{-1}\) (Table 2, scenarios 3 and 4). For pike, these expenditures corresponded to densities of 0, 159 and 3174 fry ha\(^{-1}\) (2 cm), 0, 3 and 58 fingerlings ha\(^{-1}\) (20 cm), and 0, 1 and 24 adults ha\(^{-1}\) (age-2), respectively. The left column represents the unmodified, base model (Table 2, scenario 1). The second and third columns represent lower stock productivity (\(\alpha / 2\), Table 2 scenario 3A) and lower habitat capacity resulting in stronger density-dependence (\(2 \cdot \beta\), Table 2 scenario 3B), respectively. The fourth and fifth columns represent the reduced fitness scenario (relative survival of stocked age-0 fish was 50%, of stocked adults was 90%, and relative reproductive success was 56% compared to wild fish), with zero heritability (Table 2 scenario 4A), and 100% heritability (Table 2 scenario 4B). The grey areas indicate situations where the benefit to anglers was not greater than the status quo (no stocking and no MLL), or where there was no positive net economic benefit.
Management component

Management objectives: social biological

Stocking: number size

Harvest Regulations: Minimum-length limit

Biological component

Fish population: abundance & structure (age, size)

Fishing Mortality: harvest, hooking mortality, noncompliance

Catch: number, average size, maximum size

Social component

Utility from fishing

Probability of fishing

Fishing effort (crowding)
121x66mm (300 x 300 DPI)
193x244mm (300 x 300 DPI)
Supplementary material for:

How ecological processes shape the outcomes of stock enhancement and harvest regulations in recreational fisheries

Published in Ecological Applications

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APPENDIX S1

Supplemental tables

Table S1. Bioeconomic model parameter values and their sources for northern pike (*Esox Lucius*) and common carp (*Cyprinus carpio*).

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Value or range for fish life-history types (source, where applicable)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(unit, where applicable)</td>
<td>Pike</td>
</tr>
<tr>
<td></td>
<td><strong>Index variables</strong></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>t</em> year (y)</td>
<td>0 - 150</td>
</tr>
<tr>
<td></td>
<td><em>a</em> Age class (y)</td>
<td>0 - <em>a</em>&lt;sub&gt;max&lt;/sub&gt;</td>
</tr>
<tr>
<td></td>
<td><em>a</em>&lt;sub&gt;max&lt;/sub&gt; Maximum age of a fish (y)</td>
<td>15 (5)</td>
</tr>
<tr>
<td></td>
<td><em>g</em> Growth trajectory within an age class</td>
<td>1 - 11</td>
</tr>
<tr>
<td></td>
<td><strong>Growth</strong></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>L</em>&lt;sub&gt;max&lt;/sub&gt; Mean maximum size a fish can attain at maximum age (<em>a = a</em>&lt;sub&gt;max&lt;/sub&gt;* ) in an environment free of intraspecific competition (<em>B</em>&lt;sub&gt;total&lt;/sub&gt; = 0) (cm)</td>
<td>120</td>
</tr>
<tr>
<td></td>
<td><em>L</em>&lt;sub&gt;0&lt;/sub&gt; Length of fish at hatch (cm)</td>
<td>0.8 (7)</td>
</tr>
<tr>
<td></td>
<td><em>h</em>&lt;sub&gt;max&lt;/sub&gt; Mean maximum annual growth increment (cm)</td>
<td>24.0 (10)</td>
</tr>
<tr>
<td></td>
<td><em>σ</em>&lt;sub&gt;Lg&lt;/sub&gt; Proportional deviations from the mean <em>h</em>&lt;sub&gt;max&lt;/sub&gt; in the positive and negative direction, assuming a range of 3 standard deviation units and a coefficient of variation of 0.1</td>
<td>-0.3 to 0.3</td>
</tr>
<tr>
<td></td>
<td><em>B</em>&lt;sub&gt;1/2&lt;/sub&gt; Biomass density at which the growth increment is halved (kg ha&lt;sup&gt;-1&lt;/sup&gt;)</td>
<td>100.0 (10)</td>
</tr>
<tr>
<td></td>
<td><em>G</em> Annual reproductive investment</td>
<td>0.58 (10)</td>
</tr>
<tr>
<td></td>
<td><em>w</em> Scaling constant for length-mass relationship (g cm&lt;sup&gt;-1&lt;/sup&gt;)</td>
<td>0.0048 (19)</td>
</tr>
<tr>
<td></td>
<td><em>l</em> Allometric exponent for length-mass relationship</td>
<td>3.059 (19)</td>
</tr>
<tr>
<td></td>
<td><strong>Maturation</strong></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>b</em>&lt;sub&gt;1&lt;/sub&gt; Intercept of the maturation reaction norm (cm)</td>
<td>36.6 (7)*</td>
</tr>
<tr>
<td></td>
<td><em>b</em>&lt;sub&gt;2&lt;/sub&gt; Slope of the maturation reaction norm (cm y&lt;sup&gt;-1&lt;/sup&gt;)</td>
<td>-3.25 (7)*</td>
</tr>
<tr>
<td></td>
<td><strong>Reproduction</strong></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>ω</em> Relative fecundity (g&lt;sup&gt;-1&lt;/sup&gt;)</td>
<td>34 (11)</td>
</tr>
<tr>
<td>Symbol</td>
<td>Description</td>
<td>Value</td>
</tr>
<tr>
<td>--------</td>
<td>-----------------------------------------------------------------------------</td>
<td>------------------------------</td>
</tr>
<tr>
<td>δ</td>
<td>Hatching success</td>
<td>0.75 (12)</td>
</tr>
<tr>
<td>Φ</td>
<td>Sex ratio (% female spawners)</td>
<td>0.5 (13)</td>
</tr>
<tr>
<td>ρ</td>
<td>Reproductive success of hatchery strain fish relative to wild fish</td>
<td>1.0 or 0.56 (8)</td>
</tr>
<tr>
<td></td>
<td><strong>Mortality</strong></td>
<td></td>
</tr>
<tr>
<td>α</td>
<td>Maximum survival rate of larvae to age-1</td>
<td>$1.71 \times 10^{-4}$ (10)</td>
</tr>
<tr>
<td>β</td>
<td>Strength of density-dependence on larvae to age-1 survival (ha)</td>
<td>$6.87 \times 10^{-6}$ (10)</td>
</tr>
<tr>
<td>h²</td>
<td>Proportion of hatchery larvae that transitioned to wild strain fish due to natural selection</td>
<td>0.0 or 1.0</td>
</tr>
<tr>
<td>γ</td>
<td>Relative survival of age-0 hatchery fish relative to age-0 wild fish</td>
<td>1.0 or 0.5 (8)</td>
</tr>
<tr>
<td>σₙₐₙ</td>
<td>Proportion of fish in a growth trajectory $g$ assuming a normal distribution with a mean $h_{\text{max}}$ and a coefficient of variation of 0.1</td>
<td>0.37 to $7.56 \times 10^{-6}$ (calculated)</td>
</tr>
<tr>
<td>Dₑquilib</td>
<td>Unexploited equilibrium effective density, which was considered to be the $D_L$ after model stabilization but prior to the introduction of stocking and fishing (cm² ha⁻¹)</td>
<td>32168.4 (calculated)</td>
</tr>
<tr>
<td>γ</td>
<td>Strength of density-dependence on the allometry of size-dependent natural mortality (see supplement for derivation)</td>
<td>0.27 (15)</td>
</tr>
<tr>
<td>y</td>
<td>Steepness of size-dependent vulnerability curve</td>
<td>0.3</td>
</tr>
<tr>
<td>z</td>
<td>Size as a proportion of $L_{\text{max}}$ used when calculating the size $L_{50}$ at which 50% of the fish are vulnerable to capture</td>
<td>0.18</td>
</tr>
<tr>
<td>Lₜᵢₙₜᵢₙ</td>
<td>Bias correction factor for the minimum size of fish that can be captured that is used when calculating the size $L_{50}$ (cm). See Johnston et al. 2013 for more details.</td>
<td>10</td>
</tr>
<tr>
<td>q</td>
<td>Catchability reflecting skill level (ha h⁻¹)</td>
<td>0.20</td>
</tr>
<tr>
<td>fₜ</td>
<td>Proportion of fish dying from hooking mortality</td>
<td>0.05</td>
</tr>
<tr>
<td>fₙ</td>
<td>Proportion of fish below the minimum-size limit $MSL$ harvested illegally</td>
<td>0.05</td>
</tr>
<tr>
<td>γ₂</td>
<td>Relative survival of recruited hatchery origin fish relative to wild fish</td>
<td>Immature 1.0 or 0.5 (8)</td>
</tr>
</tbody>
</table>

**Equilib**

Unexploited equilibrium effective density, which was considered to be the $D_L$ after model stabilization but prior to the introduction of stocking and fishing (cm² ha⁻¹).
### Stocking

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Values</th>
</tr>
</thead>
<tbody>
<tr>
<td>$L_s$</td>
<td>length of fish at stocking (cm)</td>
<td>2.0, 20.0, $L_{w_i}$, 4.0, 15.0, 40.0</td>
</tr>
<tr>
<td>$a_s$</td>
<td>Age at which recruited fish (adults) were stocked (y)</td>
<td>2 (2)</td>
</tr>
<tr>
<td>$J_{0s}$</td>
<td>The density of age-0 fish stocked (ha$^{-1}$)</td>
<td>Fry, Fry 0 to 4887, 0 to 1967, Fingerlings, Fingerlings 0 to 90 (2), 0 to 155 (2)</td>
</tr>
<tr>
<td>$N_{S,t}$</td>
<td>The density of recruited fish of age $a_s$ stocked (ha$^{-1}$)</td>
<td>0 to 39 (2), 0 to 23 (2)</td>
</tr>
</tbody>
</table>

### Linear coefficient of allometric stocking cost to size relationship

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\theta$</td>
<td>0.009459 (2)</td>
</tr>
<tr>
<td>$\lambda$</td>
<td>1.736 (2)</td>
</tr>
</tbody>
</table>

### Exponent of the allometric stocking cost to size relationship

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\theta$</td>
<td>0.003535 (2)</td>
</tr>
<tr>
<td>$\lambda$</td>
<td>1.923 (2)</td>
</tr>
</tbody>
</table>

### Angling regulations

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
<th>Values</th>
</tr>
</thead>
<tbody>
<tr>
<td>$MLL$</td>
<td>Minimum-length limit (cm)</td>
<td>0 - $L_{max}$</td>
</tr>
<tr>
<td>$DBL$</td>
<td>Daily bag limit (d$^{-1}$)</td>
<td>10</td>
</tr>
<tr>
<td>$A_L$</td>
<td>Density of angling licenses issued</td>
<td>1, 5, 10</td>
</tr>
<tr>
<td>$\epsilon_L$</td>
<td>Annual angling license cost (€)</td>
<td>100</td>
</tr>
</tbody>
</table>

### Angler Effort Dynamics

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
<th>Values</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\phi$</td>
<td>Persistence of fishing behaviour (= relative influence of last year’s realized fishing probability on the current year’s realized fishing probability)</td>
<td>0.5 (10)</td>
</tr>
<tr>
<td>$d_{max}$</td>
<td>Maximum number of days that an angler would fish annually irrespective of fishing quality (d)</td>
<td>20</td>
</tr>
<tr>
<td>$\Psi$</td>
<td>Average time an angler will fish in a day (h)</td>
<td>3 (2)</td>
</tr>
<tr>
<td>$\bar{T}_{ref}$</td>
<td>Reference average size of fish caught (cm)</td>
<td>37</td>
</tr>
<tr>
<td>$L_T$</td>
<td>Threshold length defining trophy-sized fish (cm)</td>
<td>100, 90</td>
</tr>
<tr>
<td>$U_{no}$</td>
<td>utility gained from not fishing</td>
<td>0.2489 (1)$\dagger$</td>
</tr>
<tr>
<td>$U_{out}$</td>
<td>utility gained from fishing elsewhere</td>
<td>0.4371 (1)$\dagger$</td>
</tr>
<tr>
<td>$U_{in}$</td>
<td>basic utility gained from fishing in the region</td>
<td>-0.686 (1)$\dagger$</td>
</tr>
<tr>
<td>$U_{Spp}$</td>
<td>PWU of fishing for most preferred species</td>
<td>0.0655 (1)$\dagger$</td>
</tr>
<tr>
<td>$u_1$</td>
<td>Cost coefficient</td>
<td>-0.518 (1)$\dagger$</td>
</tr>
<tr>
<td>$u_2$</td>
<td>Daily catch coefficient</td>
<td>0.1230 (1)$\dagger$</td>
</tr>
<tr>
<td>$u_3$</td>
<td>Average size coefficient</td>
<td>1.2357 (1)$\dagger$</td>
</tr>
<tr>
<td></td>
<td>Description</td>
<td>Value</td>
</tr>
<tr>
<td>---</td>
<td>--------------------------------------</td>
<td>------------------------</td>
</tr>
<tr>
<td>$u_4$</td>
<td>Trophy catch coefficient</td>
<td>$0.0254 \times 100$ (1)$\dagger$ $0.0357 \times 100$ (1)$\dagger$</td>
</tr>
<tr>
<td>$u_5$</td>
<td>Crowding coefficient</td>
<td>$-0.0424 \times 0.5$ (1)$\dagger$ $-0.0392 \times 0.5$ (1)$\dagger$</td>
</tr>
<tr>
<td>$u_6$</td>
<td>MLL linear coefficient</td>
<td>$0.005$ (1)$\dagger$    $0.0032$ (1)$\dagger$</td>
</tr>
<tr>
<td>$u_7$</td>
<td>MLL quadratic coefficient</td>
<td>$-0.0001$ (1)$\dagger$  $-0.0001$ (1)$\dagger$</td>
</tr>
<tr>
<td>$u_8$</td>
<td>Daily bag limit linear coefficient</td>
<td>$-0.0104$ (1)$\dagger$  $0.0085$ (1)$\dagger$</td>
</tr>
<tr>
<td>$u_9$</td>
<td>Stocking frequency coefficient</td>
<td>$0.1006$ (1)$\dagger$   $0.0632$ (1)$\dagger$</td>
</tr>
<tr>
<td>$u_{10}$</td>
<td>Catch composition coefficient</td>
<td>$0.0595$ (1)$\dagger$   $0.1013$ (1)$\dagger$</td>
</tr>
</tbody>
</table>

n.a., not applicable.

(1) Arlinghaus et al. (2014); (2) Arlinghaus et al. *Unpublished data*; (3) Babiak et al. (1997); (4) Brown and Walker (2004); (5) Craig and Kipling (1983); (6) Crivelli (1981); (7) Frost and Kipling (1967); (8) Hühn et al. (2014); (9) Jelkić et al. (2012); (10) Johnston et al. (2013); (11) Kipling and Frost (1969); (12) Kipling and Frost (1970); (13) Le Cren et al. (1977); (14) (Lorenzen 1996b) and Vilizzi et al. (2013); (15) derived from Post et al. (1999), see supplement; (16) Tempero et al. (2006); (17) Vilizzi et al. (2013), worldwide average; (18) Weber et al. (2011); (19) Willis (1989).

* calculated from the source data by determining maturity ogives and then calculating the probabilistic maturation norm. See Heino et al. (2002) and Barot et al. (2004) for methods. The slope represents the age and size at which the probability of maturation is 50%.

** calculated from source data using method described in Johnston et al. (2013).

$\dagger$ parameter values used were modified slightly from those reported by Arlinghaus et al. (2014) so that the $U_{\text{MLL}}$, the part-worth utility function of MLL, was quadratic in form rather linear. This was done because the quadratic form best described the data for pike and carp a quadratic.
Supplemental figures

Figure S1. Size-dependent vulnerability of fish to capture by anglers. The black and gray diamonds illustrate the average size at stocking of pike and carp, respectively, for fry, fingerlings and adults. The vertical dashed lines represent the average size a fish achieves by its third birthday (age-2 at the end of the year) for pike (black) and carp (gray), which we use to define the vulnerable population.
Figure S2. Species- and size-dependent stocking cost relationship determined from information provided by German angling clubs (Arlinghaus et al. 2015).
Figure S3. Part-worth utility functions describing the preferences of angler from Lower Saxony for catch related and non-catch related attributes when fishing for pike and carp, obtained from a choice experiment carried out by (Arlinghaus et al. 2014) and using the equations 9a-9i in Table 1 and the parameter set given in Table A1.
Figure S4. Relative length distribution of pike age-1 to age-4 cohorts in an unstocked population with a minimum-length limit of 42 cm and a latent fishing pressure of 5 anglers ha$^{-1}$. Values are for the beginning of the year. Other cohorts are not depicted.
Derivation of unpacked stock-recruitment

Survival of age-0 fish during the pre-stocking phase \( s_1 \) and the post-stocking phase \( s_2 \) were described by two Ricker stock-recruitment relationships. The method used by Lorenzen (2005) was modified to follow a Ricker model rather than a Beverton-Holt model to be more representative of early survival for pike (Johnston et al. 2013) and carp (Brown and Walker 2004). Overcompensation can result from cannibalism (Hilborn and Stokes 2010), a factor that is common in pike (Wright and Giles 1987, Skov et al. 2003). Cannibalism also occurs in carp populations (Tonn et al. 1994), but reduced age-0 survival at higher adult densities could also be the result of starvation, due to the overlap in diet with larger carp which have an exploitative advantage (Tonn et al. 1994). Larger reproductive investment of larger individuals at lower adult densities could also be a factor contributing to a Ricker-type stock-recruitment relationship (Weber and Brown 2013). The \( \alpha_1 \) and \( \alpha_2 \) parameters, describing the maximum survival rate of fish, and \( \beta_1 \) and \( \beta_2 \) parameters, describing the strength of the density-dependence during pre- and post-stocking, respectively, were derived in a manner similar to that used by Lorenzen (2005). Length-survival relationships and parameters from the original stock-recruitment relationship were used as follows:

Assuming under zero density the survival rate of larvae to recruitment at age-1 \( s^* \) was equal to the maximum survival rate \( \alpha \) from a Ricker stock-recruitment relationship.

\[
s^* = \alpha = \left( \frac{L_0}{L_{\text{rec}}} \right)^{M^*_1/h_{\text{max}}}
\]

where, \( L_0 \) is the larval length at hatch, \( L_{\text{rec}} \) is the average length at recruitment, \( M^*_1 \) is the natural mortality rate at 1cm, and \( h_{\text{max}} \) is the maximum somatic growth rate. The previous equation can be used to solve for \( M^*_1 \),

\[
M^*_1 = h_{\text{max}} \frac{\ln s^*}{\ln \left( \frac{L_0}{L_{\text{rec}}} \right)}
\]

Note that \( M_1 \) for unrecruited fish (age-0) is much higher than for recruited fish (Lorenzen 2005). The maximum survival rates during the two phases, pre-stocking \( \alpha_1 \) and post-stocking \( \alpha_2 \), can then be determined,

\[
\alpha_1 = \left( \frac{L_0}{L_2} \right)^{M^*_1/h_{\text{max}}} \quad \text{and} \quad \alpha_2 = \left( \frac{L_3}{L_{\text{rec}}} \right)^{M^*_2/h_{\text{max}}}
\]

such that \( \alpha = \alpha_1 \alpha_2 \).
where $L_s$ is the length of fish at the time of stocking. One can also solve for $\beta_1$ and $\beta_2$, if

$$M_i^* = h_{\max} \frac{\ln s^*}{\ln L_0, \ln L_{\text{rec}}} = h_{\max} \frac{\ln s_2}{\ln L_0, \ln L_{\text{rec}}}$$

Then by substituting in the Ricker relationships it can be simplified to

$$\beta = \frac{\ln L_0}{\ln L_{\text{rec}}} \beta$$

Assuming

$$s_1, s_2 = a_1 e^{-\beta N_0} a_2 e^{-b_2 a_1 N_0 e^{-\beta N_0}} = a e^{-\beta N_0}$$

$\beta_2$ can be determined, using $\alpha$ and $\beta_1$,

$$\beta_2 = \frac{\beta - \beta_1}{\alpha a e^{-\beta N_0}}$$
**Derivation of density-dependent allometric mortality**

It is now generally accepted that mortality in fish is related to size in the post-recruited stage (Mangel 2017). Thus, like age-0 fish, survival of age-1 and older fish was also assumed to be size-dependent and density-dependent using a relationship described by Lorenzen (1996a, 2000).

\[ M_L = M_r \left( \frac{L}{L_r} \right)^c \]

where \( M_L \) was the instantaneous natural mortality rate of a fish of length \( L \), \( M_r \) was the instantaneous natural mortality rate of a fish of reference length \( L_r \), and \( c \) was the allometric exponent of size-dependent mortality relationship. Lorenzen (2000) determined \( c = -1 \) to be the best fit model to describe the allometry of mortality, and values for \( c \) reported by Lorenzen (1996a) for unexploited lakes were in this range. Thus, in unexploited systems natural mortality is inversely proportional to length (Lorenzen 2005).

\[ M_L = M_1 \left( \frac{1}{L} \right) \]

where \( M_1 \) is defined as the natural mortality per unit length (i.e., \( L_r = 1 \text{ cm} \)) and is usually around 15 for recruited wild fish (Lorenzen 2005). Note that \( M_1 \) for unrecruited fish (age-0) is much higher than for recruited fish (Lorenzen 2005). Based on mortality estimates from the literature when size/age was known, we found that \( M_1 \approx h_{\text{max}} \) across a number of species (Figure S5).

While we did not do an exhaustive literature review, this finding is supported by other studies. In his seminal paper, (Pauly 1980) found that natural mortality was dependent on growth parameters estimated from the von Bertalanffy growth model, and more recent investigations found that size-dependent mortality was also dependent on asymptotic size and the von Bertalanffy growth rate parameter (Lorenzen 2000, Gislason et al. 2010, Charnov et al. 2013); parameters that when combined represent the growth rate near \( t_0 \) (Gallucci and Quinn 1979). Thus, we assumed that \( M_1 = h_{\text{max}} \) when deriving our density-dependent allometric mortality relationship.

Size-dependent mortality is often assumed to be the result of how susceptible fish are to gape-limited predators (e.g., Askey et al. 2013), but might also result from larger fish having an exploitative advantage over a common resource (Tonn et al. 1994). Our model assumes that mortality is a function of fish size and the density of fish in the system, which reflects the density of predators as well as competitors, given the cannibalistic nature of the species modelled. Density-dependence in the size-dependent mortality relationship was introduced by making $c$ density-dependent. This assumes that the mortality rate of large fish will likely change very little, if at all, with density, but predator density will affect smaller fish. By having the effect of density on mortality dissipate with size, we assume that there are fewer predators of sufficient size to prey upon larger fish and that larger fish have an exploitative advantage over resources (e.g., they can have riskier foraging behaviour).

Density-dependent mortality is often assumed to be more important in the regulation of the early life stages in fish, while density-dependent growth is thought to be more important in the later life stages (Lorenzen 2008). Our model reflects this finding while avoiding a knife-edge from density-dependent to density-independent survival. However, studies have documented density-
dependent survival in age-1 fish (e.g. Post et al. 1999), and Johnston et al. (2007) documented density-dependent survival in mature bull trout (*Salvelinus confluentus*), which was more severe in the younger (smaller) adults spawning for the first time. Thus, density-dependent mortality in later life stages is not unsupported.

To derive the density-dependent relationship for $c$ we first needed to determine a fixed pivot point of the size-mortality curve. We used $M_{r,t_{\text{max}}}$ as the reference mortality rate and $L_{\text{max}}$ as the reference length at this fixed point, because fish at this size are assumed to have density-independent mortality. $M_{r,t_{\text{max}}}$ was calculated as follows,

$$M_{r,t_{\text{max}}} = M_i \left( \frac{L_{\text{max}}}{L_{r,1\text{cm}}} \right)^c = h_{\text{max}} \left( \frac{L_{\text{max}}}{1} \right)^{-1} = \frac{h_{\text{max}}}{L_{\text{max}}},$$

assuming that $c = -1$ to represent an unexploited system. Thus,

$$M_L = M_{r,t_{\text{max}}} \left( \frac{L}{L_{\text{max}}} \right)^c.$$

Assuming that $c = -1$ at the equilibrium effective density when the population is unfished and unstocked, we were able to generalize a relationship for determining $c$ across species by using relative effective density $D_{rel}$ rather than absolute effective density $D_{L^2}$. Relative effective density was calculated as,

$$D_{rel} = \frac{D_{L^2} - D_{\text{Equilib}}}{D_{\text{Equilib}}},$$

Where, $D_{\text{Equilib}}$ was the unexploited equilibrium effective density achieved prior to the introduction of fishing or stocking. Relative effective density influenced $c$ as follows,

$$c = \frac{\ln[1 + (1 - \Upsilon)D_{rel}]}{\ln(M_{r,t_{\text{max}}})} - 1$$

where, $\Upsilon$ was a constant derived from combining density-dependent growth and survival relationships from Post et al. (1999). We informed our model using published relationships on density-dependent growth and growth-dependent mortality of rainbow trout (*Oncorhynchus mykiss*) reported by Post et al. (1999), because of the exceptional quality of the data.

Post et al. (1999) report two relationships in their study, density-dependent growth and growth-dependent mortality for three size classes of age-1 rainbow trout.
\[ h_g = \gamma_{1,g} + \Lambda_{1,g} D_L \]

\[ M_g = \gamma_{2,g} + \Lambda_{2,g} h_g \]

Where, \( h_g \) and \( M_g \) were the somatic growth rate and the natural mortality rate of a size-class \( g \), respectively, \( \gamma_{1,g} \) and \( \gamma_{2,g} \) were the intercept terms, and \( \Lambda_{2,g} \) and \( \Lambda_{2,g} \) the slope terms, and \( D_L \) is the effective density of the population. Combining these two equations rendered,

\[ M_g = \gamma_{2,g} + \Lambda_{2,g} (\gamma_{1,g} + \Lambda_{1,g} D_L) . \]

As there were no significant differences among slopes or intercepts for three size classes in the growth-mortality relationships presented by Post et al. (1999), for simplicity we averaged all coefficients across the three size classes and modified them from specific rates to annual rates assuming 138 days (average period from stocking to removal). Thus,

\[ M = \gamma + \Lambda D_L \] where \( \gamma = \gamma_2 + \Lambda_2 \gamma_1 \) and \( \Lambda = \Lambda_2 \Lambda_1 \).

Assuming \( L = h_{max} \), the average size of the fish at the beginning of the year, and that \( L_r = L_{max} \), a length at which mortality is fixed,

\[ M = \gamma + \Lambda D_L = M_{r,L_{max}} \left(\frac{h_{max}}{L_{max}}\right)^c = M_{r,L_{max}}^{(c+1)} , \]

because \( M_{r,L_{max}} = \left(\frac{h_{max}}{L_{max}}\right) \).

Solving for \( c \)

\[ c = \frac{\ln(\gamma + \Lambda D_L)}{\ln(M_{r,L_{max}})} - 1 \]

To make this equation general across species, one can assume that densities are relative to some reference density \( D_L^r \), and substitute relative effective densities \( D_{rel} \) for \( D_L \), where

\[ D_{rel} = \frac{D_L - D_L^r}{D_L^r} . \]

If one assumes that the reference effective density is the density at which \( c = -1 \), then \( M = 1 \) for a fish of size \( h_{max} \). Thus,
\[ M = \Upsilon + \Lambda D_{L_x}, \text{ so} \]

\[ D_{L_x} = \frac{1 - \Upsilon}{\Lambda}. \]

One can use this to simplify the calculation of \( c \), as follows

If \( D_{L_x} = D_{rel}D_{L_x} + D_{L_x} = D_{rel}\left(\frac{1 - \Upsilon}{\Lambda}\right) + \frac{1 - \Upsilon}{\Lambda}, \)

then \( c = \frac{\ln(\Upsilon + \Lambda D_{L_x})}{\ln(M_{r,t_{max}})} - 1 = \frac{\ln\left[\Upsilon + \Lambda\left(D_{rel}\left(\frac{1 - \Upsilon}{\Lambda}\right) + \frac{1 - \Upsilon}{\Lambda}\right)\right]}{\ln(M_{r,t_{max}})} - 1, \)

which can be simplified to

\[ c = \frac{\ln\left[\frac{1 + (1 - \Upsilon)D_{rel}}{\ln(M_{r,t_{max}})}\right]}{1}. \]

Calculating \( c \) for the range of effective densities reported in Post et al. (1999) (0 to 4.4 \( 10^{-5} \) cm\(^2\) ha\(^{-1}\)), the predicted values for \( c \) fell within the range of -0.26 to -1.42. Given the 95% CI for \( c \) reported by Lorenzen (1996a) for unexploited lakes (adjusted from weight to length by multiplying by 3) were around -0.67 to -1.07, this range for exploited lakes was considered to be reasonable.
Model sensitivity to density-dependent mortality in age-1 and older fish

Given the uncertainty associated with the density-dependent mortality relationship for age-1 and older fish, we investigated the model outcomes in the absence of density-dependence in this relationship (i.e., \( c \) was held constant at -1). Results were qualitatively similar (Figures S6-S8). Fingerling stocking still resulted in the greatest total density and fry stocking generally the least, at similar stocking expenditures. Stocking adults resulted in the highest density of fish vulnerable to capture and the highest catch rates. Stocking only resulted in greater net WTP than the use of MLLs alone when the population was overexploited or natural reproduction did not occur. The cost of producing fish that survive to age-3 was greatest for fry and least for adults. The net economic benefit of stocking only exceeded the use of MLLs alone when populations were overexploited or would not otherwise exist. In such cases, low stocking rates and high latent fishing pressure resulted in the greatest net benefit.

There were, however, some small qualitative differences and some quantitative differences that are worth highlighting. When stocking carp into lakes with high latent fishing pressure (10 licenses ha\(^{-1}\)), we did not find that under liberal length limits fingerling stocking resulted in greater vulnerable fish density and catch rates (Figure S7). This occurred because there was no compensatory reduction in fingerling survival in response to the low density of predators in the system caused by heavy exploitation. For similar reasons, we did not find situations where the survivor costs of fingerlings were cheaper than the production of adults when density-dependent mortality in age-1 and older fish was absent (Figure S7).

Some quantitative differences of note relate to fish abundance. Unlike the density-dependent scenarios, when density-dependent mortality in age-1 and older pike was absent, even low latent fishing pressure was sufficient to threaten the sustainability of pike populations under liberal MLLs, because the population was unable to compensate for fishing mortality through changes in small fish survival (Figure S7). This also resulted in the population being unsustainable under higher MLLs in the unstocked scenario. In comparison to the density-dependent scenarios stocking high densities of pike fingerlings and adults resulted in greater fish densities and similar or greater catch rates, because there was no density-dependent regulation limiting the survival of these stocked fish and overall abundance (Figure S7). By contrast, stocking low densities of pike or not stocking resulted in lower densities than the density-dependent scenarios, because there was no compensatory response. Carp had lower densities and catch rates when density-dependent survival was absent (Figure S7). In terms of socioeconomic outcomes, survivor costs were higher for both pike and carp in the absence of density-dependent survival. For pike, the lack of density-dependent survival resulted in higher net WTP and net benefits, and the MLL at which the net benefit of stocking exceeded the net benefit of only using MLL was higher, in the high latent effort scenarios (Figure S7) The inability for the population to compensate for high fishing mortality through changes in natural mortality resulted in populations being unsustainable at higher MLLs.
Figure S6. The effects of stocking pike fry (2 cm), fingerlings (20 cm) and adults (age-2, 35-40 cm) at a range of densities across a range of minimum-length limits (MLLs) and a range of stocking densities (Table S1) calibrated to reflect the range of annual expenditures (0-154 € ha$^{-1}$) on pike stocking by angling-clubs in Germany (Table 2, scenario 1). Effects of stocking and MLLs on total fish density, density of vulnerable fish (age-2 and older fish at year end), catch rates, change in angler welfare (net willingness-to-pay, WTP) relative to the unregulated and unstocked case, per capita costs of stocked fish surviving to a vulnerable size (their third birthday), and net economic benefit, were evaluated. Latent fishing pressure was moderate (5 licenses ha$^{-1}$). Very close contour lines indicate rapid changes in the performance measure. Model conditions were identical to those of used to produce Figure 2, with the exception that density-dependent mortality of age-2 and older fish was absent.
Figure S7. The effect of stocking pike and carp fry, fingerlings and adults at densities that represent annual stocking expenditures of 0, 5, and 100 € ha$^{-1}$ (Table 2, scenario 2). For pike, these expenditures corresponded to densities of 0, 159 and 3174 fry ha$^{-1}$ (2 cm), 0, 3 and 58 fingerlings ha$^{-1}$ (20 cm), and 0, 1 and 24 adults ha$^{-1}$ (age-2), respectively, and for carp to densities of 0, 98 and 1967 fry ha$^{-1}$ (4 cm), 0, 8 and 155 fingerlings ha$^{-1}$ (15 cm) and 0, 1 and 23 adults ha$^{-1}$ (40 cm), respectively. Effects of stocking and MLLs on total fish density, density of vulnerable fish (age-2 and older fish at year end), catch rates, change in angler welfare (net willingness-to-pay, WTP) relative to the status quo, per capita costs of stocked fish surviving to a fully vulnerable size (their third birthday), and net economic benefit, were evaluated under low and high latent fishing pressure (1 and 10 licenses ha$^{-1}$, respectively). The grey areas indicate situations where the benefit to anglers was not greater than the status quo (no stocking and no MLL), or where there was no positive net economic benefit. Model conditions were identical to those of used to produce Figure 4, with the exception that density-dependent mortality of age-2 and older fish was absent.
Figure S8. The sensitivity of pike model outcomes to changes in model assumptions, under annual stocking expenditures of 0, 5, and 100 € ha⁻¹, and moderate latent fishing pressure, 5 licenses ha⁻¹ (Table 2, scenarios 3 and 4). For pike, these expenditures corresponded to densities of 0, 159 and 3174 fry ha⁻¹ (2 cm), 0, 3 and 58 fingerlings ha⁻¹ (20 cm), and 0, 1 and 24 adults ha⁻¹ (age-2), respectively. The left column represents the unmodified, base model (Table 2, scenario 1). The second and third columns represent lower stock productivity (α/2, Table 2, scenario 3A) and lower habitat capacity resulting in stronger density-dependence (2·β, Table 2, scenario 3B), respectively. The fourth and fifth columns represent the reduced fitness scenario (relative survival of stocked age-0 fish was 50%, of stocked adults was 90%, and relative reproductive success was 56% compared to wild fish), with zero heritability (Table 2, scenario 4A), and 100% heritability (Table 2, scenario 4B). The grey areas indicate situations where the benefit to anglers was not greater than the status quo (no stocking and no MLL), or where there was no positive net economic benefit. Model conditions were identical to those of used to produce Figure 5, with the exception that density-dependent mortality of age-2 and older fish was absent.


