Managing fish or anglers: understanding trade-offs among biological, social and economic objectives in recreational fisheries using a bioeconomic model

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ABSTRACT

Fish stocking and harvest regulations are used in recreational fisheries to maintain or enhance fisheries, but their effectiveness has rarely been evaluated using a bioeconomic model. We evaluated how stocking various fish densities and sizes (fry, fingerlings and adults) performed relative to minimum-length limits alone in terms of augmenting the fish population and catch rates, increasing angler benefits, minimizing per capita stocking costs, and producing a positive net economic benefit. Our model mechanistically integrated the dynamics of the angler and fish populations. The angler model was calibrated to a choice model from German anglers and the biological model to two model species; naturally-reproducing northern pike (*Esox lucius*) and non-recruiting common carp (*Cyprinus carpio*). We found that the benefits of stocking depended on the performance measure, the species, the stocking strategy, and latent fishing pressure. Stocking often augmented the overall fish population and catch rates, but did not necessarily increase angler welfare and rarely lead to net economic benefits. In fact, stocking was only economically advisable when natural recruitment was impaired or lacking completely, and stocking rates were low. Otherwise, minimum-length limits generated similar benefits without incurring the costs of stocking. Stocking should only be considered when sufficient numbers of anglers benefit from stocking to offset the costs, and stocking adults at low densities is better than stocking fry or fingerlings. Our findings question common stocking practices of many recreational fisheries and demonstrate how a utility-based approach to measuring performance is well suited to assess trade-offs in fisheries management.

Keywords – bioeconomic model, cost-benefit analysis, discrete choice model, fish stocking, harvest regulations, stock enhancement

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INTRODUCTION

Fish stocking and harvest regulations have often been used in recreational fisheries to create, maintain or enhance fish populations and to increase angler satisfaction (Cowx 1994, Welcomme 2001, Molony et al. 2005, Halverson 2008, FAO 2012). These tools serve various purposes ranging from ecological conservation to socioeconomic benefits (Lorenzen et al. 2012). Fish stocking acts by directly increasing the supply of fishes, while harvest regulations manage the demand side by controlling harvest mortality (Welcomme 2001).The relative effectiveness of these two management approaches has rarely been comprehensively and systematically evaluated from both an ecological and social perspective (Cowx 1994, but see Lorenzen 2005, Johnston et al. 2010, Rogers et al. 2010, Camp et al. 2014).

From a fisheries biological perspective, stocking is not always successful at enhancing stocks and fishing quality (Cowx 1994, Hilborn 1999, Molony et al. 2005, Lorenzen et al. 2012). Limited recruitment and carrying capacity due to poor habitat quality, compensatory changes in growth and survival of fish populations, and a lack of local adaptation may all limit the ability of stocked fish to survive (Cowx 1994, Lorenzen 2005, Lorenzen et al. 2012). Natural recruitment is an important factor determining stocking success, because in stock-enhanced fisheries, ones where fish are stocked into a naturally recruiting population, stocked fish and wild conspecifics are forced into competition, and as a result size at stocking determines the potential for additive effects (Lorenzen 2005, Rogers et al. 2010, Lorenzen et al. 2012, Arlinghaus et al. 2015). Culture-based fisheries, where fish are stocked into systems in which natural recruitment is absent, have generally been found to have more predictable outcomes. Stocking can also have deleterious effects on wild fish populations through, for example, introduction of disease, changes in genetic diversity, trophic changes, loss of local gene pools, replacement of wild stocks by hatchery origin fishes, or alteration of water quality through bioturbation (Cowx 1994, Welcomme 2001, Molony et al. 2005, Vilizzi et al. 2015). All such impacts have to be considered when judging the relative benefits of stocking versus size-based harvest limits (FAO 2012).

From a social perspective, the effects of stocking or size-based harvest limits on angler welfare (i.e., satisfaction or utility) are generally unknown, because integrative models linking complex fish population biology and the dynamics of anglers are generally lacking (Cole and Ward 1994, Johnston et al. 2010, Fenichel et al. 2013a, but see Camp et al. 2014). Most available models dealing with stocking or size-limits only consider catch-related outcomes (e.g., catch rates and fish size) and tend to ignore or simplify angler dynamics (Post et al. 2003, Allen et al. 2009, Rogers et al. 2010). However, both catch-related and non-catch-related (e.g. regulations, license fees, crowding), attributes contribute to angler satisfaction and welfare (Cole and Ward 1994, Hunt 2005, Arlinghaus et al. 2014). Moreover, the importance of certain aspects of the fishing experience can differ substantially among anglers (Aas et al. 2000, Oh et al. 2005, Beardmore et al. 2015). As a result, it is not straightforward how changes in the fish population and catch-related attributes due to stocking or size-based harvest regulations will influence angler utility, behaviour, and the resulting distribution of anglers among multiple sites (Askey et al. 2013). Any improvements in fishery quality resulting from the use of these management tools, or even simply the act of stocking, itself, may attract increased angling effort and new anglers (e.g., Moring 1993, Johnson and Carpenter 1994, Loomis and Fix 1998, Cowley et al. 2003, Patterson and Sullivan 2013). Such changes could offset any long-term potential benefits (Parkinson et al. 2004), yielding a "success breeds failure" pathology (Cox and Walters 2002). Moreover, the benefits of stocking to fish populations (conservation) or anglers (utility) likely depend not only on the species but also on the size and density of fish stocked (Cowx 1994, Lorenzen 1995). Thus, given the lack of integrative social-ecological models in the fisheries literature, it is unclear under which conditions stocking (culture-based or stock enhancement) is likely to be more effective than using standard harvest regulations (e.g. minimum-length limits) to achieve management objectives.

How one defines the benefits of stocking or any other management action depends strongly on the underlying objectives and the trade-offs inherent in any fisheries management problem (Walters and Martell 2004, Johnston et al. 2010, Gwinn et al. 2015). Biological objectives can include conserving or enhancing existing fish populations, or creating new stocks that would not exist otherwise (Cowx 1994, Welcomme 2001). Biological objectives are often directly related to social objectives such as improving fishing quality and thereby increasing the welfare of current anglers or attracting new anglers to the system (Cowx 1994, Welcomme 2001). A single-lake bioeconomic model developed by Johnston et al. (2010, 2013) showed that regulations that maximize angler well-being can often also result in biologically sustainable fisheries. However, social objectives and conservation objectives may also conflict (Hilborn 2007, Camp et al. 2014). For example, high minimum-size limits might effectively protect stocks from overexploitation and elevate their abundances, but they might also alienate anglers interested in harvesting fish and lead to loss of angler welfare (Johnston et al. 2011). In practical terms, given different objectives and possible trade-offs, effective models of recreational fisheries have to be explicit about the objective-dependent performance measures used to judge management successes.

Management actions, such as stocking or size-based harvest limits, not only have potential benefits but they also have costs. Due to budget limitations, managers must consider how to allocate scarce resources among multiple management actions to produce the greatest benefits (Cole and Ward 1994). The financial costs of stocking include all the costs of culturing the fish, which will increase with fish size and stocking density (Santucci Jr and Wahl 1993, Loomis and Fix 1999, Lorenzen 2005). No such obvious direct financial costs are present when managers implement harvest limits, but there can be associated costs, such as the cost of enforcement. Furthermore, both stocking and harvest-limit changes may impose opportunity costs that exceed financial costs (Edwards 1991, Loomis and Fix 1999). Thus, it is prudent to compare the benefits and costs of any management action. One way to do this is to look at cost effectiveness. Studies related to stocking have looked at strategies (e.g., the combination of fish size and density stocked) to minimize the per-capita cost of fish surviving to a predetermined life-stage or to recruitment into the fishery catch (e.g., Santucci Jr and Wahl 1993, Wiley et al. 1993, Santucci et al. 1994, Leber et al. 2005, Jacobson and Anderson 2007). This approach allows direct comparison of different management measures to determine optimal stocking strategies (Aprahamian et al. 2003), but assumes that augmentation is directly proportional to angler satisfaction, which may not be the case (Cole and Ward 1994, Arlinghaus et al. 2014). Using such an approach, leaves unclear the degree to which augmentation (which is a supply effect) contributes to angler benefits (which is a demand effect); an interaction of particular interest to managers wanting to maximize angler well-being (Cole and Ward 1994).

To determine if changes in management policies produce a net economic benefit, one needs to determine if expenditures are matched by increased benefits to anglers (Dalton et al. 1998, Loomis and Fix 1999). Such a comparison requires the valuation of angler benefits and costs to be in a common monetary unit (Edwards 1991, Cole and Ward 1994). Angler utility can be measured using a number of techniques that determine the marginal utility gain (or loss) from fishing (Cole and Ward 1994, Loomis and Fix 1998, Cooke et al. 2009), for example stated and revealed preference studies (McFadden 1974, Hanemann 1984, Adamowicz et al. 1994, Cooke et al. 2009). Net willingness-to-pay (WTP), measured as the difference between scenarios with and without changes in stocking or harvest regulations, estimates a monetary value from the marginal utility derived from changes in fishery quality (Hanemann 1984, Adamowicz et al. 1994, Cole and Ward 1994). Net WTP, also referred to as consumer surplus (Edwards 1991, Cole and Ward 1994, Loomis and Fix 1999), is often used in benefit-cost analyses applied to recreational resource management (Edwards 1991, Cole and Ward 1994, Dalton et al. 1998, Loomis and Fix 1999). Thus, with utility-based models, benefit-cost analyses of various management tools can be completed that consider dynamic angler responses to the implementation of new policies. Few studies have linked angler responses to changes in angling quality as a result of stocking (but see Cowley et al.

2003, Fenichel et al. 2010, Camp et al. 2014), or other management tools such as size-limits (Johnston et al. 2010, 2013, Johnston et al. 2015). Furthermore, rigorous benefit-cost studies that link mechanistic models of angler preferences to biological conditions to determine the economic feasibility of stocking policies versus the use of size-based harvest limits are generally lacking.

The study's objective was to improve our understanding about the usefulness of stocking relative to harvest regulations, (i.e., minimum-length limits, MLLs), commonly used in recreational fisheries management (FAO 2012), and to evaluate the benefits and costs associated with the use of these management measures. Given the social-ecological complexity both in the fish population and fish-angler interactions, it is not trivial to determine the benefits accurately. Only by using an integrated model that jointly accounts for the dynamics of the angler population and the biological dynamics of the stock-enhanced fish population, can the conditions under which stocking represents an improvement over MLLs or other regulations be determined. We constructed an integrated bioeconomic model, that was calibrated to empirical data for both exploited fish stocks and anglers, to examine how well a range of stocking strategies (i.e., fish sizes and densities) and MLLs traded off among biological, social and economic management objectives. We calibrated the model to represent two freshwater fish populations, naturally-reproducing northern pike (*Esox lucius*) and non-naturally recruiting common carp (*Cyprinus carpio*). Pike was chosen because of its circumpolar distribution in the northern hemisphere and its popularity as a target species among anglers in both North America (Paukert et al. 2001) and Europe (Wedekind et al. 2001, Arlinghaus and Mehner 2004, Stålhammar et al. 2012), and because it is regularly stocked to enhance fisheries (Wedekind et al. 2001, Margenau et al. 2008, Hühn et al. 2014). Despite carp being considered a pest in North America and Australia, carp was chosen because of its importance as a culture-based recreational fishery throughout much of Europe (Wedekind et al. 2001, Arlinghaus and Mehner 2003, Vilizzi et al. 2015). In central Europe, carp populations depend almost entirely on stocking because they do not naturally recruit there (Mehner et al. 2004). We calibrated the bioeconomic model to a mechanistic model of angler behaviour as a function of multiple attributes of the fishing experience (Arlinghaus et al. 2014) to evaluate the following questions; i) under what conditions does stocking provide biological, social and economic benefits beyond the use of MLLs and what are the trade-offs among objectives?, ii) what are the optimal stocking strategies in terms of fish size and density in naturally reproducing and non-reproducing populations?, and iii) how sensitive are model predictions to changes in assumptions about habitat quality, relative fitness of stocked fish, and the social importance of stocking? We aimed at providing strategic insights about the trade-offs inherent in stock enhancement and recreational fisheries management rather than predictions for a particular fishery.

METHODS

The potential effects of stocking and harvest regulations, specifically MLLs on biological, social, and economic aspects of the recreational fishery were investigated using an integrated bioeconomic model adapted from our earlier work (Johnston et al. 2010, 2013), to incorporate a stock-enhanced fish population as introduced by Lorenzen (2005). The model included three main components, a deterministic age- and size-structured biological sub-model to describe the fish population dynamics, a social sub-model to describe angler effort dynamics, and a management component, which allowed for different MLLs, stocking sizes and stocking densities, to be investigated (Figure 1). We evaluated how well different sizes of stocked fish – fry, fingerlings and adults – performed relative to various MLLs in terms of achieving biological, social and economic management objectives for both naturally-reproducing northern pike and non- recruiting common carp populations in a single-lake fishery. Six performance measures were evaluated and resulting trade-offs were analysed qualitatively. In addition to these six performance measures, age structure and composition (wild vs hatchery origin fish) of the fish population was examined for some simulations. Simulations were run for 100 years prior to the commencement of fishing or implementation of management policies such as stocking and then run for a further 50 years to allow the model reach a new equilibrium. 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 Table A1.

Biological sub-model

The biological sub-model, which described dynamics of a stock-enhanced fish population, 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. 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 (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. To create a more realistic size distribution and simulate the cumulative effects of differential size-dependent mortality (Walters and Martell 2004), 11 size classes (growth trajectories) within an age class were modelled. For simplicity, stocked and wild fish were assumed to have the same growth rates. Maturation was assumed to be size and age dependent (Table 1, eqn. 3a). Reproduction was a function of female mass (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, Table A1 ρ). In the case of common carp, natural recruitment was assumed to be zero.

Survival of larvae to age-1 was assumed to be size and density dependent (Table 1, eqns. 4a-f and 5a-d). The representation of these processes differed from our earlier applications (Johnston et al. 2010, 2013, Johnston et al. 2015) to better represent the outcomes of stock enhancement using fry or juveniles. We 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 were described independently, allowing for effects of the stocking of young-of-year (YOY, fry or fingerlings) on density-dependence to be accounted for. 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-type recruitment is more representative of early survival for pike (Johnston et al. 2013) and carp (Brown and Walker 2004) (see supplement for derivation). By incorporating both naturally spawned (wild and hatchery origin) and stocked fish in the same density-dependent process, all fish experienced 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). In the pre-stocking phase (Table 1, eqns. 4a-f), wild and hatchery origin larvae underwent the same density-dependent bottleneck. During this phase it was assumed a proportion of hatchery larvae could transition to wild strain fish due to natural selection similar to Lorenzen (2005) (Table 1, eqn. 4f, Table A1 h^2), and the potential for differential survival of age-0 hatchery fish relative to age-0 wild fish was included in the model (Table 1, eqn. 4f, Table A1), because empirical data has shown stocked fishes can have lower relative 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 experienced further density-dependent survival, but at a reduced intensity because fish were larger and thus escaped the strong size- and density-dependent mortality that small fish experienced. 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 YOY 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 a relationship described by Lorenzen (1996, 2000) (Table 1, eqn. 6b). To introduce density-dependence, 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 size (see supplement for derivation). Thus, changes in density had large effects on the natural mortality rate of small fish but minimal impacts on larger fish. We informed our model in this context 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 (see supplement for derivation). Incorporating density-dependence in the post-recruitment survival allowed for increased mortality of small fish from predation by, and competition with, fish stocked at larger sizes and older ages than YOY. In scenarios in which recruited 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 (Table 1, eqn. 6a). The possibility of differential survival of fish of hatchery origin relative to wild fish beyond the YOY stage was explicitly included in the model as well (Table 1, eqn. 6f, Table A1 γ_2).

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, Figure S1), as is typically assumed in recreational fisheries models (Post et al. 2003, Arlinghaus et al. 2009, Allen et al. 2013), and MLLs were used to determine which fish were legally harvestable (Table 1, eqn. 6i). Assuming an unlimited daily bag limit (DBL), which is common for pike in North America (Paukert et al. 2001), all fish that were 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 also 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, Table A1 $d_{\max}$). Note that our use of the term fishing quality encompasses all dimensions that affect the utility of anglers, including: expected catch rate, average size, catch rate of trophy fish (as per Arlinghaus et al. 2014, fish larger than a threshold size L_T , Table A1) the number of other anglers seen while fishing (a measure of crowding), MLL, DBL, license fees to fish within the region, 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). The benefits anglers derived from each fishery attribute, called part-worth utilities (PWUs) (Figure 2), were summed to determine the overall utility gained from fishing (Table 1, eqn. 7a). Anglers responded dynamically to the perceived quality of the fishery. The probability of fishing was determined primarily by the utility experienced in the previous year (Table 1, eqn. 7a-b), but a fishing-behaviour persistence term (Table 1, eqn. 7c, Table A1 φ) 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 mechanistic sub-model of angler behaviour presented by Johnston et al. (2010, 2013) was adapted in the present study by including a function to describe angler behaviour that was informed empirically using a stated choice experiment conducted on anglers in northwestern Germany in the state of 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 to the present study, the parameter values (Table 2) differ somewhat from those reported by Arlinghaus et al. (2014) because the choice model was reanalyzed assuming that the PWU function of MLL (Table 1, eqn 9f) was quadratic in form rather linear, because the quadratic form best described the data for pike and carp. Furthermore, Arlinghaus et al. (2014) found that the two stocking attributes mentioned above did not have a significant influence on angler utility, because of heterogeneity among anglers related to these attributes.To account for this non-significance, in most simulation scenarios for pike, we assumed that anglers did not know that fish were stocked and were not able to identify fish of hatchery origin from wild fish in their catches. By contrast, for carp that very rarely recruit naturally in central and northern Europe, we assumed that anglers were aware that carp were stocked and that any fish caught was of hatchery origin. The parameters from the choice model were species-specific and for simplicity represented the average angler as estimated by (Arlinghaus et al. 2014). Hence, angler behaviour differed based on the species targeted, but all anglers were assumed to behave the same when fishing for the same species.

While the choice model allowed for variation in license cost, DBL, preference for target species, and stocking frequency, these aspects were not investigated in this study. Thus, levels of these attributes were held constant. Our model was designed to represent a single-lake fishery, such as those run by angling clubs in central Europe or by commercial put-and-take operators offering angling experiences. Managers of such fisheries have control over input or output regulations as well as over what size and density of fish to stock, without involvement of public agencies (Daedlow et al. 2011).

Range of MLLs, stocking strategies, and performance measures examined

In our model scenarios, MLLs ranged from zero to complete catch-and-release (i.e., the maximum size fish could achieve, Table A1). Fry, fingerling, or two-year old fish (referred to as adults) were stocked at a range of densities (Table 2) from no stocking (zero) to some of the higher densities (95 percentile) reported by a survey of over 2000 angling clubs (61% response rate) throughout Germany (Arlinghaus et al. 2015). To be realistic, two datasets were used to inform the levels of stocking tested in the model, the German-wide dataset, and information (including fishing diaries) gathered from anglers from angling clubs in Lower Saxony that participated in the Besatzfisch project, an interdisciplinary research project evaluating the practice of stocking from an ecological, economic and social perspective (Arlinghaus et al. 2015). In pike scenarios, fry, fingerlings and adults were assumed to be 2 cm, 20 cm, and age-2 (35-40 cm), respectively, and in carp scenarios 4 cm, 15 cm, and age-2 (40 cm), respectively. These sizes were commonly reported in the datasets, and complimented the sizes used in stocking experiments carried out by Besatzfish researchers (Arlinghaus et al. 2015). For comparability, the range of stocking densities modelled for each stocking size were chosen to reflect the range in annual stocking expenditures reported by angling clubs across Germany, mean 50 € ha^{-1} yr^{-1} for pike (range 3–150 € ha^{-1} yr^{-1}, 5th and 95th percentile respectively), and mean 210 € ha^{-1} yr^{-1} for carp (range 7–710 € ha^{-1} yr^{-1}, 5th and 95th percentile respectively). Thus, for each species the range of stocking densities tested (Table 2) resulted in the associated range in stocking costs being similar for all sizes stocked, thereby allowing a direct comparison of the effect of varying stocking sizes for the same monetary investment. Average angler density in Germany and in the five study clubs involved in the Besatzfisch 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.

We considered six main performance measures (see Table 1). Two measures related to biological and conservation objectives: 1) augmentation (i.e., increased density) of the overall population, and 2) the density of fish surviving until their third birthday (age-2 and older fish at the end of the year) when they were fully vulnerable to the fishery (Figure S1). To address social objectives, we estimated 3) 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, net WTP. 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), as well as 6) an integrative measure of the net economic benefit (aggregated angler welfare minus costs) for each of the policies we examined. Average angler welfare (angler benefit) at equilibrium was measured by the net average willingness-to-pay (WTP), a measure which quantifies the change in satisfaction 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 determine net economic benefit (benefit minus cost), benefit was measured by aggregated social welfare, the sum of individual angler welfare (WTP) across all licensed anglers, and financial cost was the cost of stocking. Stocking costs were determined based on empirical fish size-cost relationships estimated from Germany (Figure 3). We used these metrics to evaluate and implicitly rank policy outcomes. We also examined the size structure and composition (wild vs. hatchery origin) of the fish population in some scenarios to evaluate truncation effects from fishing and replacement of wild fish by hatchery origin fish.

Outline of analyses

In scenario 1 (Figure 4), we evaluated how well annually stocking differently sized fish – fry, fingerlings and adults – at a range of different densities compared to the use of a range of MLLs for achieving in relation to the six performance measures outlined above. This was done for both pike and carp, and latent fishing pressure was assumed to be moderate at 5 licensed anglers ha^{-1}.

Variations on the base scenario (1) were used to rank management strategies and investigate the sensitivity of outcomes to some of the model assumptions. In scenario 2 (Figure 4), the ranking of policies was determined for each of the performance measures and for both species, at low, average and high fishing pressures (1, 5, and 10 licenses ha^{-1}, respectively). The best management strategies were assumed to be the combination of stocking density and MLL that maximized the performance measure of interest.

In scenario 3 (Figure 4), we examined how a manager faced with a limited budget should best allocate resources among species, a more direct comparison among pike and carp was needed. Thus, we then examined model outcomes when stocking expenditures were the same for both species. We evaluated results at low (1 license ha^{-1}) and high (10 licenses ha^{-1}) levels of fishing pressure when range in stocking densities reflected low (5 € ha^{-1}) to moderate (100 € ha^{-1}) stocking costs for both species. For simplicity, in this and the following analyses we only present the upper and lower extremes, because intermediate values tested fell within the values presented.

Finally, for pike only, we examined how sensitive the model predictions were to modifications of some of the key model assumptions (i.e., beyond species, stocking strategy, and fishing pressure). In these scenarios (Figure 4, scenarios 4-6), we examined results for low and high stocking densities (the 5th and 95th percentiles, respectively) and average fishing pressure (5 licenses ha^{-1}). Four biological assumptions and two social assumptions were examined in three sets of scenarios. 1) In the first set of scenarios, we tested the hypothesis that stock enhancement may be more beneficial in habitats where natural recruitment is impaired (Rogers et al. 2010). To do this we examined two cases; one where the strength of density-dependence (Table 2 β) in the stock-recruitment relationship was doubled resulting in greater inter-specific competition and a reduction in habitat capacity (Figure 4, scenario 4A), and a second where the productivity parameter (Table 2 α) in the stock-recruitment relationship related to the slope near the origin was reduced by half (Figure 4, scenario 4B). In both cases, maximum recruitment was reduced. 2) In an additional set of scenarios (Figure 4, scenario 5A and B), the assumption of equal fitness of stocked fish and wild fish was relaxed in line with empirical data (Lorenzen 2006, Lorenzen et al. 2012, Hühn et al. 2014). Here, hatchery origin fish had reduced reproductive success, and reduced survival in both the juvenile and adult stages. These relative differences were parameterized from empirical data for pike stocking in natural ecosystems (see Hühn et al. 2014). In addition, we relaxed the base assumption that larvae produced by spawners of hatchery origin retained a hatchery origin phenotype (Table 1 eqn. 4f, Table A1 h^2 = 0), and tested the opposite extreme where all larvae produced by hatchery origin spawners were assumed to transition to wild type due to natural selection (Table 1 eqn. 4f, Table A1 h^2 = 1) (Lorenzen 2005). Thus, we examined two scenarios, one in which stocked fish have reduced fitness (Figure 4, scenario 5A), and a second in which stocked fish had reduced fitness but whose offspring evolved to wild-type fish in the F1 generation (Figure 4, scenario 5B). 3) Finally, we relaxed the assumption of the base scenarios for pike that anglers were unaware of stocking taking place. We examined what happened if we assumed that anglers were aware that pike stocking was occurring and that they could identify stocked and wild origin pike (Figure 4, scenario 6A), and a second scenario where anglers were aware of stocking but could not identify hatchery origin pike (Figure 4, scenario 6B). These scenarios were not examined for carp because it is highly unrealistic to assume wild recruitment of this species in central and northern Europe (Mehner et al. 2004). Thus, relative fitness scenarios were not applicable to carp because no wild fish existed. Furthermore, because carp did not occur naturally, anglers were assumed to know that they were stocked.

RESULTS

Outcomes of stocking vs. harvest regulations (MLLs)

In the base scenario (Figure 4, scenario 1), increasing MLLs generally increased overall pike density, although this pattern was least evident for fingerlings (Figure 5). Stocking also resulted in higher densities of fish overall – a pattern that increased with stocking density of all sizes stocked (Figure 5, left column). Overall fish densities were lowest when fry were stocked and highest when fingerlings were stocked (Figure 5). Small size classes experienced strong size- and density-dependent mortality. Thus, increases in fish density achieved by fry stocking was generally negligible compared to the effect of using high MLLs alone, because of the greater offspring production by surviving adult spawners. Only when

MLLs were small (< 40 cm) and the reproductive capacity of the wild stock was impaired did stocking fry increase overall fish density. By contrast, stocking pike fingerlings resulted in higher overall densities, regardless of MLLs, because fingerlings were sufficiently large to escape the strong density-dependent bottleneck that occurred in the earlier life stage. However, stocking fingerlings only increased densities of age-0 and age-1 fish (Figure S2). In fact, both fingerling and fry stocking had very little effect on the density of fish age-2 and older at the end of the year (Figure 5, second column), because of high size- and density-dependent mortality rates that small YOY experienced between stocking and their third birthday. Rather, when YOY pike were stocked, the density of age-2 and older fish – i.e., fish which were fully vulnerable to the fishery (Figure S1) – was largely dependent on the degree to which MLLs protected these larger fish from harvest. Protection from harvest by MLLs was similarly important for determining the effects of adult stocking on fish densities, but stocking density was also important. Stocking adult pike increased overall fish densities to intermediate levels compared to the other stocking sizes (Figure 5, left column) for three reasons, 1) because the density of adults stocked was much lower than the other sizes, 2) because these fish were mostly vulnerable to capture by fishing at the time of stocking (Figure S1), and 3) because offspring produced by stocked adults experienced the strong density-dependent bottleneck of early life. However, despite producing lower overall densities than fingerling stocking, stocking adults resulted in the greatest augmentation of the density of age-2 and older fish (Figure 5, second column), because stocked pike adults did not experience the strong size-dependent natural mortality that stocked YOY did.

The benefits of stocking to pike density, however, come at the cost of wild stock replacement with hatchery origin fish (Figure S2). Even at low stocking densities, stocked fingerlings and adults replaced of the majority of wild fish with hatchery origin fish. The effect was much less severe when fry were stocked in low densities but still resulted in major replacement of wild stocks at high stocking densities.

MLLs were important in moderating the magnitude of replacement effects, by protecting wild spawners and allowing them to contribute to the next generation.

Similar to the density effects just described, stocking pike had positive impacts on average catch rates. However, the catch-rate effects were much more pronounced and dependent on stocking density when adult pike were stocked relative to fry or even fingerlings, because stocked adult pike were immediately vulnerable to the fishery (Figure 5, third column). MLLs did not influence catch rates as much as they did fish densities, although low MLLs did result in the majority of stocked adult pike being harvested, essentially creating a put-and-take fishery. By contrast, stocked YOY pike were mostly invulnerable to the fishery due to their small size (Figure S1) and experienced much higher natural mortality rates before recruiting to the fishery. As a result, MLLs had little effect on the few stocked YOY pike that recruited to the fishery.

Despite large increases in pike catch rates due to stocking (e.g., adult stocking) in some cases, the average benefit to an angler, angler welfare (as measured by average net WTP), relative to the status quo (an unregulated and unstocked pike fishery) was largely uninfluenced by stocking pike of any size or density (Figure 5, fourth column). MLLs had more of an effect on net WTP, which initially increased and later decreased with increasing MLLs. Two reasons explain these contrasting outcomes. First, increased catch rates associated with stocking provided anglers with a diminishing marginal return (Figure 3), therefore they had little effect on angler welfare except when catch rates started out very low (e.g., when populations were highly overfished and unregulated). However, in such cases restrictive MLLs alone were sufficient to increase catch rates to levels beyond which additional increases in catch rates from stocking had little effect on angler welfare. Hence, for a large range of MLL, utility increases offered by enhanced catch rates due to stocking were low. Secondly, MLLs directly influenced angler welfare (Figures 3 and 5). High MLLs have a disutility, because they are perceived by anglers to constrain harvests, but intermediate MLLs are viewed positively, because they allow some harvest but offered some protection of fish from overharvest.

High stocking densities generally increased the per capita costs associated with stocked pike surviving to their third birthday (Figure 5, fifth column), because proportionally fewer fish survived due to size- and density-dependent mortality. By this metric, adult stocking was the most cost effective, followed by fingerlings, and finally by fry, which were the most expensive to produce. Survivor costs were generally highest when MLLs were low and fish were unprotected from harvest (< 40 cm), but decreased rapidly when MLLs reached 40 cm, and then slowly increased as MLLs increased due to density-dependent interactions. Furthermore, despite the effects of stocking pike on fish density, the net economic benefits of any stocking strategy were consistently negative when fishing pressure was moderate (5 licenses ha^{-1}) (Figure 5, right column). Only when stocking was absent did the use of MLLs up to about 75 cm produced a slightly positive net economic benefit (peaking at an MLL of 40 cm) at intermediate fishing pressures, and thus were considered superior to an unregulated case. The findings summarized in Figure 5 indicate that judging the value of stocking pike depended strongly on which performance metric was chosen and varied starkly between conservation and economic performance metrics.

Looking at results from the base scenario (Figure 4, scenario 1) for carp (Figure 6), we found several similarities but also important differences in the relative effects of stocking compared to MLL. Similar to pike, stocking carp fingerlings augmented the overall population the most and fry the least (Figure 6, left column). Likewise, stocking adult carp augmented the density of fish age-2 and older and increased catch rates the most, while stocking fry had the least effect in on these measures (Figure 6, second and third columns). Like pike, increased fish density and catch rate associated with stocking carp were generally greatest when large fish were protected from harvest (MLLs > 40 cm). However, the effect of MLLs on carp densities and catch rates was lower than it was for pike, while the effect of stocking density was higher. This was particularly evident when carp fry were stocked. By avoiding density-dependent competition with naturally recruited YOY, similar numbers of fish recruited at a given stocking density, and these numbers were largely unaffected by MLLs because carp fry were too small to be vulnerable to the fishery. Consequently, carp fry also augmented stock densities, resulting in a corresponding increase in carp catch rates relative to the unstocked baseline.

As for pike, MLLs were more important for determining average angler welfare (net WTP) than variation in stocking size or number (Figure 6, fourth column), because of aversion of carp anglers to restrictive MLLs. However, stocking carp increased angler welfare (Figure 6) more than stocking pike did (Figure 5), largely due to the extreme disutility of the base scenario in which no carp were stocked and thus no carp population existed. The per capita costs of fish surviving until their third birthday were generally much lower for carp than pike. Like pike, carp fry were least cost effective to stock, but the most cost effective stocking size was situation dependent. Low densities of fingerlings were generally most cost effective, but as stocking densities increased, adults became more cost effective (Figure 6, fifth column). While changes in survival costs for carp were not as extreme as they were for pike, survivor costs for carp mirrored those for pike, increasing with stocking density, and when MLLs were around 40 cm before decreasing slightly again at higher MLLs. As in the pike case, the net economic benefit of stocking carp were similar regardless of size stocked and were only slightly influenced by MLLs (Figure 6, right column). However, unlike pike where stocking generally generated a net economic cost, a net benefit was achieved at low carp stocking densities and moderate fishing pressure. Yet, as the stocking density of carp increased, the net benefit strongly diminished as angler welfare from carp fishing was not sufficient to offset costs associated with high carp stocking densities. Hence, at moderate fishing densities the economically best strategy would be to stock carp of any size at low densities with no or very low MLL while from a biological or catch rate perspective, stocking large carp at high densities would be advised. These results, similar to the pike case, allude to the important trade-offs and objective-dependent conclusions regarding the most advisable management strategy, an aspect that is further explored in the next section.

Managing fish or managing people: trade-offs in outcomes at different fishing intensities

The results from scenario 2 (Figure 4), highlight the trade-offs among management objectives when we look at configurations of MLLs and stocking measures that maximize each objective under different latent fishing pressures (Figure 7). For a manager solely interested in maximizing fish density and catch rates, we found for both pike and carp that stocking at maximum densities for all sizes of stocked fish would be the best strategy [Note that the maximum stocking density for each species in Figure 7 was constrained by the maximum monetary investments observed in angling clubs in Germany, and thus differed between species]. However, this maximum release strategy needed to be complemented by a MLL. Although there were some differences among species, when YOY (fry and fingerlings) were stocked intermediate MLLs (40-70 cm) generally maximized overall population densities, the proportion of fully vulnerable fish in the population, and catch rates at low fishing pressure (Figure 7). However, the best-performing MLL increased to complete catch-and-release as fishing pressure increased and the fish population required more protection. This positive relationship between MLL and fishing pressure was particularly apparent for pike which occurred in lower densities than carp and were more vulnerable to capture because of higher catchability. When adults were stocked, the best-performing MLLs to augment the population and maximize catch rate was generally the maximum possible, except for augmentation of the overall population of pike under low to moderate fishing pressure, in which case intermediate MLLs (40-70 cm) were best (Figure 7).

By contrast, when the objective was to maximize average angler welfare (compared to the unregulated and unstocked case), low to moderate MLLs (< 50 cm) were needed across both species and for all fishing intensities. The best stocking configuration, however, varied between the two species and with the sizes of stocked fish (Figure 7). The best stocking densities to maximize net WTP tended to be highest for stocked adults and lowest for stocked fingerlings and generally increased with fishing pressure. Furthermore, it should be noted that at low levels of latent fishing pressure, the use of MLLs alone rather than stocking either fry or juvenile pike provided anglers with the greatest benefits.

From a purely economic perspective, the best stocking densities were low in all cases, in stark contrast to management objectives directed at augmenting the population or raising catch rates (Figure 7). For both species, the lowest stocking densities examined achieved the lowest per capita cost of stocked fish surviving to their third birthday, regardless of the size of stocked fish. For both species, intermediate MLLs (40-50 cm) produced the lowest survivor costs in almost all cases with the exception of stocking adult pike, in which case total catch-and-release regulations (120 cm) were the best (Figure 7). The net economic benefit of stocking carp (of all sizes) was maximized when stocking densities were the lowest tested. For pike, this point was achieved when the population was unstocked. The main reason for this finding was diminishing marginal returns of catch rate on angler utility for both pike and carp (Figure 3). Therefore, because the social benefits from fishing were not strongly influenced by stocking, the costs of stocking needed to be strongly controlled. For pike, the MLL that maximized the net economic benefit tended to increase from low (~25cm) to intermediate (40-50 cm) levels as fishing pressure increased, while for carp a very low MLLs (~15 cm) maximized the net economic benefit because of the stronger aversion of carp anglers to restrictive harvest regulations.

Effectiveness of investing into recruiting (pike) versus non-recruiting (carp) species using stocking

A manager might next ask how to allocate scarce budgets in order to generate the most benefits. Hence, a direct comparison of the outcomes of pike and carp stocking in which the same expenditures (5 or 100 € ha^{-1}) were invested was conducted (Figure 4, scenario 3), revealing some key differences among the species (Figure 8). Stocking carp always enhanced the overall fish population, the density of adult (age-2 and older) fish and catch rates, because without stocking, even in low numbers, the population did not exist (Figure 8), whereas this was only the case for pike when the population was heavily exploited (i.e., high fishing pressure and low MLLs). Stocking pike at low densities into a self-sustaining (i.e., under low fishing pressure or when high MLLs protected most fish from harvest), had little impact on the fish population or catch rates, although stocking high densities of fingerling and adult pike were beneficial. Furthermore, unlike pike, even carp fry stocked at high densities had a positive effect on the population, because carp fry did not need to compete with naturally recruited conspecifics. Finally, unlike pike, stocking carp fingerlings, not adults, produced the highest population densities and catch rates when latent fishing pressure was high and MLLs were low, because for the same monetary investment adults were stocked in much lower numbers than fingerlings were and were immediately vulnerable to harvest when they were not protected by harvest regulations.

Stocking carp always resulted in a highly positive net WTP because of the low utility associated with the status quo scenario (i.e., no carp); however, the density and sizes of stocked carp had little additional effect (Figure 8). By contrast, the change in net WTP associated with stocking pike was only positive at high fishing pressure, and low MLLs (Figure 8). The rare positive net WTP resulted from the poor quality of the heavily exploited status quo (unstocked and unregulated) fishery. Under low fishing pressure, stocking pike did little to improve angler welfare, because the pike population in the status quo scenario was not overexploited.

Per capita costs for stocked fish surviving to their third birthday were substantially higher for pike than carp (Figure 8), because pike had higher production costs (Figure 2) and lower survival rates relative to carp. Survivor costs were highest when carp or pike fry were stocked, but unlike pike for which stocking adults was the least costly, the least costly size of stocked carp was situation dependent. Stocking low densities of fingerlings was generally better than stocking low densities of adults. However, stocking high densities of adult carp was generally more cost effective than stocking high densities of fingerlings, except when MLLs were low and fishing pressure was high, such that carp adults experienced high fishing mortality rates. Finally, stocking carp was much more likely to result in a positive net benefit (i.e., at lower fishing pressures and under a broader range of stocking densities), than stocking pike, because the net WTP was much higher than for carp then pike (Figure 8). Thus, fewer anglers were required to generate an aggregated welfare that was sufficient to offset the costs of stocking. Despite being positive, the net economic benefit from stocking pike only exceeded the net economic benefit of using MLLs alone when the fish population was not self-sustaining at low MLLs.

We can thus conclude that a manager faced with a limited budget probably can generate more positive outcomes by investing into culture-based fisheries (carp) through stocking, rather than enhancing an already naturally recruiting population (pike) by stocking. Instead the focus for managing pike population should be to implement appropriate harvest regulations. The reasons for this are manifold: for the same monetary investment stocking carp creates a larger population and a greater increase in angler benefits compared to pike; carp stocking also results in lower per capita costs associated with the survival of stocked fish and generates a greater positive net economic benefit at low stocking compared to pike stocking (Figure 8). Such a strategy would also have the benefit of eliminating replacement of a wild fish stock with hatchery origin fish. However, the objectives associated with any management action need to be examined to determine more clearly the action to take.

Model sensitivity to key assumptions

Stock enhancement might generate better outcomes for the fishery when the natural population had limited viability, moving stock enhancement activities towards culture-based fisheries of non-recruiting species where individuals are able to survive and grow, but not recruit. To investigate whether such effects could occur, we decreased the quality of pike habitat in the model by either increasing the strength of density-dependence and thereby reducing the habitat capacity or reducing population productivity (Figure 4, scenarios 4A and B). These changes reduced the population density in the unstocked state, but it also reduced the potential for stocking at any size class to augment the population, because fewer recruits were produced (Figure 9). Reduced habitat capacity and productivity also generally caused reductions in catch rates despite stocking, however, the effects on catch rates were not nearly as pronounced as the effects on population abundance. Reductions in baseline catch rates in the unstocked and unregulated scenario due to reduced productivity were orders of magnitude greater than reductions due to diminished habitat capacity (e.g., at 5 licenses ha^{-1} and no MLL; 8.9 10^{-3}, 5.7 10^{-3}, 6.5 10^{-6} fish per day, for baseline, poor habitat, and low productivity, respectively). By lowering the bar against which catch rates from stocked scenarios were compared, productivity had a much greater positive effect on net WTP induced by stocking than changes in habitat capacity.

Reductions in habitat capacity and productivity increased the per capita costs of surviving stocked fish, particularly YOY, at high stocking densities, due to stronger density dependence and more pronounced habitat bottlenecks (Figure 9). Changes in habitat capacity had little impact on net economic benefits of pike stocking, which were generally negative. By contrast, the diminished baseline caused bylower productivity increased the net benefit of stocking low densities of pike when MLLs were low, but this effect was not enough to exceed the benefit of using MLLs alone (Figure 9). Overall, there was limited evidence that habitat change differentially affected stocking outcomes. These results mirrored the previous findings that at moderate fishing pressure from an economic perspective pike stocking is unnecessary.

Stocked pike, like many other fishes, are known to suffer from lower fitness than wild fishes, and we thus also examined this key assumption for systematic effects (Figure 4, scenarios 5A and B). 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 overall pike density relative to the scenario of equal fitness, particularly when fingerlings were stocked, and resulted in pike populations that were lower in overall abundance than unstocked populations protected by high MLLs (Figure 10). However, the lower overall fish population density did not greatly reduce the densities of older pike which were only minimally affected by fitness changes. Low fitness of stocked fish increased the per capita costs of surviving stocked fry and to a lesser extent stocked fingerlings, but had little influence on the generally low welfare gain (net WTP) or net economic benefit of pike stocking found under assumptions of equal fitness. Simulating strong natural selection by introducing a heritability of one (i.e., 100% transition of hatchery spawned fish to wild origin, Figure 4, scenario 5B) reversed some of the effects on overall fish density and catch rates that low initial fitness introduced, but not all (Figure 10). Overall the already meagre benefits of stocking pike were further reduced given a realistic assumption of lower relative fitness of stocked relative to wild conspecifics.

Finally, assuming that anglers received benefits from knowing that pike stocking occurred and could identify stocked fish from wild fish (Figure 4, scenario 6A) did not change the results, except for very slight increases in angler welfare (net WTP) (Figure 11). However, any gains in PWU from the act of stocking itself were countered by the loss in utility from anglers knowing that hatchery origin fish composed large portions of their catch, assuming a positive utility of catching wild fishes (Figure 3). Allowing the act of stocking alone and assuming anglers could not identify stocked fish (Figure 4, scenario 6B) once again did not change results much, except for slight changes in net WTP caused by stocking utility (Figure 11). While angler welfare was increased by the knowledge that stocking occurred, this gain was not sufficiently large at moderate levels of fishing pressure to produce a positive net benefit even at low stocking densities. Hence, even informing anglers that stocking occurred would not render pike stocking economically viable despite any potential for stock enhancement effects on abundance or catch rate.

DISCUSSION

We present a bioeconomic model that integrated a mechanistic sub-model of angler behaviour with a size- and density-dependent fish population model that explicitly accounted for the compensatory response of the fish population to the introduction of stocked fish. Our model addresses the call for more integrative approaches to fisheries science that are explicit about the behavioural patterns of the human predator (Wilen et al. 2002, Fenichel et al. 2013a). Moreover, through the systematic analysis of various conservation and fishery-related performance metrics our model also adds to the growing body of research that examines the relative effectiveness of stock enhancement as a management tool compared to traditional harvest regulations (Rogers et al. 2010, Camp et al. 2014). While some studies have linked angler behaviour to catch-related fishery quality (e.g., Rogers et al. 2010, Askey et al. 2013, Camp et al. 2014), our study differed from others because angler behaviour was explicitly determined by numerous catch and non-catch related attributes calibrated to a recently published choice model of German anglers from Lower Saxony (Arlinghaus et al. 2014). Quantifying angler welfare allowed us to use our modelling framework 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 through a conceptually rigorous benefit-cost analysis to rank management options.

Our results suggest that the benefits of stocking versus managing the fishery with harvest regulations vary greatly depending on the performance metric used to evaluate success, as well as the ecological condition of the population being supplemented (e.g., recruiting, non-recruiting, or recruitment-impaired). The magnitude of stocking success was influenced by the size and density of stocked fish, the harvest regulation in place, and the local fishing pressure. With regard to the three key research questions, we found that: i) there is a fundamental trade-off between the biological/conservation and social/economic performance of stocking that managers need to be aware of. Stocking may elevate stock densities and catch rates in both recruiting and non-recruiting fish populations, but this comes at the cost of potentially replacing the wild component in natural recruiting species, which is of conservation concern and difficult to quantify monetarily. Moreover, from an economic perspective, stocking low densities may produce positive net economic benefits in culture-based fisheries provided that angler use is high enough to offset costs; ii) While fingerlings produce the greatest additive effects on abundance overall, in most cases larger fish produce greater additive effects on older fish density and catch rates in both recruiting and non-recruiting species. The net economic benefits are maximized at low stocking rates in non-recruiting species and by moderate harvest regulations without any form of stocking in recruiting species, particularly at high angling pressure. Moreover, the net economic benefits were substantially greater for non-recruiting species than recruiting species; iii) Poor habitat quality and a generally lower fitness of stocked fish further reduces the biological and economic performance of stocking in naturally-recruiting species, particularly for fry and fingerlings and to a lesser extent adults, while the danger of wild fish replacement increases due to a lower buffering capacity of the impaired wild stock. The economic disadvantage of stocking in recruiting species is unaffected by whether there is a utility to stocking *per se* unrelated to any fish abundance effects or to wild fishes, which is a surprising result but emphasizes that the stocking-related utility is completely channeled through its effects on catches and crowding in our model.

To summarize, for recruiting species both from conservation and economic perspectives, stocking is largely superfluous, while it is necessary for non-recruiting species. Whether conservation and economic objectives align in this case depends on the species and its wider ecological impacts. For example, for a species of conservation concern that is currently lacking reproduction, stocking is necessary to avoid extinction while allowing continuous fisheries use of a species that would otherwise not exist. In the case of carp, there is the potential that overstocking strongly affects water quality and other components of the food web, such that stocking should be kept at a minimal rate in natural ecosystems from a conservation perspective. Encouragingly, potential negative impacts of carp stocking can be minimized by following an economic rationale, which in our case suggests that a low stocking intensity strongly outperforms a large stocking intensity. Hence, our model helps to navigate among conflicting objectives and outlines areas of "new consensus" (Hilborn 2007) as relates to the controversial practice of stocking.

Trade-offs in social and economic outcomes of stocking into recruiting species

In agreement with a number of theoretical models, we found strong evidence that under density-dependent growth and mortality responses of the fish population limit stocking contributions to recruitment and in turn to catch rates when the size of the fish stocked is smaller than the size at which the main regulatory mechanism switches from mortality control to growth control (Welcomme 2001, Lorenzen 2005). When stocked into a self-sustaining population (e.g., pike at low effort or high MLLs), the strong density-dependent bottleneck that occurred during the early stage of life ensures little benefit in stocking fry relative to the use of MLLs alone in order to augment the population density and increase catch rates. The lack of additive effects of pike fry stocking agrees with empirical findings of pike fry stocking experiments (Skov et al. 2011, Jansen et al. 2013, Hühn et al. 2014). Stocking fingerlings, on the other hand, was found to produce additive effects, when we assumed the fitness of stocked and wild pike to be identical, because they escaped some of the early mortality bottleneck that fry experienced. However, despite the substantial augmentation of the overall population from stocking pike fingerlings, high natural mortality rates of these still small fish resulted in only minimal increases in the densities of larger fish or catch rates. A recent stocking experiment with pike juveniles in German gravel pits similarly found that stocking age-0 fingerlings enhanced stocks one year later (age-1), but the additive effect was no longer present at the age-2 cohort (Arlinghaus et al. 2015; Hühn et al. in prep.). In addition, when we tailored the parameter set of our model to empirical data reporting a reduced fitness of stocked relative to wild pike, the additive effects of YOY pike stocking were further reduced. The greater stocking success using large fishes that we found is generally consistent with other models (e.g., Rogers et al. 2010, Askey et al. 2013, Camp et al. 2014) and empirical studies (e.g., Wiley et al. 1993, Yule et al. 2000), and supports the general trend seen in some countries to stock larger fish including catchable fish in stock-enhancement efforts (Halverson 2008). Stocked adults experience much less natural mortality than fingerlings because of the allometry of the size-mortality relationship (Yule et al. 2000), and thus tend to have the largest effects on augmentation and increased catch rates, particularly when paired with high MLLs at high fishing pressure.

The biological determinants of stocking success differed for fish populations that were not self-sustaining. These situations were represented in our carp model and in our pike model under conditions of heavy exploitation and in the absence of sufficiently high MLLs to avoid recruitment overfishing. In these situations, stocking fish of any size was a feasible strategy when the objective was to augment the stocks and elevate catch rates. However, even then, the realistic assumption of a reduced fitness of stocked pike relative to wild conspecifics (Lorenzen et al. 2012, Hühn et al. 2014, Arlinghaus et al. 2015) prevented strong additive effects on adult density and catch rates to materialize when fry were stocked. Interestingly, we found that carp fingerlings might outperform adults in their contribution to the adult stock in two situations, 1) when stocking densities are low, and 2) when stocking densities are high, fishing pressure is high and size limits are low. Like Lorenzen (1995) and Hunt et al. (2014), we found that density-dependent processes resulted in a trade-off between the number of fish stocked and fish size, which had impacts on natural mortality rates. In contrast to adults, smaller stocked fish like fingerlings, which largely escaped the early-survival bottleneck, required more time to reach harvestable size, particularly when stocked at high densities which reduced their growth (Lorenzen 1995). Fingerlings tended to be smaller at age-2 than the adults stocked at 40 cm. Thus, carp fingerlings died from natural mortality at a greater rate than adults and as a result contributed less to the fishery generally. However, if the density of fingerlings stocked was sufficiently low that growth rate was fast and density-dependent mortality was low, or in situations of high fishing pressure, if juvenile mortality was not as great as the mortality adults suffered from angling, fingerlings were the better stocking option for augmenting the adult population. This was a surprising finding not reported before.

A key finding from our research was that, despite large differences in catch rates, angler welfare (as measured by net WTP, the change in utility from the managed to the unmanaged case) was largely unrelated to the stocking strategy. Rather, MLLs were more important in determining angler benefits because of the utility anglers directly or indirectly derived from this attribute, e.g., through stock-conserving efforts or the disutility at high MLLs due to constrained harvest. Similar to Johnston et al. (2010), our results challenge a common tenet of the recreational fisheries community who often assumes that angler catch rates primarily or even exclusively determine angler utility (or satisfaction) and hence effort (e.g., Cowley et al. 2003, Rogers et al. 2010, Askey et al. 2013). Similarly, we found that despite catch being a highly significant attribute in the choice experiment used to inform the mechanistic model of angler behaviour in our study (Arlinghaus et al. 2014), maximizing catch rates at equilibrium could yield socially and economically suboptimal outcomes. The reason for this disparity strongly relates to the lognormal form of the PWU function for catch rate which describes diminishing marginal utility gains with increased catch rates. As a result, most changes in catch rates fell in a range that did not substantially change the angler utility. It was only when catch rates were close to zero that increased catch rates had a substantial effect on net WTP. We argue that a diminishing marginal return of utility from increasing catch rates once catch rates are “good enough” (about 1 fish per day, Arlinghaus et al. 2014) is consistent with economic theory and is likely found in most recreational fisheries (Beardmore et al. 2015). By contrast, the utility of generally scarce goods, like catching large fish, may not have an attainable ceiling (Arlinghaus et al. 2014, Beardmore et al. 2015). Nevertheless, some anglers have demonstrated linear or accelerating preferences for catch rates, such as those targeting high-catch-rate small-bodied cyprinid species in Germany (Beardmore et al. 2015). While the limited effect on utility of catch rates in our model may reflect the particular fishing preferences of club anglers from Lower Saxony, Germany, our results are supported empirically by other studies (Fayram and Schmalz 2006, Schultz and Dood 2008, Patterson and Sullivan 2013). Patterson and Sullivan (2013) tested the assumption that stocking more fish and increasing catch rates would increase the effort of Albertan rainbow trout (*Oncorhynchus mykiss*) anglers. Patterson and Sullivan (2013) similarly found that catch rate was lognormally related to angler satisfaction, and that as long as catch rates were above a low threshold level that anglers were attracted to the fishery. Fayram et al. (2006) also found a nonlinear relationship between angler effort and walleye (*Sander vitreus*) density on Wisconsin lakes with daily bag limits of 3 fish.

In our model, factors other than catch strongly drove utility, in particular the harvest regulation in place. This agrees with other studies reporting that the regulations can affect angler use (Beard et al. 2003, Fayram et al. 2006, Johnston et al. 2011). Regulations can affect angler utility both directly because of the perceived restrictions it might have on harvest and indirectly through its effects on fish conservation and catch-related quality. In our study, by protecting fish vulnerable to harvest, MLLs resulted in large changes in adult fish abundance and catch rates, and also increasing trophy catches. MLLs were ineffective at low sizes because the small fish they were “protecting” simply were not vulnerable to the fishing gear, but this rapidly changed at around 40 cm as MLLs started to protect fish that were vulnerable to capture. Yet, like catch rates, the average size of fish caught and trophy catch had little impact on overall utility because these attributes changed very little. Consequently, we found that it was the direct PWU associated with MLLs that strongly influenced the net WTP for both pike and carp angling experiences, implying that harvesting is important to anglers. The effect of MLLs on angler welfare also differed with species. The social welfare of carp anglers was strongly dependent on a fishery being present, which somewhat swamped the influence of other attributes on utility. It also became apparent that carp anglers were less tolerant than pike anglers of intermediate MLLs in the range that offered some protection to the fish population.

The possibility that anglers may be relatively unresponsive to catch has implications for the successful implementation of both stocking and MLLs. Anglers may not leave fisheries at low MLLs or low fish abundances if they keep being attracted to a given fishery for social or habitual reasons (e.g., Johnston et al. 2010, Johnston et al. 2011, Allen et al. 2013), or perhaps simply due to the lack of alternative angling clubs. On the flip side, angler satisfaction and effort may not increase as expected by managers when fostering increases in catch rates and the size of fish (e.g., Beard et al. 2003, Fayram et al. 2006, Johnston et al. 2011, Patterson and Sullivan 2013). If management objectives change from a catch-rate focus to a management of angler satisfaction (Beardmore et al. 2015) or welfare (Dorow et al. 2010, Beardmore et al. 2011a), our research and others (Johnston et al. 2010, 2013, Patterson and Sullivan 2013) provides support for the fundamental shift away from metrics related to fish abundance or catch towards angler metrics, but for different reasons than those expressed by Askey et al. (2013). Askey et al. (2013) argue that effort is a better judge of success in recreational fisheries management because catch- and size-related metrics will remain relatively constant in open access fisheries due to angler effort redistribution. Aside from reservations expressed by Matsumura et al. (2010) and Hunt et al. (2011) that question the generality of the “homogenization of catch rate” hypothesis of Parkinson et al. (2004), our work suggests that catch-related metrics generally have little influence on angler welfare. Thus, based on economic theory, integrated utility is the preferred measure for angler benefits.

The effects of stocking on fish abundance, catch rates, and angler welfare ultimately affected the economic feasibility of stocking strategies. Like Wiley et al. (1993) and Leber et al. (2005), we found that the size of stocked fish was an important determinant of the cost effectiveness of various stocking strategies. Similar to other studies, we found that fingerlings were more cost effective than fry (Santucci

Jr and Wahl 1993, Leber et al. 2005), because they experienced less mortality from the early life stage bottleneck. Carp fingerlings stocked at low densities experienced lower fishing mortality because they tended to be smaller at age-2 than the adults stocked at 40 cm. Thus, even at higher densities if MLLs were liberal and adults experienced high mortality, fingerlings were still the most cost effective. This is similar to a findings by Diana and Wahl (2009) that found stocking medium-sized fingerlings was most cost effective because stocking larger fish did not provide survival benefits. Fingerlings were not always the most cost-effective size, however. When stocking pike, adults were more cost effective than fingerlings because fingerlings experienced strong natural mortality prior to entering the fishery. Thus, if management objectives move from social (increase catch rate) or mere biological (increase abundance) to the economic objectives (return on investment) different conclusions about the most appropriate stocking strategy might emerge. However, the measure of cost effectiveness that we used are still indirectly related to a management focused on fishing opportunities, rather than focusing on the potentially superior metric of angler satisfaction or well-being that fishing opportunities are thought to contribute to. Hence, a focus on net economic benefit is the cleanest measure of economic performance of different policy options.

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 reproducing and non-reproducing populations. The status quo situation (unregulated and unstocked) used to calculate the net WTP was very important for the findings. When the base situation was bad and catch rates were very low, 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 the disparity between the regulated/stocked scenario and the base case was large. Whereas, if the situation started out OK, there was much less gained from the stock-enhanced scenario. The second important factor determining the total net 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 WTP was low, more anglers and low stocking densities were required to produce a positive net economic benefit. Such situation was a rare for pike, and the net economic benefit of stocking pike was only greater than the use of MLLs alone when MLLs did little to protect fish from harvest (i.e., low MLLs). It should be cautioned again that our results are largely the result of the PWU function for catch rate that we used. As has been found in other modelling exercises (e.g., Allen et al. 2013, Camp et al. 2014), greater sensitivity of angler utility and behaviour to catch rates could change predictions about net economic benefits and the success of stocking strategies.

Our results generally found that stocking, with few exceptions, was an economic waste for pike, because MLLs were sufficient to preserve fishery benefits without the added costs from culturing fish. However, we found it was economically advisable to stock carp at low densities. Moreover, several stocking strategies elevated both numerical abundances and catch rates of both species, often involving the release of juveniles or adults and in carp also to a lesser degree fry. Overall, stocking was much more advisable in culture-based situations compared to stock enhancement scenarios, similar to other stocking models (Lorenzen 2005, Rogers et al. 2010). The trade-off among conservation, social and economic objectives in our work were largely confined to utilities derived from angling fisheries who strongly focused on catch rates (i.e., numerical harvest), size of fish and crowding. Culture-based fisheries for carp are also prominent in commercial settings both in Europe and Asia (Lorenzen 1995). Lorenzen (1995) analyzed culture-based stocking efforts in carp and found that intermediate stocking densities maximized fishery yield (i.e., biomass harvested) because high stocking densities reduced production due to higher mortality suffered as a result of density-dependent growth. Furthermore, similar to our results Lorenzen (1995) found that having lower size thresholds for harvest (i.e., MLLs) was more productive for fishery yields because fish were not lost due to density constrained growth rates and size-dependent mortality.

Given our finding that many stocking programs, particularly stock-enhancement efforts, may be economically inefficient, why then do many angling clubs in Europe in general, and Germany in particular, develop stocking as a routinized habit? Several reasons play a role. First, rarely are fishes that are released marked, preventing the anglers and the managers from learning about the lack of additive effects. Second, economic thinking is not widespread in local angling clubs, *inter alia* because there are few alternative tools managers can engage in as easily as stocking. Given that angling clubs are non-profit organizations any license revenue must be reinvested. Third, managers in angling clubs are under strong normative pressure by anglers (van Poorten et al. 2011, Arlinghaus et al. 2015). Loss aversion among club members puts considerable pressure on managers to act conservatively and avoid testing alternative management approaches. Moreover, Arlinghaus et al. (2014) showed that the strong preferences of anglers for stocking over regulatory tools are mainly caused by the belief that stocking contributes to catches, rather than a preference for the act of stocking *per se*. It is possible that results such as ours, when coupled with empirical tests of active adaptive management based on marked and released fishes, may slowly change the perspective of local club anglers, in turn reducing the normative pressure on club managers to engage in regulator stocking. We hope that such change can happen particularly for stock enhancement fisheries where stocking often delivers no benefits to anglers, but poses substantial risks for biodiversity. The situation is different for culture-based fisheries where stocking is an effective management tool, and indeed necessary to maintain non-recruiting populations (Lorenzen 2014).

Given a constrained budget, into which species – recruiting or non-recruiting - shall a manager invest?

If one has a limited budget to allocate, our results suggest that stocking carp rather than pike provides the best investment. For the same investment, the manager will create a larger population, greater benefits to carp anglers, lower survivor costs, and a larger and often positive net benefit. The lower production costs of carp relative to pike allow more fish to be stocked and make stocking more cost effective. From an economic perspective, non-recruiting carp required low stocking density of any fish size and the absence of any MLL of relevance for practical fisheries (~ 15 cm). However, the recommendation to stock a nonnative species assumes that one is not concerned with the possible negative ecological consequences (e.g., water quality impacts, habitat degradation, competition with other species, etc. Matsuzaki et al. 2009, Weber and Brown 2009, Vilizzi et al. 2015) of introducing carp to a waterbody. However, as carp do not recruit in central Europe (Mehner et al. 2004), proper monitoring of catches may offer one vehicle for a sustainable management of carp stocks that produce fisheries benefits while minimizing environmental impacts. Moreover, research has found that if overall biomass is kept within limits (< 200 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 in stocking management, the low stocking intensities suggested from our research should minimize conflicts among conservation and fisheries benefits for this species.

Allocating stocking funds to carp does not mean a loss for pike anglers, however, because effective management with MLLs alone is the best strategy for pike. For recruiting pike not stocking at all was economically optimal, and instead intermediate MLLs increasing in strength with fishing pressure were the optimal management approach. Not stocking fish into naturally recruiting populations has the additional benefit that it avoids the possible negative 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, disease, etc. (Cowx 1994) – environmental costs of importance to selected stakeholders (e.g., conservation NGOs) that we did not account for in our model. In general, our findings regarding optimal stocking strategies and stocking success bring into question the common stocking practices for pike in Germany that tend to rely heavily on stocking fry or juveniles and heavily resist the stocking of adults. In contrast, our work suggests that either one does not stock at all or engages in release of rather robust fish sizes because small sizes are bound to fail to generate any form of additive effect, particularly when the fitness of stocked fishes is less than that of wild conspecifics.

From stock enhancement to culture-based fisheries in naturally recruiting species

Impaired habitat quality is one reason why stock enhancements can fail, but it is often not accounted for in stocking programs (Cowx 1994, Molony et al. 2005). Yet, recruitment limitations due to habitat bottlenecks are among the most often cited argument (Cowx 1994) for so called compensatory stock-enhancement efforts in recruiting species (Lorenzen et al. 2012). As habitat conditions decline such enhancements increasingly move towards culture-based fisheries where natural recruitment is absent or very low and the fishery entirely depends on cultured fishes. When we investigated whether the relative benefits of stocking of pike would increase through a decline in habitat quality, we found that reductions in habitat capacity and reduced productivity did not affect the outcomes of stocking and did not render stocking relatively more beneficial to support the population or the fishery. Our results were in contrast to the theoretical study by Rogers et al. (2010) who found that stocking was beneficial when natural recruitment was impaired from habitat loss. Unlike our study, Rogers et al. (2010) assumed that habitat degradation only affected the wild spawned fish and did not affect the hatchery released fish. However, our results do agree with an empirical study by Hühn et al. (in prep.) who reported that the additive effects of pike stocking were largely independent of habitat quality. Reasons mentioned by Hühn et al. (in prep.) include that all fishes, including the offspring from surviving stocked fish, are forced through the same juvenile bottlenecks and hence even stocking of adults that usually elevate catches and increase the spawning stock in the short term will suffer from the same constraints in the water body such that no long-term increase in recruitment can be expected. This was likely the rationale behind our findings and the reason why our results differed from Rogers et al. (2010). Our results were in agreement with Rogers et al. (2010), however, in terms of the finding that stocking can benefit fisheries that experience particularly high fishing mortality. Our results were in general consistent with the idea that habitat quality limits the number of fish a system can support and that stocking can then not affect this outcome to the degree many managers and anglers desire (Cowx 1994). Perhaps counterintuitively, reduced system productivity resulted in greater increase in angler welfare due to stocking than other models. A lake's productivity, in terms of production of recruits, determines the ability of fish population to compensate for mortality from fishing (Lorenzen 2008), particularly at low population abundances. The reduced ability to produce offspring resulted in the status quo scenario (unregulated and unstocked) used in the net WTP calculation to be much lower compared to a healthy habitat, and resulted in a greater disparity between the status quo and the other scenarios even though the outcome might have been similar. This once again highlights that changes in angler welfare and net economic benefit are relative measures and as a result any conclusions drawn may strongly rely on the baseline situation used in the comparison.

Fishes stocked into ecosystems often show reduced fitness, particularly when forced into competition with wild recruits. For example, Hühn et al. (2014) found that cultured juvenile pike performed half as well when forced into competition with wild recruits. In our model, reducing the fitness of hatchery origin fish reduced the benefits associated with stocking YOY fish, in agreement with Lorenzen (2005) and Rogers et al. (2010), although releasing larger numbers of juvenile or adult pike could still produce desired outcomes simply due to numerical effects. From a conservation perspective, reductions in relative survival of hatchery fish have the advantage of potentially allowing for the persistence of wild fish despite intensive stocking (van Poorten et al. 2011). In our model, allowing for the offspring of hatchery fish to evolve into wild type fish in part compensated for the initially lowered stocking success resulting from differential survival. This assumptions is however optimistic, as research in salmonids has shown that pervasive reduction in reproductive fitness might persist for several generations (Araki et al. 2007, Christie et al. 2014). We did not examine other factors such as differential growth or catchability of hatchery and wild fish, which also likely to occur (Mezzera and Largiadèr 2001, Biro and Post 2008, Klefoth et al. 2012), but these differences might also have positive effects on the outcome of stocking programs by offering greater returns of hatchery fish that have higher catchability.

Managers face intense pressure to stock fish because anglers think it will provide some benefit (Molony et al. 2005, Halverson 2008), even though stocking rate may not translate directly into increased catch (e.g., Patterson and Sullivan 2013, Young 2013). In fact other studies have found that anglers will respond to the changes they perceive stocking will have rather than the actual changes in the fishery (Beard et al. 2003, Fayram et al. 2006). An additional consideration is that anglers may value wild and stocked fish differently (e.g., Olaussen and Liu 2011, Anderson and Lee 2013). From a conservation point of view the degree of replacement of wild fish with stocked fish is of concern (Cowx 1994, Welcomme 2001, van Poorten et al. 2011), and could affect anglers' preferences. We tested for the effects of knowledge about stocking and the origin of fishes in the pike model, but found that changes in assumptions about anglers' stocking knowledge and wild pike identification had little effect on the predicted benefits of stocking. However, it is possible that the importance of these attributes may be greater in other angler populations, particularly in fly fishers for salmonids who have a tradition to be able to differentiate stocked and wild fishes clearly based on external marks (e.g., eroded fins). Thus, the importance of attributes related to stocking for determining angler welfare should not be underestimated for fishes that naturally recruit, despite their low importance in the present work.

Limitations

Our bioeconomic model has a number of limitations. In the biological submodel, the impacts of stocking are strongly dependent on the strength of the 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 YOY 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. Thus, it is possible that our predicted outcomes from stocking are overoptimistic, because density-dependent feedbacks were not sufficiently strong. However, the predicted densities of adult pike (max 22 age-2+ pike/ha) are within the range predicted for natural populations (2.8-38 pike/ha > 35 cm Margenau et al. 1998, 3.2-59 pike/ha > 35 cm Pierce and Tomcko 2005). Likewise, carp densities predicted (max 350 kg/ha) were within the range observed in other systems (9-870 kg/ha carp Crivelli 1981). Moreover, our conclusions that stocking is generally not beneficial for pike and beneficial only in low densities for carp are unlikely to be affected by decreased mortality at higher stocking densities because catch had such little impact on angler utility.

In terms of the social sub-model, we assume that MLLs have no cost. While this may be reasonable because the framework is already in place to implement these and other commonly used regulations, other associated costs, such as enforcement costs, were not included in our model. A further limitation of our model is that our conclusions are linked to a specific mechanistic model of angler behaviour and are dependent on the utility estimate for catch and its contribution to angler welfare. Beyond species-specific differences, we made the simplifying assumption that all anglers had identical time-invariant preferences. In reality, anglers strongly differ in their preferences for catch and non-catch aspects of fishing (Aas et al. 2000, Beardmore et al. 2011b), and these preferences may shift over time (Gale 1987, Johnson and Carpenter 1994, van Poorten et al. 2011). Such dynamics were not represented in our model, but might affect model outcomes substantially, particularly assumptions about angler heterogeneity (Johnston et al. 2010, 2013, Johnston et al. 2015). Thus, further investigations using preferences from different angler populations composed of diverse angler types to inform angler behaviour are needed to test the robustness of our findings.

There is another aspect that our long-term equilibrium dynamics model did not consider – the temporal variability in the fishery. Seasonality and stochasticity are inherent characteristics of fisheries (Seekell 2011). 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 who can spent more time fishing shortly after stocking will reap more benefits and hence be happier than anglers who arrive later. Changes in fish behaviour can further inflate the disproportionate distribution of benefits if stocked fish alter their behaviour over time to become less vulnerable to the gear (van Poorten and Post 2005, Askey et al. 2006, Kuparinen et al. 2010, Klefoth et al. 2013). In our model such temporal and vulnerability dynamics were not represented. However, the short-term catch rate boosts expected from effective stockings in real fisheries exploited by a diversity of temporally varying angler types may render the relationship of stocking-induced catch and angler welfare more pronounced than implied by our model.

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 imbedded in the broader landscape and therefore require broader management perspectives (Lester et al. 2003, Post et al. 2008, Hunt et al. 2011, Post and Parkinson 2012). It is important for managers to understand how changes in regulations will effect target-species substitution and site substitution (Sutton and Ditton 2005, Gentner and Sutton 2008) in multi-species fisheries. Furthermore, stocking strategies that work locally may not be the best regional solution (Askey et al. 2013), 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 in order to investigate the optimal policy mixes in a landscape of diverse fisheries with angler heterogeneity.

Conclusions

One of the key results from our study and related work (e.g., Askey et al. 2013, Camp et al. 2014), is that the stocking strategies considered to be the most successful will strongly depend on the performance measure used to judge success. The same strategy might be seen as a success by some while being considered a failure by others. The key trade-off is generally between economic efficiency and conservation concern (Camp et al. 2013), which often results in opposing recommendations about which is the "best" strategy. Hence, managers need to be clear and transparent about their objectives and normative framework (Fenichel et al. 2013b). Stocking in culture-based fisheries may be a special exception to this trade-off if the species is of conservation concern, because stocking creates a win-win for both conservation and angler benefits. In addition, economic objectives may bring about lower stocking densities that align very well with conservation concerns associated with the introduction of stocked species (e.g. water quality and carp). The situation is very different in recruiting species. Here stocking large juveniles and adults results in additive effects over and above naturally achieved levels, but such strategies run the strong risk of the pervasive replacement of wild fishes by stocked ones (van Poorten et al. 2011) and potentially increases in wild fish mortality if fishing pressure increases after stocking (Baer et al. 2007). This dilemma can only be mitigated by engaging in a put-and-take type of fishery designed for the rapid recapture of stocked fishes, which is controversial in Germany, or avoided by omitting stocking altogether. Harvest regulations may be the wiser management strategy based on economic principle rather than stocking.

To make these difficult decisions, managers need to understand the social-ecological system that they are managing, both in terms of the biological outcomes and the impacts on the angling population utilizing that resource. If fish populations are self-sustaining, our results suggest that stocking is not economically advisable and will only rarely increase angler welfare. Managers can use MLLs or other forms of harvest control to achieve the same or higher benefits, without bearing the costs associated with stocking. For example, harvest slots may be superior to MLLs investigated here (Gwinn et al. 2015). However, our results suggest that the option to harvest contributes substantially to angler welfare, and thus overly restrictive MLLs may not be an option. Stocking can be effective for non-recruiting or recruit-limited populations (i.e., low or absent MLLs), if low densities of fish, preferably adults, are stocked. Stocking adults is very expensive though, thus low stocking densities are required to minimize costs, unless only a few lakes close to urban areas are stocked to attract anglers (Cole and Ward 1994, Post and Parkinson 2012). Such costs may not be of great concern for angling clubs in Germany that have few stocks to manage, but are a fundamental problem for agencies charged with managing hundreds if not thousands of stocks among which they must allocate a limited budget. A word of caution is warranted, however. For stocking to be cost effective, a sufficient number of anglers must benefit from the stocking program to generate an aggregated social welfare that offsets the stocking costs.

While the effects on stocking for augmenting populations and increasing catch rates found in our study mirror those of other studies (Lorenzen 2005, Rogers et al. 2010, Camp et al. 2014), the strength of our study was the ability to evaluate the success of stocking based on rigorous socioeconomic objectives and compare them with more classical conservation and fisheries objectives and associated performance metrics. Thus, our findings that stocking self-reproducing populations provided little benefit to angler welfare and that few stocking options resulted in a positive return on investment, are unique because they contradict recommendations stemming from the use of traditional metrics, such as population density or catch rate. That the anglers in our model did not respond to the catch rates they generally encountered is a key result that emerged from the particular choice model used, which demonstrates the diminishing marginal returns of catch rates measured in Lower Saxony anglers. However, in Germany there are some anglers who have accelerating utility to increasing catch rate, e.g., competitive coarse fishers (Beardmore et al. 2015), which were not represented in our work and could substantially alter the economic outcomes of the model and lead to alternate conclusions. However, since Arlinghaus et al. (2014) found diminishing marginal returns of catch rates across several key fish species, we are confident that our model produced robust conclusions that will hold in many fisheries with a similar angling culture. Our results challenge the common assumption that catch is the primary driver of angler utility and behaviour, and underscores key insights by Cole and Ward (1994) that managing according to angler benefits is bound to lead to different results than managing the fishing opportunity (i.e., catch or supply) only. Our study demonstrates the usefulness of using integrated modelling tools, because only through an integrated model with a mechanistic description of behaviour could we uncover these insights. A further benefit of using an integrated bioeconomic modelling framework to evaluate multiple performance criteria is that it helps define which costs are acceptable and which objectives are most important (Camp et al. 2014), improving transparency in the decision-making process and allowing managers to provide anglers with more realistic expectations about what the outcomes of stocking will be relative to other tools.

ACKNOWLEDGEMENTS

Financial support for this study was provided by the German Ministry for Education and Research (BMBF) through the Besatzfisch-Project, a Program for Social-Ecological Research (grant no. 01UU0907, www.besatz-fisch.de). We thank Maja Schlüter and Daniel Gwinn for contributions and discussions in an early phase of this project.

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TABLES

Table 1. Bioeconomic model equations. Parameter values and their sources northern pike (*Esox Lucius*) and common carp (*Cyprinus carpio*) are listed in Table A1. Derivations of some of the equations can be found in the supplementary material.

	Equation	Description
	Age-structured fish population	
	N_{ag}	Density of fish within age class a and growth trajectory
	L_{ag}	Length of fish within age class a and growth trajectory g
1a	$N_{\text{total}} = \sum_a \sum_g N_{ag}$	Total fish population density
1b	$B_{\text{total}} = \sum_a \sum_g N_{ag} W_{ag}$	Total fish biomass density
1c	$D_{L^2} = \sum_a \sum_g N_{ag} L_{ag}{}^2$	Total effective density
	Growth	
2a	$L_{ag,t+1} = L_{ag,t} + h_g p_{ag}$	Length of fish within age class a and growth trajectory g at time $t+1$
2b	$h_{g,t} = h_{\max} \sigma_{Lg} / [1 + B_{\text{total},t} / B_{1/2}]$	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
2c	$p_{ag} = \begin{cases} 1 - \frac{G}{3+G}(1 + L_{ag} / h_g) & \text{if mature} \\ 1 & \text{if immature} \end{cases}$	Proportion of the annual growth potential which a fish of age a and growth trajectory g allocates to growth
2d	$W_{ag} = w L_{ag}^{l}$	Mass of a fish of age a and growth trajectory g
	Maturation and Reproduction	
3a	$L_{\text{mat},a} = b_1 + b_2 a$	Threshold length a fish of age a must achieve to mature ($L_{ag} > L_{\text{mat},a}$ = mature)

3b	$N_{0_{\mathrm{W}},t} = \Phi\delta \sum_{a=a_{\mathrm{mat}}}^{a_{\max}} \sum_{g} \omega W_{ag_{\mathrm{W}},t} N_{ag_{\mathrm{W}},t}$, $N_{0_{\mathrm{H}},t} = \Phi\delta\rho \sum_{a=a_{\mathrm{mat}}}^{a_{\max}} \sum_{g} \omega W_{ag_{\mathrm{H}},t} N_{ag_{\mathrm{H}},t}$	Density of wild ($N_{0_{\mathrm{W}}}$) and hatchery ($N_{0_{\mathrm{H}}}$) origin larvae produced by spawners at time t . NOTE: $N_{0_{\mathrm{W}}}$ and $N_{0_{\mathrm{H}}}$ were assumed to be zero when modelling carp.
	Mortality age-0 pre-stocking	
4a	$s_{1,t} = \alpha_1 \mathrm{e}^{-\beta_1 (N_{0_{\mathrm{W}},t} + N_{0_{\mathrm{H}},t})}$	Survival of fish during the pre-stocking phase at time t
4b	$\alpha_1 = \left(\frac{L_0}{L_s}\right)^{\frac{M_1^*}{h_{\max}}}$	Maximum survival rate of larvae during the pre-stocking phase (see supplement for derivation)
4c	$\beta_1 = \frac{\ln \frac{L_0}{L_s}}{\ln \frac{L_0}{L_{\mathrm{rec}}}} \beta$	Strength of the density-dependence during the pre-stocking phase (see supplement for derivation)
4d	$M_1^* = h_{\max} \frac{\ln \alpha}{\ln \frac{L_0}{L_{\mathrm{rec}}}}$	natural mortality rate of an age-0 fish of 1cm at zero density
4e	$L_{\mathrm{rec}} = L_0 + h_{\max}$	Maximum average length at recruitment
4f	$J_{0_{\mathrm{W}},t} = s_{1,t}(N_{0_{\mathrm{W}},t} + h^2 N_{0_{\mathrm{H}},t})$ $J_{0_{\mathrm{H}},t} = s_{1,t}\gamma(1-h^2)N_{0_{\mathrm{H}},t}$	Density of age-0 wild $J_{0_{\mathrm{W}},t}$ and hatchery $J_{0_{\mathrm{H}},t}$ origin fish surviving the pre-stocking phase at time t
	Mortality age-0 post-stocking	
5a	$s_{2,t} = \alpha_2 \mathrm{e}^{-\beta_2 (J_{0_{\mathrm{W}},t} + J_{0_{\mathrm{H}},t} + J_{0_{\mathrm{S}},t})}$	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 supplement for derivation)
5c	$\beta_2 = \frac{\beta - \beta_1}{\alpha_1 e^{-\beta_1 (N_{0_{\mathrm{W}},t} + N_{0_{\mathrm{H}},t})}}$	Strength of the density-dependence during the post-stocking phase (see supplement for derivation)
5d	$N_{1g_{\mathrm{W}},t+1} = s_{2,t}\sigma_{Ng} J_{0_{\mathrm{W}},t}$ $N_{1g_{\mathrm{H}},t+1} = s_{2,t}\gamma\sigma_{Ng}(J_{0_{\mathrm{H}},t} + J_{0_{\mathrm{S}},t})$	Density of wild $N_{1g_{\mathrm{W}},t+1}$ and hatchery $N_{1g_{\mathrm{H}},t+1}$ origin fish of age $a=1$ and growth trajectory g at time $t+1$
	Stocking and Mortality age-1 and older fish	
6a	$N_{ag_{\mathrm{H}},t} = \begin{cases} N_{ag_{\mathrm{H}},t} + \sigma_{Ng} N_{\mathrm{S},t} & \text{if } a = a_{\mathrm{S}} \\ N_{ag_{\mathrm{H}},t} & \text{if } a \neq a_{\mathrm{S}} \end{cases}$	Density of hatchery origin fish after recruited fish were stocked

6b	$M_{ag,t} = M_{r,L_{\max}} \left(\frac{L_{ag,t}}{L_{\max}} \right)^{c}$	Instantaneous natural mortality rate of a fish of length L_{ag} at time t
6c	$M_{r,L_{\max}} = \frac{h_{\max}}{L_{\max}}$	Reference instantaneous natural mortality rate at length $L_{\max}$
6d	$c_t = \frac{\ln[1+(1-\Upsilon)D_{\mathrm{rel},t}]}{\ln(M_{r,L_{\max}})} - 1$	Allometric exponent of size-dependent mortality relationship at time t
6e	$D_{\mathrm{rel},t} = \frac{D_{L^2} - D_{\mathrm{Equilib}}}{D_{\mathrm{Equilib}}}$	Relative effective density at time t
6f	$v_{ag,t} = \frac{1}{1+\exp(-y(L_{ag,t} - L_{50}))}$	Proportion of fish of age a and growth trajectory g vulnerable to capture by anglers at time t
6g	$L_{50} = \mathrm{z}L_{\max} + L_{\mathrm{shift}}$	Size at 50% vulnerability to capture
6h	$C_{ag,t} = qE_t v_{ag,t}$	Instantaneous catch rate of fish of age a and growth trajectory g at time t
6i	$f_{\mathrm{H},ag} = \begin{cases} 1 & \text{if } L_{ag} \geq MLL \\ f_{\mathrm{n}} & \text{if } L_{ag} < MLL \end{cases}$	Proportion of fish of age a and growth trajectory g harvested by anglers
6j	$F_{ag,t} = f_{\mathrm{H},ag} C_{ag,t} + f_{\mathrm{h}} C_{ag,t} (1 - f_{\mathrm{H},ag})$	Instantaneous fishing mortality rate of fish of age a and growth trajectory g at time t
6k	$s_{ag_{\mathrm{W}},t} = \mathrm{e}^{-(M_{ag,t} + F_{ag,t})}$ $s_{ag_{\mathrm{H}},t} = \mathrm{e}^{-(M_{ag,t}/\gamma_2 + F_{ag,t})}$	Survival of wild $s_{ag_{\mathrm{W}},t}$ and hatchery $s_{ag_{\mathrm{H}},t}$ origin fish of age a and growth trajectory g
6l	$N_{a+1,g_{\mathrm{W}},t+1} = N_{ag_{\mathrm{W}},t} s_{ag_{\mathrm{W}},t}$ $N_{a+1,g_{\mathrm{H}},t+1} = N_{ag_{\mathrm{H}},t} s_{ag_{\mathrm{H}},t}$	Density of wild $N_{a+1,g_{\mathrm{W}},t+1}$ and hatchery $N_{a+1,g_{\mathrm{H}},t+1}$ origin fish of age $a+1$ and growth trajectory g at time $t+1$
	Angler-effort dynamics	
7a	$U_{\mathrm{f}} = U_{\mathrm{in}} + U_{\mathrm{Spp}} + U_{\mathrm{Cost}}$ $+ U_{\bar{c}_{\mathrm{D}}} + U_{\bar{l}} + U_{l_{\max}} + U_{\bar{A}_{\mathrm{D}}}$ $+ U_{MLL} + U_{DBL} + U_{\mathrm{Stock}} + U_{\mathrm{Comp}}$	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, $U_{\bar{c}_{\mathrm{D}}}$ is the PWU of average daily catch, $U_{\bar{l}}$ is the PWU of average size of fish caught annually, $U_{l_{\max}}$ is the PWU of trophy catch rate, $U_{\bar{A}_{\mathrm{D}}}$ is the PWU of anglers seen, U_{MSL} is the PWU of minimum-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).
7b	$p_{\mathrm{f},t} = \dfrac{3\exp(\hat{U}_{\mathrm{f}})}{[3\exp(\hat{U}_{\mathrm{f}}) + \exp(U_{\mathrm{out}}) + \exp(U_{\mathrm{no}})]}$	Probability an angler chooses to fish, over the alternatives of not fishing or fishing elsewhere (where $\hat{U}_{\mathrm{f}}$ applies to the previous year, U_{no} is the utility gained from not fishing, and U_{out} is the utility gained from fishing elsewhere)
7c	$p_{\mathrm{F}} = (1-\varphi)p_{\mathrm{f},t} + \varphi\hat{p}_{\mathrm{F}}$	Realized probability an angler of type j fishes (where $\hat{p}_{\mathrm{F}j}$ applies to the previous year)
7d	$E_t = p_{\mathrm{F}} d_{\max} A_{\mathrm{L}} \Psi$	Total annual realized fishing effort density at time t
	Response variables	
8a	$SPR = N_{0,\mathrm{F}} / N_{0,\mathrm{U}}$	Spawning-potential ratio (= annual population fecundity density $N_{0,\mathrm{F}}$ under fishing relative to annual population fecundity density $N_{0,\mathrm{U}}$ under unfished conditions)
8b	$WTP = \dfrac{U_{\mathrm{base}} - U_{\mathrm{scenario}}}{u_1}$	Willingness to pay, where
8c	$W = A_L WTP$	Aggregated social welfare
8d	$NB = W - €_{\mathrm{S}}$	Net economic benefit
8e	$€_{\mathrm{S}} = \begin{cases} J_{0_{\mathrm{S}}} \theta L_{\mathrm{S}}^{\lambda} & a_{\mathrm{S}} = 0 \\ N_{\mathrm{S}} \theta L_{\mathrm{S}}^{\lambda} & a_{\mathrm{S}} > 0 \end{cases}$	Cost of stocking
8f	$€_{\mathrm{ind}} = \begin{cases} €_{\mathrm{S}} / J_{0_{\mathrm{S}},t} s_{2,t} \gamma \sum_g \prod_{a=1}^{2} \sigma_{Ng} s_{ag_{\mathrm{H}},t} & a_{\mathrm{S}} = 0 \\ €_{\mathrm{S}} / N_{\mathrm{S},t} \sum_g \prod_{a=a_{\mathrm{S}}}^{2} \sigma_{Ng} s_{ag_{\mathrm{H}},t} & a_{\mathrm{S}} > 0 \end{cases}$	Cost per stocked individual surviving from the time of stocking until the end of age 2
	Part-worth-utility (PWU) functions	
9a	$U_{\mathrm{o}j} = u_1 €_{\mathrm{L}}$	PWU of annual license cost
9b	$U_{\bar{c}_{\mathrm{D}}} = u_2 \log_{10} \bar{C}_{\mathrm{D}}$	PWU of daily catch $\bar{C}_{\mathrm{D}}$

9c	$U_{\bar{l}} = u_3 \log_{10}\left(\frac{\bar{l}}{\bar{l}_{\text{ref}}}\right)$	PWU of average size of fish caught annually $\bar{l}$
9d	$U_{l_{\max}} = u_4 l_{\max}$	PWU of the catch rate $l_{\max}$ of trophy-sized fish ($L_{ag} > L_T$)
9e	$U_{\bar{A}_{\text{D}}} = u_5 \bar{A}_{\text{D}}$	PWU of the number of anglers seen in a day $\bar{A}_{\text{D}}$ on a 10 ha lake
9f	$U_{MLL} = u_6 MLL + u_7 MLL^2$	PWU of minimum-size limit MLL
9g	$U_{DBL} = u_8 DBL$	PWU of daily bag limit
9h	$U_{\text{Stock}} = u_9 1$	PWU of stocking frequency (stocking occurs annually)
9i	$U_{\text{Comp}} = u_{10} \frac{\bar{C}_{\text{D}_{\text{W}}}}{\bar{C}_{\text{D}_{\text{Total}}}}$	PWU of catch composition (% wild fish)

FIGURE CAPTIONS

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

Figure 2. Species- and size-dependent stocking cost relationship determined from information provided by German angling clubs (Arlinghaus et al. 2015a).

Figure 3. 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 4. Base model scenarios for pike and carp (right and left), and modifications (center) of scenario 1 in further investigations. Scenarios 2 and 3 above the dotted line, were applied to both pike and carp. Scenarios 4-6 below the dotted line were applied to pike only.

Figure 5. The effects of stocking pike fry (2.0 cm), fingerlings (20 cm) and adults (age-2, 35-40 cm) at a range of densities across a range of minimum-length limits and a range of stocking densities calibrated to reflect the range of angling-club expenditures on pike stocking in Germany (Figure 4, scenario 1). Effects on overall fish density, density of age-2 fish and older fish at year end, catch rates, change in angler welfare (net willingness-to-pay, WTP) relative to the unregulated and unstocked case, costs of fish surviving until their third birthday, and net economic benefit, relative the use of MLLs alone were evaluated. Latent fishing pressure was assumed to be moderate (5 licenses ha^{-1}). Very close contour lines indicate rapid changes in the performance measure.

Figure 6. The effects of stocking carp fry (4.0 cm), fingerlings (15 cm) and adults (40 cm) at a range of densities across a range of minimum-length limits and a range of stocking densities calibrated to reflect the range of angling club expenditures on carp stocking in Germany (Figure 4, scenario 1). Effects on overall fish density, density of age-2 fish and older fish at year end, catch rates, change in angler welfare (net willingness-to-pay, WTP) relative to the unregulated and unstocked case, costs of fish surviving until their third birthday, and net economic benefit, relative the use of MLLs alone were evaluated. Latent fishing pressure was assumed to be moderate (5 licenses ha^{-1}).

Figure 7. The normalized minimum-length limit (right panels) and stocking density (left panels) that in combination maximized various performance measures (Figure 4, scenario 2), including: overall population density, and density of age-2 fish and older (at the end of the year), average angler catch rates (ha^{-1}), average angler welfare (net willingness-to-pay, WTP, relative to an unstocked and unregulated case), costs of fish surviving until their third birthday, and net economic benefit. Minimum-length limit (MLL) and stocking density were represented as a percentage of their maximums. MLL maximum was 120 cm for pike and 110 cm for carp. Maximum stocking densities for pike were 4900, 90, and 30 fish per ha for fry, fingerlings and adults respectively. Maximum stocking densities for carp were 14000, 1100, and 166 fish per ha for fry, fingerlings and adults respectively. Stocking densities represented the species-specific range of angling club expenditures on pike and carp stocking in Germany.

Figure 8. The effect of stocking pike and carp fry, fingerlings and adults at densities that represent stocking investments of 5 € ha^{-1} and 100 € ha^{-1} (Figure 4, scenario 3). For pike, these values corresponded to densities of 3300 (2 cm), 60 (20 cm) and 20 (age-2), fry, fingerlings and adults ha^{-1}, respectively, and for carp to densities of 2000 (4 cm), 160 (15 cm) and 24 (40 cm), fry, fingerlings and adults ha^{-1}, respectively. Effects on overall population density, and density of age-2 fish and older (at the end of the year), average angler catch rates (ha^{-1}), average angler welfare (net willingness-to-pay, WTP, relative to an unstocked and unregulated case), costs of fish surviving until their third birthday, and net economic benefit, relative the use of MSLs alone under low and high fishing pressure (1 and 10 licenses ha^{-1}, respectively) were evaluated. The grey areas indicate situations where the satisfaction benefit was not greater than the status quo (no stocking and no MLL), or where there was no positive net benefit.

Figure 9. The influence of lower habitat capacity resulting in stronger density-dependence ($2 \cdot \beta$, middle column, Figure 4 scenario 4A) or lower stock productivity ($\alpha / 2$, right column, Figure 4 scenario 4B) on the effects of stocking pike fry (2.0 cm), fingerlings (20 cm) and adults (age-2, 35-40 cm) across a range minimum-size limits (MLLs) at low (110, 2, 0.65 fish ha^{-1}) and high (4900, 90, 30 fish ha^{-1}) densities, representing the 5^{th} (3 € ha^{-1}) and 95^{th} (154 € ha^{-1}) percentiles of club expenditures on pike stocking in Germany. The base model case was included for reference (left column). Effects on overall population density, and density of age-2 fish and older (at the end of the year), average angler catch rates (ha^{-1}), average angler welfare (net willingness-to-pay, WTP, relative to an unstocked and unregulated case), costs of fish surviving until their third birthday, and net economic benefit, relative the use of MSLs alone under moderate fishing pressure (5 licenses ha^{-1}, respectively) are shown. The grey areas indicate situations where the satisfaction benefit was not greater than the status quo (no stocking and no MLL), or where there was no positive net benefit.

Figure 10. The influence of reduced fitness and "heritability" (natural selection forces moving spawned offspring from stocked fish into the wild-type pool) on the outcomes of stocking pike fry (2.0 cm), fingerlings (20 cm) and adults (age-2, 35-40 cm) across a range minimum-size limits (MLLs) at low (110, 2, 0.65 fish ha^{-1}) and high (4900, 90, 30 fish ha^{-1}) densities, representing the 5^{th} (3 € ha^{-1}) and 95^{th} (154 € ha^{-1}) percentiles of club expenditures on pike stocking in Germany. In the first reduced fitness scenario

(middle column, Figure 4 scenario 5A), it was assumed that the survival of stocked age-0 fish to be 50%, survival of adult fish to be 90%, and the reproductive success of stocked pike to be 56% of their wild counterparts following empirical data (Hühn et al. 2014, Arlinghaus et al. 2015a), assuming a zero heritability (i.e., stocked fish never moved into the wild-like pool). In the second scenario (right column, Figure 4 scenario 5B), fitness was assumed to be similarly reduced, but "heritability" after stocking was 1. The base model case was included for reference (left column). Effects on overall population density, and density of age-2 fish and older (at the end of the year), average angler catch rates (ha^{-1}), average angler welfare (net willingness-to-pay, WTP, relative to an unstocked and unregulated case), costs of fish surviving until their third birthday, and net economic benefit, relative the use of MSLs alone under moderate fishing pressure (5 licenses ha^{-1}, respectively) are shown. The grey areas indicate situations where the satisfaction benefit was not greater than the status quo (no stocking and no MLL), or where there was no positive net benefit.

Figure 11. The influence of stocking awareness on the effects of stocking pike fry (2.0 cm), fingerlings (20 cm) and adults (age-2, 35-40 cm) across a range minimum-size limits (MLLs) at low (110, 2, 0.65 fish ha^{-1}) and high (4900, 90, 30 fish ha^{-1}) densities, representing the 5th (3 € ha^{-1}) and 95th (154 € ha^{-1}) percentiles of club expenditures on pike stocking in Germany. In the first scenario (middle column, Figure 4 scenario 6A), it was assumed that anglers were aware that pike were stocked and they could identify stocking individuals in their catch (for utility effects see Figure 3). In the second scenario (right column, Figure 4 scenario 6B), it was assumed anglers were aware of stocking but could not identify stocked individuals in their catch. The base model case was included for reference (left column). Effects on overall population density, and density of age-2 fish and older (at the end of the year), average angler catch rates (ha^{-1}), average angler welfare (net willingness-to-pay, WTP, relative to an unstocked and unregulated case), costs of fish surviving until their third birthday, and net economic benefit, relative the use of MSLs alone under moderate fishing pressure (5 licenses ha^{-1}, respectively) are shown. The grey areas indicate situations where the satisfaction benefit was not greater than the status quo (no stocking and no MLL), or where there was no positive net benefit.

FIGURES

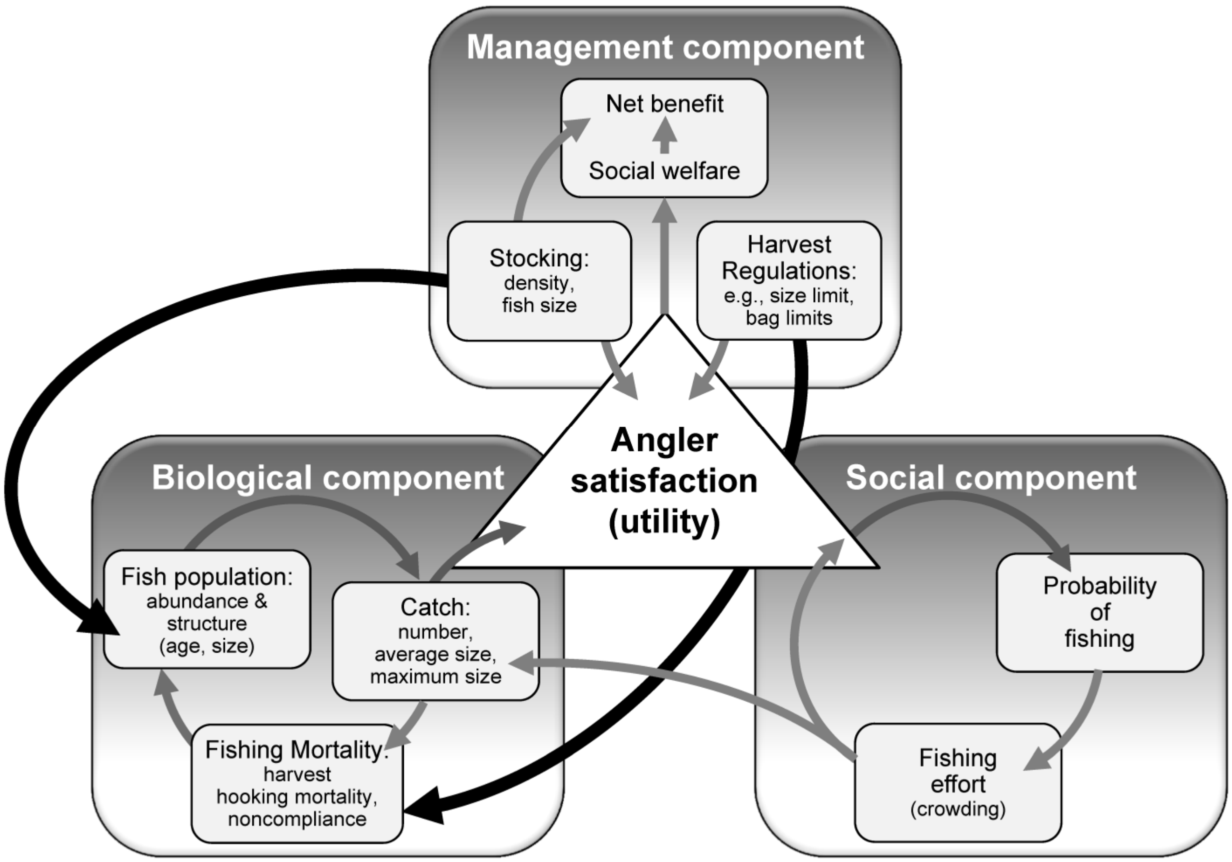
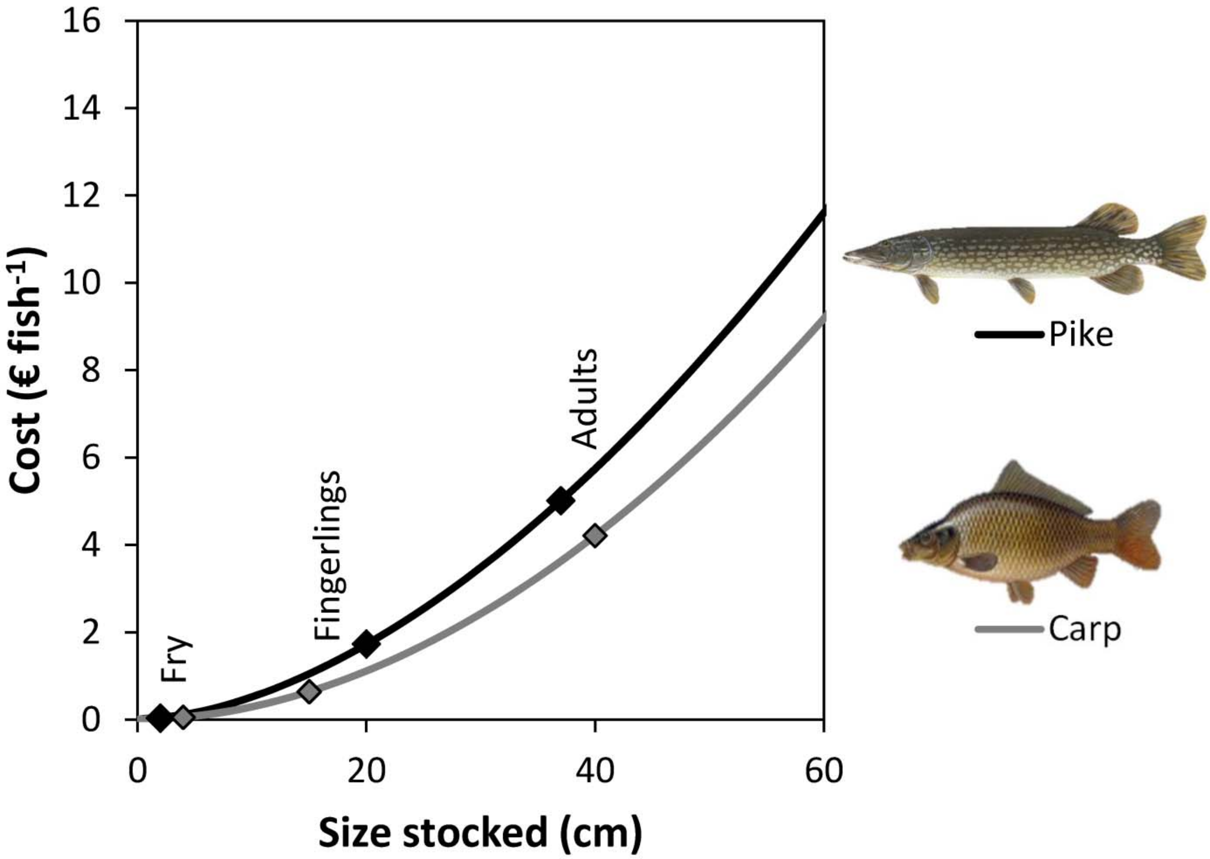


Figure 1.



1516

1517 Figure 2.

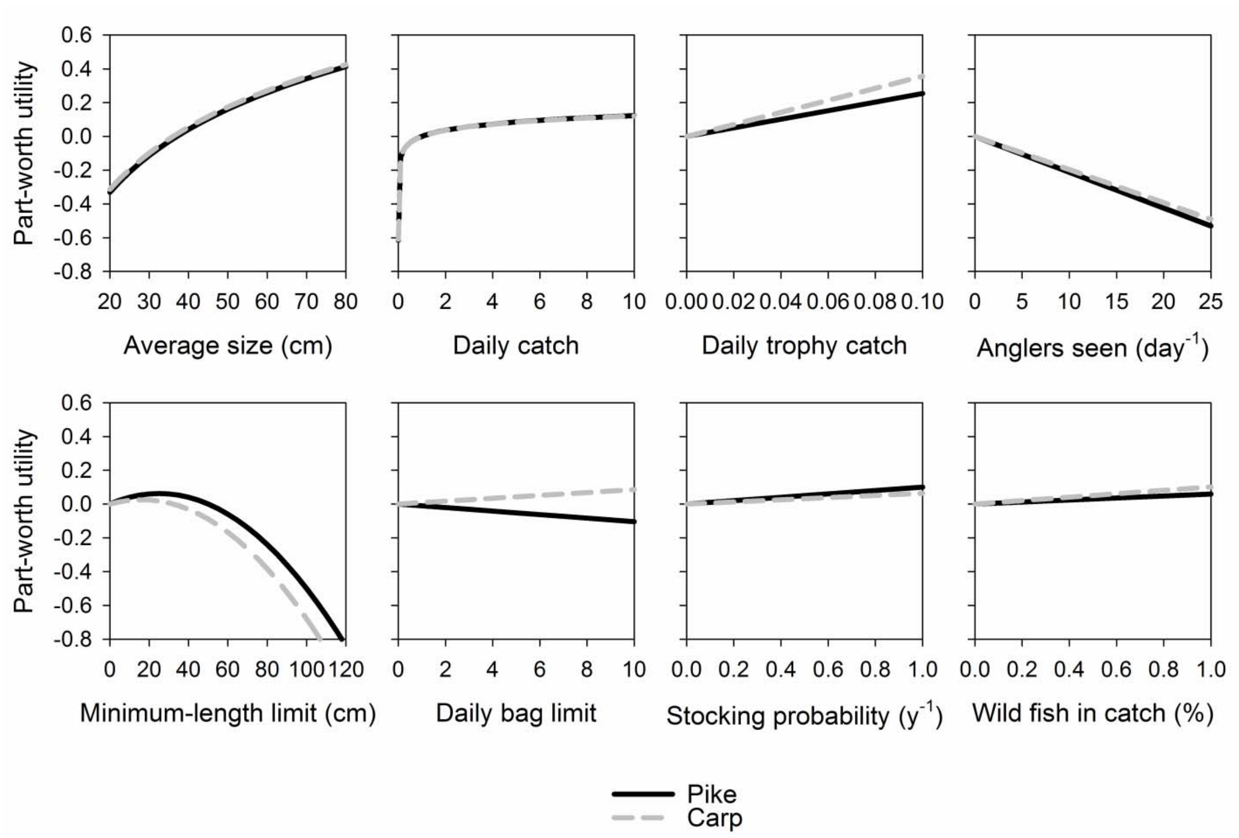

Part-worth utility
Average size (cm)
Daily catch
Daily trophy catch
Anglers seen (day^{-1})
Part-worth utility
Minimum-length limit (cm)
Daily bag limit
Stocking probability (y^{-1})
Wild fish in catch (%)
Pike
Carp

Figure 3.

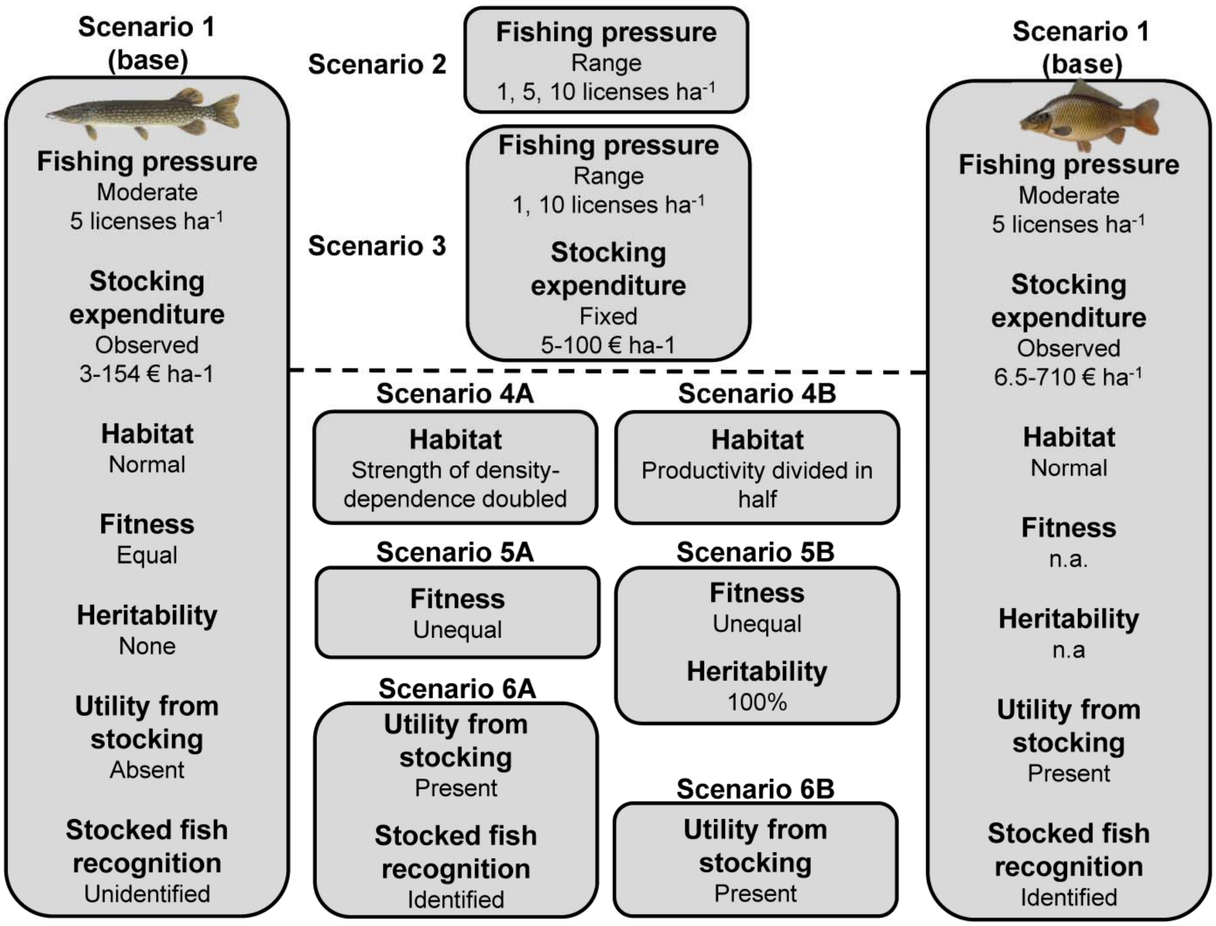
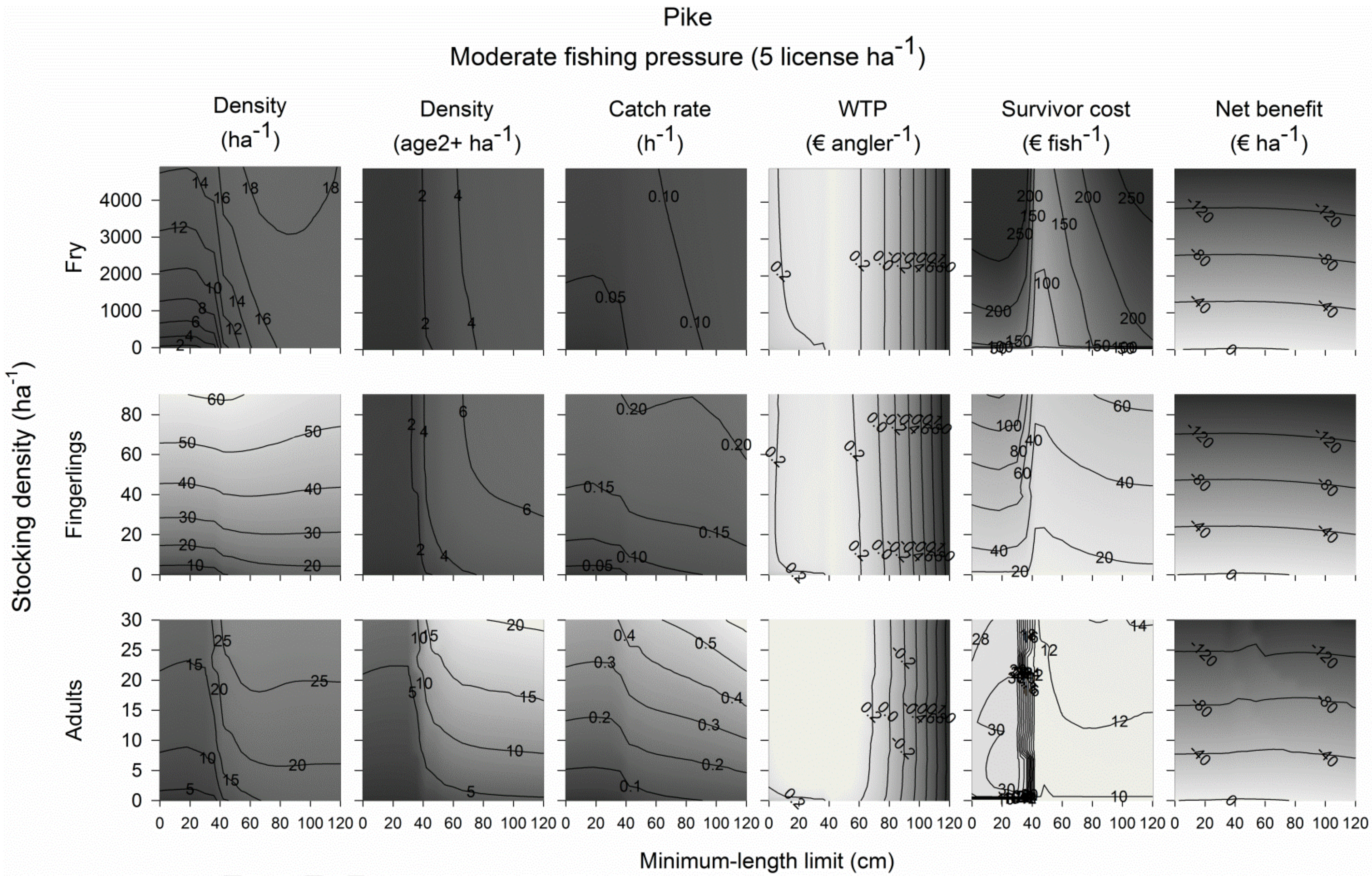

Scenario 1 (base)
Fishing pressure
Moderate
5 licenses ha-1
Stocking expenditure
Observed
3-154 € ha-1
Habitat
Normal
Fitness
Equal
Heritability
None
Utility from stocking
Absent
Stocked fish recognition
Unidentified
Scenario 2
Fishing pressure
Range
1, 5, 10 licenses ha-1
Scenario 3
Fishing pressure
Range
1, 10 licenses ha-1
Stocking expenditure
Fixed
5-100 € ha-1
Scenario 4A
Habitat
Strength of density-dependence doubled
Scenario 4B
Habitat
Productivity divided in half
Scenario 5A
Fitness
Unequal
Scenario 5B
Fitness
Unequal
Heritability
100%
Scenario 6A
Utility from stocking
Present
Stocked fish recognition
Identified
Scenario 6B
Utility from stocking
Present
Scenario 1 (base)
Fishing pressure
Moderate
5 licenses ha-1
Stocking expenditure
Observed
6.5-710 € ha-1
Habitat
Normal
Fitness
n.a.
Heritability
n.a
Utility from stocking
Present
Stocked fish recognition
Identified

Figure 4.



Pike
Moderate fishing pressure (5 license ha^{-1})
Density (ha^{-1})
Density (age2+ ha^{-1})
Catch rate (h^{-1})
WTP (€ angler^{-1})
Survivor cost (€ fish^{-1})
Net benefit (€ ha^{-1})
Fry
Fingerlings
Adults
Stocking density (ha^{-1})
Minimum-length limit (cm)

Figure 5.

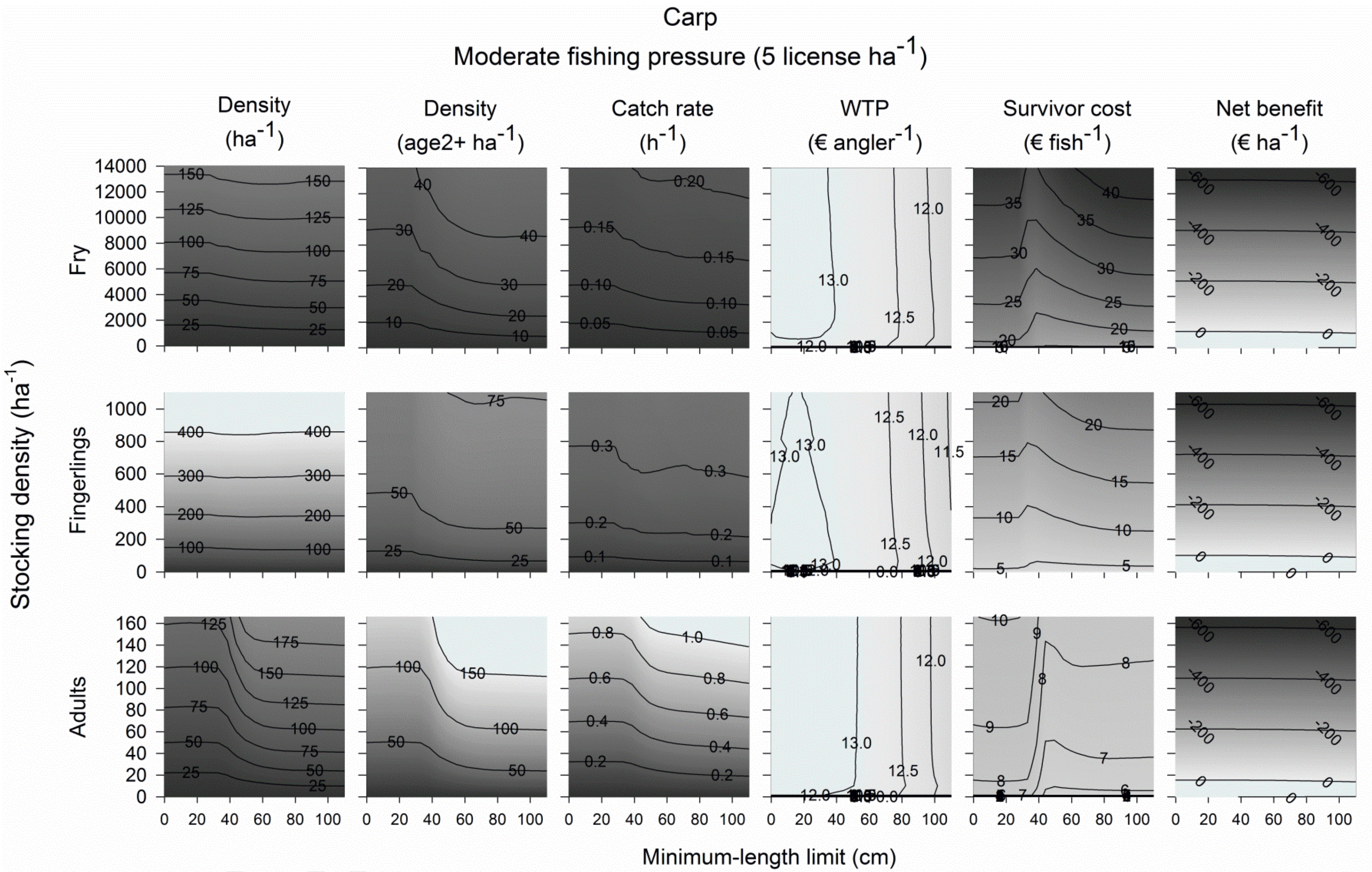

Carp
Moderate fishing pressure (5 license ha-1)
Density (ha-1)
Density (age2+ ha-1)
Catch rate (h-1)
WTP (€ angler-1)
Survivor cost (€ fish-1)
Net benefit (€ ha-1)
Fry
Fingerlings
Adults
Stocking density (ha-1)
Minimum-length limit (cm)

Figure 6.

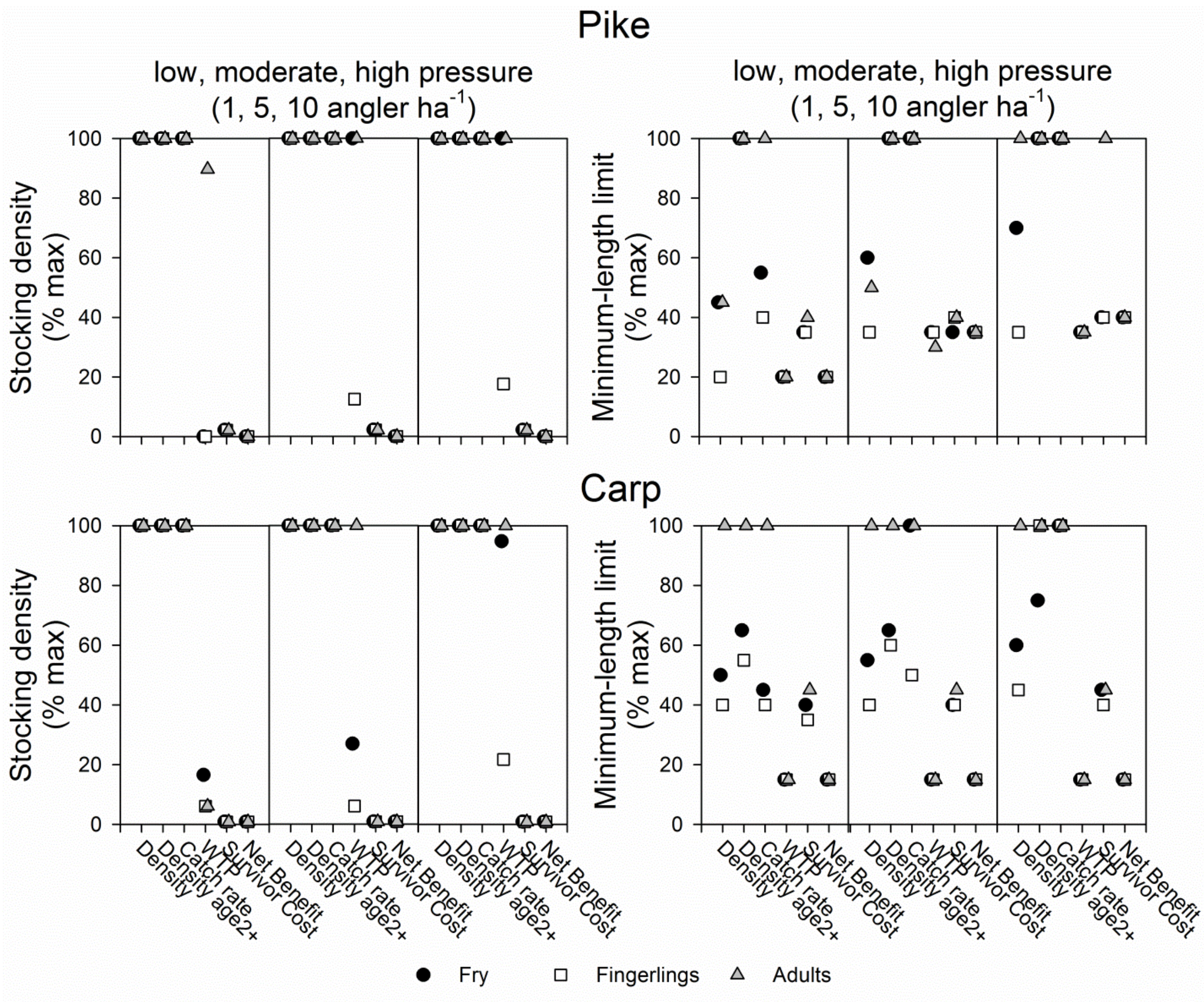
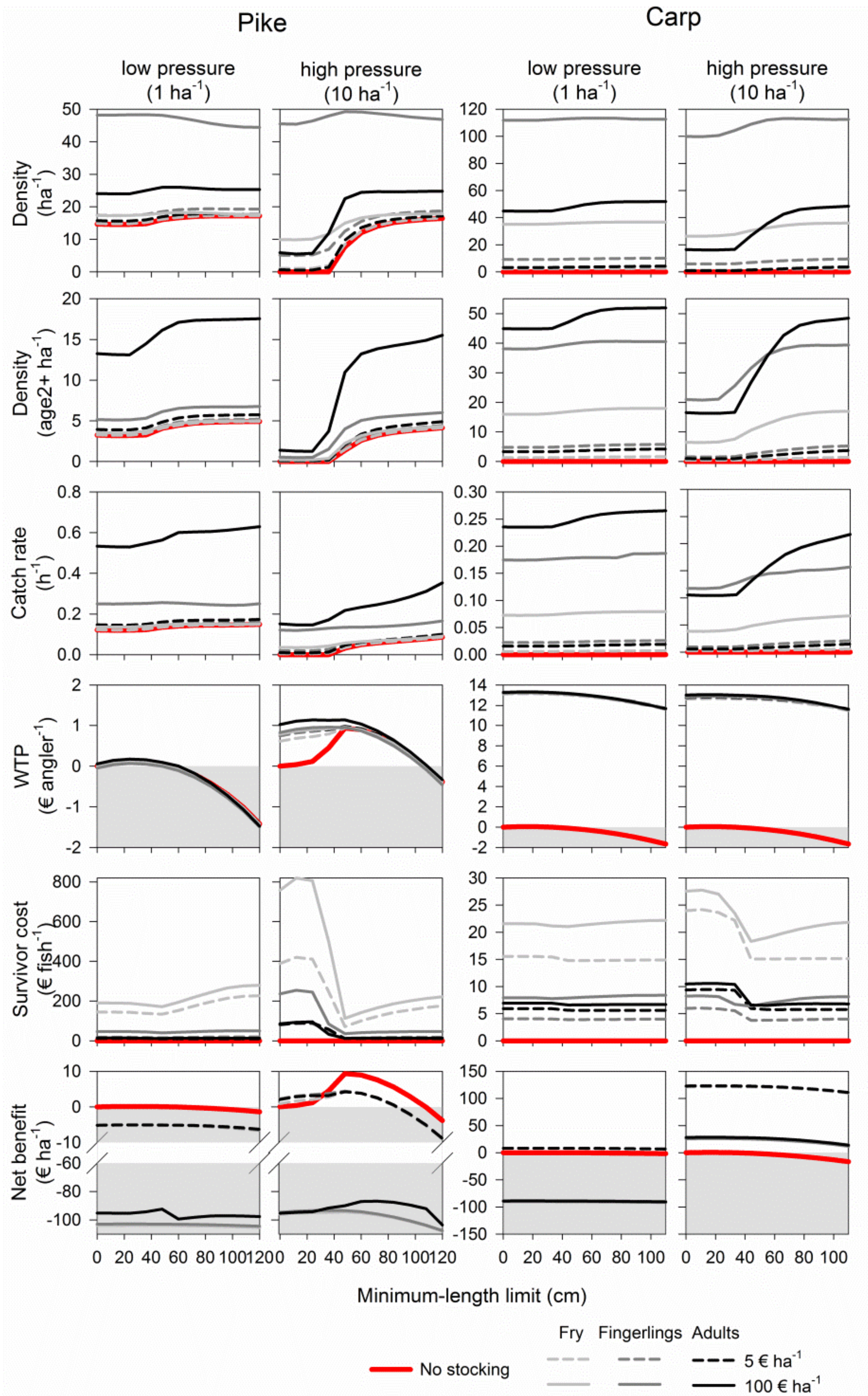
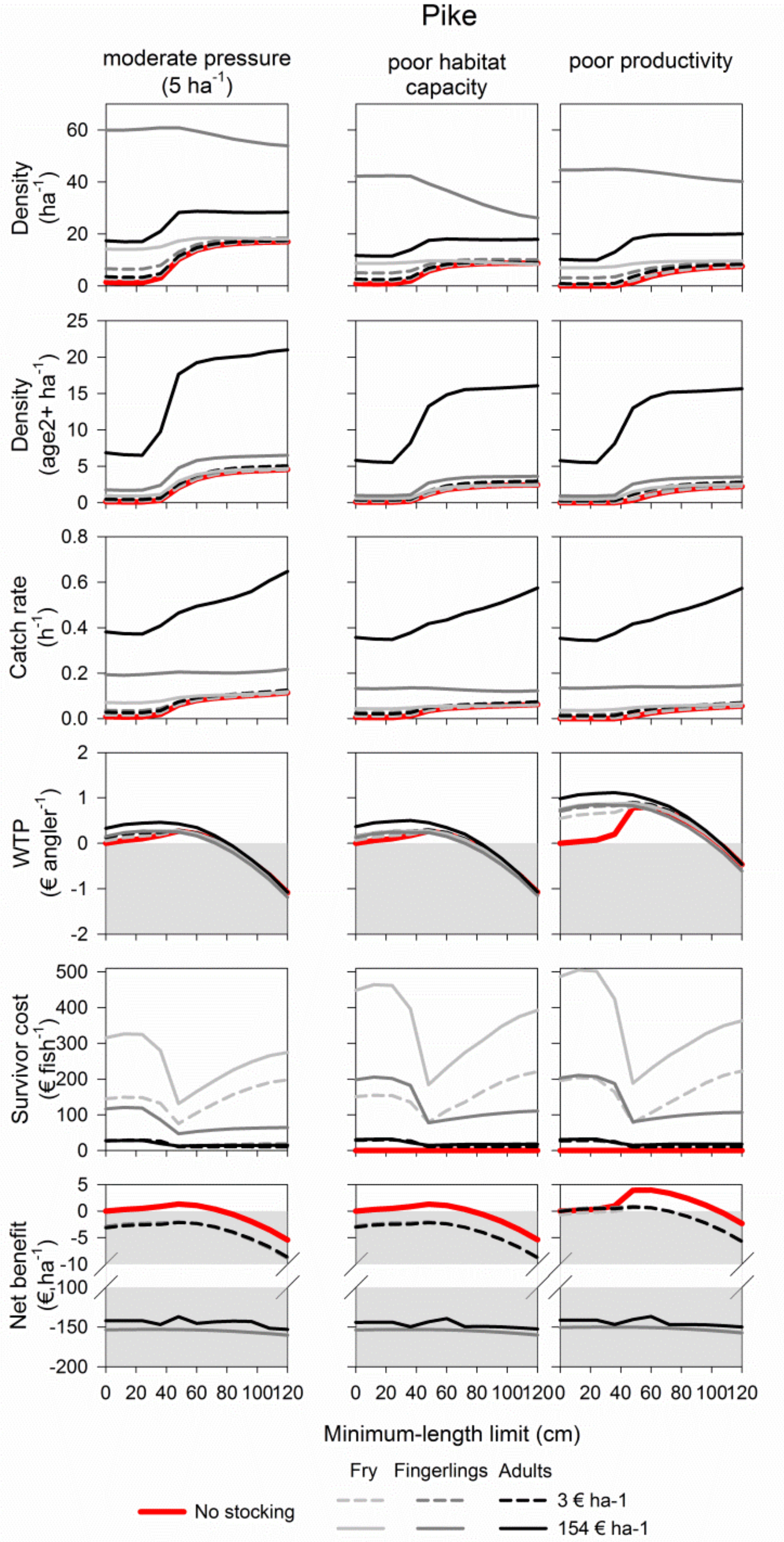

Pike
low, moderate, high pressure
(1, 5, 10 angler ha^{-1})
low, moderate, high pressure
(1, 5, 10 angler ha^{-1})
Stocking density
(% max)
Minimum-length limit
(% max)
Carp
Stocking density
(% max)
Minimum-length limit
(% max)
0
20
40
60
80
100
Density
Density age2+
Catch rate
WTP
Survivor
Survivor Cost
Net Benefit
Fry
Fingerlings
Adults

Figure 7.



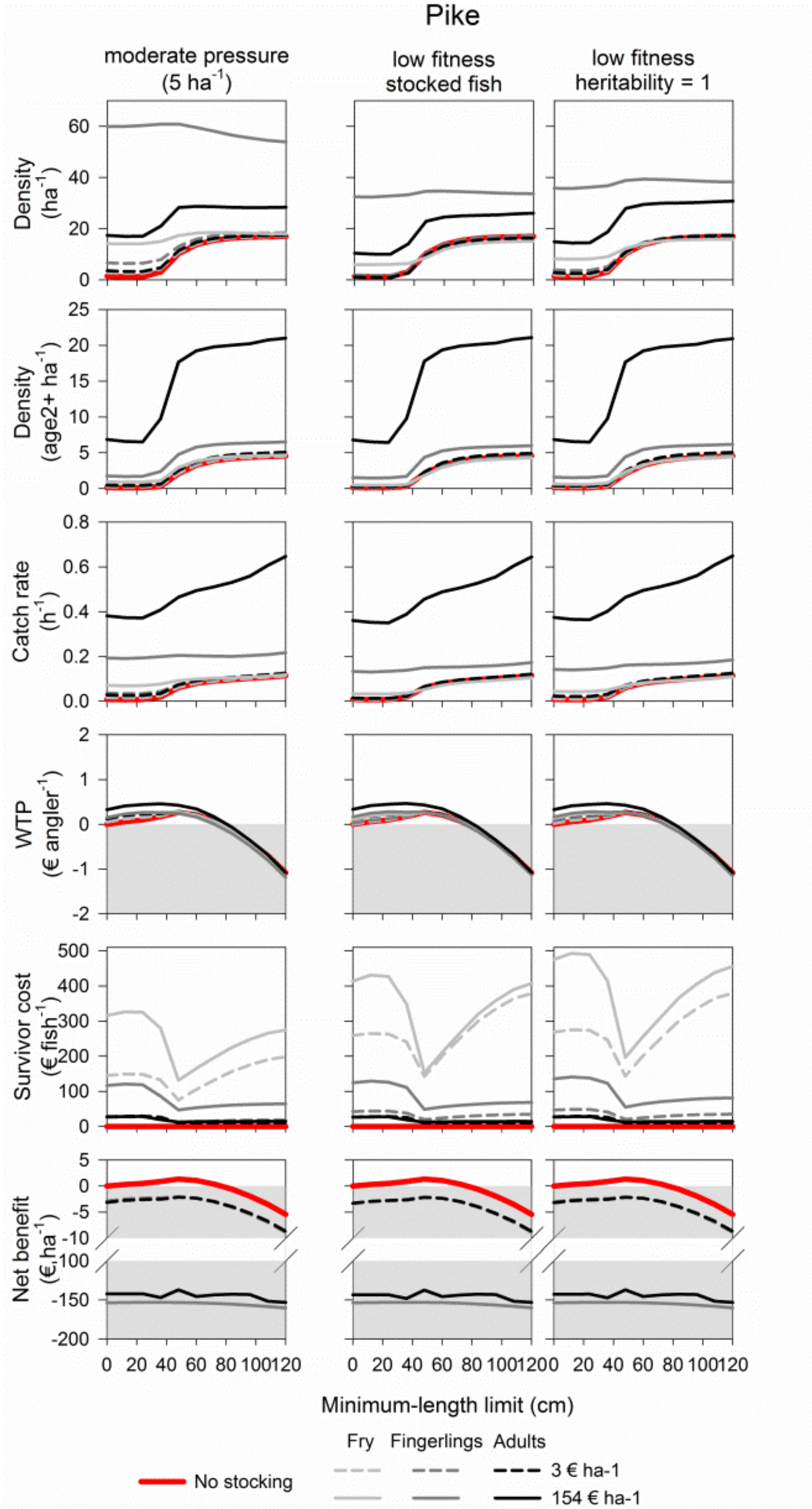
1528

1529 Figure 8.



1530

1531 Figure 9.



Pike
moderate pressure (5 ha-1)
low fitness stocked fish
low fitness heritability = 1
Density (ha-1)
Density (age2+ ha-1)
Catch rate (h-1)
WTP (€ angler-1)
Survivor cost (€ fish-1)
Net benefit (€ ha-1)
Minimum-length limit (cm)
Fry
Fingerlings
Adults
No stocking
3 € ha-1
154 € ha-1

Figure 10.

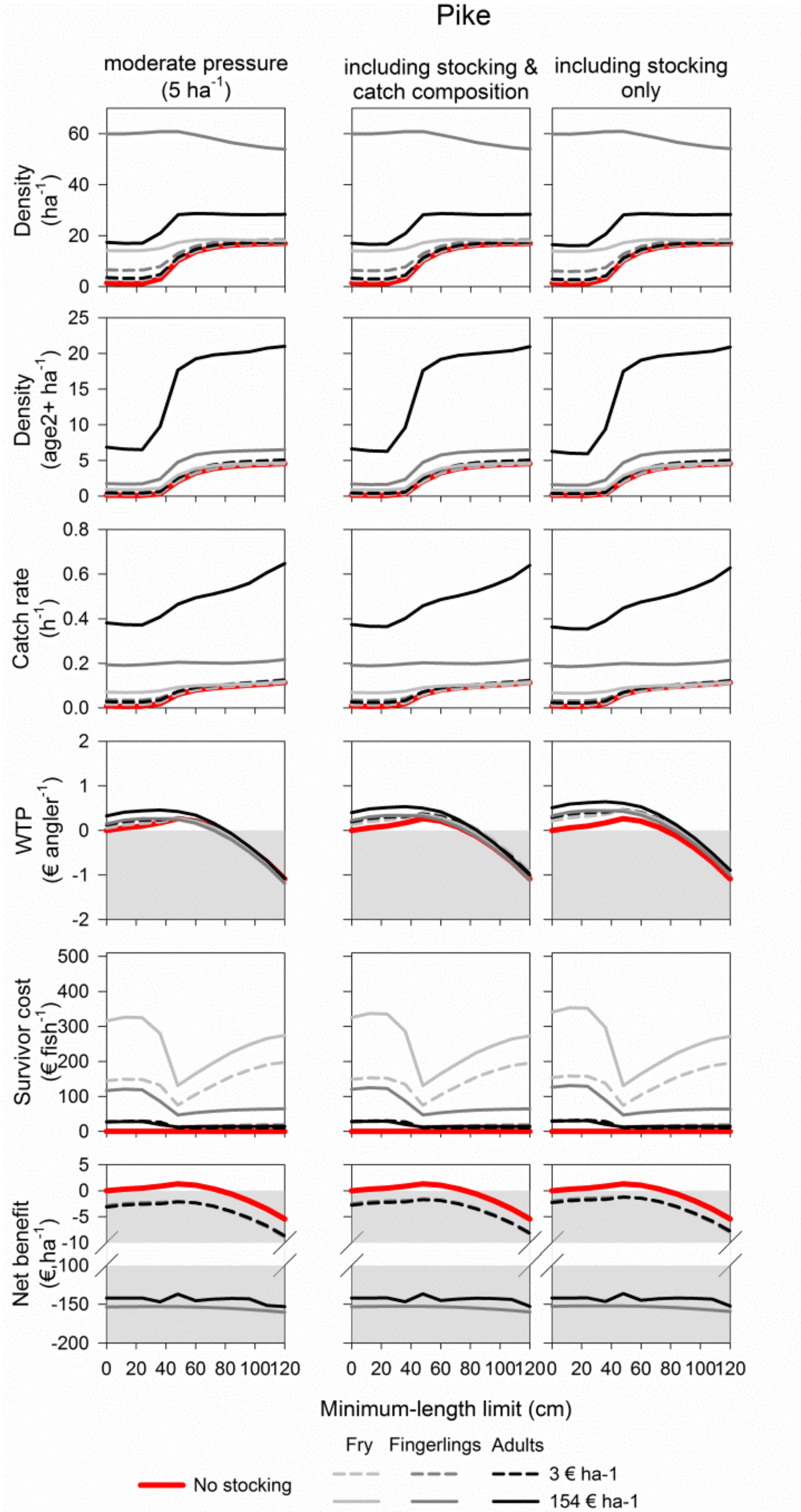

Pike
moderate pressure (5 ha-1)
including stocking & catch composition
including stocking only
Density (ha-1)
Density (age2+ ha-1)
Catch rate (h-1)
WTP (€ angler-1)
Survivor cost (€ fish-1)
Net benefit (€ ha-1)
Minimum-length limit (cm)
Fry
Fingerlings
Adults
No stocking
3 € ha-1
154 € ha-1

Figure 11.

APPENDIX

Table A1. Bioeconomic model parameter values and their sources for northern pike (*Esox Lucius*) and common carp (*Cyprinus carpio*).

Symbol	Description (unit, where applicable)	Value or range for fish life-history types (source, where applicable)	
		Pike	Carp
Index variables			
t	year (y)	0 - 150	0 - 150
a	Age class (y)	0 - $a_{\max}$	0 - $a_{\max}$
$a_{\max}$	Maximum age of a fish (y)	15 (5)	20 (18)
g	Growth trajectory within an age class	1 - 11	1 - 11
Growth			
$L_{\max}$	Mean maximum size a fish can attain at maximum age ($a = a_{\max}$) in an environment free of intraspecific competition ($B_{\text{total}} = 0$) (cm)	120	110
L_0	Length of fish at hatch (cm)	0.8 (7)	0.6 (9)
$h_{\max}$	Mean maximum annual growth increment (cm)	24.0 (10)	21.3 (14)**
σ_{Lg}	Deviations from the mean $h_{\max}$ in the positive and negative direction, assuming a range of 3 standard deviation units and a coefficient of variation of 0.1	-0.3 to 0.3	-0.3 to 0.3

$B_{1/2}$	biomass density at which the growth increment is halved (kg ha^{-1})	100.0 (10)	454.5 (14)**
G	Annual reproductive investment	0.58 (10)	0.49 (14)**
w	Scaling constant for length-mass relationship (g cm^{-l})	0.0048 (19)	0.020 (17)
l	Allometric exponent for length-mass relationship	3.059 (19)	2.97 (17)
Maturation			
b_1	Intercept of the maturation reaction norm (cm)	36.6 (7)*	30.8 (6)*
b_2	Slope of the maturation reaction norm (cm y^{-1})	-3.25 (7)*	-3.31 (6)*
Reproduction			
ω	Relative fecundity (g^{-1})	34 (11)	220 (16)
δ	Hatching success	0.75 (12)	0.75 (3)
Φ	Sex ratio (% female spawners)	0.5 (13)	0.5 (4)
ρ	reproductive success of hatchery strain fish relative to wild fish	1.0 or 0.56 (8)	n.a.
Mortality			
α	Maximum survival rate of larvae to age-1	1.71 10^{-4} (10)	2.00 10^{-5} (4)
β	Strength of density-dependence on larvae to age-1 survival (ha)	6.87 10^{-6} (10)	2.00 10^{-8} (4)
h^2	Proportion of hatchery larvae that transitioned to wild strain fish due to natural selection	0.0 or 1.0	n.a.
γ	Relative survival of age-0 hatchery fish relative to age-0 wild fish	1.0 or 0.5 (8)	n.a.

σ_{Ng}	Proportion of fish in a growth trajectory g assuming a normal distribution with a mean $h_{\max}$ and a coefficient of variation of 0.1	0.37 to 7.56 10^{-6} (calculated)	0.37 to 7.56 10^{-6} (calculated)
D_{Equilib}	Unexploited equilibrium effective density, which was considered to be the D_{L^2} after model stabilization but prior to the introduction of stocking and fishing (cm^2 ha^{-1})	32168.4 (calculated)	277123 (calculated)
Υ	Strength of density-dependence on the allometry of size-dependent natural mortality (see supplement for derivation)	0.27 (15)	0.27 (15)
y	Steepness of size-dependent vulnerability curve	0.3	0.3
z	Size as a proportion of $L_{\max}$ used when calculating the size L_{50} at which 50% of the fish are vulnerable to capture	0.18	0.18
L_{shift}	Constant used to when calculating the size L_{50} (cm)	10	10
q	Catchability reflecting skill level (ha h^{-1})	0.20	0.20
f_{h}	Proportion of fish dying from hooking mortality	0.05	0.05
f_{n}	Proportion of fish below the minimum-size limit MSL harvested illegally	0.05	0.05
γ_2	Relative survival of recruited hatchery origin fish relative to wild fish	Immature 1.0 or 0.5 (8)	n.a.

		Mature	
		1.0 or 0.9 (8)	
Stocking			
L_s	length of fish at stocking (cm)	2.0, 20.0, $\bar{L}_{a_S}$	4.0, 15.0, 40.0
a_S	Age at which recruited fish (adults) were stocked (y)	2 (2)	2 (2)
J_{0_S}	The density of age-0 fish stocked (ha^{-1})	Fry	Fry
		110 to 4900	130 to14000
		Fingerlings	Fingerlings
		2 to 90 (2)	10 to 1100 (2)
$N_{S,t}$	The density of recruited fish of age a_S stocked (ha^{-1})	0.65 to 30 (2)	1.5 to 166 (2)
θ	Linear coeffient of allometric stocking cost to size relationship	0.009459 (2)	0.003535 (2)
λ	Exponent of the allometric stocking cost to size relationship	1.736 (2)	1.923 (2)
Angling regulations			
MLL	Minimum-length limit (cm)	0 - L_{max}	0 - L_{max}
DBL	Daily-bag limit (d^{-1})	10	10
A_L	Density of angling licenses issued (= density of licensed anglers)	1, 5, 10	1, 5, 10
$€_L$	Annual angling license cost (€)	100	100
Angler Effort Dynamics			

φ	Persistence of fishing behaviour (= relative influence of last year's realized fishing probability on the current year's realized fishing probability)	0.5 (10)	0.5 (10)
d_{max}	Maximum number of days that an angler would fish per year irrespective of fishing quality (d)	20	20
Ψ	Average time an angler will fish in a day (h)	3 (2)	3 (2)
$\bar{l}_{ref}$	Reference average size of fish caught (cm)	37	36
L_T	Threshold length defining trophy-sized fish (cm)	100	90
U_{no}	utility gained from not fishing	0.2489 (1)‡	0.2489 (1)‡
U_{out}	utility gained from fishing elsewhere	0.4371 (1)‡	0.4371 (1)‡
U_{in}	basic utility gained from fishing in the region	-0.686 (1)‡	-0.686 (1)‡
U_{Spp}	PWU of fishing for most preferred species	0.0655 (1)‡	0.0655 (1)‡
u_1	Cost coefficient	-0.518 (1)‡	-0.518 (1)‡
u_2	Daily catch coefficient	0.1230 (1)‡	0.1219 (1)‡
u_3	Average size coefficient	1.2357 (1)‡	1.2263 (1)‡
u_4	Trophy catch coefficient	0.0254*100 (1)‡	0.0357*100 (1)‡
u_5	Crowding coefficient	-0.0424*0.5 (1)‡	-0.0392*0.5 (1)‡
u_6	MSL linear coefficient	0.005 (1)‡	0.0032 (1)‡
u_7	MSL quadratic coefficient	-0.0001 (1)‡	-0.0001 (1)‡
u_8	DBL linear coefficient	-0.0104 (1)‡	0.0085 (1)‡
u_9	Stocking frequency coefficient	0.1006 (1)‡	0.0632 (1)‡

u_{10}	Catch composition coefficient	0.0595 (1)‡	0.1013 (1)‡

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 (1996) 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(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).

‡ parameter values used were modified slightly from those reported by Arlinghaus et al. (2014) so that the U_{MLL}, the PWU 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.

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