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

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1　　　　　　**Running Head: Ecology, stocking and length limits**

2　　**How ecological processes shape the outcomes of stock enhancement and harvest regulations**

3　　　　　　　　　　　**in recreational fisheries**

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16

17 **ABSTRACT**

18 Fish stocking and harvest regulations are frequently used to maintain or enhance freshwater

19 recreational fisheries and contribute to fish conservation. However, their relative effectiveness

20 has rarely been systematically evaluated using quantitative models that account for key size- and

21 density-dependent ecological processes, and adaptive responses of anglers. We present a new

22 integrated model of freshwater recreational fisheries where the population dynamics of two

23 model species affect the effort dynamics of recreational anglers. With this model we examined

24 how stocking various fish densities and sizes (fry, fingerlings, and adults) performed relative to

25 minimum-length limits using a variety of biological, social and economic performance measures,

26 while evaluating trade-offs. Four key findings are highlighted. First, stocking often augmented

27 the exploited fish population, but size- and density-dependent bottlenecks limited the number of

28 fry and fingerlings surviving to a catchable size in self-sustaining populations. The greatest

29 enhancement of the catchable fish population occurred when large fish that escaped early

30 bottlenecks were stocked, but this came at the cost of wild-stock replacement, thereby

31 demonstrating a fundamental trade-off between fisheries benefits and conservation. Second, the

32 relative performance of stocking naturally reproducing populations was largely independent of

33 habitat quality and was generally low. Third, stocking was only economically advisable when

34 natural reproduction was impaired or absent, stocking rates were low, and enough anglers

35 benefitted from stocking to offset the associated costs. Fourth, in self-sustaining fish populations,

36 minimum-length limits generally outperformed stocking when judged against a range of

37 biological, social and economic objectives. By contrast, stocking in culture-based fisheries often

38 generated substantial benefits. Collectively, our study demonstrates that size- and density-

39 dependent processes, and broadly the degree of natural recruitment, drive the biological, social

40   and economic outcomes of popular management actions in recreational fisheries. To evaluate

41   these outcomes and the resulting trade-offs, integrated fisheries-management models that

42   explicitly consider the feedbacks among ecological and social processes are needed.

43   **KEYWORDS** density-dependence, size-dependent mortality, harvest regulations, fish stock

44   enhancement, human dimensions, recreational fishing, northern pike (*Esox lucius*), common carp

45   (*Cyprinus carpio*).

46

47   **INTRODUCTION**

48   Many inland fish populations are under threat due to anthropogenic impacts on habitat quality

49   and quantity, climate change, the stocking and spread of non-native fishes and genotypes and

50   resulting changes in genetic diversity, and overharvest (Dudgeon et al. 2006, Laikre et al. 2010,

51   Cooke et al. 2016). Recreational fishers are the dominant users of inland fish stocks in

52   industrialized countries (Arlinghaus et al. 2002, FAO 2012), and their activities and expenditures

53   are fundamentally important drivers for fish conservation and fisheries-management activities

54   (Arlinghaus 2006, Tufts et al. 2015). Collectively, recreational fishers can exert substantial

55   harvesting pressures on fish populations (Post et al. 2002, Cooke and Cowx 2006, Lewin et al.

56   2006). Managers tend to respond to impacts on recreational fisheries using three general

57   strategies (Arlinghaus et al. 2016): i) implementing input and output regulations that control

58   fishing effort (input) or regulate which sizes and how many fish are harvested (output), ii)

59   improving and restoring habitat, or iii) engaging in stocking-based enhancements. Among these,

60   harvest regulations and stocking are the most widespread due to tradition and ease of

61   implementation (van Poorten et al. 2011, Arlinghaus et al. 2016, Sass et al. 2017).

62   To manage fish stocking sustainably, it is important to understand when to engage in a specific

63   action and when to use alternatives (Lorenzen 2014, Arlinghaus et al. 2016, Arlinghaus et al.

64   2017). Although stocking can help fish stocks recover and enhance fisheries use and catch

65   (Lorenzen et al. 2012, Amoroso et al. 2017), the practice can also contribute to the decline of

66   wild fish populations by elevating competition or predation, fostering disease outbreaks,

67   promoting mixing of wild populations with domesticated, hatchery-reared fishes (Laikre et al.

68   2010, van Poorten et al. 2011, Lorenzen et al. 2012), and potentially increasing fishing pressure

69   on wild stocks (Baer et al. 2007). The ability of stocking to maintain or boost fisheries catches

70 beyond levels achievable by wild populations may correlate with a decline in environmental

71 quality that constrains natural recruitment, thereby freeing "niches" for hatchery fish (Rogers et

72 al. 2010, Ziegler et al. 2017). However, stocking hatchery fish may further burden an already

73 dwindling wild stock (Laikre et al. 2010, van Poorten et al. 2011, Cochran-Biederman et al.

74 2015), creating a fundamental trade-off between wild fish conservation and maintaining or

75 enhancing fisheries through (successful) stocking (Lorenzen 2005, Camp et al. 2017, Amoroso et

76 al. 2017). In light of key feedbacks among the ecological and social components of a fishery

77 (Camp et al. 2014, Lorenzen 2014, Arlinghaus et al. 2016), navigating this trade-off demands

78 careful analysis of how the outcomes from stocking vary with ecological conditions (e.g.,

79 whether a stock is self-sustaining or not) and properties of the management intervention (e.g.,

80 size and density of stocked fishes, fitness of hatchery fish in the wild). Such an analysis using an

81 integrated social-ecological model of recreational fisheries that incorporates a mechanistic model

82 of angler behavior and a realistic ecological representation of a stock-enhanced fishery regulated

83 by multiple size- and density-dependent ecological processes has so far not been completed.

84 An alternative management response common in freshwater recreational-fisheries management

85 is the implementation of harvest regulations (Arlinghaus et al. 2016). Harvest regulations are

86 used to limit fishing mortality, manage size structure, and distribute harvest more equally among

87 anglers (Radomski et al. 2001). However, constraints on an individual's ability to harvest fish

88 can have high social costs for angler groups most affected by the regulations (Beard et al. 2003,

89 Johnston et al. 2011, Haglund et al. 2016). Thus, implementing restrictive harvest controls is

90 rarely preferred by anglers over stocking or the control of perceived or real competitors (e.g.,

91 commercial fishers, fish-eating birds, Arlinghaus and Mehner 2003a, Dorow and Arlinghaus

92 2012). An analysis of fish-angler interactions that integrates ecological and social dimensions

93   and considers dynamic angler responses is needed to outline the ecological and socio-economic

94   conditions that favor one management approach (e.g. harvest restrictions) over another (e.g.,

95   stocking) (Arlinghaus et al. 2017).

96   A range of fish stocking models incorporating key ecological mechanisms, such as density- and

97   size-dependent mortality, are available to examine the ecological conditions constraining the

98   additive potentials of fish stocking (e.g., Lorenzen 2005, Rogers et al. 2010, Askey et al. 2013,

99   Camp et al. 2014). However, few of these models have explicitly considered multi-attribute

100   decision making by anglers. Both strategic and tactical recreational-fisheries models should

101   consider anglers' preferences and behavioral responses to policy interventions (Johnston et al.

102   2010), because they can strongly influence social (e.g., effort directed at a given site) and

103   ecological (e.g., fish abundance or catch rate) outcomes (Arlinghaus et al. 2017). Mechanistic

104   choice models based on economic random utility theory can be used to extrapolate complex,

105   human behavioral responses (Fenichel et al. 2013a), but no stocking model using a rigorous

106   choice-based representation of angler behavior exists. Considering both the ecological and social

107   dimensions of fisheries will likely affect management trade-offs, and the costs and benefits of

108   particular management actions. Moreover, judging the performance of any management action

109   will depend on the performance measure used, and ultimately on the underlying normative

110   framework and objectives (e.g., conservation, fisheries quality, economic benefits) upon which

111   the measures are based (Fenichel et al. 2013b, Camp et al. 2017).

112   Management actions such as harvest regulations and stocking will likely not be equally effective

113   at achieving various objectives, because they differentially affect fish populations and anglers.

114   The outcomes of stocking will be governed by a range of ecological processes that determine

115   how hatchery reared fish interact with their wild conspecifics (Lorenzen 2014). Most fish

116　populations are regulated by density-dependent compensatory mortality in the early juvenile

117　stage (Lorenzen 2005). Another key regulatory process is size-dependent mortality coupled with

118　density-dependent growth in later life stages (Lorenzen 2005). Size- and density-dependent

119　ecological processes are relevant for the success of minimum-length limits because they will

120　determine if fishing mortality is being affected (FAO 2012). These processes are also important

121　for determining stocking success, because they influence whether or not stocked fish can

122　circumvent factors limiting the wild population (Lorenzen 2005, Rogers et al. 2010, Camp et al.

123　2014). In addition, limited recruitment or productivity due to poor habitat quality, compensatory

124　changes in growth or survival of fish populations, and a lack of local adaptation of stocked fishes

125　to the wild can limit the ability of hatchery-reared fish to survive and reproduce (Cowx 1994,

126　Lorenzen et al. 2012, Cochran-Biederman et al. 2015). The situation is somewhat different in

127　non-naturally reproducing populations where stocked fish will not face intraspecific competition

128　with wild conspecifics.

129　We hypothesize that stocking should generate large social and economic benefits when natural

130　reproduction is lacking, while harvest regulations shall socio-economically outperform most

131　stocking events in self-sustaining stocks. We also hypothesize that stocking will be most

132　effective when large, recruited fishes are stocked that are no longer affected by compensatory

133　juvenile mortality (Lorenzen 2005), but that such stocking in naturally-reproducing populations

134　will create a fundamental trade-off between conservation and fisheries benefits (Amoroso et al.

135　2017, Camp et al. 2017). We test these hypotheses using a fully integrated model of fish-angler

136　interactions with explicit angler behavioral feedback grounded in economic utility theory. We

137　use this model to systematically explore how the contrasting ecology of two freshwater fishes,

138　naturally-reproducing and non-reproducing, shape the ecological, conservation and

139 socioeconomic outcomes of both stocking and a commonly applied harvest regulation, the

140 minimum-length limit (MLL). In the model, angler behavior is described mechanistically as a

141 function of multiple attributes of the fishing experience using results from an empirically

142 grounded stated preference model of anglers (Arlinghaus et al. 2014). The ecological sub-model

143 is calibrated to represent two prototypical freshwater fish populations, naturally-reproducing

144 northern pike (*Esox lucius*) that recruits to the fishery and common carp (*Cyprinus carpio*) that

145 does not naturally recruit to the fishery (referred to as non-reproducing). Pike was chosen

146 because it is a popular target species among anglers that is commonly stocked in both North

147 America (Paukert et al. 2001, Margenau et al. 2008) and Europe (Wedekind et al. 2001,

148 Arlinghaus and Mehner 2004, Hühn et al. 2014). Both stock enhancement (stocking into wild

149 populations) and culture-based stocking (into systems in which natural reproduction is absent)

150 can occur (Lorenzen et al. 2012). Despite carp being considered a pest in North America,

151 Australia and some parts of Europe (e.g. Spain), carp was chosen because of its importance as a

152 culture-based, harvest-oriented inland fishery in central Europe (Wedekind et al. 2001,

153 Arlinghaus and Mehner 2003b, Vilizzi et al. 2015). In central Europe, carp populations depend

154 almost entirely on stocking, because, while they regularly spawn, they rarely recruit to the

155 population successfully in the wild (Kottelat and Freyhof 2007). Hypotheses for why this occurs

156 include; unsuitable temperatures and flow for spawning, and competition or predation from

157 native cyprinids that usually spawn substantially earlier than carp (Kottelat and Freyhof 2007,

158 Bajer and Sorensen 2010). In the model we also considered recruitment-limited pike populations,

159 such as might occur in response to the loss of vegetated habitat (Casselman and Lewis 1996),

160 thereby studying the full range of possibilities as to how the degree of natural recruitment affects

161 stock enhancement outcomes relative to harvest regulations. Our simulation exercise was meant

162   to produce strategic insights into the trade-offs inherent in common fisheries management

163   actions in light of ecological constraints, rather than to generate tactical insights informing

164   management of a particular fishery.

165   **METHODS**

166   The potential effects of stocking and harvest regulations, specifically minimum-length limits

167   (MLLs) on biological, social, and economic outcomes were investigated using an integrated

168   bioeconomic recreational-fisheries model adapted from earlier work (Johnston et al. 2010, 2013).

169   The model included three main components: 1) a deterministic age- and size-structured

170   biological sub-model to describe the fish population dynamics, 2) a social sub-model to describe

171   angler effort dynamics, and 3) a management component, which allowed for different MLLs,

172   stocking sizes and stocking densities to be investigated (Figure 1). We used the model to

173   evaluate how well stocking different sizes of fish – fry, fingerlings, and adults (Appendix S1:

174   Figures S1 and S2) – at a variety of stocking densities performed relative to various MLLs in

175   terms of achieving biological, social, and economic management objectives, and the trade-offs

176   involved, for a single-lake fishery. This evaluation was done for naturally-reproducing northern

177   pike, representing a stock enhancement scenario, and for non-reproducing common carp,

178   representing a culture-based stocking scenario. Six performance measures covering a range of

179   commonly used ecological, social and economic objectives were evaluated. In addition, the age

180   structure and composition (wild vs. hatchery origin fish) of the fish population was examined for

181   some simulations as a further conservation objective. The simulations were run until the

182   population reached an equilibrium prior to the commencement of fishing or implementation of

183   management policies and then run for additional time until the model reached a new equilibrium

184   after the changes were introduced. In the stocking scenarios, stocking occurred annually at the

185   beginning of each year. Information from an interdisciplinary study on fish stocking and anglers

186   in Lower Saxony, Germany (www.besatz-fisch.de), was used to inform the biological and social

187   sub-models (Arlinghaus et al. 2014, Hühn et al. 2014, Arlinghaus et al. 2015). Model equations

188   can be found in Table 1 and parameter values in Appendix S1: Table S1. Software based on the

189   model presented here is freely available at http://www.ifishman.de/en/practioner/software/ in

190   English or German, which can be used to reproduce the results presented here and run

191   simulations for a range of other freshwater species.

192   *Biological sub-model*

193   The biological sub-model included the following key ecological processes: density-dependent

194   growth, reproduction, and density- and size-dependent survival during the early life stage (age-0

195   fish) and later life stages. These processes are essential to properly represent the ecological

196   changes induced by the density increase through stocking (Lorenzen 2005). A bi-phasic model

197   developed by Lester et al. (2004) was used to describe somatic growth. This model assumed that

198   the annual growth in length of immature fish was linear and dependent on biomass density to

199   represent density-dependent growth (Table 1, eqn. 2a-2b), while mature fish only realized a

200   proportion of the annual growth potential (Table 1, eqn. 2c) due to the diversion of resources to

201   reproduction. Thus, post-maturation growth was also density dependent. To create a more

202   realistic size distribution and simulate the cumulative effects of differential size-dependent

203   mortality (Walters and Martell 2004), 11 size classes (i.e., growth trajectories) within an age

204   class were modelled. For simplicity, stocked and wild fish were assumed to have the same

205   growth rates, but relative survival and reproductive fitness could differ (see below). Maturation

206   was assumed to be size and age dependent as is typical in fish (Table 1, eqn. 3a). Reproduction

207   was a linear function of female mass (Walters and Martell 2004) (Table 1, eqn. 3b), and the

208   potential for differential relative reproductive success between hatchery and wild fish (Lorenzen

209   2005) was explicitly included in the model (Table 1, eqn. 3b, ρ, Appendix S1: Table S1). In the

210   case of carp, natural reproduction was assumed to be zero, and in the pike simulations we

211   assumed various scenarios for the degree of natural recruitment to represent healthy and

212   disturbed ecosystems.

213   Differing from earlier applications (Johnston et al. 2010, 2013, Johnston et al. 2015), the survival

214   of larvae to age-1 was assumed to be size and density-dependent (Table 1, eqns. 4a-f and 5a-d) to

215   better represent the outcomes of stock enhancement using hatchery reared fry or juveniles

216   (Lorenzen 2005). To that end, we modified and implemented a method pioneered by Lorenzen

217   (2005), where recruitment to age-1 was "unpacked" so that pre- and post-stocking survival of

218   age-0 fish (fry or fingerlings) were described independently, allowing all fish to experience

219   density-dependent and size-dependent mortality - two processes which are commonly

220   experienced by fishes in this early life stage (Lorenzen 1996, 2005, Hazlerigg et al. 2012). We

221   modified the methods of Lorenzen (2005) by representing a Ricker-type stock-recruitment model

222   rather than a Beverton-Holt stock-recruit relationships, because a Ricker recruitment model has

223   been used to describe the early survival for pike (Edeline et al. 2008) and carp (Brown and

224   Walker 2004, based on data presented in Koehn et al. 2000) (see Appendix S1 for derivation). In

225   the pre-stocking phase (Table 1, eqns. 4a-f), wild and hatchery origin larvae (i.e., offspring of

226   stocked fish) underwent the same density-dependent survival bottleneck. During this phase it

227   was possible for a proportion of hatchery larvae to transition to wild strain fish due to natural

228   selection similar to Lorenzen (2005) (Table 1, eqn. 4f, h^2, Appendix S1: Table S1). The

229   potential for differential survival of age-0 hatchery fish relative to age-0 wild fish was also

230   included in the model (Table 1, eqn. 4f, γ, Appendix S1: Table S1), because empirical data has

231   shown stocked fishes often have lower relative survival fitness (Lorenzen 2006, Lorenzen et al.

232   2012, Hühn et al. 2014). In the post-stocking phase (Table 1, eqns. 5a-d), the age-0 fish that

233   survived the pre-stocking phase as well as age-0 fish stocked that year (fry or fingerlings)

234   experienced further density-dependent survival, but at a reduced intensity because fish were

235   larger and, thus, were less vulnerable to size-dependent mortality than smaller fish (Lorenzen

236   2005). Consequently, in our model, stocked fingerlings experienced lower natural mortality than

237   smaller fry. Similar to Coggins et al. (2007), fish surviving to age-1 were allocated to a growth

238   trajectory assuming a normal distribution. Although carp did not reproduce, stocked fry or

239   fingerlings were still assumed to experience size- and density-dependent mortality.

240   Natural mortality rates of age-1 and older fish were also assumed to be size- and density-

241   dependent using an empirical relationship presented by Lorenzen (1996, 2000) (Table 1, eqn.

242   6b). To introduce density-dependence in survival, we assumed that the allometric exponent of

243   size-dependent mortality relationship changed with density (Table 1, eqn. 6d), but that the

244   mortality rate of very large fish changed very little with density (see Appendix S1 for

245   derivation). Thus, changes in density had a greater impact on the natural mortality rate of small

246   fish compared to larger fish, agreeing with empirical studies and population dynamical theory of

247   stock enhancements (Lorenzen 2005). Incorporating size- and density-dependence into post-

248   recruitment survival allowed for increased mortality of small fish from predation by, and

249   competition with, larger fish, including fish stocked at larger sizes and older ages than age-0.

250   Model predictions in the absence of density-dependent survival of age-1 and older fish was

251   explored in the supplementary material (Appendix S1: Figures S6, S7, and S8). In scenarios in

252   which older fish (> age-0) were stocked, fish were added to the abundance of surviving hatchery

253   origin fish in the appropriate age category and allocated normally among the growth trajectories

12

254   (Table 1, eqn. 6a). The possibility of differential survival of fish of hatchery origin relative to

255   wild fish beyond the first year of life was also explicitly included in the model (Table 1, eqn. 6k,

256   γ_2, Appendix S1: Table S1).

257   To account for the size-dependent processes inherent to fishing mortality, a sigmoidal

258   vulnerability curve was used to determine vulnerability of fish to capture (Table 1, eqns. 6f-g,

259   Appendix S1: Figure S1), as is typical in recreational fisheries models (Post et al. 2003,

260   Arlinghaus et al. 2009, Allen et al. 2013). MLLs were used to determine which fish were legally

261   harvestable (Table 1, eqn. 6i). No bag limit was assumed; thus, all fish of legal size were

262   harvested. To account for illegal harvest (Sullivan 2002, Johnston et al. 2015), a percentage of

263   undersized fish were also harvested (Table 1, eqn. 6i). Undersized fish that were released

264   experienced hooking mortality (Table 1, eqn .6j) – an important process in recreational fisheries

265   (Post et al. 2003, Coggins et al. 2007, Johnston et al. 2015).

266   *Social sub-model*

267   In the social sub-model, annual angling effort was determined by the fishery quality of past

268   fishing experiences (Table 1, eqn. 7d), and constrained by available fishing time in line with

269   empirical data (Table 1, eqn. 7d, d_{max}, Appendix S1: Table S1). Note that our use of the term

270   fishing quality encompasses all dimensions that affect the angler utility, including: expected

271   catch rate, average size of fish caught, catch rate of trophy fish (as per Arlinghaus et al. 2014,

272   fish larger than a threshold size, L_T, Appendix S1: Table S1), the number of other anglers seen

273   while fishing (a measure of crowding), MLL (which measure preferences for retention of fish for

274   own consumption), license fees to fish within the water, preference for target species, stocking

275   frequency (an independent effect of knowing that a fishery is stocked), and the composition of

276   the catch (percent wild fish in the catch). Following random utility theory, the benefits anglers

277   derived from each fishery attribute, called part-worth utilities (Appendix S1: Figure S3), were

278   summed to determine the overall utility gained from fishing (Table 1, eqn. 7a) (Hunt et al. 2011,

279   Fenichel et al. 2013a). Using the utility model, anglers responded dynamically to changes in the

280   perceived quality of the fishery over time. The probability of fishing was determined primarily

281   by the utility experienced in the previous year (Table 1, eqn. 7a-b), but a fishing-behavior

282   persistence term (Table 1, eqn. 7c, φ, Appendix S1: Table S1) accounted for the fact that

283   previous experiences and fishing habits also influence anglers' fishing decisions (Adamowicz

284   1994) by including previous experiences at a discounted rate.

285   The theoretical utility-based sub-model of angler behavior was informed empirically by results

286   from a stated discrete-choice experiment conducted on German anglers in Lower Saxony

287   (Arlinghaus et al. 2014). This choice experiment exposed anglers to stocking-related attributes as

288   well as a large range of catch rates, thereby allowing the (dis)utility of very low catches near zero

289   to be explicitly estimated. For application in the present study, the parameter values for angler

290   preferences (u_1 - u_{10}, Appendix S1: Table S1) differ somewhat from those reported by

291   Arlinghaus et al. (2014). The choice model data were reanalyzed assuming that the part-worth

292   utility function of MLL (Table 1, eqn 9f) was quadratic rather than linear, because the quadratic

293   form best described the data for pike and carp (Arlinghaus et al. unpublished data). Arlinghaus et

294   al. (2014) found that the two stocking attributes did not have a significant influence on angler

295   utility. Thus, we assumed that anglers did not know that pike were stocked and were unable to

296   identify hatchery versus wild origin pike, which is likely. By contrast, for carp we assumed that

297   anglers were aware that carp were stocked and of hatchery origin, because these are culture-

298   based fisheries. The parameters from the choice model were species-specific, but for simplicity

299   represented the average angler as estimated by Arlinghaus et al. (2014). Hence, angler behavior

300   differed based on the species targeted, but all anglers were assumed to behave the same when

301   fishing for the same species. An exploration of angler heterogeneity is reserved for future work.

302   While the choice model allowed for variation in license cost $\text{\euro}_L$, daily bag limit DBL,

303   preference for target species, and stocking frequency, these aspects were not investigated in this

304   study. Thus, levels of these attributes were held constant (Appendix S1: Table S1). Our model

305   was designed to represent a single-lake fishery, such as those run by angling clubs in central

306   Europe. Managers of such fisheries have control over input and output regulations, as well as

307   over what size and density of fish stocked, without involvement of public agencies as is typical

308   for central Europe (Daedlow et al. 2011).

309   *Range of MLLs, stocking strategies, and performance measures examined*

310   In the model scenarios, MLLs ranged from zero to mandatory total catch-and-release (i.e., the

311   maximum size fish could achieve, 0 - L_{max}, Appendix S1: Table S1). The size of fish stocked and

312   the range of stocking densities explored reflected information from a survey of over 2000

313   angling clubs (61% response rate) throughout Germany (Arlinghaus et al. 2015). Accordingly, in

314   the pike scenarios, fry, fingerlings and adults were assumed to be about 2 cm, 20 cm, and age-2

315   (35-40 cm), respectively, and in the carp scenarios about 4 cm, 15 cm, and age-2 (40 cm),

316   respectively (L_s, Appendix S1: Table S1). These sizes were commonly reported in the datasets.

317   For pike, the range of stocking densities of all three stocking sizes initially modelled were chosen

318   to reflect the range in annual stocking expenditures reported by angling clubs across Germany,

319   i.e., a mean of 50 € ha^{-1} yr^{-1} for pike (range 3–154 € ha^{-1} yr^{-1}, 5th and 95th percentile

320   respectively). Thus, the range of stocking densities for each of the three size classes we tested (

321   J_{0_S} for fry and fingerlings, $N_{S,t}$ for adults, Appendix S1: Table S1) resulted in the associated

322   range in stocking costs being identical across size classes (Table 2), thereby allowing a direct

323   comparison of the effect of varying stocking sizes for the same monetary investment. For carp,

324   the expenditure range reported by German angling clubs was much greater (mean 210 € ha^{-1} yr^{-1},

325   range 7–710 € ha^{-1} yr^{-1}, 5th and 95th percentile respectively). For comparative purposes we

326   investigated stocking expenditures in a similar range to pike (0, 5, and 100 € ha^{-1} yr^{-1}) instead for

327   carp (Table 2), translated into numerical stocking abundance. Average angler density in

328   Germany and in the five study clubs involved in our stocking project, measured as the number of

329   anglers licensed to fish a given area of water, was approximately 5 licensed anglers ha^{-1}, ranging

330   from about 1 to 10 licensed anglers (ha^{-1}). Thus, as a surrogate for latent fishing pressure, we

331   used these three angler densities in our model simulations but allowed realized fishing pressure

332   to vary in response to changes in fishing quality following the utility model.

333   We considered six main performance measures for each of the policies we examined. Two

334   measures related to biological objectives: 1) augmentation (i.e., increased density) of the overall

335   population, and 2) the density of fish fully vulnerable to the fishery, assumed to be those

336   surviving until their third birthday (age-2 and older fish at the end of the year) (Figure S1). In

337   addition, the age structure and composition (wild vs. hatchery origin fish) of the fish population

338   was examined for some simulations as a further conservation objective. Two measures addressed

339   social objectives: 3) the average catch rate, which is often used as a surrogate of angler well-

340   being (Cox et al. 2003), and contrasted it with 4) a more integrated measure of average angler

341   welfare (benefit), net willingness-to-pay (WTP) (Table 1, eqn 8a). Net WTP is a measure which

342   quantifies the change in satisfaction (inclusive value) relative to the status quo expressed in

343   monetary terms (Edwards 1991, Cole and Ward 1994, Loomis and Fix 1999). As status quo, we

344   used the unstocked and unregulated (no MLL) scenario. To address economic considerations, we

345   calculated 5) the per capita costs associated with stocked fish surviving until they were fully

346   vulnerable to the fishery (i.e., their third birthday, Table 1, eqn 8e), as well as 6) an integrative

347   measure of the net economic benefit (aggregated angler welfare minus costs, Table 1, eqn 8c).

348   Net economic benefit was measured as aggregated social welfare, the sum of individual angler

349   welfare (WTP) across all licensed anglers, minus the financial cost of stocking. Stocking costs

350   were determined based on empirical fish size-cost relationships estimated from Germany

351   (Appendix S1: Figure S2). We used these metrics to evaluate and implicitly rank policy

352   outcomes. Additionally, we examined the size structure and composition (wild vs. hatchery

353   origin) of the fish population in some scenarios to evaluate size/age truncation effects from

354   fishing and replacement of wild fish by hatchery origin fish as a further commonly applied

355   conservation objective (Rogers et al. 2010, Camp et al. 2017).

356   *Outline of analyses*

357   In scenario 1 (Table 2), we evaluated how well annually stocking of various sizes of fish – fry,

358   fingerlings and adults – at a range of realistic densities preformed relative to the use of a range of

359   MLLs in relation to the six performance measures outlined above. This was done for pike, and

360   latent fishing pressure was assumed to be moderate at 5 licensed anglers ha^{-1}.

361   Variations on the base scenario 1 (Table 2) were then used to investigate the sensitivity of

362   outcomes to some of the model assumptions. In scenario 2 (Table 2), we compared naturally-

363   reproducing pike and non-reproducing carp, when stocking expenditures were the same for both

364   species. We evaluated results at low (1 licenses ha^{-1}) and high (10 licenses ha^{-1}) latent fishing

365   pressure, and when the range in stocking densities reflected low (5 € ha^{-1}) to moderate (100 € ha^{-}

366   ^{1}) stocking costs for both species.

367   In scenarios 3 and 4, for pike only, we examined how sensitive the model predictions were to

368   modifications of some of the key model assumptions. In these scenarios (Table 2), we examined

369   results for low and moderate stocking densities (5 € ha^{-1} to 100 € ha^{-1}, respectively) and

370   moderate latent fishing pressure (5 licenses ha^{-1}). Four biological assumptions were examined in

371   two sets of scenarios. 1) In scenarios 3A and 3B (Table 2), we tested the hypothesis that stock

372   enhancement may be more beneficial in habitats where natural reproduction is impaired (Rogers

373   et al. 2010). We examined two cases; one where the productivity parameter (α, Appendix S1:

374   Table S1) in the stock-recruitment relationship related to the slope near the origin was reduced

375   by half (Table 2, scenario 3A), and a second where the strength of density-dependence (β,

376   Appendix S1: Table S1) in the stock-recruitment relationship was doubled (Table 2, scenario

377   3B), resulting in greater inter-specific competition effectively reducing habitat capacity. In both

378   cases, maximum recruitment was reduced. 2) We examined two scenarios, one in which stocked

379   fish had reduced fitness (Table 2, scenario 4A), and a second in which stocked fish had reduced

380   fitness but whose offspring evolved to wild-type fish in the F1 generation (Table 2, scenario 4B).

381   In both scenarios 4A and 4B (Table 2), hatchery origin fish had reduced reproductive success,

382   and reduced survival in both the juvenile and adult stages (relative survival of stocked age-0 fish

383   was 50%, of stocked adults was 90%, and relative reproductive success was 56% compared to

384   wild fish) following empirical data (Hühn et al. 2014). In scenario 4B (Table 2), we relaxed the

385   base assumption that larvae produced by spawners of hatchery origin retained a hatchery origin

386   phenotype (Table 1 eqn. 4f, $h^2 = 0$), and tested the opposite extreme where all larvae produced

387   by hatchery origin spawners transitioned to wild type due to natural selection (Table 1 eqn. 4f,

388    $h^2 = 1$) (Lorenzen 2005). These scenarios were not examined for carp because it is unrealistic to

389   assume wild recruitment of this species in central and northern Europe.

390   **RESULTS**

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

392   From a biological and conservation perspective, in the base scenario (Table 2, scenario 1) where

393   hatchery and wild pike were assumed to have equal fitness, increasing MLLs generally increased

394   total pike density and the density of vulnerable pike, although this pattern was less evident for

395   total pike density when fingerlings were stocked (Figure 2). Density increased rapidly around an

396   MLL of 40 cm as MLLs began to protect the age-2 cohort from harvest (Appendix S1: Figure

397   S4). Total pike densities increased with increased stocking density for all sizes stocked,

398   particularly when MLLs were low (< 40 cm) and the pike population was overfished at a latent

399   license density of 5 angling licenses ha^{-1} in the absence of stocking. Total densities were highest

400   when fingerlings were stocked and lowest when fry were stocked, and stocking pike fry had

401   minimal effects on total pike density at all MLLs > 40 cm (Figure 2, left column). By contrast,

402   adult stocking resulted in the greatest increases in vulnerable pike density (i.e., catchable size),

403   whereas stocking fry and fingerlings had very little effect on this metric (Figure 2, second

404   column). Any benefits of stocking to pike density, however, came at the cost of severe wild stock

405   replacement by hatchery origin fish (Figure 3). Even at low annual stocking densities, stocked

406   fingerlings and adults at equilibrium replaced most of the wild fish. Replacement of wild stocks

407   was less severe when fry were stocked at low densities and MLLs were high, but was a concern

408   at high fry stocking densities, despite the lack of additive effects on the overall pike stock.

409   Replacement was less severe at high MLLs, particularly for fry, suggesting that they improve the

410   buffering capacity of wild populations against invasion by hatchery phenotypes by reducing

411   fishing mortality of adults.

412   From a social perspective of the fishing quality, stocking pike had positive impacts on average

413   catch rates, but the catch-rate effects were much more pronounced and dependent on stocking

414   density when adult pike were stocked relative to fry and fingerlings (Figure 2, third column).

415   MLLs did not influence catch rates as much when fry and fingerlings were stocked as they did

416   when adults were stocked. Yet, despite the potential for large increases in pike catch rates due to

417   stocking (particularly the stocking of immediately catchable adults), the average benefit to an

418   angler (measured by average net WTP) was largely uninfluenced by stocking pike of any size or

419   density (Figure 2, fourth column), although net WTP was generally slightly higher when adults

420   were stocked. MLLs had a stronger effect on net WTP than stocking, with the benefits initially

421   increasing and then decreasing with increasing MLLs. These findings revealed that intermediate

422   MLLs maximized angler well-being.

423   From an economic perspective, high stocking densities generally increased the per capita costs

424   associated with stocked pike surviving to be fully vulnerable to the fishery (Figure 2, fifth

425   column). By this metric, adult stocking was the most cost effective, followed by fingerlings. Fry

426   were the least cost effective. Survivor costs were generally highest when MLLs were low (< 40

427   cm) but decreased rapidly when MLLs reached 40 cm and protected fish from harvest, and then

428   slowly increased as MLLs increased further as density-dependent processes became more

429   important. Importantly, however, the net economic benefits of stocking were negative for most

430   stocking strategies evaluated (10–154 € ha^{-1} yr^{-1}) when fishing pressure was moderate (5 licenses

431   ha^{-1}) (Figure 2, right column). Only very low stocking densities (<10 € ha^{-1} yr^{-1}), resulted in a

432   positive net benefit. When stocking was absent, use of MLLs up to about 110 cm produced a

20

433   positive net economic benefit (peaking at 8.8 € ha^{-1} yr^{-1} at an MLL of ~60 cm) at intermediate

434   fishing pressures.

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

436   A direct comparison of the outcomes for reproducing pike and non-reproducing carp with the

437   same stocking expenditures (0, 5 or 100 € ha^{-1}) under low and high latent fishing pressure (1

438   angler ha^{-1} or 10 anglers ha^{-1}, Table 2 scenarios 2A and 2B) revealed several similarities to

439   results above, but also important differences in the relative effects of stocking compared to

440   MLLs. Similar to pike, stocking carp enhanced total carp density and the density of vulnerable

441   carp (Figure 4), with higher stocking densities having larger effects. Like pike, stocking carp

442   fingerlings produced the highest total densities of carp. Stocking adults generally produced

443   higher densities of vulnerable carp and higher catch rates than stocking of either fry or

444   fingerlings (Figure 4), except under high latent fishing pressure (10 anglers ha^{-1}) and low MLLs

445   (< 50 cm). Unlike pike, where stocking pike at low densities into a self-sustaining population

446   (i.e., under low latent fishing pressure, 1 angler ha^{-1}, or when MLLs > 50 cm protected adults

447   from harvest) had little impact on the fish density, the density of vulnerable fish, and catch rates,

448   stocking carp of any size was always beneficial and much less influenced by MLLs compared to

449   the pike scenarios (Figure 4). Even stocking fry improved carp density, vulnerable carp density,

450   and catch rates, whereas stocking pike fry only had an effect when the pike population was

451   heavily exploited (i.e., high latent fishing pressure of 10 anglers ha^{-1}, and low MLLs < 40 cm),

452   and only enhanced total pike density having little impact on vulnerable pike density or catch

453   rates (Figure 4).

454   Similar to pike, MLLs were more important for determining net WTP in carp than variation in

455   stocking size or number (Figure 4). However, stocking carp increased net WTP more than

456   stocking pike did, and unlike pike where stocking only performed better than MLLs at high

457   fishing pressure and low MLLs, stocking carp always resulted in a highly positive net WTP that

458   was much greater than the use of MLLs alone (Figure 4). Carp net WTP was also much less

459   influenced by latent fishing pressure than the pike's net WTP.

460   The per capita costs of fish surviving to a vulnerable age were much lower for carp than pike, but

461   as in the case of pike the costs tended to be lowest when MLLs were around 40 cm and increased

462   with stocking density (Figure 4). Also, similar to pike, carp fry were least cost-effective to stock.

463   However, unlike pike, the most cost-effective stocking size for carp was context-dependent. Low

464   densities of carp fingerlings were generally most cost-effective, but as stocking densities

465   increased, adult carp became more cost-effective than fingerlings in most cases (Figure 4).

466   Finally, like pike, the net economic benefit of stocking carp was not strongly influenced by the

467   size of fish stocked, with adults and fingerlings performing slightly better than fry (Figure 4).

468   However, unlike pike, stocking carp was much more likely to result in a positive net benefit,

469   occurring at lower latent fishing pressures, under a broader range of stocking densities, and being

470   of higher magnitude (Figure 5). It should be noted, at higher latent effort, even pike stocking

471   resulted in a positive net benefit. Moreover, the net economic benefit from stocking carp was

472   more likely to exceed the net benefit from the use of MLLs alone; something which only

473   occurred for pike at low MLLs when latent fishing pressure was high. Thus, overall stocking of

474   carp outperformed stocking of pike economically and socially.

475   *The ecological constraints on stocking wild fish populations*

476   The model outcomes were generally robust to some key assumptions made about ecological

477   constraints on the production of wild pike. Changes in population productivity and habitat

478   capacity (Table 2, scenarios 3A and 3B), as expected, reduced total pike density and vulnerable

479   pike density in both the unstocked and stocked scenarios (Figure 5). Despite these differences,

480   the patterns in terms of the performance of stocking were generally qualitatively similar to the

481   unaltered scenario, i.e., reduced habitat quality did not improve the prospects of stocking

482   generating additive effects on the pike stock and fishing quality. One exception involved

483   stocking pike fingerlings at high density when habitat capacity was poor. In this case, total pike

484   density declined with increasing MLLs rather than staying relatively static in the unaltered case

485   (Figure 5). Reduced habitat capacity and productivity also reduced catch rates, but the effects on

486   catch rates were less severe (Figure 5). That said, reductions in baseline catch rates in the

487   unstocked and unregulated scenario due to reduced productivity were orders of magnitude

488   smaller than the baseline and diminished habitat capacity scenarios (e.g., at 5 licenses ha^{-1}, and

489   no MLL or stocking; 1.9 10^{-6} pike d^{-1}, for baseline and poor habitat capacity, 2.8 10^{-13} pike d^{-1},

490   for low productivity scenario). As a result, changes in habitat capacity had no discernable effect

491   on net WTP, but reduced productivity resulted in much higher net WTP under all stocked and

492   unstocked scenarios (Figure 5). Reductions in habitat capacity and productivity increased the per

493   capita costs of stocked fry and fingerlings surviving to a vulnerable age, particularly when they

494   were stocked at high stocking densities (Figure 5). Similar to net WTP, changes in habitat

495   capacity had little impact on the net economic benefits of pike stocking, while reduced

496   productivity increased net benefit in all scenarios. However, this effect was not enough to exceed

497   the benefit of using moderate to high MLLs alone in the management of pike in a habitat-

498   constrained fishery (Figure 5).

499   Stocked pike, like many other fishes, are known to suffer from lower fitness relative to wild

500   fishes, so we also examined this key assumption for systematic effects (Table 2, scenarios 4A

501   and 4B). The realistic assumption that stocked fish had generally lower fitness (i.e., lower

502   reproductive success, and lower survival) than similarly-sized wild conspecifics caused

503   reductions in total pike density, vulnerable density, and catch rates relative to the scenario of

504   equal fitness. Reductions were most pronounced when fingerlings were stocked and least

505   pronounced when adults were stocked (Figure 5). Lowered fitness of stocked fish increased the

506   per capita costs of stocked fry and, to a lesser extent, the number stocked fingerlings surviving to

507   vulnerable sizes, but had little influence on net WTP or net economic benefit of pike stocking.

508   Simulating strong natural selection by introducing a heritability of one (i.e., 100% transition of

509   hatchery spawned fish to wild origin, Table 2, scenario 4B) reversed some of the effects on total

510   fish density that low fitness introduced but had little influence on other output measures (Figure

511   5). Thus, the results presented were robust to these model sensitivities.

512   **DISCUSSION**

513   Our model integrated a size-structured fish population model (which included multiple size- and

514   density-dependent feedbacks) with a mechanistic sub-model of adaptive angler behavior.

515   Through key size- and density-dependent ecological processes we explicitly accounted for the

516   compensatory response of the fish population and how they respond to the change in density

517   induced by stocking or harvesting. The coupled social-ecological model thus allowed the

518   systematic study of how ecological processes drive the biological, social and economic outcome

519   of commonly applied management interventions in recreational-fisheries management. We show

520   that the expected benefits of stocking versus managing the fishery solely with harvest regulations

521   vary greatly depending on the ecological condition of the population being supplemented along a

522   gradient of reproducing and self-sustaining to non-reproducing. The evaluation of outcomes also

523   varies strongly with the metric that is used to judge performance, identifying some key trade-

524   offs, e.g., among conservation and fisheries benefits in the case of stock enhancements in

525   naturally self-sustaining populations. Both hypotheses initially stated were supported. First,

526   stocking promises to have additive ecological and large social effects when natural reproduction

527   of the target species is lacking or when fish large enough to have escaped strong juvenile

528   mortality compensation are stocked in self-sustaining populations. However, in the latter case

529   this comes at the costs of replacement of wild fish by hatchery fish over time, creating a

530   fundamental trade-off among successful stock enhancement and wild fish conservation (*sensu*

531   Rogers et al. 2010, Amoroso et al. 2017, Camp et al. 2017). Second, harvest regulations socially

532   and economically outperform stocking measures when managing naturally reproducing

533   populations.

534   *Conservation and catch outcomes*

535   Our results underscore the importance of ecological processes for determining the outcomes of

536   common recreational-fisheries management actions. Like other studies (e.g., Lorenzen 2005,

537   Camp et al. 2014), we found density-dependent growth and size- and density-dependent

538   mortality responses of fish populations constrained the contribution of stocking to the exploited

539   population and limited the catch rates that anglers could enjoy. For example, stocking fry into a

540   self-sustaining population (e.g., pike at low latent effort or high MLLs where the stock was not

541   overfished) produced no additive effects to the vulnerable population and to catch rates relative

542   to the use of MLLs alone. These model predictions agree well with empirical findings for stock-

543   enhanced pike and other species (e.g., Li et al. 1996, Skov et al. 2011, Hühn et al. 2014), and

544   findings of previous stocking models (e.g., Lorenzen 2005, Camp et al. 2014). Stocked

545   fingerlings that escaped more of the early mortality bottleneck, on the other hand, were predicted

546   to augment the overall population beyond levels achieved by MLLs alone, particularly when

547   hatchery fish had a high relative fitness. However, in naturally reproducing populations high

548   size-dependent natural mortality rates of stocked fingerlings resulted in only minimal increases

549   in the densities of fish vulnerable to capture, while the largest additive effects on vulnerable

550   density and thus catch rates were predicted from the stocking of large, recruited fishes in such

551   situations. These findings are consistent with empirical results for a range of species (e.g., Li et

552   al. 1996, Baer and Brinker 2008) and theoretical studies (e.g., Rogers et al. 2010, Garlock et al.

553   2017). Our findings are also consistent with a recent pike stocking experiment that found that

554   stocking age-0 fingerlings enhanced stocks one year later (age-1), but the additive effect was no

555   longer present in the age-2 cohort when the fish became vulnerable to the fishery and size-

556   dependent mortality had regulated the cohort's abundance back to carrying capacity (Arlinghaus

557   et al. 2015, Guillerault et al. 2018). The reason for the superior performance of large-sized

558   stocked fishes in naturally recruiting situations is that stocked adults experience much less

559   natural mortality than fingerlings because of the allometry of the size-mortality relationship

560   (Lorenzen 2000). At the same time, they may be large enough to be immediate vulnerable to

561   capture by fishing gear (Lorenzen et al. 2012). The benefits from stocking large fish in both

562   naturally reproducing and non-reproducing situations that we found in our model are generally

563   consistent with other models (Askey et al. 2013, Camp et al. 2014, Garlock et al. 2017) and

564   empirical studies (e.g., Wiley et al. 1993, Yule et al. 2000, Meyer et al. 2012). Our model

565   supports the trend seen in some countries to stock increasingly larger fish including catchable

566   fish in stock-enhancement efforts (Halverson 2008), which is likely a response to fry and small

567   fingerlings rarely producing sustained outcomes for ecological reasons. However, the more

568   successful stock enhancement efforts in naturally reproducing stocks become, the more likely

569   these efforts are to replace the wild stock component (Rogers et al. 2010, van Poorten et al.

570   2011), and potentially increase angling impacts by attracting increased fishing pressure (Baer et

571   al. 2007), thereby creating a fundamental, trade-off among fisheries benefits and conservation

572   (Camp et al. 2017, Amoroso et al. 2017).

573   Despite abundant ecological risks (e.g., Laikre et al. 2010, van Poorten et al. 2011), our findings

574   and related work (Cowx 1994, Lorenzen et al. 2012, Sass et al. 2017) suggest stocking can, when

575   properly conducted, play an important role in rehabilitating fisheries that are no longer self-

576   sustaining or creating or maintaining fishing opportunities when local fishing pressures are high.

577   Specifically, we found that stocking fish populations that were not self-sustaining (e.g., carp or

578   heavily overexploited pike at low MLLs) was successful in establishing and enhancing the

579   fisheries for the benefit of anglers and conservation. In these culture-based situations, stocking

580   fish of small size also elevated catch rates, because otherwise the population would not persist.

581   Interestingly, unlike the case in pike, we found that carp fingerlings contributed more to the

582   vulnerable population than adults in two situations, 1) when stocking densities were low, and 2)

583   when stocking densities were high, fishing pressure was high, and MLLs were low (overfished

584   stocks). Ecological processes were important for determining stocking outcomes in these cases.

585   In the first case, similar to what Lorenzen (1995) and Hunt et al. (2014) found, density-

586   dependent processes resulted in a trade-off between the number of fish stocked and fish size,

587   which had impacts on natural mortality rates. At low stocking densities, fingerling growth rates

588   were fast and size- and density-dependent mortalities were reduced, resulting in more fingerlings

589   surviving to the vulnerable stage. The reverse was the case at higher stocking densities, except

590   when the catchable-sized adults experienced high fishing mortality rates under high fishing

591   pressure and liberal harvest limits, resulting in low residence times of stocked adults. Thus, the

592   possible enhancement effects of different fish sizes are tightly coupled to the degree of natural

593   recruitment, stocking rate, local harvesting pressure and the harvest regulations in place. Models

594   such as ours (available at http://www.ifishman.de/en/practioner/software/) and others (Varkey et

595   al. 2016, Garlock et al. 2017), can help to define species-specific expectations and inform

596   management policies as to which life stage is likely to perform best, but adaptive stocking

597   experiments are then needed to identify the most suitable stocking strategy for a given target

598   species and system (Arlinghaus et al. 2017).

599   Ecological processes are also responsible for the prediction that the conservation benefits from

600   stocking recruitment-limited populations may actually be slim. Recruitment limitations due to

601   habitat bottlenecks are among the most often cited arguments (Cowx 1994) for so called

602   compensatory stock-enhancement efforts in impaired populations (Lorenzen et al. 2012).

603   However, we found that reductions in maximum habitat capacity for recruits and generally a

604   reduced productivity did not render stocking relatively more beneficial to the population or the

605   fishery, particularly when small sizes were used in stocking. Our results agree with a recent

606   empirical study by Guillerault et al. (2018) who reported that the additive effects of pike stocking

607   were largely independent of the quality of the habitat for the target species in lakes. Our findings

608   contrast those of other studies (e.g., Rogers et al. 2010, Ziegler et al. 2017) who reported that

609   stocking is increasingly beneficial when natural reproduction is impaired from habitat loss.

610   However, even then the size-at-stocking is bound to determine stocking outcomes, and only sizes

611   beyond recruitment bottlenecks are likely to perform well (Lorenzen 2005). Varying assumptions

612   in related models and ours can explain the divergent study findings. For example, Rogers et al.

613   (2010) assumed that habitat degradation only affected the wild-spawned fish and did not affect

614   the hatchery-released fish. By contrast, we assumed that all fish, including the offspring from

615   surviving stocked fish, were constrained by the conditions of the waterbody. Hence in our study,

616   even stocking adults, which elevate catch rates and increase spawning stock in the short-term,

617   will not produce long-term biological benefits by improving recruitment, but it will benefit

618   anglers by creating a put-and-take or a put-grow-and-take fishery. Similarly, Ziegler et al. (2017)

619   found that stocking larger individuals allowed fish to escape the high predation mortality when

620   predation refugia utilized by young-of-year walleye (*Sander vitreus*) was removed from lakes,

621   and Li et al. (1996) reported that fingerling stocking enhanced a walleye abundance index more

622   than fry stocking, but only in lakes where natural recruitment was essentially absent. Under

623   conditions of low habitat quality where natural recruitment is constrained, stocking is a bandage

624   solution used to increase abundance and improve catch rates, rather than addressing the

625   underlying problem (Sass et al. 2017). In such situations, habitat restoration promises to be the

626   only tool able to sustainably elevate the productivity and carrying capacity of a given ecosystem

627   for fish (Sass et al. 2017). Although our model did not explicitly allow habitat management to be

628   explored, changes to the parameters of the stock-recruitment relationship can be used to inform

629   how well this practice preforms compared to stocking or MLLs.

630   The realistic assumption of reduced fitness of stocked fish relative to wild conspecifics

631   (Lorenzen et al. 2012, Hühn et al. 2014, Arlinghaus et al. 2015) can further minimize the benefits

632   of stocking. For example, in a replicated pond study, Hühn et al. (2014) found that cultured

633   juvenile pike fry performed half as well in terms of growth and juvenile mortality when forced

634   into competition with wild recruits, but did as well as wild recruits when stocked in ponds with

635   no wild pike. Despite their lower fitness, however, some stocked fry established in the stock

636   enhancement treatments leading to the replacement of wild recruits rather than increasing the

637   year class abundance (Hühn et al. 2014). The circumvention of sexual selection during artificial

638   breeding can also reduce reproductive fitness (Thériault et al. 2011). Given the lower fitness of

639   hatchery fish, even those held for only brief periods in the hatchery (Araki et al. 2007, Thériault

640   et al. 2011, Christie et al. 2014), establishment of hatchery fish in natural stocks can ultimately

641   also lead to a reduced productivity of the fishery (Chilcote et al. 2011). We found that reducing

642   the fitness of hatchery-origin fish reduced the benefits associated with stocking fry or fingerlings,

643   in agreement with Lorenzen (2005) and Rogers et al. (2010), although if, as has been suggested

644   (Lorenzen 2005), natural selection causes hatchery fish to evolve wild-type phenotypes this

645   could partially compensate for the lower stocking success resulting from differential survival.

646   Despite lower fitness, we found that releasing low fitness juvenile or adult pike in larger numbers

647   could still produce fisheries benefits, simply due to numerical effects. The caveats include the

648   possible replacement of the wild stock components by hatchery fish and a possible reduction in

649   long-term sustainability.

650   Alternatively, hatchery fish could survive well to recapture but show low reproductive success

651   relative to wild spawners (Lorenzen et al. 2012). If the phenotypes to be released survive well,

652   but do reproduce effectively, stock enhancements could be of less conservation concern, while

653   still delivering fisheries benefits. We did not examine this scenario in our model, nor did we

654   evaluate other factors such as differential growth or catchability of hatchery and wild fish

655   (Mezzera and Largiadèr 2001, Biro and Post 2008, Klefoth et al. 2012), and these processes will

656   positively affect the fisheries performance of stocking programs by offering greater returns of

657   hatchery fish that have higher catchability (Lorenzen et al. 2012). Moreover, the high

658   catchability could reduce the residence times (time between stocking and recapture) of hatchery

659   fish minimizing the risk of introgression (Mezzera and Largiadèr 2001, Baer et al. 2007).

660   Stocking triploids is an alternative to effectively avoid interbreeding of hatchery fish and wild

661   fishes, thereby minimizing the impacts of wild stocks in the long term while providing fishing

662   opportunities (Koenig et al. 2011, Lorenzen et al. 2012).

663   *Social outcomes*

664   From a social perspective, we found that stocking naturally reproducing pike populations had

665   little effect on angler well-being as long as a threshold catch rate was achieved in the fishery.

666   Socially, we found intermediate MLLs generally outperformed stock enhancements in naturally

667   reproducing situations, but, in line with Rogers et al. (2010), stocking can benefit naturally

668   reproducing fisheries that experience high fishing mortality. In the latter case, recruitment

669   overfishing limited egg production, because not enough adults were surviving to reproduce.

670   Thus, while stocking can be effective for managing heavily exploited populations, a more

671   sustainable approach would be using restrictive harvest regulations, which can then be combined

672   with put-growth-and take type of enhancements to satisfy angler demands (Arlinghaus et al.

673   2016).

674   Similar to other studies (e.g., Johnston et al. 2010, Camp et al. 2016), our results challenge a

675   common assumption that angler utility (or satisfaction), is determined primarily or exclusively

676   by angler catch rates (e.g., Carpenter et al. 1994, Post et al. 2003, Rogers et al. 2010). We found

677   the success of stocking, as measured by net WTP, was not tightly correlated with catch rates,

678   even when stocking created large differences in catch rates. Although catch rate was a highly

679   significant attribute in the choice experiment used to inform angler behavior in our study

680   (Arlinghaus et al. 2014), the lognormal form of the part-worth utility function for catch rate

681   (Appendix S1: Figure S3) meant that the marginal gains in utility that came with increased catch

682   rates rapidly diminished as catch rates exceeded a certain minimally acceptable threshold.

683   Empirical studies have found similar relationships between catch and satisfaction (e.g., Patterson

684   and Sullivan 2013, Beardmore et al. 2015, Hyman et al. 2016). In other words, anglers were very

685   dissatisfied when catch rates were extremely low, but once catch rates were "good enough"

686   (roughly 1 fish daily, Arlinghaus et al. 2014) they had little further impact on angler satisfaction.

687   As a consequence, it has been found empirically that intermediate stocking rates attract the

688   greatest fishing effort, because low stocking rates produce catch rates low enough to affect

689   anglers' behavior and high stocking rates reduce fish growth and affect anglers' satisfaction with

690   the size of fish caught, thereby attracting less fishing effort (Mee et al. 2016). We argue that a

691   diminishing marginal return in utility from increasing catch rates is consistent with economic

692   (Beardmore et al. 2015) and motivational theory (Finn and Loomis 2001), and is likely found in

693   most recreational fisheries. That said, some anglers have been implied to have linear or

694   accelerating preferences for catch rates (e.g., Varkey et al. 2016), such as those targeting high-

695   catch-rate small-bodied cyprinid species in Germany (Beardmore et al. 2015). If such

696   relationships exist, our model predictions may not hold.

697   The non-linear relationship between catch and utility explains, in part, why MLLs were much

698   more important than the stocking strategy for determining angler well-being (and thus

699   satisfaction) in naturally reproducing fish in our study. When MLLs were sufficiently high (>40

700   cm) to offer some protection to catchable fish, then catch rates were "good enough" using MLLs

701   alone and any improvements to catch rates from stocking had minimal impacts on angler

702   satisfaction and behavior. A second reason why MLLs impacted angler satisfaction was because

703   harvest regulations also affect anglers directly through the perceived restrictions they might have

704   on harvest. Other studies have confirmed that regulations can affect angler use (e.g., Beard et al.

705   2003, Johnston et al. 2011, Haglund et al. 2016). The quadratic (i.e., hump shape) form of the

706   part-worth-utility relationship for MLLs (Appendix S1: Figure S3) implies that there is a balance

707   between desires to conserve the fish resource and perceived ability to harvest (Johnston et al.

708   2010), thus, generally intermediate MLLs were preferred by the majority of anglers in our

709   model.

710   While utilizing MLLs may represent a more sustainable approach to managing naturally

711   reproducing populations, culture-based fisheries maintained by stocking can generate substantial

712   social benefits that would not occur in the absence of stocking (Arlinghaus et al. 2016). We

713   found that if fish reproduction was nonexistent (carp) or impaired (overexploited pike), then

714   stocking positively influenced angler satisfaction, because without stocking catch rates were low

715   enough to be a matter of concern. However, in such situations the differences among stocking

716   strategies were not pronounced, because all stocking strategies resulted in catch rates that were

717   "good enough". Anglers often prefer stocking over other management measures, because it is

718   relatively easy to implement, less restrictive, and generally perceived to help fish stocks and

719   maintains catch rates (Arlinghaus and Mehner 2003a, Dorow et al. 2009, Garlock and Lorenzen

720   2017). Thus, stocking in culture-based fisheries can potentially be used to provide fishing

721   opportunities that draw fishing pressure away from wild stocks or increase participation (Fayram

722   et al. 2006, Baer et al. 2007, Mee et al. 2016). That said, there is a need to inform and maybe

723   even "educate" anglers about which forms of stocking are beneficial and which are unlikely to

724   generate additive effects (Fujitani et al. 2017). Otherwise, decision-makers will continue to

725   experience strong pro-stocking social norms of anglers and be constantly challenged to re-invest

726   license money back into the waters (Riepe et al. 2017), despite knowing that many of these

727   stocking efforts will likely not benefit the fishery and challenge conservation objectives.

728   *Economic outcomes*

729   The effects of stocking on fish abundance, catch rates, and angler welfare ultimately affected the

730   economic feasibility of stocking strategies relative to the management of fisheries based on the

731   "cost-free" MLL. Stocking few fish was generally more cost effective than stocking high

732   densities due to size- and density-dependent regulatory processes, and these processes were also

733   important for determining which size of fish was most cost effective. Similar to other studies

734   (Santucci Jr and Wahl 1993, Leber et al. 2005, Garlock et al. 2017), we found that fingerlings

735   were more cost effective than fry, because fingerlings experienced less mortality from the early

736   life-stage bottleneck than fry did. Likewise, in agreement with Wiley et al. (1993) we found that

737   stocking catchable adults was generally more cost-effective than stocking sub-catchable

738   fingerlings, because of the strong natural mortality (from size and density dependence) that

739   fingerlings experienced prior to becoming vulnerable to the fishery. The faster fish reach

740   vulnerable sizes, the more effective stocking will be, making fish growth rates an important

741   predictor of stocking outcomes (Garlock et al. 2017). In addition, minimizing mortality of fish,

742   particularly fry and fingerlings, using MLLs before they become fully vulnerable to the fishery,

743   improved the cost-effectiveness of stocking, while more restrictive regulations reduced cost-

744   effectiveness because fish were "lost" due to density-dependent mortality. The benefits of

745   stocking larger fish, however, requires that there are sufficient survival benefits to offset the

746   costs of producing larger fish. For example, in carp, low stocking densities minimized size-

747   dependent mortality of fingerlings making them more cost effective than adults. Moreover, high

748   mortality rates from fishing (high latent effort) for adults, which were fully vulnerable to harvest

749   at the time of stocking, outweighed any benefits of size for determining natural mortality rates,

750   until MLLs offered some protection. Our findings are similar to Diana and Wahl (2009) who

751 reported that stocking medium-sized largemouth bass (*Micropterus salmoides*) fingerlings was

752 most cost-effective, because stocking larger fish did not provide additional survival benefits.

753 Despite adults being generally more cost-effective, they require more space and long production

754 periods making them expensive to produce even at low stocking densities. Monetary stocking

755 costs may not be of great concern if only a few lakes close to urban areas are stocked to satisfy

756 anglers (Cole and Ward 1994, Post and Parkinson 2012), or for angling clubs in Germany or

757 elsewhere in central Europe that have few stocks to manage, high license income and little

758 alternative uses for the income than stocking. But costs may be a problem for North American

759 agencies charged with managing hundreds if not thousands of stocks among which they must

760 allocate a limited budget (Cowley et al. 2003). In this context, our research suggests that low

761 stocking rates of adults may be cost-effective in many situations, not only in put-and-take urban

762 lakes. However, an evaluation of whether these fish can be produced in a cost-effective manner

763 needs to be evaluated (Garlock et al. 2017), and any additional issues from domestication and

764 long holding times in hatcheries that could reduce survival post-release need to be evaluated

765 (Lorenzen et al. 2012).

766 In practice, management objectives often focus on improving fishing opportunities or

767 maximizing license sales (Askey et al. 2013, Dabrowska et al. 2014, Hunt et al. 2017), rather

768 than on individual angler satisfaction as we did, particularly if fisheries agencies depend on

769 license income for funding. By contrast, local angling clubs under private fishing right systems

770 in central Europe who are sufficiently funded likely focus more on angler satisfaction-objectives

771 and not whether stocking or any other measures recruits new members to clubs. When we

772 examined whether the socioeconomic benefits (social welfare) of stocking outweighed the

773 financial costs of stocking (assuming financial costs of changing MLLs were zero) we found a

774   striking difference between the economic performance of stocking into naturally reproducing and

775   non-reproducing populations. Moderate MLLs in the absence of stocking maximized the net

776   economic benefit from fishing for pike, while the economic benefit of stocking pike rarely

777   exceeded the use of MLLs alone. This is because MLLs were sufficient to preserve fishery

778   benefits without the added costs from culturing fish. Stocking was only the economically best

779   option when MLLs offered little protection to the pike population and recruitment overfishing

780   was occurring under higher levels of latent fishing pressure. By contrast, we found it was

781   economically advisable to create a culture-based fishery using carp, particularly when adults

782   were stocked at low densities. Our results are in agreement with other stocking models

783   (Lorenzen 2005, Rogers et al. 2010) that reported stocking was much more advisable in culture-

784   based situations compared to stock-enhancement scenarios. Such information can inform the

785   allocation of stocking resources within the landscape of lakes, with and without natural fish

786   populations, to maximize the benefits the angling community receives while avoiding incurring

787   unneeded costs (Cowley et al. 2003).

788   The reasons behind our findings relate to the two components that determined net economic

789   benefit – net WTP and latent fishing effort. In this context, the definition of the status quo

790   situation (unregulated and unstocked) used to calculate the net WTP was very important for the

791   findings. When catch rates approached zero in the status quo scenario, as occurred when the

792   population was heavily overexploited (pike) or lacked natural reproduction (carp), anglers were

793   willing to pay much more to improve the situation because of the large disparity between the

794   regulated/stocked scenarios and the status quo case. Whereas if catch rates in the status quo

795   situation approached "good enough" in scenarios where the population was self-sustaining, then

796   there was much less gained from the stock-enhanced scenario, because of the above-mentioned

797   nonlinear relationship between angler satisfaction and catch rates. The second important factor

798   determining the net economic benefit generated by a given policy was latent fishing effort,

799   because it determined the aggregated angler welfare (net WTP multiplied by latent effort) of a

800   given policy. When net per angler WTP was low, more anglers and lower stocking densities

801   were required to produce a positive net economic benefit for the fishery as a whole. Such a

802   situation was rare for pike, even at low stocking densities, unless latent angling pressure was

803   moderate to high. By contrast, stocking carp often produced a positive net economic benefit,

804   except when there were not sufficient anglers to benefit from the culture-based fishery. It should

805   be cautioned, however, that our results are largely the result of the nonlinear relationship

806   between catch rates and angler satisfaction. A greater sensitivity of angler utility and behavior to

807   catch rates not approaching zero, as has been assumed in other modelling exercises (e.g., Allen et

808   al. 2013, Camp et al. 2014), could change predictions about the net economic benefits and

809   success of stocking strategies.

810   In the face of financial constraints, our results are good news for managers facing tough

811   budgetary decisions. If one has a limited budget to allocate, our results suggest that creating

812   culture-based fisheries with a desired species, rather than stocking naturally reproducing

813   populations provides the best investment. In doing so, managers create more fishing

814   opportunities, greater benefits to anglers, and a better return on their investment. Stocking may

815   also have the added benefit of drawing fishing effort away from wild stocks, but only if

816   additional effort attracted to the system does not put additional pressure on wild stocks (Fayram

817   et al. 2006, Baer et al. 2007, Meyer et al. 2012). The recommendation to stock a nonnative

818   species such as carp also assumes that one is not concerned with the possible negative ecological

819   consequences of high carp biomasses (e.g., water quality impacts, habitat degradation,

820   competition with other species, etc. Matsuzaki et al. 2009, Weber and Brown 2009, Vilizzi et al.

821   2015). However, as carp do not regularly recruit in central Europe (Kottelat and Freyhof 2007),

822   environmental impacts may be controlled in what effectively becomes a put-grow-and take

823   fishery. Research has found that, if overall biomass is kept within limits (< 50 kg ha^{-1}), impacts

824   on water quality (Mehner et al. 2004, Vilizzi et al. 2015) and aquatic ecosystems (Barthelmes

825   and Brämick 2003) may be limited. Thus, if anglers follow economic principles and minimize

826   costs when making stocking decisions, the low stocking intensities suggested from our research

827   should minimize conflicts among conservation and fisheries objectives for this species.

828   Allocating stocking funds to carp does not mean a loss for pike anglers (or other naturally

829   occurring species). Our study has a clear message: if fish populations are self-sustaining, we

830   suggest that stocking is not economically advisable and will only rarely increase angler welfare.

831   Managers can use MLLs or other forms of harvest controls, for example harvest slots (Gwinn et

832   al. 2015), to achieve the same or greater benefits, without bearing the costs associated with

833   stocking. However, overly restrictive MLLs may not be an option either, because harvest

834   contributes substantially to angler welfare in many cultures (Arlinghaus et al. 2014). The use of

835   harvest restrictions has the additional benefit of avoiding the possible negative ecological effects

836   of stocking fish, such as replacement of the wild stock (Rogers et al. 2010, van Poorten et al.

837   2011, Camp et al. 2014), effects on genetic integrity, spread or disease, etc. (Cowx 1994, Araki

838   et al. 2007, Lorenzen et al. 2012), as well as negative impacts of the welfare on other

839   stakeholders (e.g., conservation lobby groups) that we did not account for in our model.

840   *Limitations*

841   Our model has a number of limitations that are worth noting. In the biological sub-model, the

842   impacts of stocking were strongly dependent on the strength of the size- and density-dependent

843   compensatory responses at the different life stages. While we did observe effects from density-

844   dependent mortality, we did not observe large declines in the number of fry or fingerlings

845   surviving to age-1 at extremely high stocking densities as one might expect from a Ricker stock-

846   recruitment relationship (Fayram et al. 2005), nor did we see overall densities reaching a

847   maximum carrying capacity at high stocking densities for any fish size. This is a result of the

848   stocking densities we investigated, and density-dependent mortality in age-1 and older fish.

849   Thus, it is possible that our predicted outcomes from stocking are overly optimistic, because

850   density-dependent feedbacks were not sufficiently strong. Moreover, our conclusions that

851   stocking is generally not beneficial for naturally-reproducing pike and beneficial only in low

852   densities for non-reproducing carp are unlikely to be affected by decreased mortality at higher

853   stocking densities because catch had such little impact on angler utility. However, reduced

854   natural mortality rates of small fish due to changes in the size- and density-dependent survival

855   relationships could result in fingerlings being a more effective size to stock than adults. We did,

856   however, find that our model predictions were robust to the assumption of density-dependent

857   mortality of fish age-1 and older. Model predictions in the absence of density-dependent

858   mortality for fish of age-1 and older were qualitatively similar (Appendix S1: Figures S6, S7,

859   and S8). The only differences of note were that compared to stocking carp adults, stocking carp

860   fingerlings did not produce higher vulnerable densities and catch rates or lower survivor costs

861   under high latent effort. In addition, the inability of pike populations to compensate for the low

862   density of predators in the system caused by heavy exploitation resulted in a greater range of

863   MLLs where populations were unsustainable and higher WTP, survivor costs, and net benefits,

864   although the patterns were qualitatively the same as the density-dependent scenarios.

865   In terms of the social sub-model, we assumed that MLLs have no direct monetary cost. While

866   this may be reasonable because the implementation framework is already in place, other

867   associated costs, such as enforcement costs, were not included in our model. Our model was also

868   based on a specific, mechanistic model of angler behavior. As discussed previously, the

869   lognormal relationship between catch and utility had a strong influence on our results, and other

870   functional forms in this relationship may alter the outcomes. An additional limitation of our

871   model was that we made the simplifying assumption that all anglers had identical time-invariant

872   preferences. In reality, preferences may shift over time (Hunt et al. 2011), and particularly

873   assumptions about angler heterogeneity might affect model outcomes substantially (Johnston et

874   al. 2010, 2013, Matsumura et al. 2017). Thus, further investigations using preferences from

875   different angler populations composed of diverse angler types are needed to test the robustness of

876   our findings.

877   Another aspect that our long-term equilibrium dynamics model did not consider was the

878   temporal variability in the fishery. Seasonality and stochasticity are inherent characteristics of

879   fisheries. Differences in catch can develop because anglers differ not only in their skill (Dorow et

880   al. 2010, Ward et al. 2013) but also in when they go fishing (Hunt et al. 2007). Thus, after a

881   stocking event, particularly of large fishes, there is the potential that those anglers who come first

882   and spend more time fishing shortly after stocking will reap more benefits than anglers who

883   arrive later. Changes in fish behavior can further inflate the disproportionate distribution of

884   benefits, if stocked fish alter their behavior over time to become less vulnerable to fishing gear

885   (e.g., van Poorten and Post 2005, Askey et al. 2006, Klefoth et al. 2013). However, any short-

886   term catch rate boosts from stocking would likely not affect social outcomes, because of the non-

887   linearity in the catch-utility relationship, but they could alter predictions about biological

888   enhancement.

889   Finally, the results we presented in our study relate to the benefits of stocking a single lake with

890   a single-species population. In reality, individual fisheries are embedded in the broader landscape

891   and therefore require broader management perspectives (Lester et al. 2003, Hunt et al. 2011, Mee

892   et al. 2016). It is important for managers to understand how changes in regulations will effect

893   target-species substitution and site substitution (Gentner and Sutton 2008, Sutton and Ditton

894   2005) in multi-species fisheries. Furthermore, stocking strategies that work locally may not be

895   the best regional solution (Askey et al. 2013, Varkey et al. 2016), and managers must figure out

896   how to allocate limited stocking resources optimally within the landscape (Cowley et al. 2003).

897   Hence, our work should be extended to broader spatial scales to investigate the optimal policy

898   mixes in a landscape of diverse fisheries and diverse angler populations.

899   *Conclusions*

900   One of the key findings from our study and related work (e.g., Askey et al. 2013, Camp et al.

901   2017, Garlock et al. 2017) is that the stocking strategies considered to be the most successful will

902   strongly depend on ecological processes of the managed species and the performance measure

903   used to judge management success. We found that the presence or absence of natural

904   reproduction, and the strength of size- and density-dependent processes regulating the

905   population, were key for determining whether stocking can produce additive effects and elevate

906   fishing quality or not. However, we also found that a move away from mere biological objectives

907   (increased abundance), to social (increased angler satisfaction) or economic objectives (return on

908   investment) can result in different conclusions about the most appropriate management strategy.

909   For self-sustaining populations, from both conservation and economic perspectives, stocking is

910   rarely beneficial, while it is necessary for culture-based fisheries.

911   A strength of our study was the ability to evaluate the outcomes of various management tools

912   and strategies not only from a biological perspective, but also in terms of social benefits and

913   economic feasibility by using a conceptually rigorous cost-benefit analysis. For naturally

914   reproducing species, the additive effects promised by some forms of stocking do not necessarily

915   translate into an increase in angler well-being, and the practice is often economically inefficient.

916   In addition, stocking runs the strong risk of the pervasive replacement of wild fishes by stocked

917   ones (van Poorten et al. 2011), and potentially increases mortality of wild fish if fishing pressure

918   increases after stocking (Baer et al. 2007). By contrast, in non-reproducing species stocking has

919   additive effects, increases angler satisfaction, and when conducted properly is economically

920   advisable. These results highlight that a species' reproductive ecology in combination with

921   normative metrics creates important trade-offs. The key trade-off is generally between economic

922   efficiency and conservation concerns (Camp et al. 2017), which often results in opposing

923   recommendations about which is the "best" strategy. Yet, in some situations, for example

924   stocking fish into severely depleted populations, stocking can create a win-win for both

925   conservation and anglers' interests, particularly when local broodstock are used and stocking is a

926   temporary practice that is paired with habitat enhancement efforts. Similarly, using economic

927   objectives to inform stocking decisions may bring about lower stocking densities that minimize

928   conservation concerns (e.g. water quality and carp).

929   Our findings that stocking self-sustaining populations provided little benefit to angler welfare

930   and rarely produced a positive return on investment, despite increased abundance, are

931   noteworthy because they contradict recommendations stemming from traditional metrics, such as

932   population density or catch rate, often used to evaluate management success. Our results also

933   challenge the common assumption that catch is the primary driver of angler utility and behavior,

934   and underscores early insights by Cole and Ward (1994) that managing according to angler

935   benefits is bound to lead to different results than managing fishing opportunities (i.e., catch or

936   supply). Our study demonstrates the usefulness of using a social-ecological modelling

937   framework, because only through an integrated model with a mechanistic description of behavior

938   could we uncover these insights. While some studies have linked angler behavior to catch-related

939   fishery quality (e.g., Rogers et al. 2010, Askey et al. 2013, Camp et al. 2014), our study differed

940   from these because angler behavior was explicitly determined by numerous catch and non-catch

941   related attributes and informed by the preferences of real anglers (Arlinghaus et al. 2014). A

942   further benefit of using an integrated bioeconomic modelling framework is it forces managers to

943   be transparent about their objectives and normative framework (Fenichel et al. 2013b). It is

944   ultimately the tight interplay of ecology and the human dimensions that will determine the

945   success of any management action.

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952

953 **LITERATURE CITED**

954 Adamowicz, W. L. 1994. Habit formation and variety seeking in a discrete choice model of

955   recreational demand. Journal of Agricultural and Resource Economics **19**:19-31.

956 Allen, M. S., R. N. M. Ahrens, M. J. Hansen, and R. Arlinghaus. 2013. Dynamic angling effort

957   influences the value of minimum-length limits to prevent recruitment overfishing.

958   Fisheries Management and Ecology **20**:247-257.

959 Amoroso, R. O., M. D. Tillotson, and R. Hilborn. 2017. Measuring the net biological impact of

960   fisheries enhancement: pink salmon hatcheries can increase yield, but with apparent costs

961   to wild populations. Canadian Journal of Fisheries and Aquatic Sciences **74**:1233-1242.

962 Araki, H., B. Cooper, and M. S. Blouin. 2007. Genetic effects of captive breeding cause a rapid,

963   cumulative fitness decline in the wild. Science **318**:100-103.

964 Arlinghaus, R. 2006. Overcoming human obstacles to conservation of recreational fishery

965   resources, with emphasis on central Europe. Environmental Conservation **33**:46-59.

966 Arlinghaus, R., J. Alós, B. Beardmore, K. Daedlow, M. Dorow, M. Fujitani, D. Hühn, W.

967   Haider, L. M. Hunt, B. M. Johnson, F. Johnston, T. Klefoth, S. Matsumura, C. Monk, T.

968   Pagel, J. R. Post, T. Rapp, C. Riepe, H. Ward, and C. Wolter. 2017. Understanding and

969   managing freshwater recreational fisheries as complex adaptive social-ecological

970   systems. Reviews in Fisheries Science & Aquaculture **25**:1-41.

971 Arlinghaus, R., B. Beardmore, C. Riepe, J. Meyerhoff, and T. Pagel. 2014. Species-specific

972   preferences of German recreational anglers for freshwater fishing experiences, with

973   emphasis on the intrinsic utilities of fish stocking and wild fishes. Journal of Fish Biology

974   **85**:1843-1867.

975   Arlinghaus, R., E.-M. Cyrus, E. Eschbach, M. Fujitani, D. Hühn, F. Johnston, T. Pagel, C. Riepe,

976   and (eds.). 2015. Hand in Hand für eine nachhaltige Angelfi scherei: Ergebnisse und

977   Empfehlungen aus fünf Jahren praxisorientierter Forschung zu Fischbesatz und seinen

978   Alternativen. Berichte des IGB Vol. 28. Leibniz-Institute of Freshwater Ecology and

979   Inland Fisheries, Berlin, Germany.

980   Arlinghaus, R., K. Lorenzen, B. M. Johnson, S. J. Cooke, and I. G. Cowx. 2016. Management of

981   freshwater fisheries: addressing habitat, people and fishes. Pages 557-579 *in* J. F. Craig,

982   editor. Freshwater Fisheries Ecology. John Wiley & Sons, Ltd.

983   Arlinghaus, R., S. Matsumura, and U. Dieckmann. 2009. Quantifying selection differentials

984   caused by recreational fishing: development of modeling framework and application to

985   reproductive investment in pike (*Esox lucius*). Evolutionary Applications **2**:335-355.

986   Arlinghaus, R., and T. Mehner. 2003a. Management preferences of urban anglers: habitat

987   rehabilitation versus other options. Fisheries **28**:10-17.

988   Arlinghaus, R., and T. Mehner. 2003b. Socio-economic characterisation of specialised common

989   carp (*Cyprinus carpio* L.) anglers in Germany, and implications for inland fisheries

990   management and eutrophication control. Fisheries Research **61**:19-33.

991   Arlinghaus, R., and T. Mehner. 2004. A management-orientated comparative analysis of urban

992   and rural anglers living in a metropolis (Berlin, Germany). Environmental Management

993   **33**:331-344.

994   Arlinghaus, R., T. Mehner, and I. G. Cowx. 2002. Reconciling traditional inland fisheries

995   management and sustainability in industrialized countries, with emphasis on Europe. Fish

996   and Fisheries **3**:261-316.

997   Askey, P. A., S. A. Richards, and J. R. Post. 2006. Linking angling catch rates and fish learning

998   under catch-and-release regulations. North American Journal of Fisheries Management

999   **26**:1020-1029.

1000   Askey, P. J., E. A. Parkinson, and J. R. Post. 2013. Linking fish and angler dynamics to assess

1001   stocking strategies for hatchery-dependent, open-access recreational fisheries. North

1002   American Journal of Fisheries Management **33**:557-568.

1003   Baer, J., K. Blasel, and M. Diekmann. 2007. Benefits of repeated stocking with adult, hatchery-

1004   reared brown trout, *Salmo trutta*, to recreational fisheries? Fisheries Management and

1005   Ecology **14**:51-59.

1006   Baer, J., and A. Brinker. 2008. Are growth and recapture of hatchery-reared and resident brown

1007   trout (*Salmo trutta* L.) density dependent after stocking? Ecology of Freshwater Fish

1008   **17**:455-464.

1009   Bajer, P., and P. Sorensen. 2010. Recruitment and abundance of an invasive fish, the common

1010   carp, is driven by its propensity to invade and reproduce in basins that experience winter-

1011   time hypoxia in interconnected lakes. Biological Invasions **12**:1101-1112.

1012   Barthelmes, D., and U. Brämick. 2003. Variability of a cyprinid lake ecosystem with special

1013   emphasis on the native fish fauna under intensive fisheries management including

1014   common carp (*Cyprinus carpio*) and silver carp (*Hypophthalmichthys molitrix*).

1015   Limnologica - Ecology and Management of Inland Waters **33**:10-28.

1016   Beard, T. D., Jr., S. P. Cox, and S. R. Carpenter. 2003. Impacts of daily bag limit reductions on

1017   angler effort in Wisconsin walleye lakes. North American Journal of Fisheries

1018   Management **23**:1283-1293.

1019   Beardmore, B., L. M. Hunt, W. Haider, M. Dorow, and R. Arlinghaus. 2015. Effectively

1020   managing angler satisfaction in recreational fisheries requires understanding the fish

1021   species and the anglers. Canadian Journal of Fisheries and Aquatic Sciences **72**:500-513.

1022   Biro, P. A., and J. R. Post. 2008. Rapid depletion of genotypes with fast growth and bold

1023   personality traits from harvested fish populations. Proceedings of the National Academy

1024   of Sciences **105**:2919-2922.

1025   Brown, P., and T. I. Walker. 2004. CARPSIM: stochastic simulation modelling of wild carp

1026   (*Cyprinus carpio* L.) population dynamics, with applications to pest control. Ecological

1027   Modelling **176**:83-97.

1028   Camp, E. V., R. N. M. Ahrens, M. S. Allen, and K. Lorenzen. 2016. Relationships between

1029   angling effort and fish abundance in recreational marine fisheries. Fisheries Management

1030   and Ecology **23**:264-275.

1031   Camp, E. V., S. L. Larkin, R. N. M. Ahrens, and K. Lorenzen. 2017. Trade-offs between

1032   socioeconomic and conservation management objectives in stock enhancement of marine

1033   recreational fisheries. Fisheries Research **186, Part 2**:446-459.

1034   Camp, E. V., K. Lorenzen, R. N. M. Ahrens, and M. S. Allen. 2014. Stock enhancement to

1035   address multiple recreational fisheries objectives: an integrated model applied to red

1036   drum *Sciaenops ocellatus* in Florida. Journal of Fish Biology **85**:1868-1889.

1037   Carpenter, S. R., A. Muñoz-del-Rio, S. Newman, P. W. Rasmussen, and B. M. Johnson. 1994.

1038   Interactions of anglers and walleyes in Escanaba Lake, Wisconsin. Ecological

1039   Applications **4**:822-832.

1040   Casselman, J. M., and C. A. Lewis. 1996. Habitat requirements of northern pike (*Essox lucius*).

1041   Canadian Journal of Fisheries and Aquatic Sciences **53**:161-174.

1042   Chilcote, M. W., K. W. Goodson, and M. R. Falcy. 2011. Reduced recruitment performance in

1043   natural populations of anadromous salmonids associated with hatchery-reared fish.

1044   Canadian Journal of Fisheries and Aquatic Sciences **68**:511-522.

1045   Christie, M. R., M. J. Ford, and M. S. Blouin. 2014. On the reproductive success of early-

1046   generation hatchery fish in the wild. Evolutionary Applications:n/a-n/a.

1047   Cochran-Biederman, J. L., K. E. Wyman, W. E. French, and G. L. Loppnow. 2015. Identifying

1048   correlates of success and failure of native freshwater fish reintroductions. Conservation

1049   Biology **29**:175-186.

1050   Coggins, L. G., Jr., M. J. Catalano, M. S. Allen, W. E. Pine, III, and C. J. Walters. 2007. Effects

1051   of cryptic mortality and the hidden costs of using length limits in fishery management.

1052   Fish and Fisheries **8**:196-210.

1053   Cole, R. A., and F. A. Ward. 1994. Optimum fisheries management policy: angler opportunity

1054   versus angler benefit. North American Journal of Fisheries Management **14**:22-33.

1055   Cooke, S. J., R. Arlinghaus, B. M. Johnson, and I. G. Cowx. 2016. Recreational fisheries in

1056   inland waters. Pages 449-465 *in* J. F. Craig, editor. Freshwater Fisheries Ecology. John

1057   Wiley & Sons, Ltd.

1058   Cooke, S. J., and I. G. Cowx. 2006. Contrasting recreational and commercial fishing: Searching

1059   for common issues to promote unified conservation of fisheries resources and aquatic

1060   environments. Biological Conservation **128**:93-108.

1061   Cowley, D. E., F. A. Ward, R. Deitner, and M. D. Hatch. 2003. Optimizing the allocation of

1062   hatchery-produced fish among multiple stocking sites. North American Journal of

1063   Fisheries Management **23**:216-229.

1064   Cowx, I. G. 1994. Stocking strategies. Fisheries Management and Ecology **1**:15-30.

1065   Cox, S. P., C. J. Walters, and J. R. Post. 2003. A model-based evaluation of active management

1066   of recreational fishing effort. North American Journal of Fisheries Management **23**:1294-

1067   1302.

1068   Dabrowska, K., W. Haider, and L. Hunt. 2014. Examining the impact of fisheries resources and

1069   quality on licence sales. Journal of Outdoor Recreation and Tourism **5–6**:58-67.

1070   Daedlow, K., T. D. Beard Jr, and R. Arlinghaus. 2011. A property rights-based view on

1071   management of inland recreational fisheries: contrasting common and public fishing

1072   rights regimes in Germany and the U.S.A. Pages 13-38 *in* T. D. Beard Jr, R. Arlinghaus,

1073   and S. Sutton, editors. Proceedings of the 5th World Recreational Fishing Conference,

1074   American Fisheries Society Symposium 75. American Fisheries Society, Bethesda.

1075   Diana, M. J., and D. H. Wahl. 2009. Growth and Survival of Four Sizes of Stocked Largemouth

1076   Bass. North American Journal of Fisheries Management **29**:1653-1663.

1077   Dorow, M., and R. Arlinghaus. 2012. The relationship between personal commitment to angling

1078   and the opinions and attitudes of German anglers towards the conservation and

1079   management of the European eel *Anguilla anguilla*. North American Journal of Fisheries

1080   Management **32**:466-479.

1081   Dorow, M., B. Beardmore, W. Haider, and R. Arlinghaus. 2009. Using a novel survey technique

1082   to predict fisheries stakeholders' support for European eel (Anguilla anguilla L.)

1083   conservation programs. Biological Conservation **142**:2973-2982.

1084   Dorow, M., B. Beardmore, W. Haider, and R. Arlinghaus. 2010. Winners and losers of

1085   conservation policies for European eel, *Anguilla anguilla*: an economic welfare analysis

1086   for differently specialised eel anglers. Fisheries Management and Ecology **17**:106-125.

1087   Dudgeon, D., A. H. Arthington, M. O. Gessner, Z.-I. Kawabata, D. J. Knowler, C. Lévêque, R. J.

1088   Naiman, A.-H. Prieur-Richard, D. Soto, M. L. J. Stiassny, and C. A. Sullivan. 2006.

1089   Freshwater biodiversity: importance, threats, status and conservation challenges.

1090   Biological Reviews **81**:163-182.

1091   Edeline, E., T. B. Ari, L. A. Vøllestad, I. J. Winfield, J. M. Fletcher, J. B. James, and N. C.

1092   Stenseth. 2008. Antagonistic selection from predators and pathogens alters food-web

1093   structure. Proceedings of the National Academy of Sciences **105**:19792-19796.

1094   Edwards, S. F. 1991. A critique of three "economics" arguments commonly used to influence

1095   fishery allocations. North American Journal of Fisheries Management **11**:121-130.

1096   FAO. 2012. (Food and Agricultural Organization of the United Nations). FAO Technical

1097   Guidelines for Responsible Fisheries: Recreational Fisheries. No. 13. FAO, Rome. 176

1098   pp.

1099   Fayram, A. H., M. J. Hansen, and T. J. Ehlinger. 2006. Influence of walleye stocking on angler

1100   effort in Wisconsin. Human Dimensions of Wildlife **11**:129-141.

1101   Fayram, A. H., M. J. Hansen, and N. A. Nate. 2005. Determining optimal stocking rates using a

1102   stock-recruitment model: An example using walleye in Northern Wisconsin. North

1103   American Journal of Fisheries Management **25**:1215-1225.

1104   Fenichel, E. P., J. K. Abbott, and B. Huang. 2013a. Modelling angler behaviour as a part of the

1105   management system: synthesizing a multi-disciplinary literature. Fish and Fisheries

1106   **14**:137-157.

1107   Fenichel, E. P., B. Gentner, and R. Arlinghaus. 2013b. Normative considerations for recreational

1108   fishery management: a bioeconomic framework for linking positive science and

1109   normative fisheries policy decisions. Fisheries Management and Ecology **20**:223-233.

1110   Finn, K. L., and D. K. Loomis. 2001. The importance of catch motives to recreational anglers:

1111   the effects of catch satiation and deprivation. Human Dimensions of Wildlife **6**:173-187.

1112   Fujitani, M., A. McFall, C. Randler, and R. Arlinghaus. 2017. Participatory adaptive

1113   management leads to environmental learning outcomes extending beyond the sphere of

1114   science. Science Advances **3**.

1115   Garlock, T. M., E. V. Camp, and K. Lorenzen. 2017. Using fisheries modeling to assess

1116   candidate species for marine fisheries enhancement. Fisheries Research **186, Part 2**:460-

1117   467.

1118   Garlock, T. M., and K. Lorenzen. 2017. Marine angler characteristics and attitudes toward stock

1119   enhancement in Florida. Fisheries Research **186, Part 2**:439-445.

1120   Gentner, B., and S. Sutton. 2008. Substitution in recreational fishing. Pages 150-169 *in* Ø. Aas,

1121   editor. Global Challenges in Recreational Fisheries. Blackwell Publishing Ltd.

1122   Guillerault, N., D. Hühn, J. Cucherousset, R. Arlinghaus, and C. Skov. 2018. Stocking for pike

1123   population enhancement.*in* C. Skov and A. Nilsson, editors. Biology and Ecology of

1124   Pike. CRC Press, Boca Raton.

1125   Gwinn, D. C., M. S. Allen, F. D. Johnston, P. Brown, C. R. Todd, and R. Arlinghaus. 2015.

1126   Rethinking length-based fisheries regulations: the value of protecting old and large fish

1127   with harvest slots. Fish and Fisheries **16**:259-281.

1128   Haglund, J. M., D. A. Isermann, and G. G. Sass. 2016. Walleye population and fishery responses

1129   after elimination of legal harvest on Escanaba Lake, Wisconsin. North American Journal

1130   of Fisheries Management **36**:1315-1324.

1131   Halverson, M. A. 2008. Stocking trends: a quantitative review of governmental fish stocking in

1132   the United States, 1931 to 2004. Fisheries **33**:69-75.

1133   Hazlerigg, C. R. E., K. Lorenzen, P. Thorbek, J. R. Wheeler, and C. R. Tyler. 2012. Density-

1134   dependent processes in the life history of fishes: evidence from laboratory populations of

1135   zebrafish *Danio rerio*. PLoS ONE **7**:e37550.

1136   Hühn, D., K. Lübke, C. Skov, and R. Arlinghaus. 2014. Natural recruitment, density-dependent

1137   juvenile survival, and the potential for additive effects of stock enhancement: an

1138   experimental evaluation of stocking northern pike (Esox lucius) fry. Canadian Journal of

1139   Fisheries and Aquatic Sciences **71**:1508-1519.

1140   Hunt, L. M., R. Arlinghaus, N. Lester, and R. Kushneriuk. 2011. The effects of regional angling

1141   effort, angler behavior, and harvesting efficiency on landscape patterns of overfishing.

1142   Ecological Applications **21**:2555-2575.

1143   Hunt, L. M., A. E. Bannister, D. A. R. Drake, S. A. Fera, and T. B. Johnson. 2017. Do fish drive

1144   recreational fishing license sales? North American Journal of Fisheries Management

1145   **37**:122-132.

1146   Hunt, L. M., B. N. Boots, and P. C. Boxall. 2007. Predicting fishing participation and site choice

1147   while accounting for spatial substitution, trip timing, and trip context. North American

1148   Journal of Fisheries Management **27**:832-847.

1149   Hunt, T. L., K. Giri, P. Brown, B. A. Ingram, P. L. Jones, L. J. B. Laurenson, and A. M. Wallis.

1150   2014. Consequences of fish stocking density in a recreational fishery. Canadian Journal

1151   of Fisheries and Aquatic Sciences **71**:1554-1560.

1152   Hyman, A. A., S. L. McMullin, and V. DiCenzo. 2016. Dispelling assumptions about stocked-

1153   trout fisheries and angler satisfaction. North American Journal of Fisheries Management

1154   **36**:1395-1404.

1155   Johnston, F. D., R. Arlinghaus, and U. Dieckmann. 2010. Diversity and complexity of angler

1156   behaviour drive socially optimal input and output regulations in a bioeconomic

1157   recreational-fisheries model. Canadian Journal of Fisheries and Aquatic Sciences

1158   **67**:1507-1531.

1159   Johnston, F. D., R. Arlinghaus, and U. Dieckmann. 2013. Fish life history, angler behaviour and

1160   optimal management of recreational fisheries. Fish and Fisheries **14**:554-579.

1161   Johnston, F. D., R. Arlinghaus, J. Stelfox, and J. R. Post. 2011. Decline in angler use despite

1162   increased catch rates: anglers' response to the implementation of a total catch-and-release

1163   regulation. Fisheries Research **110**:189-197.

1164   Johnston, F. D., B. Beardmore, and R. Arlinghaus. 2015. Optimal management of recreational

1165   fisheries in the presence of hooking mortality and noncompliance — predictions from a

1166   bioeconomic model incorporating a mechanistic model of angler behavior. Canadian

1167   Journal of Fisheries and Aquatic Sciences **72**:37–53.

1168   Klefoth, T., T. Pieterek, and R. Arlinghaus. 2013. Impacts of domestication on angling

1169   vulnerability of common carp, Cyprinus carpio: the role of learning, foraging behaviour

1170   and food preferences. Fisheries Management and Ecology **20**:174-186.

1171   Klefoth, T., C. Skov, J. Krause, and R. Arlinghaus. 2012. The role of ecological context and

1172   predation risk-stimuli in revealing the true picture about the genetic basis of boldness

1173   evolution in fish. Behavioral Ecology and Sociobiology **66**:547-559.

1174   Koehn, J., A. Brumley, and P. Gehrke. 2000. Managing the impacts of carp. Bureau of Rural

1175   Sciences, Department of Agriculture, Fisheries and Forestry, Canberra, Australia.

1176   Koenig, M. K., J. R. Kozfkay, K. A. Meyer, and D. J. Schill. 2011. Performance of diploid and

1177   triploid rainbow trout stocked in Idaho alpine lakes. North American Journal of Fisheries

1178   Management **31**:124-133.

1179   Kottelat, M., and J. Freyhof. 2007. Handbook of European Freshwater Fishes. Kottelat, Cornol,

1180   Switzerland and Freyhof, Berlin, Germany.

1181   Laikre, L., M. K. Schwartz, R. S. Waples, and N. Ryman. 2010. Compromising genetic diversity

1182   in the wild: unmonitored large-scale release of plants and animals. Trends in Ecology &

1183   Evolution **25**:520-529.

1184   Leber, K. M., R. N. Cantrell, and P. S. Leung. 2005. Optimizing cost-effectiveness of size at

1185   release in stock enhancement programs. North American Journal of Fisheries

1186   Management **25**:1596-1608.

1187   Lester, N. P., T. R. Marshall, K. Armstrong, W. I. Dunlop, and B. Ritchie. 2003. A broad scale

1188   approach to management of Ontario's recreational fisheries. North American Journal of

1189   Fisheries Management **23**:1312-1328.

1190   Lester, N. P., B. J. Shuter, and P. A. Abrams. 2004. Interpreting the von Bertalanffy model of

1191   somatic growth in fishes: the cost of reproduction. Proceedings of the Royal Society of

1192   London. Series B: Biological Sciences **271**:1625-1631.

1193   Lewin, W. C., R. Arlinghaus, and T. Mehner. 2006. Documented and potential biological

1194   impacts of recreational fishing: insights for management and conservation. Reviews in

1195   Fisheries Science **14**:305-367.

1196   Li, J., Y. Cohen, D. H. Schupp, and I. R. Adelman. 1996. Effects of walleye stocking on

1197   population abundance and fish size. North American Journal of Fisheries Management

1198   **16**:830-839.

1199   Loomis, J., and P. Fix. 1999. A statistical approach to estimating costs of propagating hatchery

1200   rainbow trout. North American Journal of Fisheries Management **19**:110-119.

1201   Lorenzen, K. 1995. Population dynamics and management of culture-based fisheries. Fisheries

1202   Management and Ecology **2**:61-73.

1203   Lorenzen, K. 1996. The relationship between body weight and natural mortality in juvenile and

1204   adult fish: a comparison of natural ecosystems and aquaculture. Journal of Fish Biology

1205   **49**:627-642.

1206   Lorenzen, K. 2000. Allometry of natural mortality as a basis for assessing optimal release size in

1207   fish-stocking programmes. Canadian Journal of Fisheries and Aquatic Sciences **57**:2374-

1208   2381.

1209   Lorenzen, K. 2005. Population dynamics and potential of fisheries stock enhancement: practical

1210   theory for assessment and policy analysis. Philosophical Transactions of the Royal

1211   Society B: Biological Sciences **360**:171-189.

1212   Lorenzen, K. 2006. Population management in fisheries enhancement: Gaining key information

1213   from release experiments through use of a size-dependent mortality model. Fisheries

1214   Research **80**:19-27.

1215   Lorenzen, K. 2014. Understanding and managing enhancements: why fisheries scientists should

1216   care. Journal of Fish Biology **85**:1807-1829.

1217   Lorenzen, K., M. C. M. Beveridge, and M. Mangel. 2012. Cultured fish: integrative biology and

1218   management of domestication and interactions with wild fish. Biological Reviews

1219   **87**:639-660.

1220   Margenau, T., S. AveLallemant, D. Giehtbrock, and S. Schram. 2008. Ecology and management

1221   of northern pike in Wisconsin. Hydrobiologia **601**:111-123.

1222   Matsumura, S., B. Beardmore, W. Haider, U. Dieckmann, and R. Arlinghaus. 2017. Ecological,

1223   angler and spatial heterogeneity drive social and ecological outcomes in an integrated

1224   landscape model of freshwater recreational fisheries. bioRxiv.

1225   Matsuzaki, S.-i., N. Usio, N. Takamura, and I. Washitani. 2009. Contrasting impacts of invasive

1226   engineers on freshwater ecosystems: an experiment and meta-analysis. Oecologia

1227   **158**:673-686.

1228   Mee, J. A., J. R. Post, H. Ward, K. L. Wilson, E. Newton, and A. Cantin. 2016. Interaction of

1229   ecological and angler processes: experimental stocking in an open access, spatially

1230   structured fishery. Ecological Applications **26**:1693-1707.

1231   Mehner, T., R. Arlinghaus, S. Berg, H. Dörner, L. Jacobsen, P. Kasprzak, R. Koschel, T.

1232   Schulze, C. Skov, C. Wolter, and K. Wysujack. 2004. How to link biomanipulation and

1233   sustainable fisheries management: a step-by-step guideline for lakes of the European

1234   temperate zone. Fisheries Management and Ecology **11**:261-275.

1235   Meyer, K. A., B. High, and F. S. Elle. 2012. Effects of stocking catchable-sized hatchery

1236   rainbow trout on wild rainbow trout abundance, survival, growth, and recruitment.

1237   Transactions of the American Fisheries Society **141**:224-237.

1238   Mezzera, M., and C. R. Largiadèr. 2001. Evidence for selective angling of introduced trout and

1239   their hybrids in a stocked brown trout population. Journal of Fish Biology **59**:287-301.

1240   Patterson, W. F., and M. G. Sullivan. 2013. Testing and refining the assumptions of put-and-take

1241   rainbow trout fisheries in Alberta. Human Dimensions of Wildlife **18**:340-354.

1242   Paukert, C. P., J. A. Klammer, R. B. Pierce, and T. D. Simonson. 2001. An overview of northern

1243   pike regulations in North America. Fisheries **26**:6-13.

1244   Post, J. R., C. Mushens, A. Paul, and M. Sullivan. 2003. Assessment of alternative harvest

1245   regulations for sustaining recreational fisheries: model development and application to

1246   bull trout. North American Journal of Fisheries Management **23**:22-34.

1247   Post, J. R., and E. A. Parkinson. 2012. Temporal and spatial patterns of angler effort across lake

1248   districts and policy options to sustain recreational fisheries. Canadian Journal of Fisheries

1249   and Aquatic Sciences **69**:321-329.

1250   Post, J. R., M. Sullivan, S. Cox, N. P. Lester, C. J. Walters, E. A. Parkinson, A. J. Paul, L.

1251   Jackson, and B. J. Shuter. 2002. Canada's recreational fisheries: the invisible collapse?

1252   Fisheries **27**:6-17.

1253   Radomski, P. J., G. C. Grant, P. C. Jacobson, and M. F. Cook. 2001. Visions for recreational

1254   fishing regulations. Fisheries **26**:7-18.

1255   Riepe, C., M. Fujitani, J. Cucherousset, T. Pagel, M. Buoro, F. Santoul, R. Lassus, and R.

1256   Arlinghaus. 2017. What determines the behavioral intention of local-level fisheries

1257   managers to alter fish stocking practices in freshwater recreational fisheries of two

1258   European countries? Fisheries Research **2017**.

1259   Rogers, M. W., M. S. Allen, P. Brown, T. Hunt, W. Fulton, and B. A. Ingram. 2010. A

1260   simulation model to explore the relative value of stock enhancement versus harvest

1261   regulations for fishery sustainability. Ecological Modelling **221**:919-926.

1262   Santucci Jr, V. J., and D. H. Wahl. 1993. Factors influencing survival and growth of stocked

1263   walleye (*Stizostedion vitreum*) in a centrarchid-dominated impoundment. Canadian

1264   Journal of Fisheries and Aquatic Sciences **50**:1548-1558.

1265   Sass, G. G., A. L. Rypel, and J. D. Stafford. 2017. Inland fisheries habitat management: lessons

1266   learned from wildlife ecology and a proposal for change. Fisheries **42**:197-209.

1267   Skov, C., A. Koed, L. Baastrup-Spohr, and R. Arlinghaus. 2011. Dispersal, growth, and diet of

1268   stocked and wild northern pike fry in a shallow natural lake, with implications for the

1269   management of stocking programs. North American Journal of Fisheries Management

1270   **31**:1177-1186.

1271   Sullivan, M. G. 2002. Illegal angling harvest of walleyes protected by length limits in Alberta.

1272   North American Journal of Fisheries Management **22**:1053-1063.

1273   Sutton, S. G., and R. B. Ditton. 2005. The substitutability of one type of fishing for another.

1274   North American Journal of Fisheries Management **25**:536-546.

1275   Thériault, V., G. R. Moyer, L. S. Jackson, M. S. Blouin, and M. A. Banks. 2011. Reduced

1276   reproductive success of hatchery coho salmon in the wild: insights into most likely

1277   mechanisms. Molecular Ecology **20**:1860-1869.

1278   Tufts, B. L., J. Holden, and M. DeMille. 2015. Benefits arising from sustainable use of North

1279   America's fishery resources: economic and conservation impacts of recreational angling.

1280   International Journal of Environmental Studies **72**:850-868.

1281   van Poorten, B. T., R. Arlinghaus, K. Daedlow, and S. S. Haertel-Borer. 2011. Social-ecological

1282   interactions, management panaceas, and the future of wild fish populations. Proceedings

1283   of the National Academy of Sciences.

1284   van Poorten, B. T., and J. R. Post. 2005. Seasonal fishery dynamics of a previously unexploited

1285   rainbow trout population with contrasts to established fisheries. North American Journal

1286   of Fisheries Management **25**:329-345.

1287   Varkey, D. A., M. K. McAllister, P. J. Askey, E. Parkinson, A. Clarke, and T. Godin. 2016.

1288   Multi-criteria decision analysis for recreational trout fisheries in British Columbia,

1289   Canada: A Bayesian network implementation. North American Journal of Fisheries

1290   Management **36**:1457-1472.

1291 Vilizzi, L., A. S. Tarkan, and G. H. Copp. 2015. Experimental evidence from causal criteria

1292   analysis for the effects of common carp *Cyprinus carpio* on freshwater ecosystems: a

1293   global perspective. Reviews in Fisheries Science & Aquaculture **23**:253-290.

1294 Walters, C. J., and S. J. D. Martell. 2004. Fisheries Ecology and Management. Princeton

1295   University Press, Princeton, NJ, USA.

1296 Ward, H. G. M., P. J. Askey, and J. R. Post. 2013. A mechanistic understanding of hyperstability

1297   in catch per unit effort and density-dependent catchability in a multistock recreational

1298   fishery. Canadian Journal of Fisheries and Aquatic Sciences **70**:1542-1550.

1299 Weber, M. J., and M. L. Brown. 2009. Effects of common carp on aquatic ecosystems 80 years

1300   after "carp as a dominant": ecological insights for fisheries management. Reviews in

1301   Fisheries Science **17**:524-537.

1302 Wedekind, H., V. Hilge, and W. Steffens. 2001. Present status, and social and economic

1303   significance of inland fisheries in Germany. Fisheries Management and Ecology **8**:405-

1304   414.

1305 Wiley, R. W., R. A. Whaley, J. B. Satake, and M. Fowden. 1993. Assessment of stocking

1306   hatchery trout: a Wyoming perspective. North American Journal of Fisheries

1307   Management **13**:160-170.

1308 Yule, D. L., R. A. Whaley, P. H. Mavrakis, D. D. Miller, and S. A. Flickinger. 2000. Use of

1309   strain, season of stocking, and size at stocking to improve fisheries for rainbow trout in

1310   reservoirs with walleyes. North American Journal of Fisheries Management **20**:10-18.

1311   Ziegler, J. P., E. J. Golebie, S. E. Jones, B. C. Weidel, and C. T. Solomon. 2017. Social-

1312   ecological outcomes in recreational fisheries: the interaction of lakeshore development

1313   and stocking. Ecological Applications **27**:56–65.

1314

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1316   **TABLES**

1317   **Table 1**. Bioeconomic model equations. Parameter values and their sources for northern pike

1318   (*Esox lucius*) and common carp (*Cyprinus carpio*) are listed in Appendix S1: Table S1.

1319   Derivations of some of the equations can be found in Appendix S1. PWU = part-worth utility.

	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	$L_{ag,t+1} = L_{ag,t} + h_{g,t} p_{ag}$	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	$p_{ag} = \begin{cases} 1 - \dfrac{G}{3+G}(1 + L_{ag}/h_g) & \text{if mature} \\ 1 & \text{if immature} \end{cases}$	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	$$s_{1,t} = \alpha_1 e^{-\beta_1(N_{0_{\mathrm{W}},t}+N_{0_{\mathrm{H}},t})}$$	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 Appendix S1 for derivation)
4c	$$\beta_1 = \frac{\ln\dfrac{L_0}{L_s}}{\ln\dfrac{L_0}{L_{\mathrm{rec}}}}\beta$$	Strength of the density-dependence during the pre-stocking phase (see Appendix S1 for derivation)
4d	$$M_1^* = h_{\max}\frac{\ln\alpha}{\ln\dfrac{L_0}{L_{\mathrm{rec}}}}$$	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	$$s_{2,t} = \alpha_2 e^{-\beta_2(J_{0_{\mathrm{W}},t}+J_{0_{\mathrm{H}},t}+J_{0_{\mathrm{S}},t})}$$	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 Appendix S1 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 Appendix S1 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	$M_{ag,t} = M_{r,L_{max}} \left(\dfrac{L_{ag,t}}{L_{max}} \right)^{c_t}$	Instantaneous natural mortality rate of a fish of length L_{ag} at time t
6c	$M_{r,L_{max}} = \dfrac{h_{max}}{L_{max}}$	Reference instantaneous natural mortality rate at length L_{max}
6d	$c_t = \dfrac{\ln[1+(1-\Upsilon)D_{rel,t}]}{\ln(M_{r,L_{max}})} - 1$	Allometric exponent of size-dependent mortality relationship at time t
6e	$D_{rel,t} = \dfrac{D_{L^2} - D_{Equilib}}{D_{Equilib}}$	Relative effective density at time t
6f	$v_{ag,t} = \dfrac{1}{1 + \exp(-y(L_{ag,t} - L_{50}))}$	Proportion of fish of age a and growth trajectory g vulnerable to capture by anglers at time t
6g	$L_{50} = zL_{max} + L_{shift}$	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	$f_{H,ag} = \begin{cases} 1 & \text{if } L_{ag} \geq MLL \\ f_n & \text{if } L_{ag} < MLL \end{cases}$	Proportion of captured fish of age a and growth trajectory g harvested by anglers
6j	$F_{ag,t} = f_{H,ag} C_{ag,t} + f_h C_{ag,t}(1 - f_{H,ag})$	Instantaneous fishing mortality rate of fish of age a and growth trajectory g at time t
6k	$s_{ag_W,t} = e^{-(M_{ag,t} + F_{ag,t})}$ $s_{ag_H,t} = e^{-(M_{ag,t}/\gamma_2 + F_{ag,t})}$	Survival of wild $s_{ag_W,t}$ and hatchery $s_{ag_H,t}$ origin fish of age a and growth trajectory g
6l	$N_{a+1,g_W,t+1} = N_{ag_W,t} s_{ag_W,t}$ $N_{a+1,g_H,t+1} = N_{ag_H,t} s_{ag_H,t}$	Density of wild $N_{a+1,g_W,t+1}$ and hatchery $N_{a+1,g_H,t+1}$ origin fish of age $a+1$ and growth trajectory g at time $t+1$
	Angler-effort dynamics	
7a	$U_f = U_{in} + U_{Spp} + U_{Cost}$ $+ U_{\bar{c}_D} + U_{\bar{l}} + U_{l_{max}} + U_{\bar{A}_D}$ $+ U_{MLL} + U_{DBL} + U_{Stock} + U_{Comp}$	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, $U_{\bar{c}_D}$ 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, $U_{\bar{A}_D}$ 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	$p_{f,t} = \dfrac{\exp(\hat{U}_f)}{[\exp(\hat{U}_f) + \exp(U_{out}) + \exp(U_{no})]}$	Probability an angler chooses to fish, over the alternatives of not fishing or fishing elsewhere (where $\hat{U}_f$ 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	$p_{F,t} = (1-\varphi)p_{f,t} + \varphi\hat{p}_F$	Realized probability an angler of type j fishes (where $\hat{p}_{Fj}$ applies to the previous year)
7d	$E_t = p_{F,t}d_{max}A_L\Psi$	Total annual realized fishing effort density at time t
	Response variables	
8a	$WTP = \dfrac{U_{base} - U_{scenario}}{u_1}$	Willingness to pay
8b	$W = A_L WTP$	Aggregated social welfare
8c	$NB = W - \text{€}_S$	Net economic benefit
8d	$\text{€}_S = \begin{cases} J_{0_S}\theta L_S{}^\lambda & a_S = 0 \\ N_S\theta L_S{}^\lambda & a_S > 0 \end{cases}$	Cost of stocking
8e	$\text{€}_{ind} = \begin{cases} \text{€}_S / J_{0_S,t}s_{2,t}\gamma\sum\limits_g\prod\limits_{a=1}^{2}\sigma_{Ng}s_{ag_H,t} & a_S = 0 \\ \text{€}_S / N_{S,t}\sum\limits_g\prod\limits_{a=a_S}^{2}\sigma_{Ng}s_{ag_H,t} & a_S > 0 \end{cases}$	Cost per stocked individual surviving from the time of stocking until the end of age 2
	Part-worth-utility (PWU) functions	
9a	$U_{oj} = u_1\text{€}_L$	PWU of annual license cost
9b	$U_{\bar{c}_D} = u_2\log_{10}\bar{C}_D$	PWU of daily catch $\bar{C}_D$
9c	$U_{\bar{l}} = u_3\log_{10}\left(\dfrac{\bar{l}}{\bar{l}_{ref}}\right)$	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	$U_{\bar{A}_D} = u_5 \bar{A}_D$	PWU of the number of anglers seen in a day $\bar{A}_D$ per 10 ha
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	$U_{Stock} = u_9 1$	PWU of stocking frequency (stocking occurs annually)
9i	$U_{Comp} = u_{10} \dfrac{\bar{C}_{D_W}}{\bar{C}_{D_{Total}}}$	PWU of catch composition (% wild fish)

1320 **Table 2**. Parameters used in model scenarios. Bold font indicates changes in the parameters relative to the base case, scenario 1.

1321 Scenarios 2A and 2B compare pike and carp, scenarios 3A and 3B compare assumptions about productivity and habitat changes, and

1322 scenarios 4A and 4B compare assumptions about relative fitness and heritability.

Variable	Scenarios						
	1 (Base)	2A	2B	3A	3B	4A	4B
Species	Pike	Pike	**Carp**	Pike	Pike	Pike	Pike
Latent Fishing Pressure	Moderate 5 licenses ha^{-1}	**Low, High 1, 10 licenses ha$_{-1}$**	**Low, High 1, 10 licenses ha$_{-1}$**	Moderate 5 licenses ha^{-1}	Moderate 5 licenses ha^{-1}	Moderate 5 licenses ha^{-1}	Moderate 5 licenses ha^{-1}
Stocking Expenditure	Observed 0-154 € ha^{-1}	**Fixed 0,5,100 € ha^{-1}**	**Fixed 0,5,100 € ha^{-1}**	**Fixed 0,5,100 € ha^{-1}**	**Fixed 0,5,100 € ha^{-1}**	**Fixed 0,5,100 € ha^{-1}**	**Fixed 0,5,100 € ha^{-1}**
Habitat	Normal	Normal	Normal	**Reduced $\alpha / 2$**	**Reduced $2 * \beta$**	Normal	Normal
Relative Fitness	Equal	Equal	**n.a.**	Equal	Equal	**Unequal**	**Unequal**
Heritability	None	None	**n.a.**	None	None	None	**100%**
Utility from Stocking	Absent	Absent	**Present**	Absent	Absent	Absent	Absent
Stocked Fish Recognition	Unidentified	Unidentified	**Identified**	Unidentified	Unidentified	Unidentified	Unidentified

1323

1324   **FIGURE CAPTIONS**

1325   **Figure 1**. Schematic of modelled fishery components and their interactions (modified from

1326   Johnston et al. 2013).

1327   **Figure 2**. The effects of stocking pike fry (2 cm), fingerlings (20 cm) and adults (age-2, 35-40

1328   cm) at a range of densities across a range of minimum-length limits (MLLs) and a range of

1329   stocking densities (0 - L_{max}) calibrated to reflect the range of annual expenditures (0-154 € ha^{-1})

1330   on pike stocking by angling-clubs in Germany (Table 2, scenario 1). Effects of stocking and

1331   MLLs on total fish density, density of vulnerable fish (age-2 and older fish at year end), catch

1332   rates, change in angler welfare (net willingness-to-pay, WTP) relative to the unregulated and

1333   unstocked case, per capita costs of stocked fish surviving to a vulnerable size (their third

1334   birthday), and net economic benefit, were evaluated. Latent fishing pressure was moderate (5

1335   licenses ha^{-1}). Very close contour lines indicate rapid changes in the performance measure.

1336   **Figure 3.** Age structure of a pike population under three different minimum-length limits

1337   (MLLs, no MLL, 48 cm, and 120 cm), when fry, fingerlings and adults were stocked at low (3 €

1338   ha^{-1}), or high (154 € ha^{-1}) densities, or not stocked at all. The abundance of fish older than age-6

1339   were not presented for visual clarity. The percentages listed in the corner of each panel represent

1340   the percent of the population that is composed of wild-origin fish under low (tightly hashed bar)

1341   and high (coarsely hashed bar) stocking densities.

1342   **Figure 4**. The effect of stocking pike and carp fry, fingerlings and adults at densities that

1343   represent annual stocking expenditures of 0, 5, and 100 € ha^{-1} (Table 2, scenario 2). For pike,

1344   these expenditures corresponded to densities of 0, 159 and 3174 fry ha^{-1} (2 cm), 0, 3 and 58

1345   fingerlings ha^{-1} (20 cm), and 0, 1 and 24 adults ha^{-1} (age-2), respectively, and for carp to

1346 densities of 0, 98 and 1967 fry ha^{-1} (4 cm), 0, 8 and 155 fingerlings ha^{-1} (15 cm) and 0, 1 and 23

1347 adults ha^{-1} (40 cm), respectively. Effects of stocking and MLLs on total fish density, density of

1348 vulnerable fish (age-2 and older fish at year end), catch rates, change in angler welfare (net

1349 willingness-to-pay, WTP) relative to the status quo, per capita costs of stocked fish surviving to a

1350 fully vulnerable size (their third birthday), and net economic benefit, were evaluated under low

1351 and high latent fishing pressure (1 and 10 licenses ha^{-1}, respectively). The grey areas indicate

1352 situations where the benefit to anglers was not greater than the status quo (no stocking and no

1353 MLL), or where there was no positive net economic benefit.

1354 **Figure 5**. The sensitivity of pike model outcomes to changes in model assumptions, under

1355 annual stocking expenditures of 0, 5, and 100 € ha^{-1}, and moderate latent fishing pressure, 5

1356 licenses ha^{-1} (Table 2, scenarios 3 and 4). For pike, these expenditures corresponded to densities

1357 of 0, 159 and 3174 fry ha^{-1} (2 cm), 0, 3 and 58 fingerlings ha^{-1} (20 cm), and 0, 1 and 24 adults ha^{-}

1358 ^{1} (age-2), respectively. The left column represents the unmodified, base model (Table 2, scenario

1359 1). The second and third columns represent lower stock productivity ($\alpha / 2$, Table 2 scenario 3A)

1360 and lower habitat capacity resulting in stronger density-dependence ($2 \cdot \beta$, Table 2 scenario 3B),

1361 respectively. The fourth and fifth columns represent the reduced fitness scenario (relative

1362 survival of stocked age-0 fish was 50%, of stocked adults was 90%, and relative reproductive

1363 success was 56% compared to wild fish), with zero heritability (Table 2 scenario 4A), and 100%

1364 heritability (Table 2 scenario 4B). The grey areas indicate situations where the benefit to anglers

1365 was not greater than the status quo (no stocking and no MLL), or where there was no positive net

1366 economic benefit.

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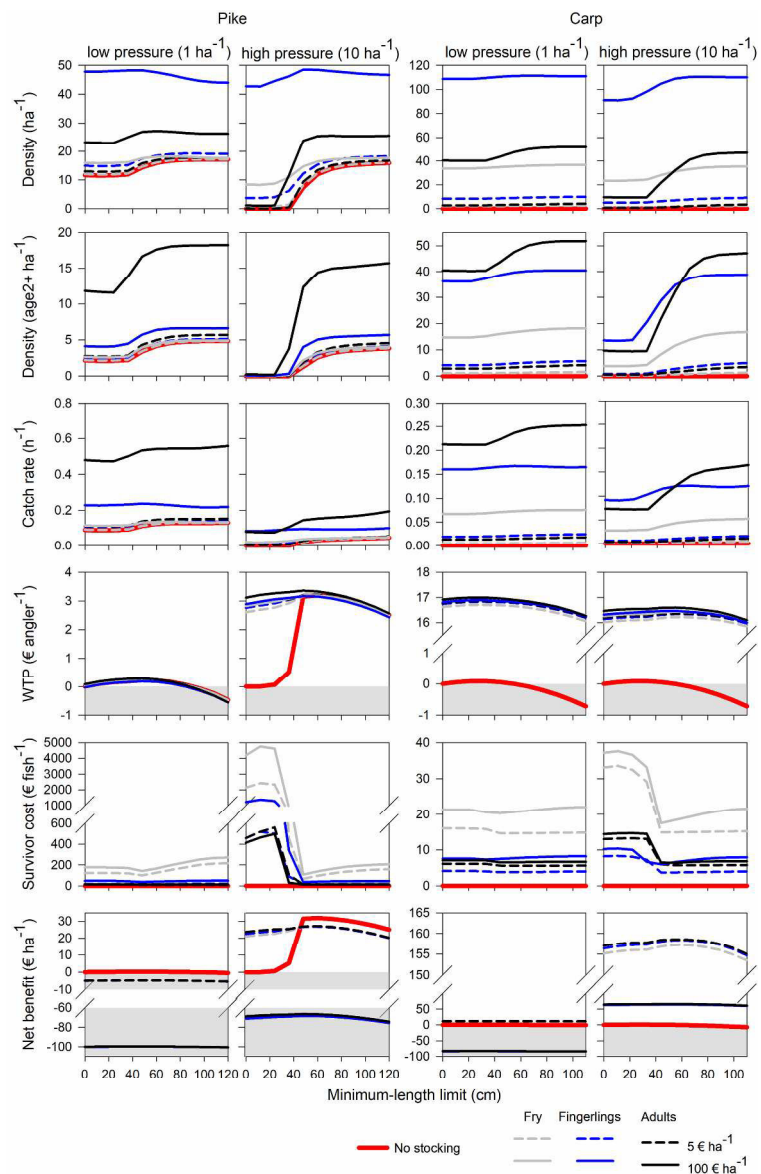
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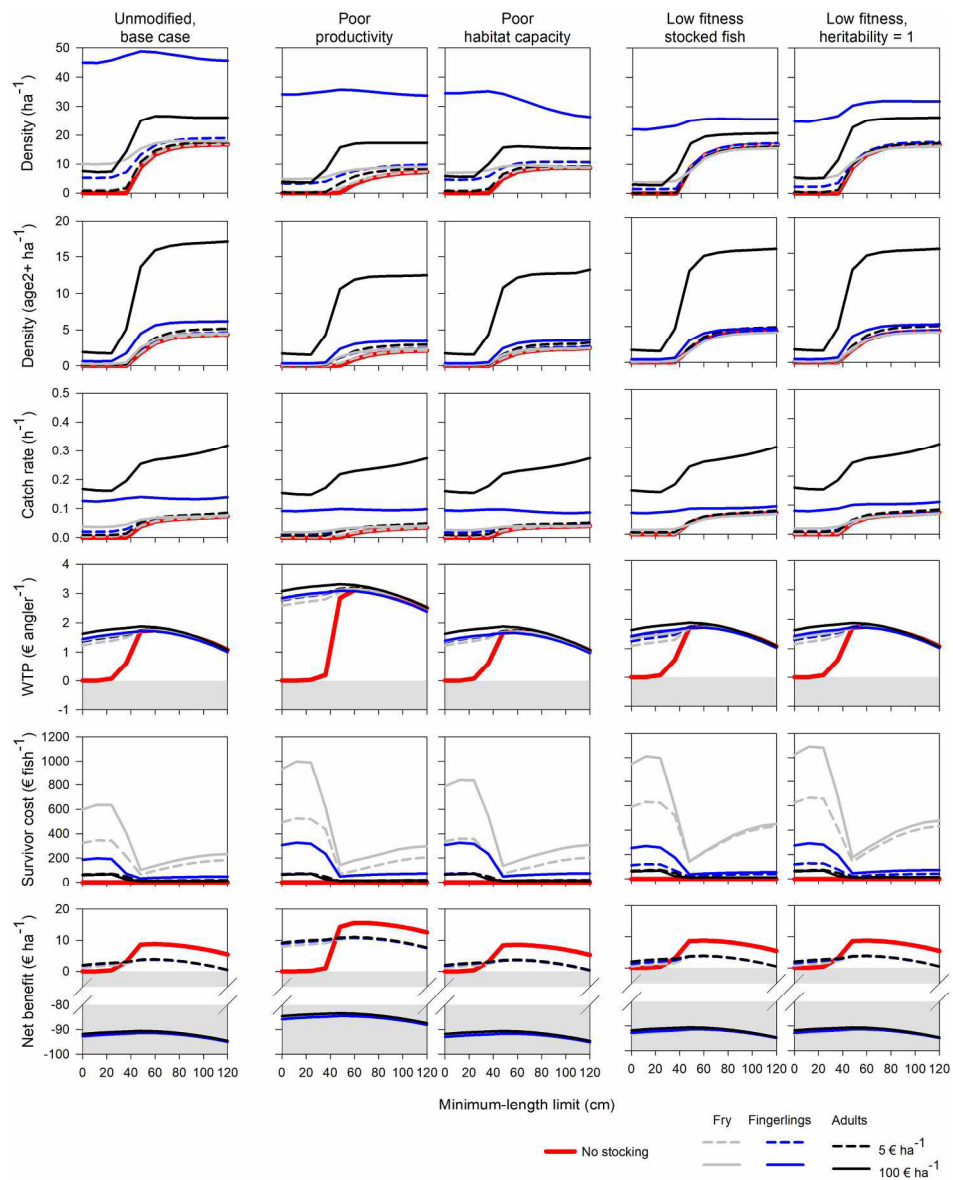
193x244mm (300 x 300 DPI)

Supplementary material for:

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

Published in Ecological Applications

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APPENDIX S1

Supplemental tables

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

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 ($B_{total} = 0$) (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}	Proportional 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}	Bias correction factor for the minimum size of fish that can be captured that is used when calculating the size L_{50} (cm). See Johnston et al. 2013 for more details.	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) Mature 1.0 or 0.9 (8)	n.a.

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 0 to 4887 Fingerlings 0 to 90 (2)	Fry 0 to 1967 Fingerlings 0 to 155 (2)
$N_{S,t}$	The density of recruited fish of age a_S stocked (ha^{-1})	0 to 39 (2)	0 to 23 (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 annually 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	MLL linear coefficient	0.005 (1)‡	0.0032 (1)‡
u_7	MLL quadratic coefficient	-0.0001 (1)‡	-0.0001 (1)‡
u_8	Daily bag limit 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 1996b) and Vilizzi et al. (2013); (15) derived from Post et al. (1999), see supplement; (16) Tempero et al. (2006); (17) Vilizzi et al. (2013), worldwide average; (18) Weber et al. (2011); (19) Willis (1989).

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

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

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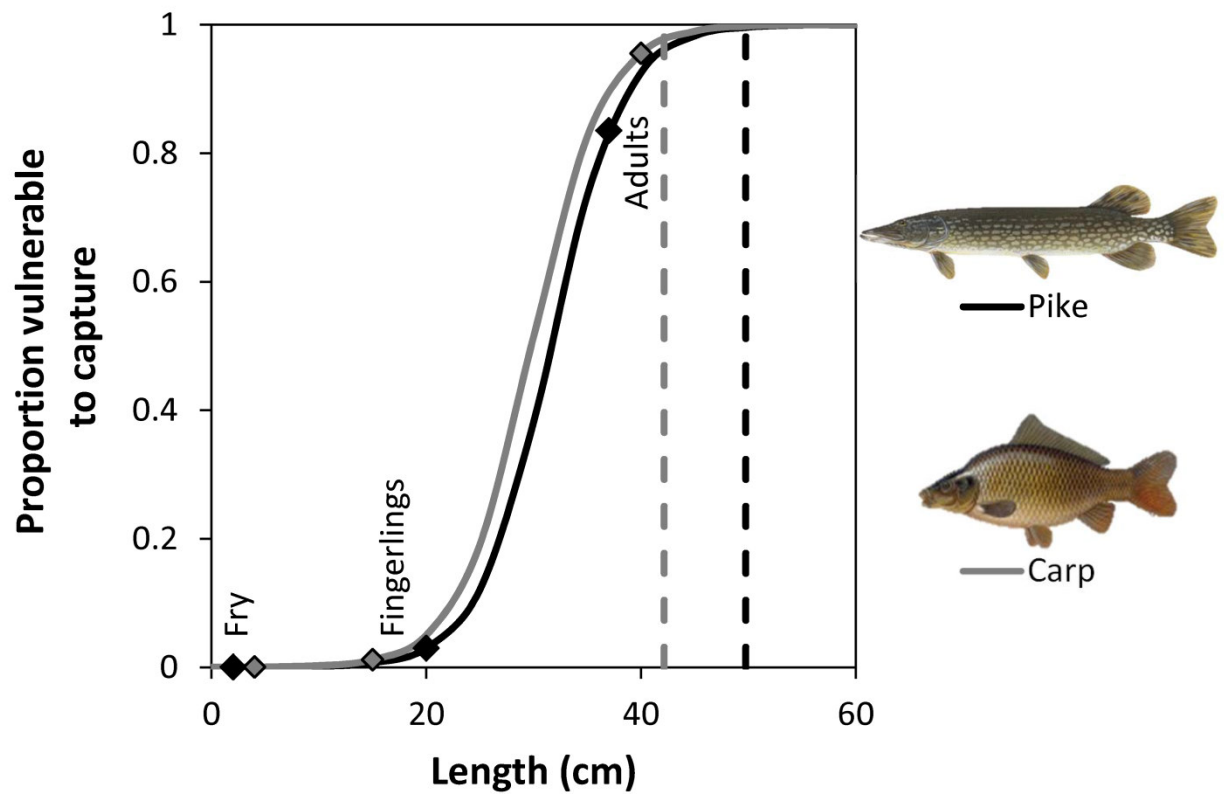
Figure S1. Size-dependent vulnerability of fish to capture by anglers. The black and gray diamonds illustrate the average size at stocking of pike and carp, respectively, for fry, fingerlings and adults. The vertical dashed lines represent the average size a fish achieves by its third birthday (age-2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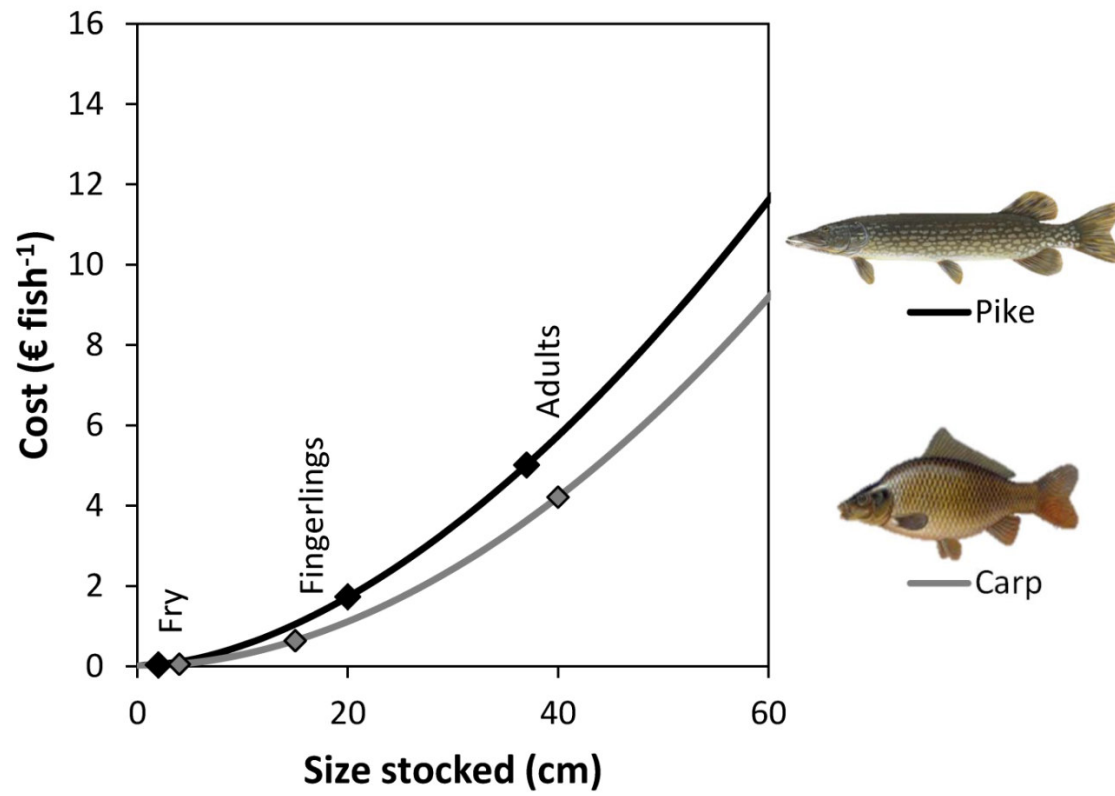
Figure S2. Species- and size-dependent stocking cost relationship determined from information provided by German angling clubs (Arlinghaus et al. 2015).
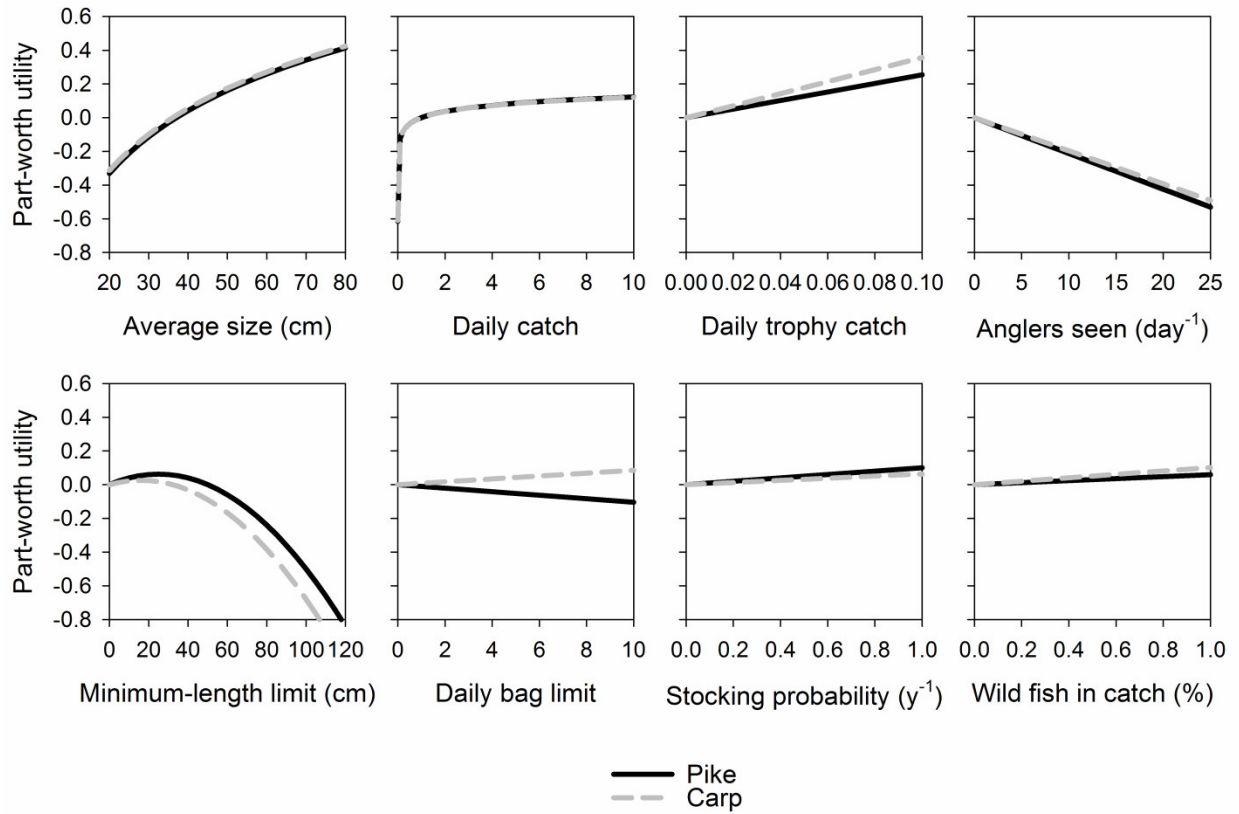
Figure S3. Part-worth utility functions describing the preferences of angler from Lower Saxony for catch related and non-catch related attributes when fishing for pike and carp, obtained from a choice experiment carried out by (Arlinghaus et al. 2014) and using the equations 9a-9i in Table 1 and the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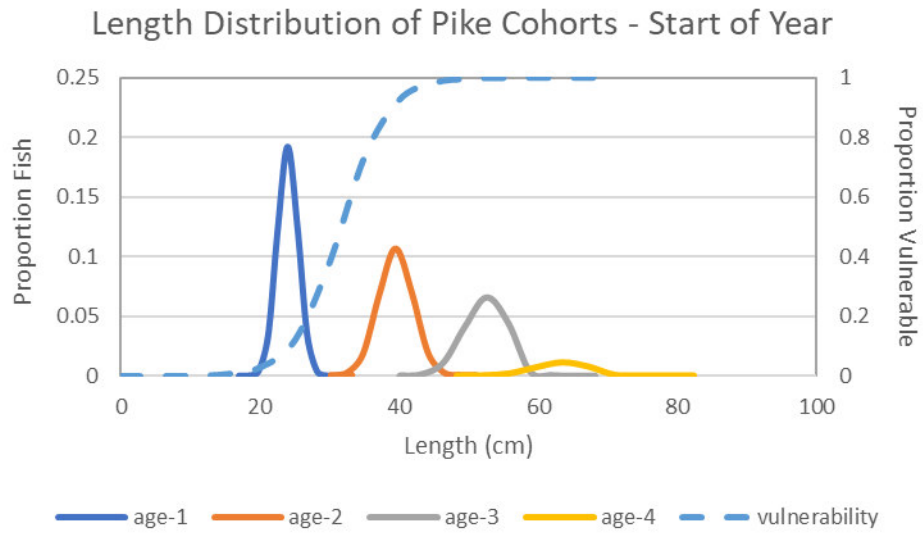
Figure S4. Relative length distribution of pike age-1 to age-4 cohorts in an unstocked population with a minimum-length limit of 42 cm and a latent fishing pressure of 5 anglers ha^{-1}. Values are for the beginning of the year. Other cohorts are not depicted.

Derivation of unpacked stock-recruitment

Survival of age-0 fish during the pre-stocking phase s_1 and the post-stocking phase s_2 were described by two Ricker stock-recruitment relationships. The method used by Lorenzen (2005) was modified to follow a Ricker model rather than a Beverton-Holt model to be more representative of early survival for pike (Johnston et al. 2013) and carp (Brown and Walker 2004). Overcompensation can result from cannibalism (Hilborn and Stokes 2010), a factor that is common in pike (Wright and Giles 1987, Skov et al. 2003). Cannibalism also occurs in carp populations (Tonn et al. 1994), but reduced age-0 survival at higher adult densities could also be the result of starvation, due to the overlap in diet with larger carp which have an exploitative advantage (Tonn et al. 1994). Larger reproductive investment of larger individuals at lower adult densities could also be a factor contributing to a Ricker-type stock-recruitment relationship (Weber and Brown 2013). The α_1 and α_2 parameters, describing the maximum survival rate of fish, and β_1 and β_2 parameters, describing the strength of the density-dependence during pre- and post-stocking, respectively, were derived in a manner similar to that used by Lorenzen (2005). Length-survival relationships and parameters from the original stock-recruitment relationship were used as follows:

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

$$s^* = \alpha = \left(\frac{L_0}{L_{rec}} \right)^{\frac{M_1^*}{h_{max}}}$$

where, L_0 is the larval length at hatch, L_{rec} is the average length at recruitment, M_1^* is the natural mortality rate at 1cm, and h_{max} is the maximum somatic growth rate. The previous equation can be used to solve for M_1^*,

$$M_1^* = h_{max} \frac{\ln s^*}{\ln \frac{L_0}{L_{rec}}} .$$

Note that M_1 for unrecruited fish (age-0) is much higher than for recruited fish (Lorenzen 2005). The maximum survival rates during the two phases, pre-stocking α_1 and post-stocking α_2, can then be determined,

$$\alpha_1 = \left(\frac{L_0}{L_s} \right)^{\frac{M_1^*}{h_{max}}} \text{ and } \alpha_2 = \left(\frac{L_s}{L_{rec}} \right)^{\frac{M_1^*}{h_{max}}} \text{ such that } \alpha = \alpha_1 \alpha_2,$$

where L_s is the length of fish at the time of stocking. One can also solve for β_1 and β_2 , if

$$M_1^* = h_{max} \frac{\ln s^*}{\ln \dfrac{L_0}{L_{rec}}} = h_{max} \frac{\ln s_2}{\ln \dfrac{L_s}{L_{rec}}}$$

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

$$\beta_1 = \frac{\ln \dfrac{L_0}{L_s}}{\ln \dfrac{L_0}{L_{rec}}} \beta$$

Assuming

$$s_1 s_2 = \alpha_1 e^{-\beta_1 N_0} a_2 e^{-b_2 \alpha_1 N_0 e^{-\beta_1 N_0}} = \alpha e^{-\beta N_0}$$

β_2 can be determined, using α_1 and β_1 ,

$$\beta_2 = \frac{\beta - \beta_1}{\alpha_1 e^{-\beta_1 N_0}}$$

Derivation of density-dependent allometric mortality

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

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

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

$$M_L = M_1 \left(\frac{1}{L} \right),$$

where M_1 is defined as the natural mortality per unit length (i.e., $L_r = 1$ cm) and is usually around 15 for recruited wild fish (Lorenzen 2005). Note that M_1 for unrecruited fish (age-0) is much higher than for recruited fish (Lorenzen 2005). Based on mortality estimates from the literature when size/age was known, we found that $M_1 \cong h_{max}$ across a number of species (Figure S5). While we did not do an exhaustive literature review, this finding is supported by other studies. In his seminal paper, (Pauly 1980) found that natural mortality was dependent on growth parameters estimated from the von Bertalanffy growth model, and more recent investigations found that size-dependent mortality was also dependent on asymptotic size and the von Bertalanffy growth rate parameter (Lorenzen 2000, Gislason et al. 2010, Charnov et al. 2013); parameters that when combined represent the growth rate near t_0 (Gallucci and Quinn 1979). Thus, we assumed that $M_1 = h_{max}$ when deriving our density-dependent allometric mortality relationship.
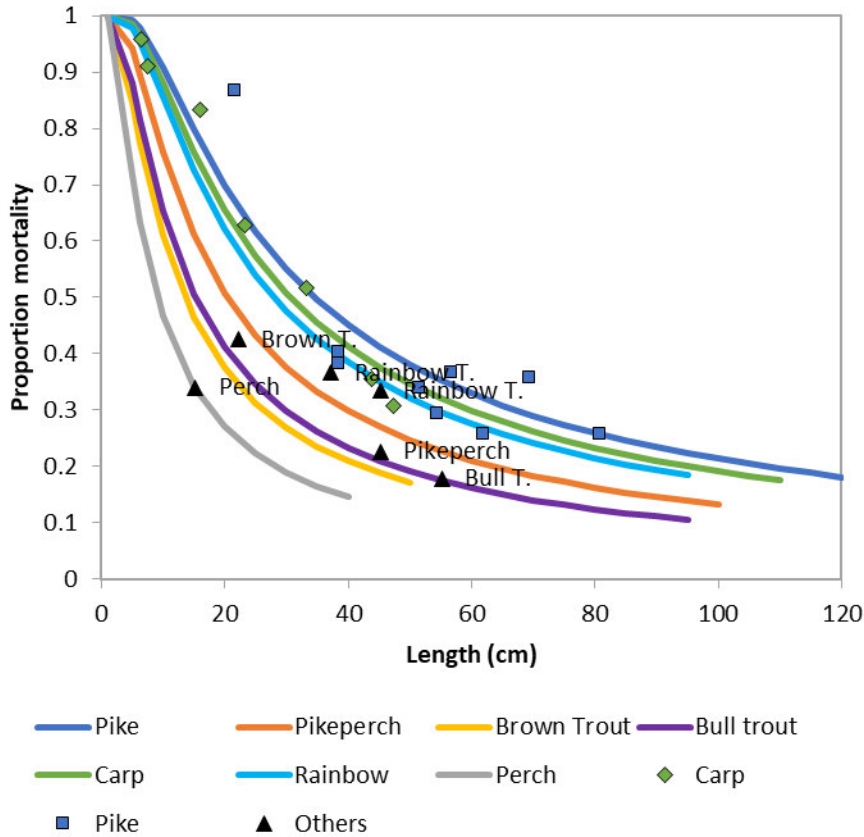
Figure S5. Comparison of some data to predictions from the size-dependent mortality function based on the assumption that $M_1 = h_{max}$. Sources: pike (Kipling and Frost 1970, Treasurer et al. 1992), carp (Koehn et al. 2000, Brown et al. 2005, Vilizzi et al. 2015), others (Le Cren et al. 1977, Lind 1977, Crisp 1994, Cox 2000, Post et al. 2003)

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

Density-dependent mortality is often assumed to be more important in the regulation of the early life stages in fish, while density-dependent growth is thought to be more important in the later life stages (Lorenzen 2008). Our model reflects this finding while avoiding a knife-edge from density-dependent to density-independent survival. However, studies have documented density-

dependent survival in age-1 fish (e.g, Post et al. 1999), and Johnston et al. (2007) documented density-dependent survival in mature bull trout (*Salvelinus confluentus*), which was more severe in the younger (smaller) adults spawning for the first time. Thus, density-dependent mortality in later life stages is not unsupported.

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

$$M_{r,L_{max}} = M_1 \left(\frac{L_{max}}{L_{r,1cm}} \right)^c = h_{max} \left(\frac{L_{max}}{1} \right)^{-1} = \frac{h_{max}}{L_{max}},$$

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

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

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

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

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

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

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

Post et al. (1999) report two relationships in their study, density-dependent growth and growth-dependent mortality for three size classes of age-1 rainbow trout.

$$h_g = \Upsilon_{1,g} + \Lambda_{1,g} D_{L^2}$$

$$M_g = \Upsilon_{2,g} + \Lambda_{2,g} h_g$$

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

$$M_g = \Upsilon_{2,g} + \Lambda_{2,g}(\Upsilon_{1,g} + \Lambda_{1,g} D_{L^2}).$$

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

$$M = \Upsilon + \Lambda D_{L^2} \text{ where } \Upsilon = \Upsilon_2 + \Lambda_2 \Upsilon_1 \text{ and } \Lambda = \Lambda_2 \Lambda_1.$$

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

$$M = \Upsilon + \Lambda D_{L^2} = M_{r,L_{max}} \left(\frac{h_{max}}{L_{max}} \right)^c = M_{r,L_{max}}^{(c+1)},$$

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

Solving for c

$$c = \frac{\ln(\Upsilon + \Lambda D_{L^2})}{\ln(M_{r,L_{max}})} - 1$$

To make this equation general across species, one can assume that densities are relative to some reference density $D_{L^2,r}$ and substitute relative effective densities D_{rel} for D_{L^2}, where

$$D_{rel} = \frac{D_{L^2} - D_{L^2,r}}{D_{L^2,r}}.$$

If one assumes that the reference effective density is the density at which $c = -1$, then $M = 1$ for a fish of size h_{max}. Thus,

$M = \Upsilon + \Lambda D_{L^2 . r}$, so

$$D_{L^2,r} = \frac{1 - \Upsilon}{\Lambda}.$$

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

If $D_{L^2} = D_{rel}D_{L^2,r} + D_{L^2,r} = D_{rel}\left(\frac{1-\Upsilon}{\Lambda}\right) + \frac{1-\Upsilon}{\Lambda}$,

then $c = \dfrac{\ln(\Upsilon + \Lambda D_{L^2})}{\ln(M_{r,L_{max}})} - 1 = \dfrac{\ln\left[\Upsilon + \Lambda\left[D_{rel}\left(\dfrac{1-\Upsilon}{\Lambda}\right) + \dfrac{1-\Upsilon}{\Lambda}\right]\right]}{\ln(M_{r,L_{max}})} - 1$,

which can be simplified to

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

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

Model sensitivity to density-dependent mortality in age-1 and older fish

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

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

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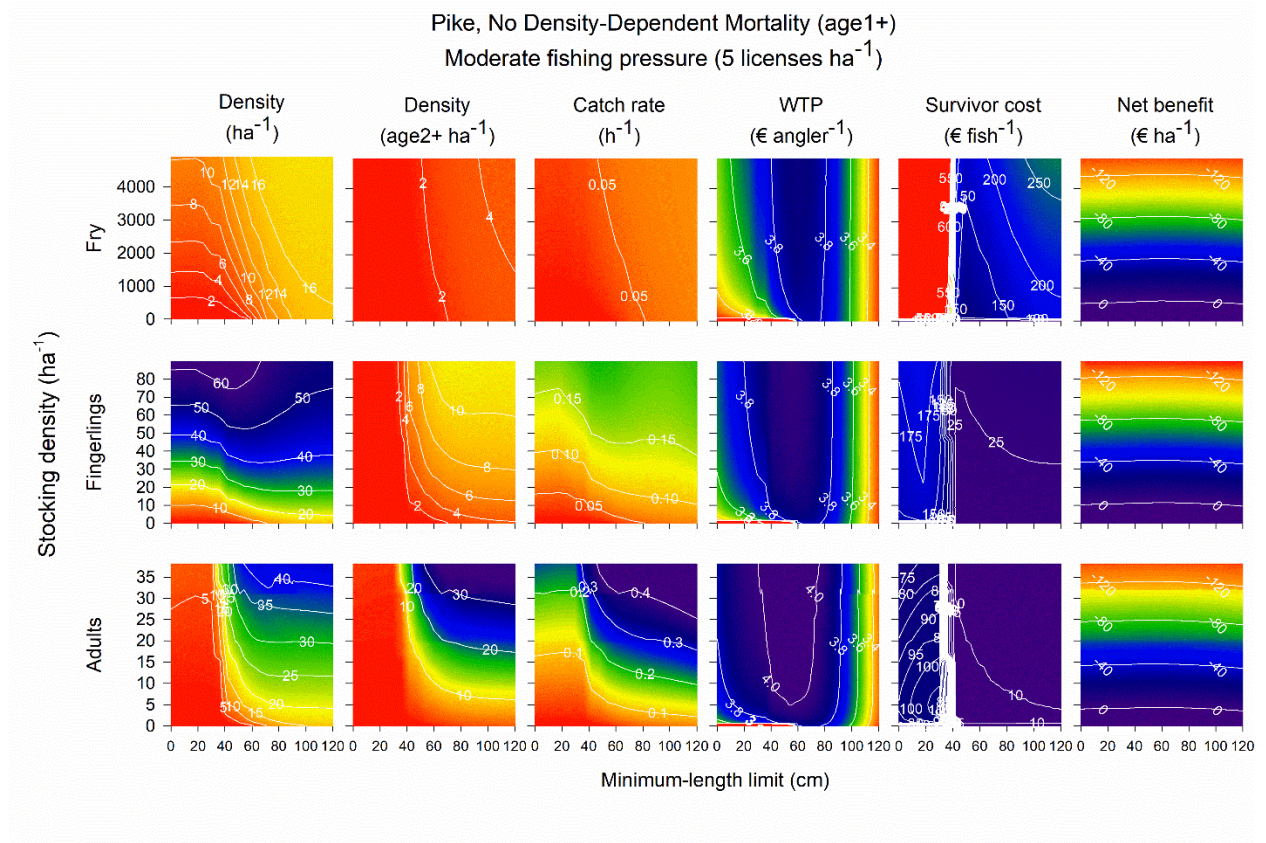
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Figure S6. The effects of stocking pike fry (2 cm), fingerlings (20 cm) and adults (age-2, 35-40 cm) at a range of densities across a range of minimum-length limits (MLLs) and a range of stocking densities (Table S1) calibrated to reflect the range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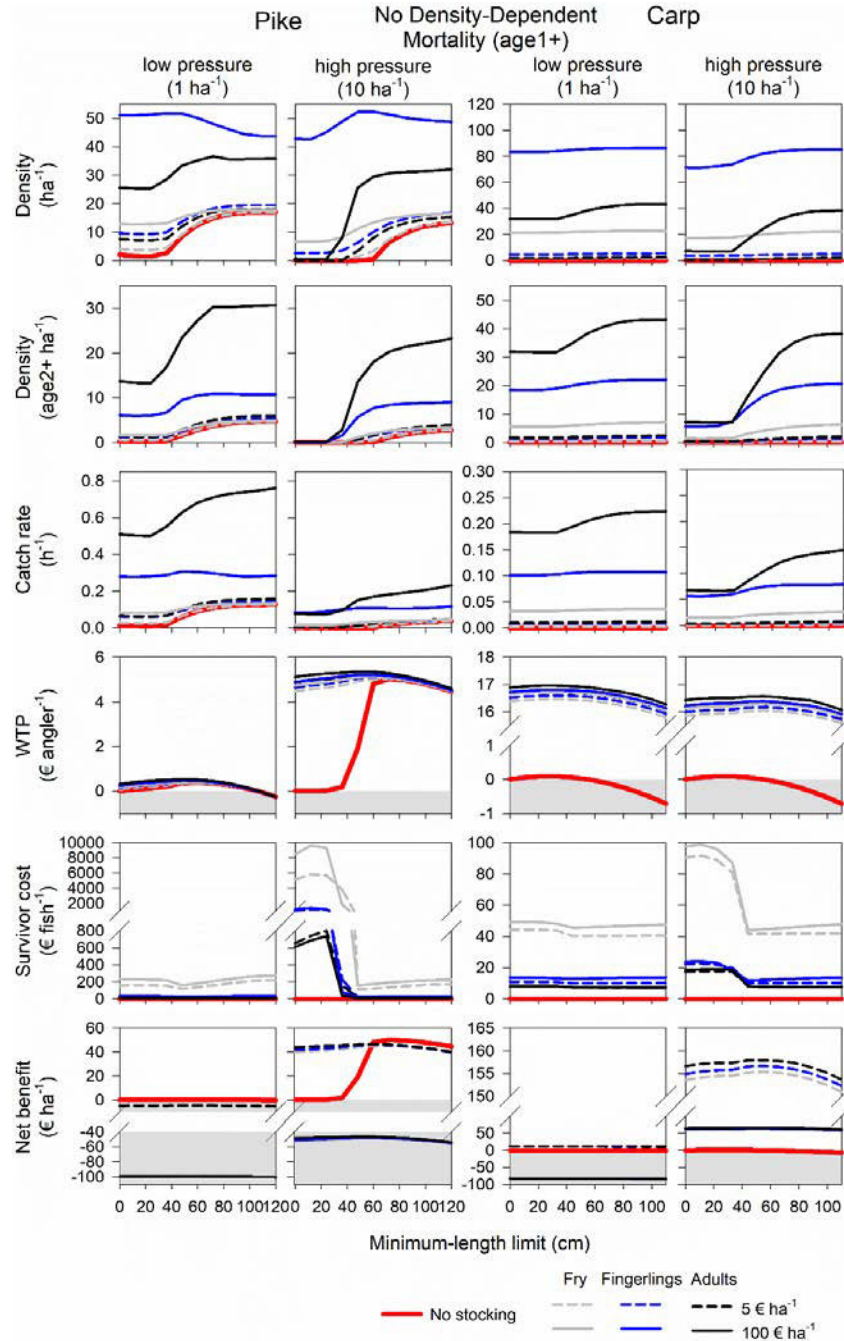
Figure S7. The effect of stocking pike and carp fry, fingerlings and adults at densities that represent annual stocking expenditures of 0, 5, and 100 € ha^{-1} (Table 2, scenario 2). For pike, these expenditures corresponded to densities of 0, 159 and 3174 fry ha^{-1} (2 cm), 0, 3 and 58 fingerlings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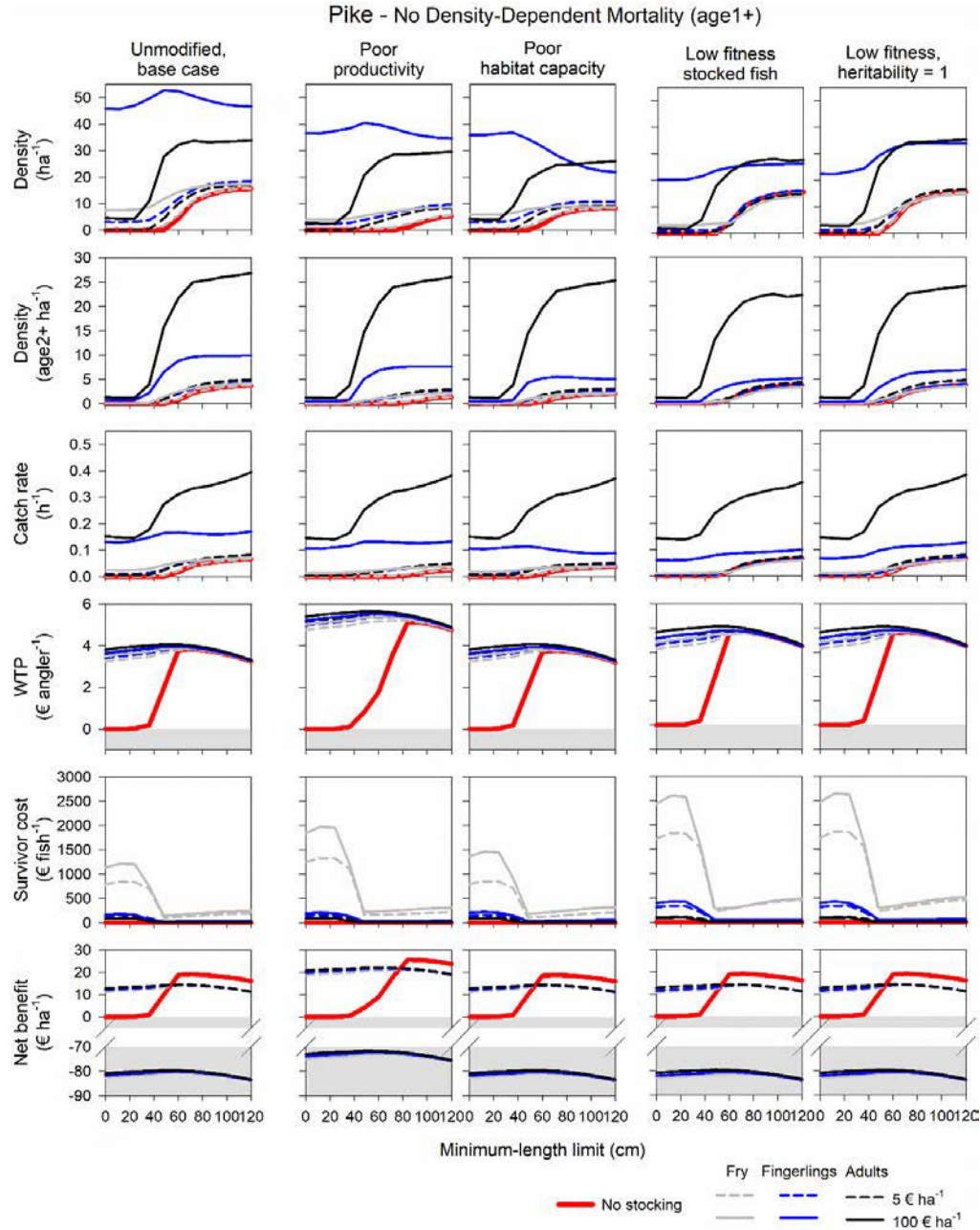
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Figure S8. The sensitivity of pike model outcomes to changes in model assumptions, under annual stocking expenditures of 0, 5, and 100 € ha^{-1}, and moderate latent fishing pressure, 5 licenses ha^{-1} (Table 2, scenarios 3 and 4). For pike, these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

Appendix S1: Literature Cited

Arlinghaus, R., B. Beardmore, C. Riepe, J. Meyerhoff, and T. Pagel. 2014. Species-specific preferences of German recreational anglers for freshwater fishing experiences, with emphasis on the intrinsic utilities of fish stocking and wild fishes. Journal of Fish Biology **85**:1843-1867.

Arlinghaus, R., E.-M. Cyrus, E. Eschbach, M. Fujitani, D. Hühn, F. Johnston, T. Pagel, C. Riepe, and (eds.). 2015. Hand in Hand für eine nachhaltige Angelfi scherei: Ergebnisse und Empfehlungen aus fünf Jahren praxisorientierter Forschung zu Fischbesatz und seinen Alternativen. Berichte des IGB Vol. 28. Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany.

Askey, P. J., E. A. Parkinson, and J. R. Post. 2013. Linking fish and angler dynamics to assess stocking strategies for hatchery-dependent, open-access recreational fisheries. North American Journal of Fisheries Management **33**:557-568.

Babiak, I., J. Glogowski, E. Brzuska, J. Szumiec, and J. Adamek. 1997. Cryopreservation of sperm of common carp, *Cyprinus carpio* L. Aquaculture Research **28**:567-571.

Barot, S., M. Heino, L. O'Brien, and U. Dieckmann. 2004. Estimating reaction norms of age and size at maturation when age at first reproduction is unknown. Evolutionary Ecology Research **6**:659-678.

Brown, P., K. P. Sivakumaran, D. Stoessel, and A. Giles. 2005. Population biology of carp (*Cyprinus carpio* L.) in the mid-Murray River and Barmah Forest Wetlands, Australia. Marine and Freshwater Research **56**:1151-1164.

Brown, P., and T. I. Walker. 2004. CARPSIM: stochastic simulation modelling of wild carp (*Cyprinus carpio* L.) population dynamics, with applications to pest control. Ecological Modelling **176**:83-97.

Charnov, E. L., H. Gislason, and J. G. Pope. 2013. Evolutionary assembly rules for fish life histories. Fish and Fisheries **14**:213-224.

Cox, S. P. 2000. Angling quality, effort response, and exploitation in recreational fisheries: field and modeling studies on British Columbia rainbow trout (*Oncorhynchus mykiss*) lakes. PhD Thesis. University of British Columbia.

Craig, J. F., and C. Kipling. 1983. Reproduction effort versus the environment; case-histories of Windermere perch, *Perca fluviatilis* L., and pike, *Esox lucius* L. Journal of Fish Biology **22**:713-727.

Crisp, D. T. 1994. Reproductive investment of female brown trout, *Salmo trutta* L., in a stream and reservoir system in northern England. Journal of Fish Biology **44**:343-349.

Crivelli, A. J. 1981. The biology of the common carp, *Cyprinus carpio* L. in the Camargue, southern France. Journal of Fish Biology **18**:271-290.

Frost, W. E., and C. Kipling. 1967. A study of reproduction, early life, weight-length relationship and growth of pike, *Esox lucius* L., in Windermere. Journal of Animal Ecology **36**:651-693.

Gallucci, V. F., and T. J. Quinn. 1979. Reparameterizing, fitting, and testing a simple growth model. Transactions of the American Fisheries Society **108**:14-25.

Gislason, H., N. Daan, J. C. Rice, and J. G. Pope. 2010. Size, growth, temperature and the natural mortality of marine fish. Fish and Fisheries **11**:149-158.

Heino, M., U. Dieckmann, and O. R. Godø. 2002. Estimating reaction norms for age and size at maturation with reconstructed immature size distributions: a new technique illustrated by application to Northeast Arctic cod. ICES Journal of Marine Science **59**:562-575.

Hilborn, R., and K. Stokes. 2010. Defining overfished stocks: have we lost the plot? Fisheries **35**:113-120.

Hühn, D., K. Lübke, C. Skov, and R. Arlinghaus. 2014. Natural recruitment, density-dependent juvenile survival, and the potential for additive effects of stock enhancement: an experimental evaluation of stocking northern pike (Esox lucius) fry. Canadian Journal of Fisheries and Aquatic Sciences **71**:1508-1519.

Jelkić, D., A. Opačak, I. Stević, S. Ozimec, J. Jug Dujaković, and R. Safner. 2012. Rearing carp larvae (*Cyprinus carpio*) in closed recirculatory system (RAS). Ribarstvo **70**:9-17.

Johnston, F. D., R. Arlinghaus, and U. Dieckmann. 2013. Fish life history, angler behaviour and optimal management of recreational fisheries. Fish and Fisheries **14**:554-579.

Johnston, F. D., J. R. Post, C. J. Mushens, J. D. Stelfox, A. J. Paul, and B. Lajeunesse. 2007. The demography of recovery of an overexploited bull trout, *Salvelinus confluentus*, population. Canadian Journal of Fisheries and Aquatic Sciences **64**:113-126.

Kipling, C., and W. E. Frost. 1969. Variations in the fecundity of pike *Esox lucius* L. in Windermere. Journal of Fish Biology **1**:221-237.

Kipling, C., and W. E. Frost. 1970. A study of mortality, population numbers, year class strengths, production and food consumption of pike, *Esox lucius* L., in Windermere from 1944 to 1962. Journal of Animal Ecology **39**:115-157.

Koehn, J., A. Brumley, and P. Gehrke. 2000. Managing the impacts of carp. Bureau of Rural Sciences, Department of Agriculture, Fisheries and Forestry, Canberra, Australia.

Le Cren, E. D., C. Kipling, and J. C. McCormack. 1977. A study of the numbers, biomass and year-class strengths of perch (*Perca fluviatilis* L.) in Windermere from 1941 to 1966. Journal of Animal Ecology **46**:281-207.

Lind, E. A. 1977. A review of pikeperch (*Stizostedion lucioperca*), Eurasian perch (*Perca fluviatilis*), and ruff (*Gymnocephalus cernua*) in Finland. Journal of the Fisheries Research Board of Canada **34**:1684-1695.

Lorenzen, K. 1996a. The relationship between body weight and natural mortality in juvenile and adult fish: a comparison of natural ecosystems and aquaculture. Journal of Fish Biology **49**:627-642.

Lorenzen, K. 1996b. A simple von Bertalanffy model for density-dependent growth in extensive aquaculture, with an application to common carp (*Cyprinus carpio*). Aquaculture **142**:191-205.

Lorenzen, K. 2000. Allometry of natural mortality as a basis for assessing optimal release size in fish-stocking programmes. Canadian Journal of Fisheries and Aquatic Sciences **57**:2374-2381.

Lorenzen, K. 2005. Population dynamics and potential of fisheries stock enhancement: practical theory for assessment and policy analysis. Philosophical Transactions of the Royal Society B: Biological Sciences **360**:171-189.

Lorenzen, K. 2008. Fish population regulation beyond stock and recruitment: the role of density-dependent growth in the recruited stock. Bulletin of Marine Science **83**:181-196.

Mangel, M. 2017. The inverse life-history problem, size-dependent mortality and two extensions of results of Holt and Beverton. Fish and Fisheries **18**:1192-1200.

Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. ICES Journal of Marine Science **39**:175-192.

Post, J. R., C. Mushens, A. Paul, and M. Sullivan. 2003. Assessment of alternative harvest regulations for sustaining recreational fisheries: model development and application to bull trout. North American Journal of Fisheries Management **23**:22-34.

Post, J. R., E. A. Parkinson, and N. T. Johnston. 1999. Density-dependent processes in structured fish populations: interaction strengths in whole-lake experiments. Ecological Monographs **69**:155-175.

Skov, C., L. Jacobsen, and S. Berg. 2003. Post-stocking survival of 0+ year pike in ponds as a function of water transparency, habitat complexity, prey availability and size heterogeneity. Journal of Fish Biology **62**:311-322.

Tempero, G. W., N. Ling, B. J. Hicks, and M. W. Osborne. 2006. Age composition, growth, and reproduction of koi carp (*Cyprinus carpio*) in the lower Waikato region, New Zealand. New Zealand Journal of Marine and Freshwater Research **40**:571-583.

Tonn, W. M., I. J. Holopainen, and C. A. Paszkowski. 1994. Density-dependent effects and the regulations of crucian carp populations in single-species ponds. Ecology **75**:824-834.

Treasurer, J. W., R. Owen, and E. Bowers. 1992. The population dynamics of pike, *Esox lucius*, and perch, *Perca fluviatilis*, in a simple predator-prey system. Environmental Biology of Fishes **34**:65-78.

Vilizzi, L., F. G. Ekmekçi, A. S. Tarkan, and Z. J. Jackson. 2015. Growth of common carp *Cyprinus carpio* in Anatolia (Turkey), with a comparison to native and invasive areas worldwide. Ecology of Freshwater Fish **24**:165-180.

Vilizzi, L., A. S. Tarkan, and F. G. Ekmekçi. 2013. Stock characteristics and management insights for common carp (*Cyprinus carpio*) in Anatolia: a review of weight–length relationships and condition factors. Turkish Journal of Fisheries and Aquatic Sciences **13**:759-775.

Weber, M. J., and M. L. Brown. 2013. Density-dependence and environmental conditions regulate recruitment and first-year growth of common carp in shallow lakes. Transactions of the American Fisheries Society **142**:471-482.

Weber, M. J., M. J. Hennen, and M. L. Brown. 2011. Simulated population responses of
common carp to commercial exploitation. North American Journal of Fisheries
Management **31**:269-279.

Willis, D. W. 1989. Proposed standard length-weight equation for northern pike. North
American Journal of Fisheries Management **9**:203-208.

Wright, R. M., and N. Giles. 1987. The survival, growth and diet of pike fry, *Esox lucius* L.,
stocked at different densities in experimental ponds. Journal of Fish Biology **30**:617-629.