Fish life history, angler behaviour, and optimal management of recreational fisheries

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Interim Report IR-12-044

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February 2015

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Abstract

To predict recreational-fishing impacts on freshwater fish species, it is important to understand the interplay among fish populations, anglers, and management actions. We use an integrated bioeconomic model to study the importance of fish life-history type (LHT) for determining (*i*) vulnerability to overexploitation by diverse angler types (generic, consumptive, and trophy anglers), who respond dynamically to fishing-quality changes; (*ii*) regulations (i.e., minimum-size limits and license densities) that maximize the social welfare of angler populations; and (*iii*) biological and social conditions resulting under such socially optimal regulations. We examine five prototypical freshwater species: European perch (*Perca fluviatilis*), brown trout (*Salmo trutta*), pikeperch (*Sander lucioperca*), pike (*Esox lucius*), and bull trout (*Salvelinus confluentus*). We find that LHT is important for determining the vulnerability of fish populations to overfishing, with pike, pikeperch, and bull trout being more vulnerable than perch and brown trout. Angler type influences the magnitude of fishing impacts, due to differences in fishing practices and angler-type-specific effects of LHT on angling effort. Our results indicate that angler types are systematically attracted to particular LHTs. Socially optimal minimum-size limits generally increase with LHT vulnerability, whereas optimal license densities are similar across LHTs. Yet, both regulations vary among angler types. Despite this variation, we find that biological sustainability occurs under socially optimal regulations, with one exception. Our results highlight the importance of jointly considering fish diversity, angler diversity, and regulations when predicting sustainable management strategies for recreational fisheries. Failure to do so could result in socially suboptimal management, fishery collapse, or both.

Introduction

Commercial harvesting can cause severe declines in fish stocks (Worm et al., 2009). Similarly, recreational fisheries can also have substantial negative impacts on the world's fisheries (McPhee et al., 2002, Coleman et al., 2004, Cooke and Cowx, 2004, Lewin et al., 2006), although they often remain "invisible" due to absent or insufficient monitoring (Post et al., 2002). The lack of sustainability in some fisheries may relate to simplification or neglect of three interrelated factors, which need to be jointly considered in fisheries management: (*i*) the life history of the exploited population and its influence on vulnerability to overexploitation (Reynolds et al., 2001, Rose et al., 2001, Winemiller, 2005), (*ii*) the heterogeneity and dynamics of fishers exploiting the fishery (Radomski et al., 2001, Wilen et al., 2002, Johnston et al., 2010, Fulton et al., 2011), and (*iii*) the influence of management objectives and regulations on the ecological and social dynamics of the fishery (Radomski et al., 2001, Cox and Walters, 2002, Wilen et al., 2002). Only by integrating these three main components – biological, social and managerial – into fisheries-projection models (Figure 1) can fisheries dynamics be understood and more robust management predictions be achieved (Johnston et al., 2010). While earlier studies have illustrated the importance of considering how differences in fish biology (e.g., productivity) can influence the efficacy of harvest regulations (e.g., Beamesderfer and North, 1995), progress in integrated angler-fish population modelling has been slow (Fenichel et al., 2012). To our knowledge, no previous modelling study has rigorously explored the importance of considering the interrelationships among fish life history, angler diversity, and various management measures for sustainable fisheries management. To advance our understanding, here we examine these interrelationships and study how the resulting dynamics of both fish and anglers affect optimal management strategies in recreational fisheries.

105   A key factor determining the dynamics of a fishery is fish life history (described by

106   the combination of life-history traits that characterize a species), because it influences a fish

107   population's vulnerability to overexploitation (Reynolds et al., 2001, Rose et al., 2001,

108   Winemiller, 2005). Life-history traits (describing, e.g., growth, maturation, or fecundity) vary

109   substantially among species (Reynolds et al., 2001), and are often phenotypically plastic

110   (Pigliucci, 2005). Fish that exhibit different life-history strategies will thus differ in their

111   production and in the degree to which density-dependent processes regulate the population,

112   thus altering their ability to compensate for fishing mortality (Rose et al., 2001, Winemiller,

113   2005, Goodwin et al., 2006). For example, fish that mature late, attain large maximum size,

114   and have low potential rates of population increase have been reported to be more vulnerable

115   to overexploitation than fish with the opposite characteristics (Jennings et al., 1998).

116   However, for freshwater fish species the relationships between risk of decline and

117   anthropogenic factors are often not clear-cut (Duncan and Lockwood, 2001, Reynolds et al.,

118   2005). Thus, to provide more robust predictions about the vulnerability of freshwater fish

119   populations to overexploitation by recreational angling, a quantitative modelling approach

120   that describes life-history characteristics of commonly targeted species is warranted.

121   A second key, yet often ignored, factor determining the impacts of fishing on fish

122   populations is the structure and dynamics of fishers exploiting the fishery (Wilen et al., 2002,

123   Johnston et al., 2010, Fulton et al., 2011). While commercial fishers are primarily motivated

124   by maximizing yield or economic revenue (Hilborn, 2007), multiple catch-related and non-

125   catch-related attributes of a fishery (e.g., catch rates, fish size, angler congestion, aesthetic

126   appeal, facilities, permit costs; reviewed in Hunt, 2005) influence the fishing decisions. of

127   recreational anglers Furthermore, angler populations are almost always composed of diverse

128   angler types (e.g., Arlinghaus, 2004), each exhibiting specific fishing preferences and fishing

129   practices (e.g., Aas et al., 2000, Beardmore et al., 2011). For example, some anglers prioritize

130 fish harvest whereas others preferentially target trophy-sized fish and voluntarily release

131 them (Hahn, 1991, Jacobson, 1996, Fisher, 1997). Thus, angling impacts likely differ with the

132 type of anglers fishing (Johnston et al., 2010) and the life-history type of exploited fish.

133 Predicting the long-term outcome of fish-angler interactions requires an integrated modelling

134 approach that incorporates population dynamics of diverse fish life histories and behavioural

135 responses of diverse angler types to changes in fishery quality (Johnston et al., 2010).

136   A third key factor influencing any fishery system is its management component. Fish-

137 angler dynamics do not occur in isolation from fishing regulations. Harvest regulations

138 commonly employed in recreational fisheries influence which fish are caught and/or

139 harvested (in terms of, e.g., species and size), but they also influence angler behaviour (Beard

140 et al., 2003, Fulton et al., 2011) and therefore are of crucial importance for describing angler

141 dynamics (Johnston et al., 2010). Fish-angler dynamics will influence how effective

142 regulations are at meeting the management objectives they are designed to achieve;

143 objectives which often include balancing the sometimes conflicting interests of different

144 stakeholders with the maintenance of a biologically sustainable fishery (Cochrane, 2000, Cox

145 and Walters, 2002, Hilborn, 2007). Optimum social yield (OSY) incorporates numerous

146 management objectives by integrating social, economic, and biological considerations into a

147 single measure of the utility (in terms of benefits, satisfaction, and/or social welfare) a

148 recreational fishery provides to society (Roedel, 1975, Malvestuto and Hudgins, 1996). The

149 OSY approach is rarely used in practice (possibly because of the difficulty in measuring the

150 underlying quantities), but has shown promise for the management of a northern-pike (*Esox*

151 *lucius*, Esocidae) recreational fishery: a study modelling this species revealed that regulations

152 maximizing social welfare also maintained a biologically sustainable fish population

153 (Johnston et al., 2010). However, because life history influences a fish population's response

154 to fishing, and in turn the behaviour of the anglers exploiting it, it is unknown if this

155 prediction holds across life histories commonly targeted by freshwater recreational anglers.

156   To explore the importance of jointly considering fish life history, dynamic and diverse

157 angler behaviour, alternative management options, and the nonlinear interplay among the

158 three fishery components (Figure 1) when managing recreational fisheries, here we use an

159 integrated bioeconomic model. Our model is parameterized to describe five fish life-history

160 types (LHTs) representing recreationally important freshwater fish species, in conjunction

161 with three plausible angler behavioural types (Johnston et al., 2010). We use this model to

162 evaluate how differences in LHT and angler type influence recreational-fishing impacts and

163 the socially optimal management of fisheries. Specifically, we investigate (*i*) how LHT

164 influences vulnerability to overfishing under different levels of constant and, more

165 realistically, dynamic fishing effort by various angler types; (*ii*) how angling regulations (e.g.,

166 minimum-size limits and license densities) that maximized social welfare vary among LHTs

167 and angler types; and finally (*iii*) how biological sustainability and social conditions under

168 socially optimal regulations differ across LHTs and angler types. Our intention here is not to

169 provide predictions for a particular fishery, but to gain general insights into the influence of

170 LHT and angler diversity on the dynamics of a coupled social-ecological system, by bridging

171 the traditional divide between fisheries science and social science (Arlinghaus et al., 2008,

172 Fulton et al., 2011, Fenichel et al., 2012). Our framework can nevertheless be calibrated to a

173 particular fishery, if appropriate data on the fish population and the preferences of angler

174 types are collected using fisheries-biological and human-dimensions research methods.

Methods

Model overview

177   We use an integrated bioeconomic model (Table A1), developed by Johnston et al.

178 (2010) for a northern-pike recreational fishery, that links dynamic angler behaviour with a

179   deterministic age-structured fish population model for a single-species single-lake fishery.

180   The model includes three components (Figures 1 and 2): (*i*) a biological component that

181   determines the fish population dynamics of different LHTs, (*ii*) a social component that

182   determines the angler-effort dynamics of different angler types based on angler-type-specific

183   preference functions, and (*iii*) a management component that prescribes the angling

184   regulations. In this study, we extend the model by Johnston et al. (2010) to describe five

185   distinct LHTs representing northern pike, European perch (*Perca fluviatilis*, Percidae),

186   pikeperch (*Sander lucioperca*, Percidae), brown trout (*Salmo trutta*, Salmonidae), and bull

187   trout (*Salvelinus confluentus*, Salmonidae) (Figure 3; Table S1). These LHTs were chosen

188   because they span diverse life-history characteristics (Wootton, 1984), and represent a broad

189   range of LHTs commonly targeted by freshwater recreational anglers (e.g., Post et al., 2002,

190   Almodóvar and Nicola, 2004, Isermann et al., 2007). The LHTs vary in body size and growth

191   rate, age- and size-at-maturation, offspring size, fecundity, lifespan, natural mortality rate,

192   and the degree to which density regulates early juvenile survival (stock-recruitment

193   relationships) and individual growth rates (Figure 3). Thus, the LHTs examined here differ in

194   unexploited abundance, biomass, and age and size structure (Table 1). To allow for a direct

195   comparison of model outcomes, the same age-structured fish population model is used for all

196   LHTs. In all scenarios we investigate, fish populations reach demographic equilibrium prior

197   to the introduction of fishing, and the presented results reflect equilibrium conditions after

198   fishing is introduced (i.e., we investigate long-term dynamics). A model overview is provided

199   below (see also Figure 2); additional details are described in Johnston et al. (2010). Model

200   equations are given in Table A1 and variables are given in Table A2, qualitative descriptions

201   of LHTs and angler types are shown in Figures 3 and 4, and detailed parameters and part-

202   worth-utility equations are provided in the supplementary material (Tables S1-S4).

203   ***Model components***

204   The biological model component determines fish population dynamics, describing

205 reproduction, growth, and survival (Figure 2, element A). Reproduction is pulsed at the

206 beginning of the year.To account for LHT differences in spawning time (not present in

207 Johnston et al. 2010), fecundities (total egg numbers) are determined by spawner sizes and

208 spawner numbers either at the beginning of each year (spring spawners) or in the fall of the

209 previous year (fall spawners) (Table A1, equation 5a; Table S1). Two important density-

210 dependent processes, growth in body size and early offspring survival, allow for

211 compensatory responses to exploitation (Rose et al., 2001, Lorenzen, 2008). Density-

212 dependent offspring survival from spawning to post-hatch occurs at the beginning of each

213 year, described by either a Beverton-Holt type (Beverton and Holt, 1957) or a Ricker-type

214 stock-recruitment relationship (Ricker, 1954b) (Table A1, equation 5c). Growth is modelled

215 using a biphasic growth model (Lester et al., 2004) (Table A1, equations 4a-4c), and. Growth,

216 as well as mortality from both fishing and natural sources (for fish aged 1 year and older;

217 Table A1, equation 6i), are modelled in continuous time. Continuous growth allows fish to

218 become more vulnerable to capture within a year. Continuous mortality allows for recapture

219 and repeated exposure of released fish to hooking mortality; the latter can have serious

220 negative impacts on some recreational fish species especiallyif effort is high (Coggins et al.,

221 2007). The number and size of fish caught are determined jointly by the abundance and

222 structure of the fish population, fishing effort, anglers' skills (affecting catchability), and the

223 size-dependent vulnerability to capture (Table A1, equation 6a), which varies among angler

224 types (see below) (Table A1, equation 6c; Figure 2, element B). Fishing mortality depends on

225 the number and size distribution of the catch, the regulated minimum-size limit and harvest

226 practices of angler types fishing (Table A1, equation 6h; Figure 2, element C). Thus, fishing

227 mortality is size-dependent through both capture vulnerability and minimum-size limits.

228   The social model component determines annual fishing effort. Random utility theory

229   assumes that anglers will have a higher probability to fish when conditions provide them with

230   more utility (Hunt, 2005) (Figure 2, element D). Following Johnston et al. (2010), angling

231   effort is determined by angler-type-specific multi-attribute utility functions, based on catch-

232   related attributes (catch rates, average and maximum size of fish caught) and non-catch-

233   related attributes (angler crowding, minimum-size limits, and license costs) of the fishery that

234   are known to affect anglers' utility and hence participation decisions (Hunt, 2005) (Table A1,

235   equation 1; Figure 2, element E). In addition, angler types can differ in their fishing practices

236   (in terms of the size of fish they target, their skill level, and their propensity to voluntarily

237   release fish), as well as in their preferences for the considered fishery attributes (Aas et al.,

238   2000, Hunt, 2005, Oh and Ditton, 2006). Here we describe three angler types – generic,

239   consumptive, and trophy anglers – differing in their fishing practices and preferences (Figure

240   2, elements F1 to F3; see also Figure 4). Our parameterization of utility functions for these

241   three angler types (Table S3) is based on angler specialization theory (Bryan, 1977) as

242   described in detail in Johnston et al. (2010).

243   The management model component prescribes input regulations through license

244   densities (A_L s) and output regulations through minimum-size limits (MSL s) (Figure 2,

245   element G). In our model, license density is the number of licenses issued to anglers for a

246   single 100 ha lake, and ranges up to a maximum of one license per hectare. We focus on

247   minimum-size limits, as these are commonly used in recreational fisheries to limit harvest

248   (Radomski et al., 2001). In open-access recreational fisheries, output regulations often only

249   reduce an individual angler's harvest, and not total harvest (Radomski et al., 2001, Cox et al.,

250   2002, Cox and Walters, 2002), whereas input regulations more directly control angler effort

251   and thus fishing mortality (Cox et al., 2002); therefore, license densities are also varied in our

252   model. We do not include daily bag limits in our model for three reasons. First, we want to

253   concentrate our analyses on comparing one input regulation and one output regulation.

254   Second, the effectiveness of daily bag limits has been questioned, because in practice daily

255   quotas are often not met (Cook et al., 2001) and, moreover are only successful if fishing

256   effort, and thus total harvest, are not too high (Post and Parkinson, 2012). Third, our model

257   includes angler-type-specific harvest preferences, which work similar to daily bag limits, by

258   limiting some angler types' daily harvest through their propensity to voluntarily release fish

259   (Table S3). The management component of our model is also used to determine regulations

260   that achieve an optimal social yield (OSY). We assume such optimal regulations to be given

261   by combinations of minimum-size limit (MSL_{opt}) and license density ($A_{L,opt}$) that maximize

262   the total utility (an aggregation of individual utilities across anglers; Table A1, equation 7b)

263   gained by the angler population at equilibrium (Figure 2, element H). We use total utility to

264   measure social welfare; naturally, results may differ when other welfare measures are used

265   (Johnston et al., 2010).

266   ***Standardizing across LHTs***

267   To allow direct comparison among our results for different LHTs, the vulnerability of

268   fish to capture, as well as some baseline attribute levels used for determining angler utility

269   that depend on fish size or abundance, need to be standardized for LHT differences in

270   maximum body size (L_{max}) and unexploited abundance (Table 1).

271   *Vulnerability to capture*

272   The size dependence of capture vulnerability is described by a sigmoidal function that

273   varies among LHTs and angler types. These functions are characterized by the size L_{50} at

274   which vulnerability reaches 50%, and by the steepness y with which vulnerability increases

275   around L_{50} (Table A1, equation 6a). In choosing L_{50} and y, we need to account for three

276   considerations. First, to standardize the vulnerability curve among LHTs we allow L_{50} to

277   increase roughly proportionally with a LHT's maximum size L_{max}. Second, to produce

278   realistic size structures of catch, we need to account for a systematic bias in L_{50}: the general

279   lack of interest in catching very small fish, presumably because they provide minimal

280   consumptive or trophy value, reduces the relative range of sizes captured for smaller LHTs

281   much more than it does for larger LHTs. Empirical findings show that even when anglers

282   target smaller-bodied predatory freshwater species, they catch few very small fish (e.g., van

283   Poorten and Post, 2005, Wilberg et al., 2005). We account for this bias by introducing an

284   offset L_{shift} into the sigmoidal function that shifts L_{50} to the right. This shift is more

285   consequential for smaller LHTs than for larger LHTs, and thus accounts for the

286   aforementioned bias. Third, different angler types impose different size-selective capture

287   vulnerabilities, with trophy anglers targeting larger fish. We account for these three facts by

288   determining L_{50} as a linear function of L_{max}, $L_{50} = z_j L_{max} + L_{shift}$ (Table A1, equation 6b) where

289   z_j depends on the angler type j. To estimate y and z_j for generic and consumptive

290   anglers, we use a least-square approximation of the vulnerability of pike reported by Johnston

291   et al. (2010). For trophy anglers, z_j is increased by 10% relative to generic and consumptive

292   anglers (Table S3), since trophy anglers value, and thus target, larger fish by using different

293   gear than the other angler types (Jacobson, 1996, Aas et al., 2000). To the extent that

294   empirical data is available, we find that the capture vulnerabilities thus specified produce size

295   structures of catch that generally match empirical observations for the described LHTs or

296   closely relates species (e.g., Paul et al., 2003, Post et al., 2003, van Poorten and Post, 2005,

297   Wilberg et al., 2005, Arlinghaus et al., 2009; see footnote Table S3).

298   *Part-worth-utility functions*

299   In our model, multiple fishery attributes contribute to an angler's utility (Table A1,

300   equation 1) and thus influence the participation decisions of anglers (Table A1, equation 2a).

301 Part-worth-utility (PWU) functions from welfare economics (illustrated in Johnston et al.

302 2010, Figure 3) are used to describe the relative importance of each catch-related and non-

303 catch-related attribute to an angler's overall utility (Table S2). The PWU functions also

304 involve scaling attribute levels relative to baseline attribute levels (defined as the levels at

305 which the focal PWU value equals 0,and the probability to fish thus equals 50%, when all

306 other PWU values equal 0; Table S4). However, some baseline attribute levels depend on fish

307 size or fish abundance in a way that varies with LHT. For example, a perch angler likely

308 gains more utility from catching a 30 cm perch than a pike angler does from catching a 30 cm

309 pike, due to the intrinsic size differences between these two species. Thus, several baseline

310 attribute levels are standardized so as to achieve such the desired relative scaling across

311 LHTs.

312 First, minimum-size limits are set as a proportion of L_{max} ranging between 0 and 1

313 (Table S4). Second, the baseline catch rates C_{De} (Table S4) are assumed to equal 50% of the

314 maximum catch rate achievable for a given LHT by a mixed angler population (comprising

315 40%, 30%, and 30%; generic, consumptive, and trophy anglers, respectively) imposing no

316 harvest, non-compliance, or hooking mortality on the fish population. For all LHT, the thus

317 established baseline catch rates are generally within the range reported for the modeled, or

318 closely related, species (see Table S4). Third, proportional-stock-density (PSD) categories

319 (Gabelhouse, 1984), also known as proportional size structure (Guy et al., 2006), which

320 describe the recreational value of fish based on their size relative to the species' world-record

321 length, are used to set baseline values for the average size $\bar{L}_e$ and maximum size L_{xe} of

322 caught fish. Specifically, we assume that "quality" fish (40% of L_{max}) represent the baseline

323 value for $\bar{L}_e$, and fish bordering the "preferred" and "memorable" categories (55% of L_{max})

324 represent the baseline value for L_{xe} (Table S4).

Outline of analysis

326   To examine how biological impacts from recreational fishing varies among LHTs, we

327 first run our model across a range of minimum-size limits (MSL; Table S1) and fishing

328 efforts, both of which are held constant within a model run. In these model runs, anglers

329 therefore do not behave dynamically (Figure 2, element I) and are furthermore assumed to be

330 consumptive anglers killing all harvestable fish: this makes it possible to compare the

331 biological response of LHTs at equilibrium to identical levels of fishing effort. Changes in

332 fish abundance and biomass relative to unexploited levels (Table 1), and in the weighted

333 spawning-potential ratio SPR (Table A1, equation 7a), are examined. The SPR is commonly

334 used to assess fisheries sustainability: values below 0.2-0.3 are considered critical (Goodyear,

335 1993), whereas maintaining SPR above 0.35-0.40 is likely to prevent recruitment overfishing

336 (Mace, 1994, Clark, 2002).

337   In a second stage of our analysis, we allow angler types to respond dynamically to the

338 perceived quality of the fishery, i.e., utility affected anglers' probability to fish (Figure 2,

339 element D). We examine model runs across a range of minimum-size limits MSL and license

340 densities A_L (Table A2), for homogeneous angler populations composed of one angler type,

341 and more realistically, for four specific compositions of mixed angler populations (Table S3).

342 These mixed angler populations are comprised of either relatively equal proportions of the

343 three angler types (40%:30%:30%; generic, consumptive, and trophy anglers, respectively),

344 or strongly skewed towards generic (70%:15%:15%), consumptive (15%:70%:15%), or

345 trophy (15%:15%:70%) anglers. We evaluate how the interplay among life-histories,

346 dynamic angler behaviours, and regulations differentially affect overfishing vulnerability,

347 angler behaviour, and optimal regulations (in terms of MSL_{opt} and $A_{L,opt}$) across LHTs and

348 anglers populations under equilibrium conditions. The biological conditions (in terms of SPR

349) and social conditions (in terms of total utility and fishing effort) under optimal regulations

350 are also examined, to assess whether trends across LHTs exist and whether optimal

351 regulations imply biological sustainability. We also analyse the relative participation of

352 angler types in mixed angler populations (in terms of the proportion of the fishing effort

353 exerted by a given angler type relative to that type's proportion of the angler population;

354 Table A1, equation 7c) across LHTs, to determine if angler types are differentially attracted

355 to, or excluded from, particular fisheries.

356   Finally, we evaluate the sensitivity of fish-angler dynamics to LHT parameterization

357 using elasticity analyses (e.g., Allen et al., 2009). For this purpose, we vary each life-history

358 parameter by ±10% from its original value (except for age-at-maturation and maximum age,

359 which are discrete and are therefore varied by ±1 year) and calculate the relative change in

360 MSL_{opt} and $A_{L,opt}$. Relative changes exceeding 10% indicate that the fish-angler dynamics are

361 sensitive to those parameters. SPR levels predicted under the new optimal regulations are

362 also examined, to evaluate if predictions about biological sustainability under socially

363 optimal regulations are robust to changes in life-history parameters.

364 ## Results

365 *Biological impacts under constant fishing effort*

366   In the absence of exploitation, the five life-history types (LHTs) in our model differ

367 substantially in their population characteristics. Perch is most abundant, with an unexploited

368 equilibrium density (of fish aged 1 year and older) approaching 800 fish·ha^{-1}, followed by

369 brown trout and pikeperch (300 and 90 fish·ha^{-1}, respectively; Table 1). Pike and bull trout

370 are least abundant (less than 25 fish·ha^{-1}; Table 1). Predicted abundance under unexploited

371 conditions generally fall within the range predicted in the literature, although pikeperch in our

372 model are more abundant than what may be considered average literature values, and the

373 predicted abundances of perch and bull trout are at the low end of the range reported in the

374 literature (supplementary material – "Parameterization of stock-recruitment relationships").

375   The unexploited biomasses (of fish aged 1 year and older) predicted by our model range

376   between 10 kg·ha^{-1} and 60 kg·ha^{-1} across all LHTs. Pikeperch exhibits the highest unexploited

377   biomass, followed by perch, brown trout, pike, and bull trout.

378   When recreational fishing is introduced with a constant consumptive angling effort,

379   the biological impacts on the five LHTs, measured relative to unexploited conditions, differ

380   greatly (Figure 5). Fishing reduces the abundance, biomass, and *SPR* of pike, bull trout, and

381   pikeperch relative to unexploited levels, particularly under low to moderately restrictive

382   minimum-size limits (0-50% of L_{max}) and moderate to high fishing efforts (30-80 h·ha^{-1};

383   Figure 5). Similarly, fishing reduces the biomass and *SPR* of perch and brown trout (Figure

384   5), although their relative magnitudes of decline are generally smaller than for the other

385   LHTs. However, unlike all other LHTs, exploitation increases perch abundance above

386   unexploited levels under all examined minimum-size limits and fishing efforts (Figure 5).

387   Fishing also increases brown-trout abundance (Figure 5), but only under liberal minimum-

388   size limits and for fishing efforts below 20 h·ha^{-1}, or under more restrictive minimum-size

389   limits above 60% of L_{max}.

390   Overall, these results suggest that the susceptibility of LHTs to declines in abundance,

391   biomass, and *SPR* are greatest to least as follows (ranked by the proportion of model runs in

392   which *SPR* was smaller than 0.35): bull trout, pikeperch/pike (similar responses), brown

393   trout, and perch. Hereafter, we use the term LHT vulnerability to refer the degree to which

394   LHTs in our model are susceptible to recruitment overfishing from recreational angling. The

395   obtained ranking suggests that LHT vulnerability to overexploitation by consumptive anglers

396   is negatively related to unexploitedabundance and maximum recruitment, positively related

397   to maximum body size and size-at-maturation, and not strongly related to age-at-maturation,

398   relative fecundity, or natural mortality (see Table 1 and Table S1 for values).

399   ***Biological impacts under dynamic angler behaviour***

16

400   Allowing anglers to respond dynamically to the perceived quality of the fishery alters

401   the incidence of recruitment overfishing, and also causes fishing efforts to vary substantially

402   among LHTs and angler populations (Figure 6). Despite this influence of LHT on the angling

403   effort a fishery attracts, the pattern of differential vulnerability of LHTs to overexploitation

404   by anglers remains qualitatively unchanged, regardless of the composition of the angler

405   population. Consistent with our aforementioned findings for the biological impacts of

406   consumptive anglers that fish with constant effort, the biological impacts (measured by SPR)

407   of dynamic angler populations are greatest to least across LHTs as follows: (again ranked as

408   described above) bull trout, pikeperch/pike, brown trout, and perch (Figure 6).

409   However, the angler population's composition does alter the quantitative magnitudes

410   of the biological impacts anglers exert on the fished populations. Under liberal minimum-size

411   limits, the consumptive angler population reduces SPR more than other angler populations

412   across LHTs, whereas under more restrictive minimum-size limits, SPR is most reduced by

413   the trophy anglers (Figure 6).

414   Biological impacts on less vulnerable LHTs vary much more among angler

415   populations, despite being generally less severe, than on more vulnerable LHTs. For example,

416   only certain angler populations (consumptive, or consumptive and mixed) overfish perch and

417   brown trout, whereas all angler populations overfish pike, pikeperch, and bull trout under

418   some regulations. Across the range of regulations examined, consumptive angler populations

419   reduce the SPR below 0.35 more often than other angler populations when targeting

420   pikeperch, perch, and brown trout, whereas the trophy-angler population had the greatest

421   impact on bull trout, and impacts on pike are similar for populations of consumptive, trophy,

422   and mixed (40%:30%:30%) anglers.

423   ***Socially optimal regulations***

424   We also find that socially optimal regulations differ among LHTs: the optimal

425   minimum-size limit MSL_{opt} (measured as a fraction of L_{max}) increases with LHT

426   vulnerability, generally being lowest for perch (23-44% of L_{max}, 9-17 cm), followed by

427   brown trout (29-54%, 15-28 cm), pikeperch (54-70%, 56-72 cm), pike (52-84%, 61-98 cm),

428   and bull trout (44-80%, 43-78 cm; Figure 7a). In addition, MSL_{opt} varies greatly (over a range

429   wider than 20% of L_{max}) among angler populations (Figure 7a): for all LHTs except brown

430   trout, MSL_{opt} is highest for trophy-dominated angler populations (composed solely of, or

431   dominated by, trophy anglers) and lowest for consumptive-dominated angler populations

432   (defined analogously). For brown trout, MSL_{opt} is highest for consumptive-dominated angler

433   populations and lowest for generic-dominated angler populations (Figure 7a).For all LHTs,

434   MSL_{opt} values for all mixed angler populations fall within the ranges predicted for the three

435   homogeneous angler populations.

436   Unlike MSL_{opt}, the optimal license density $A_{L,opt}$ shows no general trend across

437   LHTs, ranging from 0.4-0.6 ha^{-1} for most LHTs, but varying by 0.15-0.20 ha^{-1} among angler

438   populations (Figure 7b). One exception to this pattern occurs for bull trout, for which $A_{L,opt}$

439   for the consumptive angler population is very low (0.11 ha^{-1}; Figure 7b). Despite the general

440   consistency of $A_{L,opt}$ across LHTs, the highest $A_{L,opt}$ for pikeperch, perch, and brown trout

441   occur when these LHTs are targeted by a generic angler population, whereas for pike and bull

442   trout, $A_{L,opt}$ is highest for the mixed (40%:30%:30%) angler population (Figure 7b). On the

443   other extreme, $A_{L,opt}$ for pike and brown trout is lowest when exploited by trophy-dominated

444   angler populations, while for pikeperch, perch, and bull trout, the consumptive-dominated

445   angler populations have the lowest $A_{L,opt}$. Thus, unlike MSL_{opt}, $A_{L,opt}$ for mixed angler

446   populations can exceed the range predicted for homogeneous angler populations.

Conditions under socially optimal regulations

Under socially optimal regulations (MSL_{opt} and $A_{L,opt}$), which maximized anglers'

total utility, fish populations are generally not at risk of recruitment overfishing.The *SPR*

remains above 0.35 across all LHTs and angler populations, except when bull trout is

exploited by solely consumptive anglers (in which case *SPR* drops to 0.26; Figure 7c).

However, *SPR* under optimal regulations tends to be lower for LHTs that are generally more

vulnerable, although it varies substantially among angler populations (Figure 7c). Across

LHTs, *SPR* is generally lowest for the solely consumptive angler population, except for

brown trout, for which the mixed angler population skewed towards generic anglers has the

lowest *SPR* (Figure 7c). The trophy-dominated angler populations reduces the *SPR* of

pikeperch, perch, and brown trout the least under optimal regulations, while the mixed

(40%:30%:30%) angler population had the least impact on pike, and the generic angler

populationhad the least impact on bull trout (Figure 7c).

The maximum total utility gained by an angler population varies with LHT and angler

population. Under socially optimal regulations, trophy-dominated angler populations gain the

most total utility and consumptive-dominated angler populations the least, across LHTs

(Figure 7d). Total utility tends to be higher and vary less for less vulnerable LHTs than for

more vulnerable LHTs (Figure 7d), revealing distinct angler-type-specific LHT preferences.

While total utility is high for all angler populations exploiting perch and brown trout, the total

utility gained by trophy-dominated angler populations tends to increase with LHT

vulnerability, being highest for bull trout and pike. By contrast, the total utility gained by

generic-dominated and consumptive-dominated angler populations is highest for perch and

brown trout, and tends to decline with LTH vulnerability (Figure 7d).

The annual fishing efforts that the modelled fisheries attract under optimal regulations

are reasonable, when compared with the corresponding ranges reported for the different

472   LHTs in the literature [e.g., yellow perch (*Perca flavescens*, Percidae) 3-109 h ha^{-1} (Isermann

473   et al., 2005), pike 38-91 h ha^{-1} (Pierce et al., 1995), and walleye (*Sander vitreus*, Percidae)

474   29-112 h ha^{-1} (Beard et al., 2003)], potentially being on the high side for some LHTs [e.g.,

475   bull trout, 10-20 h ha^{-1} (Post et al., 2003)]. Like $A_{L,opt}$, optimal fishing efforts show little

476   variation among LHTs (45-70 h·ha^{-1} for most LHTs), but vary more markedly among angler

477   populations (Figure 7e). Consequently, optimal fishing effort shows little relationship with

478   LHT vulnerability, only differing substantially (14.2 h·ha^{-1}) for the consumptive angler

479   population targeting bull trout. Across most LHTs, consumptive-dominated angler

480   populations fish less than the other angler populations under optimal regulations, except for

481   the trophy-dominated angler populations fishing for brown trout (Figure 7e). Pike, perch, and

482   brown trout attract the most fishing effort from generic-dominated angler populations,

483   whereas trophy-dominated angler populations fish more for pikeperch and bull trout (Figure

484   7e). The optimal fishing efforts of mixed angler populations generally fall within the range

485   predicted for the three homogeneous angler populations.

486   The relative participation of different angler types in the mixed angler populations

487   show clear trends in relation to LHTs under optimal regulations (Figure 8). These trends

488   occur despite differences among mixed angler populations in MSL_{opt} and $A_{L,opt}$, as well as in

489   the conditions associated with optimal regulations (e.g., total utility and fishing effort).

490   Regardless of LHT, generic anglers tend to be underrepresented or proportionally represented

491   in the total angling effort compared with their relative abundance in the mixed angler

492   population (ca. 1; Figure 8a). By contrast, the relative participation of consumptive anglers

493   decreases (Figure 8b), and the relative participation of trophy anglers increases (Figure 8c),

494   as LHT vulnerability increases. Thus, consumptive anglers tend to be overrepresented when

495   fishing for perch and brown trout and underrepresented when fishing for pike, pikeperch, and

496   bull trout, whereas trophy anglers show the opposite pattern, being systematically attracted to

497   the larger-bodied LHTs.

498   *Sensitivity analyses*

499   We find that MSL_{opt} is generally less sensitive to changes in life-history parameters

500   than $A_{L,opt}$ (Tables S5 and S6), and that both are most sensitive to changes in age-at-

501   maturation a_m, maximum growth increment h_{max}, and instantaneous natural mortality rate

502   m_{na} (note, however, that because the change in a_m is ±1 year, the relative change in a_m is

503   much greater than ±10%). Sensitivity varies across combinations of LHT and angler type.

504   The robustness of MSL_{opt} and $A_{L,opt}$ tends to decrease with LHT vulnerability (e.g., fewer

505   relative changes exceeding 10% for perch compared with bull trout).The sensitivity of

506   MSL_{opt} is relatively similar among angler types, whereas, across all LHTs, $A_{L,opt}$ is more

507   sensitive to changes in life-history parameters when exploited by consumptive anglers,

508   followed by trophy anglers and generic anglers.

509   Despite the sensitivity of optimal regulations to changes in life-history parameters,

510   predictions about the biological sustainability of the fishery under optimal regulations are

511   fairly robust (Table S7).For pike and pikeperch under optimal regulations, the *SPR* never

512   drops below 0.35. For perch and brown trout under optimal regulations, consumptive anglers

513   reduce *SPR* below 0.35 when age-at-maturation a_m is increased, but remains above 0.35 in

514   all other cases. Similar to our main results, bull trout under optimal regulations cannot

515   biologically sustain exploitation by consumptive anglers, except when the natural mortality

516   rate m_{na} is decreased. Angling of bull trout by generic and trophy anglers also result in *SPR*

517   values below 0.35 when a_m is increased, but remains above 0.35 in all other cases involving

518   those angler types.

519   **Discussion**

520   Here we have used a novel bioeconomic model developed by Johnston et al. (2010) to

521   integrate fish life-history diversity, angler diversity and dynamics, and input and output

522   regulations, to evaluate the importance of jointly considering these components   for

523   determining optimal regulations and the vulnerability of different fish life-history types

524   (LHTs) to recreational overfishing. Our study is the first to systematically investigate the

525   response of different LHTs in an integrated framework using realistic assumptions about

526   distinct angler types and their dynamic responses to changes in fishing quality. Thereby, our

527   study addresses recent calls for more integrative analyses in recreational fisheries (Fenichel et

528   al., 2012).

529   We find that LHTs are crucially important for determining the vulnerability of

530   recreational fish populations to recruitment overfishing. LHTs differentially affect the

531   fishing-participation decisions of angler types. We also find that, because angler types differ

532   in their effort dynamics and fishing practices, the angler population's composition influences

533   the biological impacts of fishing on LHTs. These complex feedbacks between fish LHTs and

534   angler populations result in large variations, across both LHTs and angler populations, in

535   regulations that maximize social welfare. For example, more vulnerable LHTs in our model

536   tend to have higher optimal maximum-size limits MSL_{opt} than less vulnerable LHTs, and as a

537   second example, trophy anglers generally prefer the highest MSL_{opt} for a given LHT, while

538   consumptive anglers prefer the lowest. Yet, despite differences in regulations that achieved

539   optimal social yield OSY, our model predicts optimal regulations to result in biologically

540   sustainable exploitation for all LHTs, except when bull trout are exploited solely by

541   consumptive anglers. A management approach based on social objectives (e.g., OSY), rather

542   than one based solely on biological objectives (e.g., maximum sustainable yield), can thus

543   facilitate biologically sustainable exploitation. This is because biological objectives are

544   inherently part of the social-welfare metric, through their effects on catch-related utility

545   attributes.

546   Results of our study underscore the importance of considering all three components of

547   a recreational fishery – LHTs, angler types, and management regulations – in an integrated

548   framework when predicting sustainable management strategies for recreational fisheries.

549   Simplification of any of these components may lead to erroneous predictions about fish-

550   angler dynamics, which may result in socially suboptimal management, biological collapse,

551   or both.

LHT vulnerability to overfishing

553   Life-history traits are important for determining the vulnerability of fish populations

554   to overfishing (Reynolds et al., 2001, Rose et al., 2001, Winemiller, 2005). Thus, it is not

555   surprising we have found differences in the susceptibility of LHTs to recreational

556   exploitation. Numerous studies suggest that fish with certain life-history characteristics (i.e.,

557   late maturation, large maximum size, low population growth rate) are prone to experience

558   greater population declines from fishing than others (Jennings et al., 1998, Reynolds et al.,

559   2001, Dulvy et al., 2003); our model-based results are in general agreement with those

560   empirical findings

561   Specifically, we find that the naturally-less-abundant and large-bodied LHTs in our

562   model (bull trout, pikeperch and pike) experience more severe population declines in

563   response to recreational angling than the naturally-more-abundant and smaller-bodied LHTs

564   (perch and brown trout,) which can sustain greater fishing mortality. In fact, in agreement

565   with warnings by Post et al. (2003) about the extreme susceptibility of bull trout to

566   overfishing, we find that bull trout requires minimum-size limits approaching complete catch-

567   and-release fishing, to sustain even low fishing efforts. Thus, our results corroborate other

568   studies (Jennings et al., 1998, Reynolds et al., 2001, Dulvy et al., 2003) suggesting that

569   maximum body size is correlated with vulnerability to overexploitation by fishing.

570   Furthermore, our results show that indicators such as unexploited abundance, maximum

571   recruitment, and potentially also size-at-maturation (although this may simply be a correlate

572   of maximum body size) could also be useful for identifying fish populations susceptible to

573   overfishing, where information on those indicators is available. Moreover, our results suggest

574   that age-at-maturation, fecundity, and natural mortality are not likely to be good indicators of

575   vulnerable LHTs, contrary to earlier suggestions (Jennings et al., 1998, Reynolds et al.,

576   2001).

577   The differences among LHTs in vulnerability to overfishing relate in part to their

578   overall productivity and their abilities to compensate for fishing-related mortality through

579   density-dependent gains in survivorship and/or reproductive success (Rose et al., 2001). This

580   ability depends on species' life-history characteristics and on the strength and frequency of

581   the density-dependent processes to which they are adapted (Rose et al., 2001, Winemiller,

582   2005, Goodwin et al., 2006). For example, density-dependent survival during early life

583   stages, which is common in many fish species (Myers et al., 1995), influences a population's

584   ability to offset fishing mortality (Rose et al., 2001, Goodwin et al., 2006, Lorenzen, 2008).

585   At high population densities, even overcompensation can occur (e.g., in the form of a Ricker

586   stock-recruitment relationship), due to cannibalism, density-dependent disease transmission,

587   or spawning interference (Ricker, 1954a, Hilborn and Stokes, 2010). This means that with

588   reductions in spawning stock recruitment initially rises before declining (Hilborn and Stokes,

589   2010). In our model, perch experiences large gains in recruitment because of

590   overcompensation when egg production is reduced by fishing, ultimately resulting in an

591   increase in population density. Overcompensation and cannibalism have been reported for

592   this species (Ohlberger et al., 2011). Overcompensation for low fishing mortality also occurs

593   for brown trout, but not when fishing effort, and thus mortality, increases under liberal

594   minimum-size limits. All other LHTs, even highly fecund pikeperch, are unable to replace,

595   through compensatory population growth, individuals removed by fishing. In addition to this

596   relatively low compensatory potential, the greater vulnerability of these naturally-less-

597   abundant and larger-bodied LHTs to overexploitation reflects the low maximum recruitment

598   and population density (Table 1) of these top predators relative to perch and brown trout.

599   When considered alone, stock-recruitment relationships can underestimate population

600   responses to fishing (Rochet et al., 2000, Rose et al., 2001, Rose, 2005), even though they

601   strongly influence the compensatory potential of exploited populations, because other

602   density-dependent processes may co-determine those responses (Rose et al., 2001, Rose,

603   2005, Lorenzen, 2008). For example, density-dependent growth, which is included in our

604   model, can alter a population's compensatory potential, because fish size influences

605   fecundity, maturation, and survival (Rose et al., 2001, Rose, 2005, Lorenzen, 2008).

606   However, stock-recruitment relationships are likely more important than density-dependent

607   growth for determining the compensatory potential of heavily exploited populations

608   (Lorenzen, 2008). Indeed, the reductions in biomass and SPR we observe across LHTs in our

609   model underscore that density-dependent changes in size-at-age cannot compensate fully for

610   density losses caused by high fishing mortality. Density-dependent changes in fecundity,

611   maturation, and reproductive frequency, and fisheries-induced evolutionary changes are not

612   considered in our study, but could also be important for determining a fish population's

613   response to exploitation (Rochet et al., 2000, Rose et al., 2001, Jørgensen et al., 2007). We

614   therefore recommend that model extensions aim at including all salient processes influencing

615   a population's compensatory potential.

616   It has been suggested that, in the absence of detailed information, qualitative "rules of

617   thumb" based on the life-history characteristics of exploited fish populations could aid

618   fisheries managers in identifying those populations that are most vulnerable to overfishing

619 (Reynolds et al., 2001, Winemiller, 2005). For example, according to Winemiller and Rose's

620 (1992) classification scheme, "periodic strategists" (featuring high fecundity, late maturation,

621 and low juvenile survival) are predicted to exhibit the highest resilience to fishing, whereas

622 "equilibrium strategists" (with low fecundity, late maturation, and high juvenile survival)

623 should have lower resilience (Winemiller and Rose, 1992, Winemiller, 2005). Our results

624 regarding the extreme vulnerability of bull trout, a salmonid likely classified as intermediate

625 between periodic and equilibrium strategists (Winemiller and Rose, 1992), and indeed its

626 current status – "vulnerable" in the IUCN's Red List (Gimenez Dixon, 1996), and

627 "threatened" in coterminous USA (US Fish and Wildlife Service 2010), provide some

628 support for these predictions, as do our findings related to pike, pikeperch, perch, and brown

629 trout, which are all broadly classified as periodic strategists (Rose et al., 2001, Vila-Gispert

630 and Moreno-Amich, 2002) and are all listed as species of least concern (Freyhof and Kottelat,

631 2008a, Freyhof and Kottelat, 2008b, Freyhof and Kottelat, 2008c, Freyhof, 2011).

632   However, our results caution that coarse life-history classifications, such as

633 Winemiller and Rose's (1992), risk obscuring important life-history differences that exist

634 within the broadly defined strategies (Rose et al., 2001): as we have shown here these life-

635 history differences can substantially influence vulnerability to overexploitation. For example,

636 despite four of our LHTs being classified as periodic strategists (Vila-Gispert and Moreno-

637 Amich, 2002), we found pike and pikeperch to be much more vulnerable to recruitment

638 overfishing than brown trout or perch. Indeed, pike and walleye, a congeneric of pikeperch,

639 have been shown to be highly vulnerable to overexploitation by recreational angling (e.g.,

640 Post et al., 2002). Declines in brown-trout stocks as a result of recreational fishing have also

641 been documented (e.g., Almodóvar and Nicola, 2004). Thus, in the absence of more detailed

642 information, body size and life-history classification can provide directions for identifying

643 LHTs vulnerable to overfishing. However, the present study and other work (Rose, 2005,

644 Coggins et al., 2007) suggest that, where possible, a quantitative modelling approach should

645 be used to provide more robust predictions about the response of different LHTs to

646 recreational angling.

647 ***Angler dynamics***

648   When predicting the impacts of recreational fishing, one needs to consider not only

649 fish life history but also the preferences and dynamics of anglers utilizing a fishery (Post et

650 al., 2003, Johnston et al., 2010). Our results show that dynamic angler behaviour, regardless

651 of angler type, does not alter the general trend in vulnerability to recruitment overfishing

652 across LHTs our model predicts for constant consumptive fishing effort: with and without

653 dynamic angler behaviour, bull trout are most vulnerable and perch are least vulnerable to

654 fishing-induced *SPR* declines. Yet, the composition of the angler population and its effort

655 dynamics are important for determining the magnitude of the impact angling has on LHTs in

656 our model.

657   We find that differences in fishing practices (skill levels, propensity for voluntary

658 catch-and-release, fish size targeted; Table S3) among angler types influence catch and

659 harvest rates. Under liberal minimum-size limits, consumptive anglers have greater impacts

660 than other anglers types on less vulnerable LHTs in our model (perch and brown trout),

661 because catch rates of these naturally-abundant LHTs (e.g., maximum 11.3, 20.0, 15.0

662 harvestable-sized perch day^{-1} and 5.5, 8.6, 7.7 harvestable-sized brown trout day^{-1} for generic,

663 consumptive, and trophy anglers, respectively) are generally high, and consumptive anglers

664 harvest all legal-sized fish caught (i.e., fish are not voluntarily released). On the other hand,

665 trophy anglers in our model, while also enjoying high catch rates, only harvest one fish every

666 second day. Thus, a large disparity in harvest rates results among angler types. By contrast,

667 catch rates of naturally-less-abundant LHTs, bull trout and pike, in our model (with a

668 maximum of 0.17, 0.19, 0.14 harvestable-sized bull trout per day and 0.55, 0.75, 0.80

669   harvestable-sized pike per day for generic, consumptive, and trophy anglers, respectively) are

670   generally low and thus do not allow a similar disparity in harvest rates to develop. In our

671   model, catch rates of harvestable fish often do not exceed even the conservative personal

672   daily harvest limits set by trophy anglers, similar to reports for regulated daily bag limits

673   (Cook et al., 2001). This implies that regulated daily bag limits may also have little effect,

674   unless they are low enough to be achieved. Voluntary release by any angler type rarely occurs

675   in our model, and therefore is less important for determining the fishing impacts on the more

676   vulnerable LHTs. Instead, the variation in the impact of anglers on those more vulnerable

677   LHTs emerges through differences in angler behaviour, and thus fishing effort.

678   In addition to harvesting practices, dynamic angler behaviour also determines angling

679   impacts on LHTs. First, regardless of angler type, and despite substantial declines in fish

680   abundances and catch rates under liberal harvest regulations, some anglers continued to be

681   attracted to the modelled fishery. This has the potential to collapse fisheries (Post et al.,

682   2002), demonstrating the importance of considering multi-attribute angler behaviour in

683   recreational fisheries models (see also Johnston et al., 2010), rather than assuming that catch

684   rates alone dictate the fishing decisions of anglers (e.g., Cox et al., 2003). Second, our results

685   show how differences in behaviour among angler populations, because of angler-type-

686   specific fishing preferences, alter angling impacts, in some cases leading to counterintuitive

687   outcomes. For example, despite the tendency of trophy anglers to practice voluntary catch-

688   and-release (Arlinghaus et al., 2007), across LHTs populations of trophy anglers reduce the

689   *SPR* more than other angler populations under moderate to restrictive minimum-size limits.

690   This reflects that more specialized anglers often prefer or tolerate restrictive harvest

691   regulations (Aas et al., 2000, Oh and Ditton, 2006, Arlinghaus et al., 2007) and respond to

692   them differently than other anglers (Beard et al., 2003). Thus, under constrained harvest

693   conditions, while the angling efforts by consumptive and generic anglers declined, in our

694 models effort by trophy anglers remain high, resulting in trophy anglers killing more fish than

695 other angler types. In some cases, this mortality is sufficient to put populations at risk of

696 recruitment overfishing (e.g., for bull trout with license densities exceeding 0.7 ha^{-1}), even

697 under total catch-and-release regulations.

698 　　　　Our results thus support claims that discard mortality can substantially impact the

699 biological sustainability of some fisheries (Coggins et al., 2007). In combination, the fishing

700 practices and fishing preferences of trophy anglers, counterintuitively, result in their having

701 the greatest overall impact on bull trout. among all studied angler populations These findings

702 highlight that, to prevent unexpected results, managers and researchers need to better

703 understand the types of anglers utilizing a fishery, as well as the dynamics resulting from

704 their differential practices and preferences, to achieve more robust predictions about

705 recreational fishing impacts. Where sufficient information is available, our modelling

706 approach can be used to explore implications of management changes prior to their

707 enactment, so as to help select practically implemented management changes based on their

708 efficacy.

709 *Optimal management*

710 　　　　In our model, differences in LHT vulnerability and fish-angler interactions influence

711 the regulations that maximize an angler population's total utility, measured in terms of OSY.

712 For example, although the optimal density $A_{L,opt}$ of licenses does not show a general trend

713 with LHT vulnerability, MSL_{opt} has a strong tendency to increase with LHT vulnerability

714 (with MSL_{opt} being generally most liberal for perch and most restrictive for bull trout).

715 　　　　Minimum-size limits are often set in recreational fisheries to be as low as possible (so

716 as to maximize harvest) while allowing fish to spawn at least once (Johnson and Martinez,

717 1995, Diana and Smith, 2008), This tactic, however, may not be appropriate for all species.

718 Whereas low minimum-size limits may be suitable for perch, minimum-size limits for pike –

719 set at, e.g., 46-76 cm in North America (Paukert et al., 2001) – are often below, or at the

720 lower margin of,the range of MSL_{opt} predicted by our model (61-98 cm). Our findings thus

721 suggest that species-specific considerations when setting minimum-size limits could generate

722 greater social benefits from a fishery, supporting concerns that "one size fits all" policies may

723 erode ecological and social resilience (Carpenter and Brock, 2004). The increase of MSL_{opt}

724 with vulnerability suggests that unexploited abundance, maximum recruitment, maximum

725 body size, and potentially also size-at-maturation (if known) can aid managers in setting more

726 socially advantageous minimum-size limits, due to the correlation of those indicators with

727 vulnerability.

728   Accounting not only for LHTs but also angler diversity, however, is crucially

729 important when establishing management regulations (Radomski et al., 2001, Johnston et al.,

730 2010). In agreement with findings that more-specialized anglers are more tolerant of

731 restrictive harvest regulations (Aas et al., 2000, Oh and Ditton, 2006), MSL_{opt} in our model,

732 as a general rule, tends to be lowest for consumptive-dominated angler populations and

733 highest for trophy-dominated angler populations. However, in the case of brown trout,

734 consumptive-dominated angler populations have the highest MSL_{opt}, whereas generic-

735 dominated angler populations have the lowest. The reason for this finding is that the greater

736 harvest orientation and skill level of consumptive anglers relative to generic anglers requires

737 a higher minimum-size limit to maintain a sustainable fishery for consumptive anglers. On

738 the other hand, the less-consumptive generic anglers can fish with high effort under the more

739 liberal harvest regulations they preferred, because of the relatively productive nature of

740 brown trout.

741   Angler population composition is also important for determining the optimal density

742 $A_{\text{L,opt}}$ of licenses, including subtle interactions with LHT differences. For example, we find

743   that the generic angler population exhibit the highest $A_{L,opt}$ when LHT vulnerability is low,

744   whereas mixed angler populations have an even higher $A_{L,opt}$ when LHT vulnerability is high

745   (as it is, e.g., for pike and bull trout). This result highlights the importance of considering the

746   complex interplay among angler types within an angler population.

747   More broadly, our findings support suggestions that managing for diverse angling

748   opportunities could better conserve fish populations and increase the social welfare provided

749   by a fishery (e.g., Aas et al., 2000, Carpenter and Brock, 2004, Johnston et al., 2010). Given

750   that angler types generally display consistent preferences for optimal regulations, some

751   knowledge of the angler population could assist managers with meeting this challenge.

752   However, as our previously discussed results underscore, management decisions should be

753   based on both the life history of an exploited fish population and the diversity of interests in

754   the corresponding angler population (e.g., Diana and Smith, 2008).

755   Of relevance for managers faced with the challenge of maximizing angler satisfaction

756   and participation while maintaining a viable fishery (Radomski et al., 2001, Cox and Walters,

757   2002, Peterson and Evans, 2003), is the our promising result that adopting a socially optimal

758   approach (based on OSY) to recreational fisheries management achieves both objectives.

759   Specifically, *SPR* in our model is maintained above 0.35 except for bull trout, a LHT that

760   due to its extreme vulnerability to overfishing cannot biologically sustain a satisfied solely

761   consumptive angler population under optimal regulations. In most cases, however, managing

762   for OSY is more likely to achieve management objectives and result in lower fishing

763   mortality than managing for maximum sustainable yield (Radomski et al., 2001), because a

764   viable recreational fishery provides social and cultural benefits that are not measured by yield

765   alone (Roedel, 1975, Malvestuto and Hudgins, 1996). Notwithstanding these findings, given

766   the decrease in *SPR* that occurs in our model with increased LHT vulnerability under optimal

767 regulations, a precautionary approach should be adopted when setting optimal regulations for

768 naturally-more-vulnerable LHTs.

769 ***Emergent LHT preferences***

770 A final key finding of this study is the emergent preferences of angler types for

771 particular LHTs. For example, generic and consumptive angler populations tend to gain more

772 total utility from less vulnerable LHTs than from more vulnerable LHTs, creating an

773 emergent preference for the naturally-more-abundant and smaller-bodied LHTs. By contrast,

774 the total utility of populations of trophy anglers tends to increase with LHT vulnerability,

775 creating an emergent preference for the naturally-less-abundant and larger-bodied LHTs.

776 These trends occur despite standardizing anglers' PWU baseline expectations for life-history

777 differences in fish size and abundance. The social welfare provided by perch is high for all

778 angler populations, because perch can maintain high relative catch rates even when fishing

779 mortality is high under liberal minimum-size limits. However, relatively low catch rates and

780 aversions to restrictive regulations made the more vulnerable LHTs (pike, pikeperch, and bull

781 trout) less attractive to consumptive or generic anglers. Trophy anglers, by contrast, prefer the

782 naturally-less-abundant and larger-bodied bull trout and pike, because of their tolerance for

783 restrictive regulations and their ability to catch relatively larger fish. The greater average and

784 maximum relative size achieved for these LHTs likely results from stronger density

785 dependence in growth and reduced truncation of the size distribution under restrictive

786 minimum-size limits. These novel findings suggest that the intrinsic life history of fish

787 populations strongly influence which species or LHTs an angler type prefers. Indeed, in

788 support of these results Beardmore et al. (2011), found that more specialized, trophy-oriented

789 German anglers were particularly attracted to larger-bodied species such as pike.

790 One implication of angler-type-specific LHT preferences is that the socially optimal

791 management of a given recreational fishery may systematically exclude or attract certain

792   angler types. For example, as LHT vulnerability increases, the relative participation of trophy

793   anglers in our modelled mixed angler populations under optimal regulations also increases,

794   and the reverse is true for consumptive anglers. These trends occur despite large differences

795   in the optimal regulations underlying them. Therefore, depending on the social welfare

796   measure used (Johnston et al., 2010), managing for OSY may come at a greater cost to

797   certain angler types than others, which might lead to conflict among different segments of the

798   angling community (Loomis and Ditton, 1993, Arlinghaus et al., 2007). However, our

799   modelling approach can be used by managers to identify likely conflict situations, and it

800   provides them with a tool for transparently illustrating the benefits of regulation changes to

801   the angler community as a whole. Furthermore, understanding which angler types will be

802   attracted to specific LHTs will aid managers in setting appropriate socially optimal

803   regulations.

804   ***Limitations and extensions***

805   While the present study provides important insights into the interplay among fish

806   populations, anglers, and management measures, there are several limitations to our work,

807   and resultant opportunities for extensions, that deserve to be highlighted A first set is related

808   to angler dynamics, while a second set is related to fish dynamics; we now discuss these in

809   turn.

810   First, our model constitutes a single-species, single-lake model omitting a regional

811   perspective and multi-species interactions. Movement among various fisheries in a landscape

812   (Post et al., 2008, Hunt et al., 2011, Post and Parkinson, 2012), or a multispecies fishery

813   (Worm et al., 2009), could affect the outcomes presented here. Extending our model to

814   include multispecies interactions or a spatial component of lakes connected by mobile anglers

815   would be interesting avenues to pursue in future studies.

816   Second, by standardizing the baseline expectations of angler types for LHT

817   differences in body size and abundance, we have assumed that angler-type-specific PWU

818   functions are identical across LHTs. However, although Beardmore et al. (unpublished data)

819   found no significant differences in the relative preferences (e.g., standardized for catch rate

820   and body size) of different German angler types for several species, it is still possible that the

821   preferences of angler types may differ among species. Species-specific or even regional

822   differences in the utility functions of anglers could result in lower fishing effort under optimal

823   regulations than those predicted in this study.

824   Third, we did not include inverse density-dependent catchability in our model. The

825   existence of such a relationship could strongly affect the threshold effort that leads to severe

826   overfishing (Hunt et al., 2011). Thus, the omission of density-dependent catchability may

827   make our model results overly optimistic, by underestimating the risk of collapse for some

828   species.

829   Fourth, other harvest regulations, such as daily bag limits, could potentially alter our

830   study's predictions, by minimizing the disparity in fishing mortality imposed by different

831   angler types. For example, our model may overemphasize the fishing impacts of consumptive

832   anglers relative to other angler types, because the former are assumed to harvest all fish

833   caught. However, this bias would only be relevant for the less vulnerable LHTs examined

834   here, for which catch rates greatly exceed voluntary-release thresholds, and moreover, only

835   when regulated bag limits are set low enough that catch rates can exceed them with sufficient

836   frequency. For example, in many places anglers are allowed to harvest as many as 25 yellow

837   perch per day, or even more (Isermann et al., 2007), while the maximum achieved catch rate

838   in our model was 21.5 fish per day. For the more vulnerable LHTs we have examined, angler

839   types rarely manage to catch even the most conservative daily quota (personal or regulated),

840   resulting in harvest rates that are similar among angler types. Thus, as suggested in the

841 literature (Cook et al., 2001), anglers are often not limited by daily bag limits: they harvest

842 less fish than their daily bag limit would allow, either because they voluntarily choose not to

843 harvest so many fish or because they do not manage to catch their daily limit. Nevertheless,

844 the inclusion of daily bag limits might still alter the effort dynamics of anglers in our model,

845 either through regulation aversions (Beard et al., 2003) or through resultant changes in fish

846 population dynamics, which would therefore make an interesting extension for future

847 research.

848 Other limitations of our model relate to fish dynamics. First, our results are based on

849 the parameterization of a single-species system without any consideration of food-web

850 interactions. Thus, for more realistic predictions about a specific fishery, the model will need

851 to be calibrated appropriately. However, the purpose of this work has been to encompass a

852 range of LHTs experienced by anglers, rather than to model any one specific population.

853 Second, as previously highlighted, some realistic density-dependent processes

854 resulting from phenotypic plasticity (e.g., in maturation), which could be important for

855 determining a LHT's compensatory (Rochet et al., 2000) potential and thus its predicted

856 vulnerability, were not included in our model. In addition, we did not account for any

857 harvest-induced evolutionary changes in life-history traits (e.g., Jørgensen et al., 2007) that

858 might influence a species' response to fishing, e.g., through changes in its reproductive

859 ecology (Enberg et al., 2010). Plastic or genetic changes that result in earlier maturation at

860 smaller sizes, for example, could allow a fish population to withstand higher fishing pressure,

861 especially the larger-bodied, more vulnerable LHTs. Such changes would often also influence

862 angler behaviour, by altering the perceived quality of a fishery, e.g., if mean fish size

863 declined.

864 Third, unaccounted changes in demographic structure, through juvenescence or size-

865 dependent maternal effects, could alter reproductive potential and population stability

866 (Anderson et al., 2008, Arlinghaus et al., 2010, Hsieh et al., 2010). Size-dependent maternal

867 effects would likely have more of an influence on LHTs that have lower proportions of adults

868 in the population and fewer first-time spawners in the mature population (e.g., bull trout;

869 Table 1), as well as on the more vulnerable LHTs. The impacts reported here are likely to be

870 conservative if large females are preferentially removed by fishing and size-dependent

871 maternal effects impair recruitment at low fish population abundance.

872 The influences of phenotypic plasticity, fisheries-induced evolution, and maternal

873 effects on predictions about optimal regulations would be fascinating to examine, but were

874 beyond the scope of the present study. Future research should also investigate alternative

875 regulations, e.g., slots-length limits designed to protect large spawners (Arlinghaus et al.,

876 2010).

877 *Conclusions*

878 Our study, to our knowledge, is the first to use an integrated modelling approach,

879 based on theories from ecology, economics, and human-dimensions research, to

880 systematically investigate how fish life history and angler types influence the vulnerabilityof

881 fish populations to recreational overfishing and the behaviour of angler populations

882 exploiting them. Using such an approach has revealed some unexpected results and some

883 general patterns that could not have been exposed if the interplay among fish populations,

884 anglers, and management measures had not been considered. We have also shown that

885 socially optimal management generally achieves both social and biological sustainability, a

886 result that can be taken as encouraging for recreational fisheries managers. In combination,

887 our results demonstrate the benefit of integrating the traditionally separate fields of fisheries

888 ecology and social sciences to facilitate the sustainable management of recreational fisheries.

889 In this context, our results caution that managing all species according to the same rationale

890 may result in the loss of social welfare and put fish populations at risk of overexploitation.

Acknowledgments

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Table 1. Characteristics of fish life-history types under unexploited conditions.

	Life-history type				
	Perch	Brown trout	Pikeperch	Pike	Bull trout
Maximum body size (cm; L_{max}, Table S1)	38.5	51.5	103	117	98
Density of fish aged 1 year and older (ha^{-1})	779	300	97	23	12
Biomass fish aged 1 year and older (kg·ha^{-1})	49.1	29.5	61.0	16.1	10.0
Maximum annual growth increment of juveniles (cm)	5.5	8.4	10.0	20.7	7.7
Proportion of adults in population	0.44	0.57	0.45	0.63	0.36
Proportion of first-time spawners in mature population	0.34	0.43	0.24	0.37	0.19
Mean age (y)	2.97	2.33	4.11	2.70	5.14
Age-at-maturation (y; a_m, Table S1)	3	2	4	2	6
Mean length (cm)	13.0	17.6	31.8	40.0	33.7
Size-at-maturation (cm)	14.8	18.4	36.1	35.3	45.7
Relative fecundity (g^{-1})	65.6	1.9	150.0	25.5	1.9

Maximum recruitment density** of fish aged 0 (ha^{-1})	601.2	160.8	24.6	9.2	2.5

1146 * See details in Table S1

1147 ** Either asymptotic value of Beverton-Holt stock-recruitment relationship or peak value of Ricker stock-recruitment relationship.

Figure captions

1148

1149 **Figure 1**. Fishery components and their interactions. For an overview of the corresponding

1150 integrated bioeconomic model, see Figure 2.

1151 **Figure 2**. Schematic overview of the integrated bioeconomic model. Alphabetized black

1152 circles indicate model elements described in the section "Methods, Model components"

1153 Dashed lines highlight differences between model scenarios with constant vs. dynamic

1154 fishing effort.

1155 **Figure 3**. Qualitative description of variation in biological characteristics among the five

1156 considered fish life-history types. Small, medium, and large circles represent low/small,

1157 intermediate, and high/large levels, respectively.

1158 **Figure 4**. Qualitative description of angler type diversity in preferences for fishery attributes

1159 and fishing practices. Small, medium, and large-sized dots indicate low/small, intermediate,

1160 and high/large levels, respectively.

1161 **Figure 5**. Impacts of fishing, over a range of minimum-size limits (as a percentage of L_{max})

1162 and annual fishing efforts, on the density of aged 1 year and older, on the biomass of fish

1163 aged 1 year and older, and on the spawning-potential ratio *SPR* (rows), across the five

1164 considered fish life-history types (columns). The shown levels correspond to fished

1165 conditions relative to unexploited conditions. Continuous contours represent relative levels

1166 smaller than 1 (greyscale bar). Dotted contours represent values relative levels greater than 1.

1167 All panels are based on considering consumptive anglers fishing with constant effort and

1168 harvesting all harvestable fish caught.

1169 **Figure 6**. Impacts of fishing, over a range of minimum-size limits (as a percentage of L_{max}),

1170 and license densities, on the spawning-potential ratio (grey contour areas) and on the annual

1171 fishing efforts (h·ha^{-1}; grey contour curves), across the five considered fish life-history types

1172 (columns) and four different populations of angler types (rows); both homogeneous (rows 1-

1173 3) and mixed angler populations (row 4; with a composition of 40%:30%:30% generic,

1174 consumptive, and trophy anglers, respectively). Grey diamonds indicate optimal regulations.

1175 All panels are based on considering anglers responding dynamically to the quality of their

1176 fishing experience.

1177 **Figure 7**. Predicted optimal regulations, and biological and social conditions under these

1178 regulations, for the five considered fish life-history types. (a) Optimal minimum-size limit (as

1179 a percentage of L_{max}), (b) optimal license density, (c) spawning-potential ratio SPR, (d) total

1180 utility, and (e) annual fishing effort. Grey symbols correspond to homogeneous angler

1181 populations and black symbols to mixed angler populations (with percentages as shown for

1182 generic, consumptive, and trophy anglers, respectively). In (c), a SPR below the dashed line

1183 indicates a risk of recruitment overfishing ($SPR < 0.35$) and a SPR below the dotted line

1184 indicates critical overfishing ($SPR < 0.20$).

1185 **Figure 8**. Relative participation, under optimal regulations, of the three considered angler

1186 types– (a) generic, (b) consumptive, and (c) trophy anglers – in four mixed angler populations

1187 (indicated by differently shaped symbols) targeting one of the five considered fish life-history

1188 types. Here, relative participation is defined (Table A1, equation 7c) as the ratio between the

1189 proportion of the fishing effort attributed to an angler type, and the corresponding proportion

1190 of that angler type in the mixed angler population.
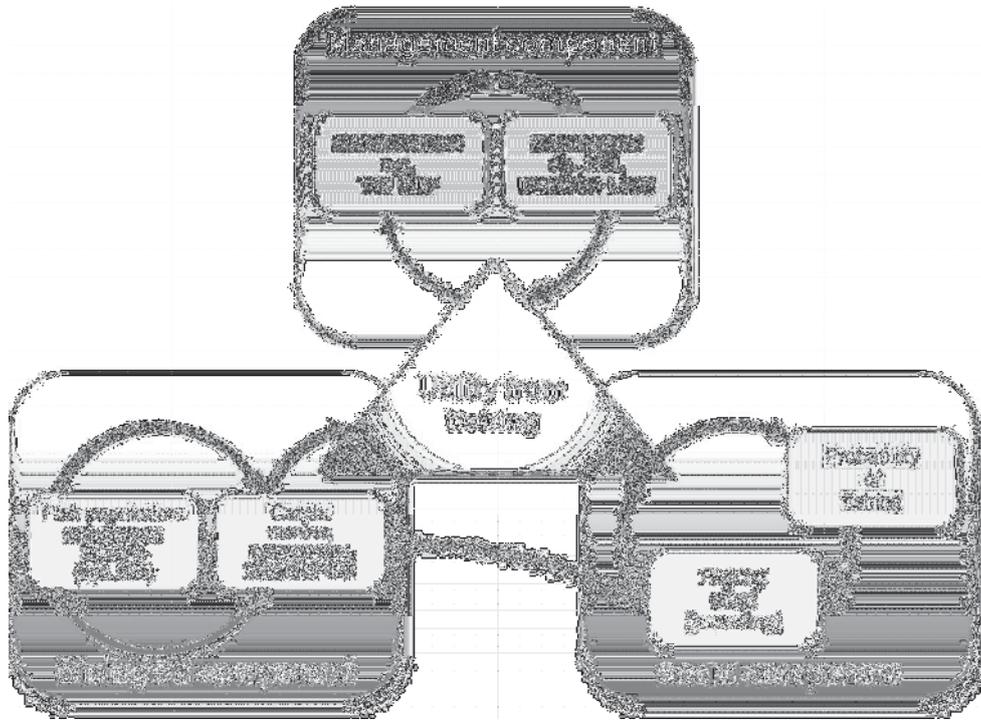
Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6

Figure 7

Figure 8

Appendix A

Table A1. Bioeconomic model equations. Variables are listed in Table A2. Parameter values,

and their sources for the fish life-history types studied here are listed in Table S1. Equations

for part-worth utility (PWU) functions are given in Table S2. Parameters describing angler

types and PWU functions are specified in Table S3.

	Equation	Description
	Individual-angler utility	
1	$$U_{fj} = U_{0j} + U_{cj} + U_{sj} + U_{xj} + U_{aj} + U_{rj} + U_{oj}$$	Conditional indirect utility gained by an angler of type j from choosing to fish (where U_{0j} is the basic utility gained from fishing, U_{cj} is the PWU of daily catch, U_{sj} is the PWU of average size of fish caught annually, U_{xj} is the PWU of maximum size of fish caught annually, U_{aj} is the PWU of angler crowding, U_{rj} is the PWU of minimum-size limit, and U_{oj} is the PWU of annual license cost).
	Angler-effort dynamics	
2a	$$p_{fj} = \exp(\hat{U}_{fj}) / [\exp(U_n) + \exp(\hat{U}_{fj})]$$	Probability an angler of type j chooses to fish, over the alternative to not fish (where $\hat{U}_{fj}$ applies to the previous year and U_n is the utility gained from not fishing)
2b	$$p_{Fj} = (1-\varphi)p_{fj} + \varphi \hat{p}_{Fj}$$	Realized probability an angler of type j chooses to fish (where $\hat{p}_{Fj}$ applies to the previous year)

2c	$D_j = p_{Fj} D_{max}$	Number of days an angler of type j chooses to fish during a year
2d	$A_{Lj} = \rho_j A_L$	Density of licensed anglers of type j
2e	$E_j = D_j A_{Lj} \Psi$	Total annual realized fishing effort density by anglers of type j
2f	$e_{jt} = \begin{cases} E_j / S_F & \text{if } t \le S_F \\ 0 & \text{if } t > S_F \end{cases}$	Instantaneous fishing effort density at time t by anglers of type j
	Age-structured fish population	
3a	$N_{total} = \sum\limits_{a=0}^{a_{max}} N_a$	Total fish population density
3b	$B_{total} = \sum\limits_{a=0}^{a_{max}} N_a W_a$	Total fish biomass density
	Growth	
4a	$h = h_{max} / [1 + B_{total} / B_{1/2}]$	Maximum annual growth of a fish dependent on the total fish biomass density at the beginning of the year
4b	$p_a = \begin{cases} 1 - \dfrac{G}{3+G}(1 + L_{a0}/h) & \text{if } a \ge a_m - 1 \\ 1 & \text{if } a < a_m - 1 \end{cases}$	Proportion of the growing season during which a fish of age a allocates energy to growth
4c	$g_{at} = \begin{cases} h / S_G & \text{if } t \le p_a S_G \\ 0 & \text{if } t > p_a S_G \end{cases}$	Instantaneous growth rate in length of a fish of age a at time t
4d	$L_{at} = L_{a0} + g_{at} t$	Length of a fish of age a at time t
4e	$W_{at} = w L_{at}^l$	Mass of a fish of age a at time t
	Reproduction	
5a	$R_a = \begin{cases} \delta W_{at_R} GSI / W_e & \text{if } a \ge a_m \\ 0 & \text{if } a < a_m \end{cases}$	Annual fecundity of a female of age a given their

		mass at time t_R
5b	$b = \Phi \sum_{a=a_m}^{a_{max}} R_a N_a$	Annual population fecundity density (pulsed at the beginning of the year)
5c	Beverton-Holt: $s_0 = \alpha_{BH} / (1 + \beta_{BH} b)$ Ricker: $s_0 = \alpha_R \exp(-\beta_R b)$	Survival probability from spawning to post-hatch of fish of age 0 (applied at the beginning of the year)
5d	$N_0 = s_0 b$	Density of fish of age 0 at the beginning of the year
	Mortality	
6a	$v_{ajt} = \dfrac{1}{1 + \exp(-y(L_{at} - L_{50j}))}$	Proportion of fish of age a that are vulnerable to capture by anglers of type j at time t
6b	$L_{50} = z_j L_{max} + L_{shift}$	Size at 50% vulnerability to capture
6c	$c_{ajt} = q_j e_{jt} v_{ajt}$	Instantaneous per capita catch rate of fish of age a by anglers of type j at time t
6d	$H_{ajt} = \begin{cases} 1 & \text{if } L_{at} \geq MSL \\ f_{nj} & \text{if } L_{at} < MSL \end{cases}$	Proportion of fish of age a that are harvestable by anglers of type j at time t
6e	$C_{jt} = \sum_{a=0}^{a_{max}} c_{ajt} N_a H_{ajt}$	Instantaneous catch rate of fish that are harvestable by anglers of type j at time t
6f	$C_{Hjt} = \min(C_{jt}, c_{max\,j} e_{jt} / \Psi)$	Instantaneous harvest rate by anglers of type j at time t
6g	$f_{Hjt} = \dfrac{C_{Hjt}}{C_{jt}} + f_{hj} \dfrac{C_{jt} - C_{Hjt}}{C_{jt}}$	Proportion of harvestable fish killed by anglers of type j at time t
6h	$m_{fajt} = f_{Hjt} c_{ajt} H_{ajt} + f_{hj} c_{ajt}(1 - H_{ajt})$	Instantaneous per capita fishing mortality rate of fish of age a from anglers of type j at time t

6i	$d_{at} = m_{\mathrm{n}a} + \sum_{j} m_{\mathrm{f}ajt}$	Instantaneous per capita mortality rate of fish of age a at time t
6j	$\dfrac{dN_a}{dt} = -d_{at} N_a$	Instantaneous rate of change in the density of fish of age a at time t
	Response variables	
7a	$SPR = b_{\mathrm{F}} / b_{\mathrm{U}}$	Spawning-potential ratio (= annual population fecundity density b_{F} under fishing relative to annual population fecundity density b_{U} under unfished conditions)
7b	$U_{\mathrm{TU}} = \sum_{j} U_{\mathrm{f}j} D_j A_{\mathrm{L}j}$	Annual total utility
7c	$P_{\mathrm{R}j} = \dfrac{E_j / \sum_{i} E_i}{\rho_j}$	Relative participation of anglers of type j in a mixed angler population

6   **Table A2**. Model variables. Bioeconomic model equations are listed in Table A1 and parameters for life-history types are listed in Table S1.

7   Angler types and their dynamics are specified in Tables S2 and S3.

Symbol	Description (unit, where applicable)	Value or range
Index variables		
t	Time within the year (y)	0.0 - 1.0
a	Age class (y)	$0 - a_{max}$
j	Angler type	Generic; consumptive; trophy
Angling regulations		
MSL	Minimum-size limit (cm)	$0 - L_{max}$
A_{L}	License density (= number of licenses issued for a given area) (ha^{-1})	0 - 1
Age-structured fish population		
N_a	Density of fish of age a (ha^{-1})	$0 - \infty$
L_{a0}	Length of fish of age a at the beginning of a year (cm)	$0 - L_{max}$

8

Supplementary material

Parameters for life-history types

Table S1. Parameters, with their units, values, and sources, for the five modelled fish life-history types (LHTs). Sources are indicated by numbers and listed below. Where a single parameter value is given, it is used for all five LHTs. Bioeconomic model equations are listed in Table A1. Angler types and their dynamics are specified in Tables S2 and S3.

Symbol	Description (unit, where applicable)	Equation	Value or range for fish life-history types (source, where applicable)				
			Perch	Brown trout	Pikeperch	Pike	Bull trout
Growth							
a_{max}	Maximum age of a fish (y)		20 (7)	15 (3)	16 (4)	15 (2)	20 (12)
L_{max}	Maximum size a fish can attain at maximum age ($a = a_{max}$) in an environment free of intraspecific competition ($B_{total} = 0$) (cm)	6b	38.5	51.5	103	117	98
h_{max}	Maximum annual growth increment (cm)	4a	6.3 (†)	9.4 (†)	14.2 (†)	24.0 (†)	10.6 (†)
$B_{l/2}$	Total fish biomass density at which the growth increment is halved (kg·ha^{-1})	4a	344.8 (†)	256.4 (†)	144.9 (†)	100.0 (†)	26.3 (†)

Symbol	Description	Eq.					
G	Annual reproductive investment	4b	0.47 (†)	0.51 (†)	0.36 (†)	0.58 (†)	0.29 (†)
a_{m}	Age at first spawning (y)	4b, 5a	3 (7)	3 (18) (*)	4 (16)	2 (13)	7 (11) (*)
L_0	Length of fish at hatch (cm)	4b	0.6 (24)	1.5 (14)	0.5 (21)	0.8 (5)	1.5 (6)
S_{G}	Annual duration of the growing season (y)	4c			1.0		
w	Scaling constant for length-mass relationship (g·cm^{-l})	4e	0.0104 (1)	0.0107 (4)	0.0058 (4)	0.0048 (23)	0.0085 (11)
l	Allometric exponent for length-mass relationship	4e	3.14 (1)	3.003 (4)	3.148 (4)	3.059 (23)	3.059 (11)

Reproduction

Symbol	Description	Eq.					
t_R	Relative time in the year when spawning occurs (spring vs. fall)	5a	0.00 = Spring (7)	-0.17 = Fall (14)	0.00 = Spring (16)	0.00 = Spring (12)	-0.17 = Fall (12)
GSI	Gonadosomatic index (= gonadic mass/somatic mass)	5a	0.21 (19)	0.18 (18)	0.10 (21)	0.17 (8)	0.15 (9)
W_{e}	Average egg mass (g)	5a	0.0024 (19)	0.0700 (3)	0.0005 (20)	0.0050 (8)	0.0600 (9)
δ	Proportion of eggs that hatch	5a			0.75 (13, 21)		
Φ	Proportion of female fish in the spawning	5b			0.5		

population

			Ricker	Ricker	Ricker	Ricker	Beverton-Holt
α	Maximum proportion of offspring surviving from spawning to post-hatch (Ricker, R; Beverton-Holt, BH)	5c	$\alpha_R = 3.25 \cdot 10^{-3}$ (‡)	$\alpha_R = 3.26 \cdot 10^{-2}$ (‡)	$\alpha_R = 2.32 \cdot 10^{-5}$ (‡)	$\alpha_R = 1.71 \cdot 10^{-4}$ (‡)	$\alpha_{BH} = 3.32 \cdot 10^{-3}$ (‡)
			Ricker	Ricker	Ricker	Ricker	Beverton-Holt
β	Inverse population density at which offspring survival is divided by $e = 2.71$ (Ricker, R) or by 2 (Beverton-Holt, BH) (ha)	5c	$\beta_R = 1.99 \cdot 10^{-6}$ (‡)	$\beta_R = 7.46 \cdot 10^{-5}$ (‡)	$\beta_R = 3.47 \cdot 10^{-7}$ (‡)	$\beta_R = 6.87 \cdot 10^{-6}$ (‡)	$\beta_{BH} = 1.34 \cdot 10^{-3}$ (‡)

Mortality

m_{na}	Instantaneous natural mortality rate of fish of age a (y^{-1})	6i	0.00 if $a = 0$ 0.41 if $a > 0$ (15)	0.00 if $a = 0$ 0.56 if $a > 0$ (3)	0.00 if $a = 0$ 0.26 if $a > 0$ (17)	0.00 if $a = 0$ 0.46 if $a > 0$ (22)	0.00 if $a = 0$ 0.20 if $a > 0$ (10)
a_{max}	Maximum age of fish (y)		20 (7)	15 (3)	16 (4)	15 (2)	20 (12)

Sources: (1) Buijse et al. (1992), (2) Craig and Kipling (1983), (3) Crisp (1994), (4) Froese and Pauly (2010), (5) Frost and Kipling (1967), (6) Gould (1987), (7) Heibo et al.(2005), (8) Hubenova et al. (2007), (9) unpublished data (F. Johnston), (10) Johnston et al. (2007), (11) Johnston and Post (2009), (12) Joynt and Sullivan (2003), (13) Kipling and Frost (1970), (14) Klemetsen et al. (2003), (15) Le Cren et al. (1977), (16) Lehtonen et al. (1996), (17) Lind (1977), (18) Lobón-Cerviá et al. (1986), (19) Øxnevad et al. (2002),

(20) Rónyai (2007) (21) Schlumberger and Proteau (1996), (22) Treasurer et al. (1992), (23) Willis (1989), (24) Ylikarjula et al. (2002).

Species names: European perch (*Perca fluviatilis*, Percidae), brown trout (*Salmo trutta*, Salmonidae), pikeperch (*Sander lucioperca*, Percidae), northern pike (*Esox lucius*, Esocidae), and bull trout (*Salvelinus confluentus*, Salmonidae).

* This specifies a first-time-spawner's age when the eggs hatch; however these fish matured and spawned during the previous fall.

† For sources and details, see section "Parameterization of density-dependent somatic growth" below.

‡ For sources and details, see section "Parameterization of stock-recruitment relationships" below.

Equations for part-worth-utility functions

Table S2. Equations for angler part-worth-utility (PWU) functions, standardized for fish life-history type. Parameters are listed in Table S3, and baseline values are listed in Table S4.

	Equation	Description
	Standardized fishery attributes	
S1a	$c_{\mathrm{D}} = C_{\mathrm{Do}} / C_{\mathrm{De}} \Psi - 1$ (*)	Standardized relative daily catch
S1b	$\bar{l} = \bar{L}_{\mathrm{o}} / \bar{L}_{\mathrm{e}} - 1$ (*)	Standardized relative average size of fish caught annually
S1c	$l_{\mathrm{x}} = L_{\mathrm{xo}} / L_{\mathrm{xe}} - 1$ (*)	Standardized relative maximum size of fish caught annually
S1d	$A = \sum_{j} D_{j} A_{\mathrm{L}j} \phi / (365\, S_{\mathrm{F}})$	Observed average number of anglers fishing in a day (Table A1, equation 2c)
S1e	$r = MSL / L_{\max}$	Standardized minimum-size limit MSL
S1f	$o = O_{\mathrm{o}} - O_{\mathrm{e}}$ (*)	Standardized relative annual license cost
	Part-worth-utility (PWU) functions	
S2a	$U_{\mathrm{c}j} = u_{1j} c_{\mathrm{D}} + u_{2j} c_{\mathrm{D}}^{2}$	PWU of daily catch
S2b	$U_{\mathrm{s}j} = u_{3j} \bar{l} + u_{4j}$	PWU of average size of fish caught annually
S2c	$U_{\mathrm{x}j} = \begin{cases} u_{5j} l_{\mathrm{x}}^{2} & \text{if } l_{\mathrm{x}} \geq 0 \\ -u_{5j} l_{\mathrm{x}}^{2} & \text{if } l_{\mathrm{x}} < 0 \end{cases}$	PWU of maximum size of fish caught annually
S2d	$U_{\mathrm{a}j} = u_{6j} A + u_{7j} A^{2} + u_{8j}$	PWU of angler crowding
S2e	$U_{\mathrm{r}j} = u_{9j} r + u_{10j} r^{2} + u_{11j}$	PWU of minimum-size limit MSL
S2f	$U_{\mathrm{o}j} = u_{12j} o$	PWU of annual license cost

4   * O_o is the observed annual fishing license cost, C_{Do} is the observed average daily catch, $\bar{L}_o$

5   is the observed average size of fish caught annually, and L_{xo} is the observed maximum size

6   of fish caught annually (defined as the 95th percentile of the size distribution of fish caught

7   annually).

8 Parameters for angler types

9 **Table S3**. Parameters, with their units and values, for the three modelled angler types

10 (generic, consumptive, and trophy anglers). Where a single parameter value is given, it is

11 used for all three angler types. The referenced equations are listed in Table A1 and Table S2.

Symbol	Description (unit, where applicable)	Equation	Value (generic; consumptive; trophy)
	Fishing practices		
y (*)	Steepness of size-dependent vulnerability curve	6a	0.36
z_j (*)	Size as a proportion of L_{max} used when calculating the size L_{50} at which 50% of the fish are vulnerable to capture	6b	0.18; 0.18; 0.28
L_{shift}	Constant used to when calculating the size L_{50} (cm)	6b	10
q_j	Catchability reflecting skill level (ha h^{-1})	6c	0.011; 0.020; 0.025
$c_{max\,j}$	Desired average number of fish an angler will harvest daily	6f	2; ∞; 0.5
f_{hj}	Proportion of fish dying from hooking mortality	6g, 6h	0.05
f_{nj}	Proportion of fish below the minimum-size limit *MSL* harvested	6d	0.05

	illegally		
	Angler population		
ρ_j	Proportion of angler population composed of anglers of type j	2d, 7c	non-mixed: 1.0 for one j; 0.0 for the others mixed-0: 0.4; 0.3; 0.3 mixed-1: 0.70; 0.15; 0.15 mixed-2: 0.15; 0.70; 0.15 mixed-3: 0.15; 0.15; 0.70
	Angler-effort dynamics		
U_n	Conditional indirect utility gained by an angler from choosing not to fish	2a	0
φ	Persistence of fishing behaviour (= relative influence of last year's realized fishing probability on the current year's realized fishing probability)	2b	0.5
D_{max}	Maximum number of days that an angler would fish per year irrespective of fishing quality	2c	40
Ψ	Average time an angler will fish in a day (h)	2e, 6f, S1a	4
ϕ	Lake area (ha)	S1d	100
S_F	Annual duration of fishing season (y)	2f, S1d	9/12

	Part-worth-utility functions		
U_{0j}	Basic utility gained by an angler of type j from choosing to fish	1	-0.405; 0.000; 0.405
u_{1j}	PWU linear coefficient	S2a	0.968; 1.318; 0.825
u_{2j}	PWU quadratic coefficient	S2a	-0.121; -0.220; -0.206
u_{3j}	PWU linear coefficient	S2b	2.476; 3.389; 4.394
u_{4j}	PWU constant coefficient	S2b	0.000; 0.000; -0.220 (†)
u_{5j}	PWU quadratic coefficient	S2c	9.414; 6.878; 12.207
u_{6j}	PWU linear coefficient	S2d	0.244; 0.149; 0.136
u_{7j}	PWU quadratic coefficient	S2d	-0.031; -0.025; -0.034
u_{8j}	PWU constant coefficient	S2d	0.610; 0.396; 0.712
u_{9j}	PWU linear coefficient	S2e	2.321; 3.766; 2.534
u_{10j}	PWU quadratic coefficient	S2e	-3.869; -9.414; -2.534
u_{11j}	PWU constant coefficient	S2e	0.271; 0.471; -0.228
u_{12j}	PWU linear coefficient	S2f	-0.015; -0.011; -0.008

12   * Predicted vulnerability values are in fairly good agreement with empirical information for

13   similar species, e.g.:, yellow perch at 27 cm is 100% vulnerable (Wilberg et al., 2005),

14   compared with 95% for European perch in our model; rainbow trout at 30-35 cm is 100%

15   vulnerable (van Poorten and Post, 2005), compared with 96%-99% for brown trout in our

16   model; pike at 55 cm is 100% vulnerable (Arlinghaus et al., 2009), compared with 100% for

17   pike in our model; bull trout at 35 cm is 100% vulnerable (Paul et al., 2003), compared with

18   90% for bull trout in our model.

19 † The intercept u_{4j}, from the PWU function of average size of fish caught annually, for

20 trophy anglers represents a 5% increase of the average-size baseline value relative to that of

21 generic and consumptive anglers. This reflects the fact that more specialized anglers have

22 been found to use a larger minimum length when defining quality-sized fish (Hahn, 1991).

Table S4. LHT-dependent baseline values for fishery attributes used in part-worth-utility functions. These baseline values specify the fishery-attribute level at which the corresponding part-worth utility gained by anglers equals zero. Where baseline values do not differ among LHT, only one value, or set of values, is given. Where baseline values differ among angler types, three values are given for generic, consumptive, and trophy anglers, respectively. Where applicable, values reported in the literature for similar or closely related species are provided in square brackets for comparative purposes. Sources are indicated by numbers and listed below.

Fishery attribute (units) (relevant table and equation)	Symbol	Life-history type [literature values (source)]				
		Perch	Brown trout	Pikeperch	Pike	Bull trout
Catch rate (h⁻¹) (Table S2, equation 8a)	C_{De}	1.90 [yellow perch 0.05-5.0 (4), European perch 1.2-4.3 (2)]	0.95 [Spanish rivers 1.3-6.9 (1), UK upland lakes 0.46-1.44 (7)]	0.41 [0.11-0.69 (2)]	0.12 [0.10-0.38 (6)]	0.06 [0.11-0.34 (5)]
Average size (cm) (Table S2, equation 8b)	$\overline{L}_e$	20 [yellow perch 21 (3)]	26 [anadromous 41 (3), UK lakes 25-28 (7)]	46 [walleye 42 (3)]	52 [58 (3)]	44 [dolly varden 41 (3)]
Maximum size (cm) (Table S2, equation 8c)	L_{xe}	26 [yellow perch 29 (3)]	33 [anadromous 54 (3)]	62 [walleye 59 (3)]	69 [80 (3)]	58 [dolly varden 56 (3)]

Crowding (d^{-1})		10; 8; 7
Minimum-size limit (as a proportion of L_{max})		0.7; 0.5; 0.9
Cost (€)	O_e	75
(Table S2, equation 8f)		

28   Sources: (1) Almodóvar and Nicola (1998), (2) unpublished data (M. Dorow and R. Arlinghaus), (3) Gabelhouse (1984), (4) Isermann et al.

29   (2005), (5) Paul et al. (2003), (6) Pierce et al. (1995), (7) Swales and Fish (1986).

30   Species names: Yellow perch (*Perca flavescens*, Percidae), walleye (*Sander vitreus*, Percidae), dolly varden (*Salvelinus malma*, Salmonidae).

Parameterization of density-dependent somatic growth

To parameterize the density-dependent growth relationships (Table A1, equation 4a), empirical length-at-age data and biomass-density data from various studies were used to estimate the maximum annual growth increment h_{max}, the total fish biomass density $B_{1/2}$ at which the growth increment is halved, and the annual reproductive investment G, by minimizing the corresponding sums of squares (using the Solver® function of Microsoft® Office Excel 2003).

The empirical studies from which this data was extracted are as follows: pike (Kipling and Frost, 1970, Kipling, 1983a, Treasurer et al., 1992, Pierce and Tomcko, 2003, Pierce et al., 2003, Pierce and Tomcko, 2005); pikeperch (Buijse et al., 1992) unpublished data, H. Winkler); perch (Le Cren, 1958, Craig et al., 1979, Treasurer et al., 1992, Treasurer, 1993); brown trout (Jenkins et al., 1999, Nicola and Almodóvar, 2002, Almodóvar and Nicola, 2004); bull trout (Johnston and Post, 2009) unpublished data, F. Johnston).

The estimated maximum annual growth increments h_{max} are in general agreement with literature values: 24.0 cm for pike in our model, compared with 27.1 cm (Arlinghaus et al., 2009); 10 cm for pikeperch in our model, compared with 9-12 cm (Biró, 1985); 5.5 cm for perch in our model, compared with 5-15 cm (Heibo et al., 2005); 8.4 cm for brown trout in our model, compared with 8-11 cm (Jenkins et al., 1999); 7.7 cm for bull trout in our model, compared with 10 cm (Paul et al., 2003).

Parameterization of stock-recruitment relationships

50

51   To parameterize the Ricker (R) and Beverton-Holt (BH) stock-recruitment

52 relationships (Table A1, equation 5c), empirical length-at-age and biomass-density data from

53 various studies were used to estimate the maximum proportion of offspring surviving from

54 spawning to post-hatch (α_R or α_{BH}) and the inverse population density at which offspring

55 survival is divided by $e = 2.71$ (β_R) or 2 (β_{BH}).

56   For pike, egg density was determined using a relative fecundity relationship (Craig

57 and Kipling, 1983), adult biomass (Kipling, 1983b), and corresponding area (1480 ha, Le

58 Cren et al., 1977), with the density of pike aged 1 year back-calculated from natural mortality

59 (Kipling and Frost, 1970) and the abundance of pike aged 2 years (Le Cren et al., 1977). For

60 pikeperch, egg density was determined using the relative fecundity relationship

61 (Schlumberger and Proteau, 1996), adult biomass, and corresponding area (19700 ha,

62 unpublished data, H. Winkler), with adult biomass back-calculated from commercial catch

63 (Lehtonen et al., 1996) and exploitation rate (Gröger et al., 2007), and the density of

64 pikeperch aged 1 year back-calculated from natural mortality information (Lind, 1977) and

65 the abundance of pikeperch aged 2 years (Gröger et al., 2007). For perch, egg density was

66 determined using a relative fecundity relationship (Treasurer, 1981), adult biomass (Craig et

67 al., 1979), and corresponding area (1480 ha, Le Cren et al., 1977), with the density of perch

68 aged 1 year back-calculated from natural mortality information (Le Cren et al., 1977) and the

69 abundance of perch aged 2 years (Le Cren et al., 1977). For brown trout, a stock-recruitment

70 relationship for a migratory brown-trout population from England (Elliott, 1985) was scaled

71 so that egg density and the density of brown trout aged 1 year (May/June) in the spawning

72 stream result in a population density in line with literature values: the chosen target fish

73 density of 300 ha^{-1} is roughly based on the density of 229 ha^{-1} observed for a British lake

74 (Swales, 1986), although this is low compared with the density of 560-4900 ha^{-1} observed for

75 more productive rivers in Spain (Nicola and Almodóvar, 2002). For bull trout, the stock-

76 recruitment relationship reported by Post et al. (2003) was scaled to account for the

77 corresponding lake area (646 ha, (Johnston et al., 2007).

78   The population densities predicted using these estimates under unexploited conditions

79 generally fall within the ranges reported in the literature (although pikeperch are likely more

80 abundant in our model than in average natural settings, whereas the densities of perch and bull

81 trout in our model are on the low side of the reported empirical ranges): for perch, 779 ha^{-1} in

82 our model, compared with 675-4189 ha^{-1} (Craig et al., 1979); for brown trout, 300 ha^{-1} in our

83 model, compared with 229 ha^{-1} in a British lake (Swales, 1986) and 560-4900 ha^{-1} in more

84 productive rivers in Spain (Nicola and Almodóvar, 2002); for pikeperch aged 3 years and

85 older, 56 ha^{-1} in our model, compared with 26-42 ha^{-1} (Lehtonen, 1979); for pike, 23 ha^{-1} in

86 our model, compared with 11.0-55.1 ha^{-1} (Pierce et al., 1995); for bull trout, 12 ha^{-1} in our

87 model, and for adult bull trout, 4.4 ha^{-1} in our model, compared with, respectively, 12-38 ha^{-1}

88 (Parker et al., 2007) and less than 2.7 ha^{-1} (Johnston et al., 2011).

Sensitivity analyses

Table S5. Sensitivities of predicted optimal minimum-size limits to changes (±10%) in life-history parameters of different fish life-history types exploited by homogeneous populations of generic, consumptive, or trophy anglers. The table shows the relative changes in optimal minimum-size limits compared with those predicted by the original model. Changes greater than 10% (highlighted by a grey background) indicate a particular sensitivity to changes in the considered life-history parameter.

Life-history type	Angler type	Parameter change	Life-history parameter									
			h_{max}	$B_{1/2}$	G	W_e	GSI	α	β	m_{na}	a_m	a_{max}
Perch	Generic	+10%	2.6%	0.0%	0.0%	0.0%	0.0%	0.0%	2.6%	0.0%	0.0%	0.0%
		-10%	0.0%	2.6%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
	Consumptive	+10%	0.0%	-2.6%	0.0%	0.0%	0.0%	-2.6%	-2.6%	0.0%	0.0%	0.0%
		-10%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	-2.6%	-2.6%	-2.6%	0.0%
	Trophy	+10%	5.2%	0.0%	5.2%	0.0%	0.0%	0.0%	0.0%	2.6%	5.2%	0.0%
		-10%	2.6%	0.0%	-5.2%	0.0%	0.0%	0.0%	2.6%	5.2%	2.6%	0.0%
Brown trout	Generic	+10%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	-1.9%	-1.9%	0.0%
		-10%	-3.9%	0.0%	0.0%	0.0%	0.0%	-1.9%	0.0%	-3.9%	-1.9%	0.0%
	Consumptive	+10%	-3.9%	0.0%	-1.9%	0.0%	0.0%	0.0%	0.0%	0.0%	-5.8%	0.0%
		-10%	-3.9%	0.0%	1.9%	0.0%	0.0%	0.0%	0.0%	0.0%	-3.9%	0.0%
	Trophy	+10%	7.8%	0.0%	3.9%	1.9%	-1.9%	3.9%	-1.9%	5.8%	11.7%	0.0%
		-10%	7.8%	-1.9%	-1.9%	0.0%	0.0%	-1.9%	0.0%	3.9%	1.9%	1.9%
Pikeperch	Generic	+10%	0.0%	-1.0%	2.9%	0.0%	0.0%	-1.0%	0.0%	0.0%	2.9%	0.0%
		-10%	-1.0%	1.0%	1.0%	0.0%	0.0%	0.0%	-1.0%	-1.0%	-1.0%	0.0%
	Consumptive	+10%	-1.0%	-1.0%	-1.9%	0.0%	-1.0%	-1.0%	0.0%	0.0%	1.0%	-1.0%
		-10%	-1.0%	0.0%	-2.9%	-1.0%	-1.0%	0.0%	-1.0%	-1.0%	-1.9%	-1.0%
	Trophy	+10%	5.8%	-1.0%	-2.9%	0.0%	0.0%	-1.0%	1.9%	2.9%	0.0%	4.9%
		-10%	-1.9%	2.9%	2.9%	0.0%	0.0%	1.9%	-1.0%	1.9%	2.9%	0.0%
Pike	Generic	+10%	6.8%	0.0%	7.7%	0.0%	0.0%	0.0%	0.9%	0.9%	11.1%	0.0%
		-10%	-4.3%	0.9%	2.6%	10.3%	0.0%	0.9%	0.0%	9.4%	10.3%	0.0%
	Consumptive	+10%	4.3%	0.0%	-1.7%	0.0%	0.0%	0.0%	-6.8%	-6.8%	3.4%	0.0%
		-10%	1.7%	0.9%	1.7%	0.0%	0.0%	0.0%	0.0%	0.9%	-1.7%	0.0%
	Trophy	+10%	-4.3%	-0.9%	-5.1%	0.0%	0.0%	-0.9%	0.9%	-9.4%	-9.4%	0.0%
		-10%	-10.3%	0.9%	6.0%	0.0%	0.0%	0.9%	-0.9%	-5.1%	-1.7%	0.0%

Bull trout	Generic	+10%	4.1%	-1.0%	-3.1%	0.0%	0.0%	-1.0%	0.0%	2.1%	-45.4%	0.0%
		-10%	-5.2%	1.0%	2.1%	0.0%	0.0%	1.0%	0.0%	-1.0%	-1.0%	0.0%
	Consumptive	+10%	-44.3%	1.0%	1.0%	1.0%	0.0%	0.0%	0.0%	-24.7%	-11.3%	0.0%
		-10%	-10.3%	0.0%	0.0%	-1.0%	-1.0%	-1.0%	-1.0%	20.6%	1.0%	0.0%
	Trophy	+10%	6.2%	-2.1%	-5.2%	1.0%	1.0%	-1.0%	1.0%	-2.1%	-50.5%	0.0%
		-10%	-4.1%	1.0%	4.1%	-1.0%	1.0%	1.0%	1.0%	-4.1%	-1.0%	0.0%

Table S6. Sensitivities of predicted optimal license densities to changes (±10%) in life-history parameters of different fish life-history types exploited by homogeneous populations of generic, consumptive, and trophy anglers. The table shows the relative changes in optimal license densities compared with those predicted by the original model. Changes greater than 10% (highlighted by a grey background) indicate a particular sensitivity to changes in the considered life-history parameter.

Life-history prototype	Angler type	Parameter change	h_{max}	$B_{1/2}$	G	W_e	GSI	α	β	m_{na}	a_m	a_{max}
Perch	Generic	+10%	-3.4%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	-1.7%	1.7%	0.0%
		-10%	-3.4%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	-1.7%	-1.7%	0.0%
	Consumptive	+10%	18.4%	0.0%	-2.6%	0.0%	0.0%	2.6%	-2.6%	-10.5%	-13.2%	0.0%
		-10%	10.5%	-2.6%	2.6%	-2.6%	0.0%	-2.6%	0.0%	2.6%	5.3%	0.0%
	Trophy	+10%	11.4%	4.5%	4.5%	-4.5%	4.5%	4.5%	-4.5%	6.8%	9.1%	0.0%
		-10%	2.3%	-2.3%	-2.3%	4.5%	-2.3%	-2.3%	4.5%	6.8%	4.5%	0.0%
Brown trout	Generic	+10%	3.7%	0.0%	-1.9%	0.0%	-1.9%	1.9%	-1.9%	-3.7%	-3.7%	0.0%
		-10%	-11.1%	0.0%	0.0%	-1.9%	0.0%	-1.9%	0.0%	-7.4%	-1.9%	0.0%
	Consumptive	+10%	-2.1%	8.3%	6.3%	2.1%	0.0%	8.3%	4.2%	0.0%	-52.1%	0.0%
		-10%	-4.2%	0.0%	10.4%	0.0%	0.0%	4.2%	4.2%	8.3%	-4.2%	0.0%
	Trophy	+10%	16.7%	0.0%	4.8%	-4.8%	0.0%	-2.4%	-2.4%	9.5%	16.7%	0.0%
		-10%	4.8%	-2.4%	-2.4%	-4.8%	-7.1%	0.0%	0.0%	14.3%	7.1%	-2.4%
Pikeperch	Generic	+10%	-3.7%	0.0%	-3.7%	-1.9%	3.7%	-1.9%	-1.9%	-1.9%	1.9%	0.0%
		-10%	1.9%	5.6%	1.9%	3.7%	-1.9%	0.0%	-3.7%	-1.9%	0.0%	0.0%
	Consumptive	+10%	-2.3%	-4.7%	-9.3%	-2.3%	-14.0%	-2.3%	-9.3%	-9.3%	-11.6%	-9.3%
		-10%	-14.0%	2.3%	-2.3%	-16.3%	-7.0%	-7.0%	-4.7%	0.0%	-2.3%	-9.3%
	Trophy	+10%	-6.3%	0.0%	-8.3%	0.0%	0.0%	-2.1%	-6.3%	-8.3%	-4.2%	-16.7%
		-10%	-10.4%	-2.1%	-6.3%	0.0%	0.0%	-6.3%	0.0%	-10.4%	-12.5%	-6.3%
Pike	Generic	+10%	7.5%	3.8%	7.5%	0.0%	0.0%	5.7%	1.9%	-3.8%	7.5%	0.0%
		-10%	0.0%	0.0%	-3.8%	1.9%	0.0%	3.8%	0.0%	9.4%	7.5%	0.0%
	Consumptive	+10%	2.4%	-2.4%	-14.3%	2.4%	-7.1%	-2.4%	-21.4%	-31.0%	-9.5%	0.0%
		-10%	-9.5%	11.9%	-7.1%	-7.1%	4.8%	-19.0%	-4.8%	2.4%	-14.3%	0.0%
	Trophy	+10%	25.0%	0.0%	5.0%	0.0%	0.0%	-2.5%	-2.5%	17.5%	20.0%	0.0%
		-10%	10.0%	-2.5%	-7.5%	0.0%	0.0%	-2.5%	2.5%	15.0%	12.5%	0.0%
Bull trout	Generic	+10%	-5.4%	3.6%	1.8%	1.8%	0.0%	1.8%	0.0%	-8.9%	25.0%	1.8%
		-10%	-8.9%	-1.8%	-14.3%	0.0%	1.8%	0.0%	1.8%	-12.5%	0.0%	0.0%
	Consumptive	+10%	690.9%	9.1%	9.1%	9.1%	0.0%	0.0%	0.0%	-18.2%	700.0%	0.0%

	-10%	-18.2%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	172.7%	9.1%	0.0%
Trophy	+10%	-4.5%	0.0%	0.0%	4.5%	2.3%	4.5%	2.3%	9.1%	77.3%	0.0%
	-10%	-9.1%	-2.3%	0.0%	-4.5%	6.8%	0.0%	6.8%	4.5%	2.3%	0.0%

Table S7. Predicted spawning-potential ratios (*SPR* s) under optimal minimum-size limits and license densities resulting from changes (±10%)

in life-history parameters of different fish life-history types exploited by homogeneous populations of generic, consumptive, and trophy anglers.

SPR values below 0.35 (highlighted by a grey background) indicate a risk of recruitment overfishing.

Life-history type	Angler type	Parameter change	Life-history parameter									
			h_{max}	$B_{1/2}$	G	W_e	GSI	α	β	m_{na}	a_m	a_{max}
Perch	Generic	+10%	0.87	0.87	0.88	0.87	0.87	0.88	0.86	0.88	0.85	0.87
		-10%	0.88	0.87	0.86	0.87	0.87	0.86	0.88	0.87	0.88	0.87
	Consumptive	+10%	0.41	0.48	0.50	0.50	0.47	0.49	0.49	0.51	0.32	0.48
		-10%	0.50	0.48	0.47	0.47	0.50	0.47	0.48	0.47	0.57	0.48
	Trophy	+10%	0.91	0.93	0.93	0.93	0.93	0.93	0.93	0.93	0.91	0.93
		-10%	0.94	0.93	0.92	0.93	0.93	0.93	0.93	0.92	0.93	0.93
Brown trout	Generic	+10%	0.67	0.67	0.67	0.68	0.66	0.69	0.66	0.65	0.57	0.67
		-10%	0.68	0.67	0.67	0.66	0.68	0.64	0.69	0.71	0.73	0.67
	Consumptive	+10%	0.44	0.59	0.58	0.61	0.58	0.60	0.59	0.60	0.32	0.60
		-10%	0.58	0.59	0.59	0.58	0.62	0.57	0.59	0.58	0.67	0.60
	Trophy	+10%	0.83	0.86	0.85	0.86	0.85	0.86	0.85	0.83	0.75	0.85
		-10%	0.85	0.86	0.85	0.85	0.87	0.84	0.86	0.84	0.87	0.86
Pikeperch	Generic	+10%	0.62	0.65	0.73	0.67	0.63	0.66	0.65	0.65	0.66	0.64
		-10%	0.67	0.64	0.64	0.63	0.66	0.64	0.65	0.64	0.67	0.65
	Consumptive	+10%	0.47	0.52	0.53	0.54	0.52	0.53	0.54	0.54	0.48	0.52
		-10%	0.57	0.51	0.43	0.52	0.54	0.52	0.51	0.51	0.54	0.53
	Trophy	+10%	0.69	0.68	0.69	0.68	0.66	0.69	0.69	0.69	0.62	0.73
		-10%	0.71	0.68	0.68	0.66	0.68	0.67	0.67	0.71	0.75	0.69
Pike	Generic	+10%	0.69	0.65	0.76	0.68	0.64	0.67	0.66	0.68	0.75	0.66
		-10%	0.61	0.66	0.67	0.76	0.68	0.64	0.65	0.75	0.76	0.66
	Consumptive	+10%	0.54	0.49	0.49	0.49	0.46	0.50	0.39	0.41	0.47	0.47
		-10%	0.55	0.46	0.50	0.46	0.49	0.49	0.49	0.47	0.49	0.47
	Trophy	+10%	0.70	0.76	0.75	0.77	0.74	0.77	0.76	0.69	0.64	0.75
		-10%	0.71	0.76	0.77	0.74	0.77	0.75	0.75	0.72	0.73	0.76
Bull trout	Generic	+10%	0.61	0.59	0.60	0.60	0.59	0.60	0.59	0.64	0.00	0.59
		-10%	0.61	0.59	0.62	0.59	0.60	0.59	0.60	0.63	0.62	0.60
	Consumptive	+10%	0.00	0.25	0.25	0.25	0.26	0.27	0.26	0.21	0.00	0.26
		-10%	0.27	0.25	0.26	0.25	0.25	0.25	0.25	0.46	0.30	0.27
	Trophy	+10%	0.46	0.44	0.44	0.44	0.43	0.44	0.43	0.39	0.00	0.44

-10%	0.49	0.44	0.43	0.44	0.43	0.43	0.43	0.42	0.48	0.45

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