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

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

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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.

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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.

A key factor determining the dynamics of a fishery is fish life history (described by the combination of life-history traits that characterize a species), because it influences a fish population's vulnerability to overexploitation (Reynolds et al., 2001, Rose et al., 2001, Winemiller, 2005). Life-history traits (describing, e.g., growth, maturation, or fecundity) vary substantially among species (Reynolds et al., 2001), and are often phenotypically plastic (Pigliucci, 2005). Fish that exhibit different life-history strategies will thus differ in their production and in the degree to which density-dependent processes regulate the population, thus altering their ability to compensate for fishing mortality (Rose et al., 2001, Winemiller, 2005, Goodwin et al., 2006). For example, fish that mature late, attain large maximum size, and have low potential rates of population increase have been reported to be more vulnerable to overexploitation than fish with the opposite characteristics (Jennings et al., 1998). However, for freshwater fish species the relationships between risk of decline and anthropogenic factors are often not clear-cut (Duncan and Lockwood, 2001, Reynolds et al., 2005). Thus, to provide more robust predictions about the vulnerability of freshwater fish populations to overexploitation by recreational angling, a quantitative modelling approach that describes life-history characteristics of commonly targeted species is warranted.

A second key, yet often ignored, factor determining the impacts of fishing on fish populations is the structure and dynamics of fishers exploiting the fishery (Wilen et al., 2002, Johnston et al., 2010, Fulton et al., 2011). While commercial fishers are primarily motivated by maximizing yield or economic revenue (Hilborn, 2007), multiple catch-related and non-catch-related attributes of a fishery (e.g., catch rates, fish size, angler congestion, aesthetic appeal, facilities, permit costs; reviewed in Hunt, 2005) influence the fishing decisions. of recreational anglers Furthermore, angler populations are almost always composed of diverse angler types (e.g., Arlinghaus, 2004), each exhibiting specific fishing preferences and fishing practices (e.g., Aas et al., 2000, Beardmore et al., 2011). For example, some anglers prioritize fish harvest whereas others preferentially target trophy-sized fish and voluntarily release them (Hahn, 1991, Jacobson, 1996, Fisher, 1997). Thus, angling impacts likely differ with the type of anglers fishing (Johnston et al., 2010) and the life-history type of exploited fish. Predicting the long-term outcome of fish-angler interactions requires an integrated modelling approach that incorporates population dynamics of diverse fish life histories and behavioural responses of diverse angler types to changes in fishery quality (Johnston et al., 2010).

A third key factor influencing any fishery system is its management component. Fish-angler dynamics do not occur in isolation from fishing regulations. Harvest regulations commonly employed in recreational fisheries influence which fish are caught and/or harvested (in terms of, e.g., species and size), but they also influence angler behaviour (Beard et al., 2003, Fulton et al., 2011) and therefore are of crucial importance for describing angler dynamics (Johnston et al., 2010). Fish-angler dynamics will influence how effective regulations are at meeting the management objectives they are designed to achieve; objectives which often include balancing the sometimes conflicting interests of different stakeholders with the maintenance of a biologically sustainable fishery (Cochrane, 2000, Cox and Walters, 2002, Hilborn, 2007). Optimum social yield (OSY) incorporates numerous management objectives by integrating social, economic, and biological considerations into a single measure of the utility (in terms of benefits, satisfaction, and/or social welfare) a recreational fishery provides to society (Roedel, 1975, Malvestuto and Hudgins, 1996). The OSY approach is rarely used in practice (possibly because of the difficulty in measuring the underlying quantities), but has shown promise for the management of a northern-pike (*Esox lucius*, Esocidae) recreational fishery: a study modelling this species revealed that regulations maximizing social welfare also maintained a biologically sustainable fish population (Johnston et al., 2010). However, because life history influences a fish population’s response to fishing, and in turn the behaviour of the anglers exploiting it, it is unknown if this prediction holds across life histories commonly targeted by freshwater recreational anglers.

To explore the importance of jointly considering fish life history, dynamic and diverse angler behaviour, alternative management options, and the nonlinear interplay among the three fishery components (Figure 1) when managing recreational fisheries, here we use an integrated bioeconomic model. Our model is parameterized to describe five fish life-history types (LHTs) representing recreationally important freshwater fish species, in conjunction with three plausible angler behavioural types (Johnston et al., 2010). We use this model to evaluate how differences in LHT and angler type influence recreational-fishing impacts and the socially optimal management of fisheries. Specifically, we investigate (*i*) how LHT influences vulnerability to overfishing under different levels of constant and, more realistically, dynamic fishing effort by various angler types; (*ii*) how angling regulations (e.g., minimum-size limits and license densities) that maximized social welfare vary among LHTs and angler types; and finally (*iii*) how biological sustainability and social conditions under socially optimal regulations differ across LHTs and angler types. Our intention here is not to provide predictions for a particular fishery, but to gain general insights into the influence of LHT and angler diversity on the dynamics of a coupled social-ecological system, by bridging the traditional divide between fisheries science and social science (Arlinghaus et al., 2008, Fulton et al., 2011, Fenichel et al., 2012). Our framework can nevertheless be calibrated to a particular fishery, if appropriate data on the fish population and the preferences of angler types are collected using fisheries-biological and human-dimensions research methods.

Methods

Model overview

We use an integrated bioeconomic model (Table A1), developed by Johnston et al. (2010) for a northern-pike recreational fishery, that links dynamic angler behaviour with a deterministic age-structured fish population model for a single-species single-lake fishery. The model includes three components (Figures 1 and 2): (*i*) a biological component that determines the fish population dynamics of different LHTs, (*ii*) a social component that determines the angler-effort dynamics of different angler types based on angler-type-specific preference functions, and (*iii*) a management component that prescribes the angling regulations. In this study, we extend the model by Johnston et al. (2010) to describe five distinct LHTs representing northern pike, European perch (*Perca fluviatilis*, Percidae), pikeperch (*Sander lucioperca*, Percidae), brown trout (*Salmo trutta*, Salmonidae), and bull trout (*Salvelinus confluentus*, Salmonidae) (Figure 3; Table S1). These LHTs were chosen because they span diverse life-history characteristics (Wootton, 1984), and represent a broad range of LHTs commonly targeted by freshwater recreational anglers (e.g., Post et al., 2002, Almodóvar and Nicola, 2004, Isermann et al., 2007). The LHTs vary in body size and growth rate, age- and size-at-maturation, offspring size, fecundity, lifespan, natural mortality rate, and the degree to which density regulates early juvenile survival (stock-recruitment relationships) and individual growth rates (Figure 3). Thus, the LHTs examined here differ in unexploited abundance, biomass, and age and size structure (Table 1). To allow for a direct comparison of model outcomes, the same age-structured fish population model is used for all LHTs. In all scenarios we investigate, fish populations reach demographic equilibrium prior to the introduction of fishing, and the presented results reflect equilibrium conditions after fishing is introduced (i.e., we investigate long-term dynamics). A model overview is provided below (see also Figure 2); additional details are described in Johnston et al. (2010). Model equations are given in Table A1 and variables are given in Table A2, qualitative descriptions of LHTs and angler types are shown in Figures 3 and 4, and detailed parameters and part-worth-utility equations are provided in the supplementary material (Tables S1-S4).

Model components

The biological model component determines fish population dynamics, describing reproduction, growth, and survival (Figure 2, element A). Reproduction is pulsed at the beginning of the year.To account for LHT differences in spawning time (not present in Johnston et al. 2010), fecundities (total egg numbers) are determined by spawner sizes and spawner numbers either at the beginning of each year (spring spawners) or in the fall of the previous year (fall spawners) (Table A1, equation 5a; Table S1). Two important density-dependent processes, growth in body size and early offspring survival, allow for compensatory responses to exploitation (Rose et al., 2001, Lorenzen, 2008). Density-dependent offspring survival from spawning to post-hatch occurs at the beginning of each year, described by either a Beverton-Holt type (Beverton and Holt, 1957) or a Ricker-type stock-recruitment relationship (Ricker, 1954b) (Table A1, equation 5c). Growth is modelled using a biphasic growth model (Lester et al., 2004) (Table A1, equations 4a-4c), and. Growth, as well as mortality from both fishing and natural sources (for fish aged 1 year and older; Table A1, equation 6i), are modelled in continuous time. Continuous growth allows fish to become more vulnerable to capture within a year. Continuous mortality allows for recapture and repeated exposure of released fish to hooking mortality; the latter can have serious negative impacts on some recreational fish species especiallyif effort is high (Coggins et al., 2007). The number and size of fish caught are determined jointly by the abundance and structure of the fish population, fishing effort, anglers' skills (affecting catchability), and the size-dependent vulnerability to capture (Table A1, equation 6a), which varies among angler types (see below) (Table A1, equation 6c; Figure 2, element B). Fishing mortality depends on the number and size distribution of the catch, the regulated minimum-size limit and harvest practices of angler types fishing (Table A1, equation 6h; Figure 2, element C). Thus, fishing mortality is size-dependent through both capture vulnerability and minimum-size limits.

The social model component determines annual fishing effort. Random utility theory assumes that anglers will have a higher probability to fish when conditions provide them with more utility (Hunt, 2005) (Figure 2, element D). Following Johnston et al. (2010), angling effort is determined by angler-type-specific multi-attribute utility functions, based on catch-related attributes (catch rates, average and maximum size of fish caught) and non-catch-related attributes (angler crowding, minimum-size limits, and license costs) of the fishery that are known to affect anglers' utility and hence participation decisions (Hunt, 2005) (Table A1, equation 1; Figure 2, element E). In addition, angler types can differ in their fishing practices (in terms of the size of fish they target, their skill level, and their propensity to voluntarily release fish), as well as in their preferences for the considered fishery attributes (Aas et al., 2000, Hunt, 2005, Oh and Ditton, 2006). Here we describe three angler types – generic, consumptive, and trophy anglers – differing in their fishing practices and preferences (Figure 2, elements F1 to F3; see also Figure 4). Our parameterization of utility functions for these three angler types (Table S3) is based on angler specialization theory (Bryan, 1977) as described in detail in Johnston et al. (2010).

The management model component prescribes input regulations through license densities (A_Ls) and output regulations through minimum-size limits (MSLs) (Figure 2, element G). In our model, license density is the number of licenses issued to anglers for a single 100 ha lake, and ranges up to a maximum of one license per hectare. We focus on minimum-size limits, as these are commonly used in recreational fisheries to limit harvest (Radomski et al., 2001). In open-access recreational fisheries, output regulations often only reduce an individual angler's harvest, and not total harvest (Radomski et al., 2001, Cox et al., 2002, Cox and Walters, 2002), whereas input regulations more directly control angler effort and thus fishing mortality (Cox et al., 2002); therefore, license densities are also varied in our model. We do not include daily bag limits in our model for three reasons. First, we want to concentrate our analyses on comparing one input regulation and one output regulation. Second, the effectiveness of daily bag limits has been questioned, because in practice daily quotas are often not met (Cook et al., 2001) and, moreover are only successful if fishing effort, and thus total harvest, are not too high (Post and Parkinson, 2012). Third, our model includes angler-type-specific harvest preferences, which work similar to daily bag limits, by limiting some angler types' daily harvest through their propensity to voluntarily release fish (Table S3). The management component of our model is also used to determine regulations that achieve an optimal social yield (OSY). We assume such optimal regulations to be given by combinations of minimum-size limit (MSL_{opt}) and license density ($A_{\text{L,opt}}$) that maximize the total utility (an aggregation of individual utilities across anglers; Table A1, equation 7b) gained by the angler population at equilibrium (Figure 2, element H). We use total utility to measure social welfare; naturally, results may differ when other welfare measures are used (Johnston et al., 2010).

Standardizing across LHTs

To allow direct comparison among our results for different LHTs, the vulnerability of fish to capture, as well as some baseline attribute levels used for determining angler utility that depend on fish size or abundance, need to be standardized for LHT differences in maximum body size (L_{max}) and unexploited abundance (Table 1).

Vulnerability to capture

The size dependence of capture vulnerability is described by a sigmoidal function that varies among LHTs and angler types. These functions are characterized by the size L_{50} at which vulnerability reaches 50%, and by the steepness y with which vulnerability increases around L_{50} (Table A1, equation 6a). In choosing L_{50} and y, we need to account for three considerations. First, to standardize the vulnerability curve among LHTs we allow L_{50} to increase roughly proportionally with a LHT's maximum size $L_{\max}$. Second, to produce realistic size structures of catch, we need to account for a systematic bias in L_{50}: the general lack of interest in catching very small fish, presumably because they provide minimal consumptive or trophy value, reduces the relative range of sizes captured for smaller LHTs much more than it does for larger LHTs. Empirical findings show that even when anglers target smaller-bodied predatory freshwater species, they catch few very small fish (e.g., van Poorten and Post, 2005, Wilberg et al., 2005). We account for this bias by introducing an offset L_{shift} into the sigmoidal function that shifts L_{50} to the right. This shift is more consequential for smaller LHTs than for larger LHTs, and thus accounts for the aforementioned bias. Third, different angler types impose different size-selective capture vulnerabilities, with trophy anglers targeting larger fish. We account for these three facts by determining L_{50} as a linear function of $L_{\max}$, $L_{50} = z_j L_{\max} + L_{\text{shift}}$ (Table A1, equation 6b) where z_j depends on the angler type j. To estimate y and z_j for generic and consumptive anglers, we use a least-square approximation of the vulnerability of pike reported by Johnston et al. (2010). For trophy anglers, z_j is increased by 10% relative to generic and consumptive anglers (Table S3), since trophy anglers value, and thus target, larger fish by using different gear than the other angler types (Jacobson, 1996, Aas et al., 2000). To the extent that empirical data is available, we find that the capture vulnerabilities thus specified produce size structures of catch that generally match empirical observations for the described LHTs or closely relates species (e.g., Paul et al., 2003, Post et al., 2003, van Poorten and Post, 2005, Wilberg et al., 2005, Arlinghaus et al., 2009; see footnote Table S3).

Part-worth-utility functions

In our model, multiple fishery attributes contribute to an angler's utility (Table A1, equation 1) and thus influence the participation decisions of anglers (Table A1, equation 2a).

Part-worth-utility (PWU) functions from welfare economics (illustrated in Johnston et al. 2010, Figure 3) are used to describe the relative importance of each catch-related and non-catch-related attribute to an angler's overall utility (Table S2). The PWU functions also involve scaling attribute levels relative to baseline attribute levels (defined as the levels at which the focal PWU value equals 0,and the probability to fish thus equals 50%, when all other PWU values equal 0; Table S4). However, some baseline attribute levels depend on fish size or fish abundance in a way that varies with LHT. For example, a perch angler likely gains more utility from catching a 30 cm perch than a pike angler does from catching a 30 cm pike, due to the intrinsic size differences between these two species. Thus, several baseline attribute levels are standardized so as to achieve such the desired relative scaling across LHTs.

First, minimum-size limits are set as a proportion of L_{max} ranging between 0 and 1 (Table S4). Second, the baseline catch rates C_{De} (Table S4) are assumed to equal 50% of the maximum catch rate achievable for a given LHT by a mixed angler population (comprising 40%, 30%, and 30%; generic, consumptive, and trophy anglers, respectively) imposing no harvest, non-compliance, or hooking mortality on the fish population. For all LHT, the thus established baseline catch rates are generally within the range reported for the modeled, or closely related, species (see Table S4). Third, proportional-stock-density (PSD) categories (Gabelhouse, 1984), also known as proportional size structure (Guy et al., 2006), which describe the recreational value of fish based on their size relative to the species' world-record length, are used to set baseline values for the average size $\bar{L}_{\mathrm{e}}$ and maximum size L_{xe} of caught fish. Specifically, we assume that "quality" fish (40% of L_{max}) represent the baseline value for $\bar{L}_{\mathrm{e}}$, and fish bordering the "preferred" and "memorable" categories (55% of L_{max}) represent the baseline value for L_{xe} (Table S4).

Outline of analysis

To examine how biological impacts from recreational fishing varies among LHTs, we first run our model across a range of minimum-size limits (MSL; Table S1) and fishing efforts, both of which are held constant within a model run. In these model runs, anglers therefore do not behave dynamically (Figure 2, element I) and are furthermore assumed to be consumptive anglers killing all harvestable fish: this makes it possible to compare the biological response of LHTs at equilibrium to identical levels of fishing effort. Changes in fish abundance and biomass relative to unexploited levels (Table 1), and in the weighted spawning-potential ratio SPR (Table A1, equation 7a), are examined.The SPR is commonly used to assess fisheries sustainability: values below 0.2-0.3 are considered critical (Goodyear, 1993), whereas maintaining SPR above 0.35-0.40 is likely to prevent recruitment overfishing (Mace, 1994, Clark, 2002).

In a second stage of our analysis, we allow angler types to respond dynamically to the perceived quality of the fishery, i.e., utility affected anglers' probability to fish (Figure 2, element D). We examine model runs across a range of minimum-size limits MSL and license densities A_{L} (Table A2), for homogeneous angler populations composed of one angler type, and more realistically, for four specific compositions of mixed angler populations (Table S3). These mixed angler populations are comprised of either relatively equal proportions of the three angler types (40%:30%:30%; generic, consumptive, and trophy anglers, respectively), or strongly skewed towards generic (70%:15%:15%), consumptive (15%:70%:15%), or trophy (15%:15%:70%) anglers. We evaluate how the interplay among life-histories, dynamic angler behaviours, and regulations differentially affect overfishing vulnerability, angler behaviour, and optimal regulations (in terms of MSL_{opt} and $A_{\mathrm{L,opt}}$) across LHTs and anglers populations under equilibrium conditions. The biological conditions (in terms of SPR) and social conditions (in terms of total utility and fishing effort) under optimal regulations are also examined, to assess whether trends across LHTs exist and whether optimal regulations imply biological sustainability. We also analyse the relative participation of angler types in mixed angler populations (in terms of the proportion of the fishing effort exerted by a given angler type relative to that type's proportion of the angler population; Table A1, equation 7c) across LHTs, to determine if angler types are differentially attracted to, or excluded from, particular fisheries.

Finally, we evaluate the sensitivity of fish-angler dynamics to LHT parameterization using elasticity analyses (e.g., Allen et al., 2009). For this purpose, we vary each life-history parameter by ±10% from its original value (except for age-at-maturation and maximum age, which are discrete and are therefore varied by ±1 year) and calculate the relative change in MSL_{opt} and $A_{\mathrm{L,opt}}$. Relative changes exceeding 10% indicate that the fish-angler dynamics are sensitive to those parameters. SPR levels predicted under the new optimal regulations are also examined, to evaluate if predictions about biological sustainability under socially optimal regulations are robust to changes in life-history parameters.

Results

Biological impacts under constant fishing effort

In the absence of exploitation, the five life-history types (LHTs) in our model differ substantially in their population characteristics. Perch is most abundant, with an unexploited equilibrium density (of fish aged 1 year and older) approaching 800 fish·ha^{-1}, followed by brown trout and pikeperch (300 and 90 fish·ha^{-1}, respectively; Table 1). Pike and bull trout are least abundant (less than 25 fish·ha^{-1}; Table 1). Predicted abundance under unexploited conditions generally fall within the range predicted in the literature, although pikeperch in our model are more abundant than what may be considered average literature values, and the predicted abundances of perch and bull trout are at the low end of the range reported in the literature (supplementary material – "Parameterization of stock-recruitment relationships").

The unexploited biomasses (of fish aged 1 year and older) predicted by our model range between 10 kg·ha^{-1} and 60 kg·ha^{-1} across all LHTs. Pikeperch exhibits the highest unexploited biomass, followed by perch, brown trout, pike, and bull trout.

When recreational fishing is introduced with a constant consumptive angling effort, the biological impacts on the five LHTs, measured relative to unexploited conditions, differ greatly (Figure 5). Fishing reduces the abundance, biomass, and SPR of pike, bull trout, and pikeperch relative to unexploited levels, particularly under low to moderately restrictive minimum-size limits (0-50% of $L_{\max}$) and moderate to high fishing efforts (30-80 h·ha^{-1}; Figure 5). Similarly, fishing reduces the biomass and SPR of perch and brown trout (Figure 5), although their relative magnitudes of decline are generally smaller than for the other LHTs. However, unlike all other LHTs, exploitation increases perch abundance above unexploited levels under all examined minimum-size limits and fishing efforts (Figure 5). Fishing also increases brown-trout abundance (Figure 5), but only under liberal minimum-size limits and for fishing efforts below 20 h·ha^{-1}, or under more restrictive minimum-size limits above 60% of $L_{\max}$.

Overall, these results suggest that the susceptibility of LHTs to declines in abundance, biomass, and SPR are greatest to least as follows (ranked by the proportion of model runs in which SPR was smaller than 0.35): bull trout, pikeperch/pike (similar responses), brown trout, and perch. Hereafter, we use the term LHT vulnerability to refer the degree to which LHTs in our model are susceptible to recruitment overfishing from recreational angling. The obtained ranking suggests that LHT vulnerability to overexploitation by consumptive anglers is negatively related to unexploitedabundance and maximum recruitment, positively related to maximum body size and size-at-maturation, and not strongly related to age-at-maturation, relative fecundity, or natural mortality (see Table 1 and Table S1 for values).

Biological impacts under dynamic angler behaviour

Allowing anglers to respond dynamically to the perceived quality of the fishery alters the incidence of recruitment overfishing, and also causes fishing efforts to vary substantially among LHTs and angler populations (Figure 6). Despite this influence of LHT on the angling effort a fishery attracts, the pattern of differential vulnerability of LHTs to overexploitation by anglers remains qualitatively unchanged, regardless of the composition of the angler population. Consistent with our aforementioned findings for the biological impacts of consumptive anglers that fish with constant effort, the biological impacts (measured by SPR) of dynamic angler populations are greatest to least across LHTs as follows: (again ranked as described above) bull trout, pikeperch/pike, brown trout, and perch (Figure 6).

However, the angler population's composition does alter the quantitative magnitudes of the biological impacts anglers exert on the fished populations. Under liberal minimum-size limits, the consumptive angler population reduces SPR more than other angler populations across LHTs, whereas under more restrictive minimum-size limits, SPR is most reduced by the trophy anglers (Figure 6).

Biological impacts on less vulnerable LHTs vary much more among angler populations, despite being generally less severe, than on more vulnerable LHTs. For example, only certain angler populations (consumptive, or consumptive and mixed) overfish perch and brown trout, whereas all angler populations overfish pike, pikeperch, and bull trout under some regulations. Across the range of regulations examined, consumptive angler populations reduce the SPR below 0.35 more often than other angler populations when targeting pikeperch, perch, and brown trout, whereas the trophy-angler population had the greatest impact on bull trout, and impacts on pike are similar for populations of consumptive, trophy, and mixed (40%:30%:30%) anglers.

Socially optimal regulations

We also find that socially optimal regulations differ among LHTs: the optimal minimum-size limit MSL_{opt} (measured as a fraction of $L_{\max}$) increases with LHT vulnerability, generally being lowest for perch (23-44% of $L_{\max}$, 9-17 cm), followed by brown trout (29-54%, 15-28 cm), pikeperch (54-70%, 56-72 cm), pike (52-84%, 61-98 cm), and bull trout (44-80%, 43-78 cm; Figure 7a). In addition, MSL_{opt} varies greatly (over a range wider than 20% of $L_{\max}$) among angler populations (Figure 7a): for all LHTs except brown trout, MSL_{opt} is highest for trophy-dominated angler populations (composed solely of, or dominated by, trophy anglers) and lowest for consumptive-dominated angler populations (defined analogously). For brown trout, MSL_{opt} is highest for consumptive-dominated angler populations and lowest for generic-dominated angler populations (Figure 7a).For all LHTs, MSL_{opt} values for all mixed angler populations fall within the ranges predicted for the three homogeneous angler populations.

Unlike MSL_{opt}, the optimal license density $A_{\mathrm{L,opt}}$ shows no general trend across LHTs, ranging from 0.4-0.6 ha^{-1} for most LHTs, but varying by 0.15-0.20 ha^{-1} among angler populations (Figure 7b). One exception to this pattern occurs for bull trout, for which $A_{\mathrm{L,opt}}$ for the consumptive angler population is very low (0.11 ha^{-1}; Figure 7b). Despite the general consistency of $A_{\mathrm{L,opt}}$ across LHTs, the highest $A_{\mathrm{L,opt}}$ for pikeperch, perch, and brown trout occur when these LHTs are targeted by a generic angler population, whereas for pike and bull trout, $A_{\mathrm{L,opt}}$ is highest for the mixed (40%:30%:30%) angler population (Figure 7b). On the other extreme, $A_{\mathrm{L,opt}}$ for pike and brown trout is lowest when exploited by trophy-dominated angler populations, while for pikeperch, perch, and bull trout, the consumptive-dominated angler populations have the lowest $A_{\mathrm{L,opt}}$. Thus, unlike MSL_{opt}, $A_{\mathrm{L,opt}}$ for mixed angler populations can exceed the range predicted for homogeneous angler populations.

Conditions under socially optimal regulations

Under socially optimal regulations (MSL_{opt} and $A_{\text{L,opt}}$), 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

LHTs in the literature [e.g., yellow perch (*Perca flavescens*, Percidae) 3-109 h ha^{-1} (Isermann et al., 2005), pike 38-91 h ha^{-1} (Pierce et al., 1995), and walleye (*Sander vitreus*, Percidae) 29-112 h ha^{-1} (Beard et al., 2003)], potentially being on the high side for some LHTs [e.g., bull trout, 10-20 h ha^{-1} (Post et al., 2003)]. Like $A_{\mathrm{L,opt}}$, optimal fishing efforts show little variation among LHTs (45-70 h·ha^{-1} for most LHTs), but vary more markedly among angler populations (Figure 7e). Consequently, optimal fishing effort shows little relationship with LHT vulnerability, only differing substantially (14.2 h·ha^{-1}) for the consumptive angler population targeting bull trout. Across most LHTs, consumptive-dominated angler populations fish less than the other angler populations under optimal regulations, except for the trophy-dominated angler populations fishing for brown trout (Figure 7e). Pike, perch, and brown trout attract the most fishing effort from generic-dominated angler populations, whereas trophy-dominated angler populations fish more for pikeperch and bull trout (Figure 7e). The optimal fishing efforts of mixed angler populations generally fall within the range predicted for the three homogeneous angler populations.

The relative participation of different angler types in the mixed angler populations show clear trends in relation to LHTs under optimal regulations (Figure 8). These trends occur despite differences among mixed angler populations in MSL_{opt} and $A_{\mathrm{L,opt}}$, as well as in the conditions associated with optimal regulations (e.g., total utility and fishing effort). Regardless of LHT, generic anglers tend to be underrepresented or proportionally represented in the total angling effort compared with their relative abundance in the mixed angler population (ca. 1; Figure 8a). By contrast, the relative participation of consumptive anglers decreases (Figure 8b), and the relative participation of trophy anglers increases (Figure 8c), as LHT vulnerability increases. Thus, consumptive anglers tend to be overrepresented when fishing for perch and brown trout and underrepresented when fishing for pike, pikeperch, and bull trout, whereas trophy anglers show the opposite pattern, being systematically attracted to the larger-bodied LHTs.

Sensitivity analyses

We find that MSL_{opt} is generally less sensitive to changes in life-history parameters than $A_{\mathrm{L,opt}}$ (Tables S5 and S6), and that both are most sensitive to changes in age-at-maturation a_{m}, maximum growth increment h_{max}, and instantaneous natural mortality rate $m_{\mathrm{n}a}$ (note, however, that because the change in a_{m} is ±1 year, the relative change in a_{m} is much greater than ±10%). Sensitivity varies across combinations of LHT and angler type. The robustness of MSL_{opt} and $A_{\mathrm{L,opt}}$ tends to decrease with LHT vulnerability (e.g., fewer relative changes exceeding 10% for perch compared with bull trout).The sensitivity of MSL_{opt} is relatively similar among angler types, whereas, across all LHTs, $A_{\mathrm{L,opt}}$ is more sensitive to changes in life-history parameters when exploited by consumptive anglers, followed by trophy anglers and generic anglers.

Despite the sensitivity of optimal regulations to changes in life-history parameters, predictions about the biological sustainability of the fishery under optimal regulations are fairly robust (Table S7).For pike and pikeperch under optimal regulations, the SPR never drops below 0.35. For perch and brown trout under optimal regulations, consumptive anglers reduce SPR below 0.35 when age-at-maturation a_{m} is increased, but remains above 0.35 in all other cases. Similar to our main results, bull trout under optimal regulations cannot biologically sustain exploitation by consumptive anglers, except when the natural mortality rate $m_{\mathrm{n}a}$ is decreased. Angling of bull trout by generic and trophy anglers also result in SPR values below 0.35 when a_{m} is increased, but remains above 0.35 in all other cases involving those angler types.

Discussion

Here we have used a novel bioeconomic model developed by Johnston et al. (2010) to integrate fish life-history diversity, angler diversity and dynamics, and input and output regulations, to evaluate the importance of jointly considering these components for determining optimal regulations and the vulnerability of different fish life-history types (LHTs) to recreational overfishing. Our study is the first to systematically investigate the response of different LHTs in an integrated framework using realistic assumptions about distinct angler types and their dynamic responses to changes in fishing quality. Thereby, our study addresses recent calls for more integrative analyses in recreational fisheries (Fenichel et al., 2012).

We find that LHTs are crucially important for determining the vulnerability of recreational fish populations to recruitment overfishing. LHTs differentially affect the fishing-participation decisions of angler types. We also find that, because angler types differ in their effort dynamics and fishing practices, the angler population's composition influences the biological impacts of fishing on LHTs. These complex feedbacks between fish LHTs and angler populations result in large variations, across both LHTs and angler populations, in regulations that maximize social welfare. For example, more vulnerable LHTs in our model tend to have higher optimal maximum-size limits MSL_{opt} than less vulnerable LHTs, and as a second example, trophy anglers generally prefer the highest MSL_{opt} for a given LHT, while consumptive anglers prefer the lowest. Yet, despite differences in regulations that achieved optimal social yield OSY, our model predicts optimal regulations to result in biologically sustainable exploitation for all LHTs, except when bull trout are exploited solely by consumptive anglers. A management approach based on social objectives (e.g., OSY), rather than one based solely on biological objectives (e.g., maximum sustainable yield), can thus facilitate biologically sustainable exploitation. This is because biological objectives are inherently part of the social-welfare metric, through their effects on catch-related utility attributes.

Results of our study underscore the importance of considering all three components of a recreational fishery – LHTs, angler types, and management regulations – in an integrated framework when predicting sustainable management strategies for recreational fisheries. Simplification of any of these components may lead to erroneous predictions about fish-angler dynamics, which may result in socially suboptimal management, biological collapse, or both.

LHT vulnerability to overfishing

Life-history traits are important for determining the vulnerability of fish populations to overfishing (Reynolds et al., 2001, Rose et al., 2001, Winemiller, 2005). Thus, it is not surprising we have found differences in the susceptibility of LHTs to recreational exploitation. Numerous studies suggest that fish with certain life-history characteristics (i.e., late maturation, large maximum size, low population growth rate) are prone to experience greater population declines from fishing than others (Jennings et al., 1998, Reynolds et al., 2001, Dulvy et al., 2003); our model-based results are in general agreement with those empirical findings

Specifically, we find that the naturally-less-abundant and large-bodied LHTs in our model (bull trout, pikeperch and pike) experience more severe population declines in response to recreational angling than the naturally-more-abundant and smaller-bodied LHTs (perch and brown trout,) which can sustain greater fishing mortality. In fact, in agreement with warnings by Post et al. (2003) about the extreme susceptibility of bull trout to overfishing, we find that bull trout requires minimum-size limits approaching complete catch-and-release fishing, to sustain even low fishing efforts. Thus, our results corroborate other studies (Jennings et al., 1998, Reynolds et al., 2001, Dulvy et al., 2003) suggesting that maximum body size is correlated with vulnerability to overexploitation by fishing. Furthermore, our results show that indicators such as unexploited abundance, maximum recruitment, and potentially also size-at-maturation (although this may simply be a correlate of maximum body size) could also be useful for identifying fish populations susceptible to overfishing, where information on those indicators is available. Moreover, our results suggest that age-at-maturation, fecundity, and natural mortality are not likely to be good indicators of vulnerable LHTs, contrary to earlier suggestions (Jennings et al., 1998, Reynolds et al., 2001).

The differences among LHTs in vulnerability to overfishing relate in part to their overall productivity and their abilities to compensate for fishing-related mortality through density-dependent gains in survivorship and/or reproductive success (Rose et al., 2001). This ability depends on species' life-history characteristics and on the strength and frequency of the density-dependent processes to which they are adapted (Rose et al., 2001, Winemiller, 2005, Goodwin et al., 2006). For example, density-dependent survival during early life stages, which is common in many fish species (Myers et al., 1995), influences a population's ability to offset fishing mortality (Rose et al., 2001, Goodwin et al., 2006, Lorenzen, 2008). At high population densities, even overcompensation can occur (e.g., in the form of a Ricker stock-recruitment relationship), due to cannibalism, density-dependent disease transmission, or spawning interference (Ricker, 1954a, Hilborn and Stokes, 2010). This means that with reductions in spawning stock recruitment initially rises before declining (Hilborn and Stokes, 2010). In our model, perch experiences large gains in recruitment because of overcompensation when egg production is reduced by fishing, ultimately resulting in an increase in population density. Overcompensation and cannibalism have been reported for this species (Ohlberger et al., 2011). Overcompensation for low fishing mortality also occurs for brown trout, but not when fishing effort, and thus mortality, increases under liberal minimum-size limits. All other LHTs, even highly fecund pikeperch, are unable to replace, through compensatory population growth, individuals removed by fishing. In addition to this relatively low compensatory potential, the greater vulnerability of these naturally-less-abundant and larger-bodied LHTs to overexploitation reflects the low maximum recruitment and population density (Table 1) of these top predators relative to perch and brown trout.

When considered alone, stock-recruitment relationships can underestimate population responses to fishing (Rochet et al., 2000, Rose et al., 2001, Rose, 2005), even though they strongly influence the compensatory potential of exploited populations, because other density-dependent processes may co-determine those responses (Rose et al., 2001, Rose, 2005, Lorenzen, 2008). For example, density-dependent growth, which is included in our model, can alter a population's compensatory potential, because fish size influences fecundity, maturation, and survival (Rose et al., 2001, Rose, 2005, Lorenzen, 2008). However, stock-recruitment relationships are likely more important than density-dependent growth for determining the compensatory potential of heavily exploited populations (Lorenzen, 2008). Indeed, the reductions in biomass and SPR we observe across LHTs in our model underscore that density-dependent changes in size-at-age cannot compensate fully for density losses caused by high fishing mortality. Density-dependent changes in fecundity, maturation, and reproductive frequency, and fisheries-induced evolutionary changes are not considered in our study, but could also be important for determining a fish population's response to exploitation (Rochet et al., 2000, Rose et al., 2001, Jørgensen et al., 2007). We therefore recommend that model extensions aim at including all salient processes influencing a population's compensatory potential.

It has been suggested that, in the absence of detailed information, qualitative "rules of thumb" based on the life-history characteristics of exploited fish populations could aid fisheries managers in identifying those populations that are most vulnerable to overfishing

(Reynolds et al., 2001, Winemiller, 2005). For example, according to Winemiller and Rose's (1992) classification scheme, "periodic strategists" (featuring high fecundity, late maturation, and low juvenile survival) are predicted to exhibit the highest resilience to fishing, whereas "equilibrium strategists" (with low fecundity, late maturation, and high juvenile survival) should have lower resilience (Winemiller and Rose, 1992, Winemiller, 2005). Our results regarding the extreme vulnerability of bull trout, a salmonid likely classified as intermediate between periodic and equilibrium strategists (Winemiller and Rose, 1992), and indeed its current status – "vulnerable" in the IUCN's Red List (Gimenez Dixon, 1996), and "threatened" in coterminous USA (US Fish and Wildlife Service 2010), provide some support for these predictions, as do our findings related to pike, pikeperch, perch, and brown trout, which are all broadly classified as periodic strategists (Rose et al., 2001, Vila-Gispert and Moreno-Amich, 2002) and are all listed as species of least concern (Freyhof and Kottelat, 2008a, Freyhof and Kottelat, 2008b, Freyhof and Kottelat, 2008c, Freyhof, 2011).

However, our results caution that coarse life-history classifications, such as Winemiller and Rose's (1992), risk obscuring important life-history differences that exist within the broadly defined strategies (Rose et al., 2001): as we have shown here these life-history differences can substantially influence vulnerability to overexploitation. For example, despite four of our LHTs being classified as periodic strategists (Vila-Gispert and Moreno-Amich, 2002), we found pike and pikeperch to be much more vulnerable to recruitment overfishing than brown trout or perch. Indeed, pike and walleye, a congeneric of pikeperch, have been shown to be highly vulnerable to overexploitation by recreational angling (e.g., Post et al., 2002). Declines in brown-trout stocks as a result of recreational fishing have also been documented (e.g., Almodóvar and Nicola, 2004). Thus, in the absence of more detailed information, body size and life-history classification can provide directions for identifying LHTs vulnerable to overfishing. However, the present study and other work (Rose, 2005, Coggins et al., 2007) suggest that, where possible, a quantitative modelling approach should be used to provide more robust predictions about the response of different LHTs to recreational angling.

Angler dynamics

When predicting the impacts of recreational fishing, one needs to consider not only fish life history but also the preferences and dynamics of anglers utilizing a fishery (Post et al., 2003, Johnston et al., 2010). Our results show that dynamic angler behaviour, regardless of angler type, does not alter the general trend in vulnerability to recruitment overfishing across LHTs our model predicts for constant consumptive fishing effort: with and without dynamic angler behaviour, bull trout are most vulnerable and perch are least vulnerable to fishing-induced *SPR* declines. Yet, the composition of the angler population and its effort dynamics are important for determining the magnitude of the impact angling has on LHTs in our model.

We find that differences in fishing practices (skill levels, propensity for voluntary catch-and-release, fish size targeted; Table S3) among angler types influence catch and harvest rates. Under liberal minimum-size limits, consumptive anglers have greater impacts than other anglers types on less vulnerable LHTs in our model (perch and brown trout), because catch rates of these naturally-abundant LHTs (e.g., maximum 11.3, 20.0, 15.0 harvestable-sized perch day^{-1} and 5.5, 8.6, 7.7 harvestable-sized brown trout day^{-1} for generic, consumptive, and trophy anglers, respectively) are generally high, and consumptive anglers harvest all legal-sized fish caught (i.e., fish are not voluntarily released). On the other hand, trophy anglers in our model, while also enjoying high catch rates, only harvest one fish every second day. Thus, a large disparity in harvest rates results among angler types. By contrast, catch rates of naturally-less-abundant LHTs, bull trout and pike, in our model (with a maximum of 0.17, 0.19, 0.14 harvestable-sized bull trout per day and 0.55, 0.75, 0.80

harvestable-sized pike per day for generic, consumptive, and trophy anglers, respectively) are generally low and thus do not allow a similar disparity in harvest rates to develop. In our model, catch rates of harvestable fish often do not exceed even the conservative personal daily harvest limits set by trophy anglers, similar to reports for regulated daily bag limits (Cook et al., 2001). This implies that regulated daily bag limits may also have little effect, unless they are low enough to be achieved. Voluntary release by any angler type rarely occurs in our model, and therefore is less important for determining the fishing impacts on the more vulnerable LHTs. Instead, the variation in the impact of anglers on those more vulnerable LHTs emerges through differences in angler behaviour, and thus fishing effort.

In addition to harvesting practices, dynamic angler behaviour also determines angling impacts on LHTs. First, regardless of angler type, and despite substantial declines in fish abundances and catch rates under liberal harvest regulations, some anglers continued to be attracted to the modelled fishery. This has the potential to collapse fisheries (Post et al., 2002), demonstrating the importance of considering multi-attribute angler behaviour in recreational fisheries models (see also Johnston et al., 2010), rather than assuming that catch rates alone dictate the fishing decisions of anglers (e.g., Cox et al., 2003). Second, our results show how differences in behaviour among angler populations, because of angler-type-specific fishing preferences, alter angling impacts, in some cases leading to counterintuitive outcomes. For example, despite the tendency of trophy anglers to practice voluntary catch-and-release (Arlinghaus et al., 2007), across LHTs populations of trophy anglers reduce the SPR more than other angler populations under moderate to restrictive minimum-size limits. This reflects that more specialized anglers often prefer or tolerate restrictive harvest regulations (Aas et al., 2000, Oh and Ditton, 2006, Arlinghaus et al., 2007) and respond to them differently than other anglers (Beard et al., 2003). Thus, under constrained harvest conditions, while the angling efforts by consumptive and generic anglers declined, in our models effort by trophy anglers remain high, resulting in trophy anglers killing more fish than other angler types. In some cases, this mortality is sufficient to put populations at risk of recruitment overfishing (e.g., for bull trout with license densities exceeding 0.7 ha^{-1}), even under total catch-and-release regulations.

Our results thus support claims that discard mortality can substantially impact the biological sustainability of some fisheries (Coggins et al., 2007). In combination, the fishing practices and fishing preferences of trophy anglers, counterintuitively, result in their having the greatest overall impact on bull trout. among all studied angler populations These findings highlight that, to prevent unexpected results, managers and researchers need to better understand the types of anglers utilizing a fishery, as well as the dynamics resulting from their differential practices and preferences, to achieve more robust predictions about recreational fishing impacts. Where sufficient information is available, our modelling approach can be used to explore implications of management changes prior to their enactment, so as to help select practically implemented management changes based on their efficacy.

Optimal management

In our model, differences in LHT vulnerability and fish-angler interactions influence the regulations that maximize an angler population's total utility, measured in terms of OSY. For example, although the optimal density $A_{\mathrm{L,opt}}$ of licenses does not show a general trend with LHT vulnerability, MSL_{opt} has a strong tendency to increase with LHT vulnerability (with MSL_{opt} being generally most liberal for perch and most restrictive for bull trout).

Minimum-size limits are often set in recreational fisheries to be as low as possible (so as to maximize harvest) while allowing fish to spawn at least once (Johnson and Martinez, 1995, Diana and Smith, 2008), This tactic, however, may not be appropriate for all species. Whereas low minimum-size limits may be suitable for perch, minimum-size limits for pike –

set at, e.g., 46-76 cm in North America (Paukert et al., 2001) – are often below, or at the lower margin of,the range of MSL_{opt} predicted by our model (61-98 cm). Our findings thus suggest that species-specific considerations when setting minimum-size limits could generate greater social benefits from a fishery, supporting concerns that "one size fits all" policies may erode ecological and social resilience (Carpenter and Brock, 2004). The increase of MSL_{opt} with vulnerability suggests that unexploited abundance, maximum recruitment, maximum body size, and potentially also size-at-maturation (if known) can aid managers in setting more socially advantageous minimum-size limits, due to the correlation of those indicators with vulnerability.

Accounting not only for LHTs but also angler diversity, however, is crucially important when establishing management regulations (Radomski et al., 2001, Johnston et al., 2010). In agreement with findings that more-specialized anglers are more tolerant of restrictive harvest regulations (Aas et al., 2000, Oh and Ditton, 2006), MSL_{opt} in our model, as a general rule, tends to be lowest for consumptive-dominated angler populations and highest for trophy-dominated angler populations. However, in the case of brown trout, consumptive-dominated angler populations have the highest MSL_{opt}, whereas generic-dominated angler populations have the lowest. The reason for this finding is that the greater harvest orientation and skill level of consumptive anglers relative to generic anglers requires a higher minimum-size limit to maintain a sustainable fishery for consumptive anglers. On the other hand, the less-consumptive generic anglers can fish with high effort under the more liberal harvest regulations they preferred, because of the relatively productive nature of brown trout.

Angler population composition is also important for determining the optimal density $A_{\mathrm{L,opt}}$ of licenses, including subtle interactions with LHT differences. For example, we find that the generic angler population exhibit the highest $A_{\mathrm{L,opt}}$ when LHT vulnerability is low, whereas mixed angler populations have an even higher $A_{\mathrm{L,opt}}$ when LHT vulnerability is high (as it is, e.g., for pike and bull trout). This result highlights the importance of considering the complex interplay among angler types within an angler population.

More broadly, our findings support suggestions that managing for diverse angling opportunities could better conserve fish populations and increase the social welfare provided by a fishery (e.g., Aas et al., 2000, Carpenter and Brock, 2004, Johnston et al., 2010). Given that angler types generally display consistent preferences for optimal regulations, some knowledge of the angler population could assist managers with meeting this challenge. However, as our previously discussed results underscore, management decisions should be based on both the life history of an exploited fish population and the diversity of interests in the corresponding angler population (e.g., Diana and Smith, 2008).

Of relevance for managers faced with the challenge of maximizing angler satisfaction and participation while maintaining a viable fishery (Radomski et al., 2001, Cox and Walters, 2002, Peterson and Evans, 2003), is the our promising result that adopting a socially optimal approach (based on OSY) to recreational fisheries management achieves both objectives. Specifically, SPR in our model is maintained above 0.35 except for bull trout, a LHT that due to its extreme vulnerability to overfishing cannot biologically sustain a satisfied solely consumptive angler population under optimal regulations. In most cases, however, managing for OSY is more likely to achieve management objectives and result in lower fishing mortality than managing for maximum sustainable yield (Radomski et al., 2001), because a viable recreational fishery provides social and cultural benefits that are not measured by yield alone (Roedel, 1975, Malvestuto and Hudgins, 1996). Notwithstanding these findings, given the decrease in SPR that occurs in our model with increased LHT vulnerability under optimal regulations, a precautionary approach should be adopted when setting optimal regulations for naturally-more-vulnerable LHTs.

Emergent LHT preferences

A final key finding of this study is the emergent preferences of angler types for particular LHTs. For example, generic and consumptive angler populations tend to gain more total utility from less vulnerable LHTs than from more vulnerable LHTs, creating an emergent preference for the naturally-more-abundant and smaller-bodied LHTs. By contrast, the total utility of populations of trophy anglers tends to increase with LHT vulnerability, creating an emergent preference for the naturally-less-abundant and larger-bodied LHTs. These trends occur despite standardizing anglers' PWU baseline expectations for life-history differences in fish size and abundance. The social welfare provided by perch is high for all angler populations, because perch can maintain high relative catch rates even when fishing mortality is high under liberal minimum-size limits. However, relatively low catch rates and aversions to restrictive regulations made the more vulnerable LHTs (pike, pikeperch, and bull trout) less attractive to consumptive or generic anglers. Trophy anglers, by contrast, prefer the naturally-less-abundant and larger-bodied bull trout and pike, because of their tolerance for restrictive regulations and their ability to catch relatively larger fish. The greater average and maximum relative size achieved for these LHTs likely results from stronger density dependence in growth and reduced truncation of the size distribution under restrictive minimum-size limits. These novel findings suggest that the intrinsic life history of fish populations strongly influence which species or LHTs an angler type prefers. Indeed, in support of these results Beardmore et al. (2011), found that more specialized, trophy-oriented German anglers were particularly attracted to larger-bodied species such as pike.

One implication of angler-type-specific LHT preferences is that the socially optimal management of a given recreational fishery may systematically exclude or attract certain angler types. For example, as LHT vulnerability increases, the relative participation of trophy anglers in our modelled mixed angler populations under optimal regulations also increases, and the reverse is true for consumptive anglers. These trends occur despite large differences in the optimal regulations underlying them. Therefore, depending on the social welfare measure used (Johnston et al., 2010), managing for OSY may come at a greater cost to certain angler types than others, which might lead to conflict among different segments of the angling community (Loomis and Ditton, 1993, Arlinghaus et al., 2007). However, our modelling approach can be used by managers to identify likely conflict situations, and it provides them with a tool for transparently illustrating the benefits of regulation changes to the angler community as a whole. Furthermore, understanding which angler types will be attracted to specific LHTs will aid managers in setting appropriate socially optimal regulations.

Limitations and extensions

While the present study provides important insights into the interplay among fish populations, anglers, and management measures, there are several limitations to our work, and resultant opportunities for extensions, that deserve to be highlighted A first set is related to angler dynamics, while a second set is related to fish dynamics; we now discuss these in turn.

First, our model constitutes a single-species, single-lake model omitting a regional perspective and multi-species interactions. Movement among various fisheries in a landscape (Post et al., 2008, Hunt et al., 2011, Post and Parkinson, 2012), or a multispecies fishery (Worm et al., 2009), could affect the outcomes presented here. Extending our model to include multispecies interactions or a spatial component of lakes connected by mobile anglers would be interesting avenues to pursue in future studies.

Second, by standardizing the baseline expectations of angler types for LHT differences in body size and abundance, we have assumed that angler-type-specific PWU functions are identical across LHTs. However, although Beardmore et al. (unpublished data) found no significant differences in the relative preferences (e.g., standardized for catch rate and body size) of different German angler types for several species, it is still possible that the preferences of angler types may differ among species. Species-specific or even regional differences in the utility functions of anglers could result in lower fishing effort under optimal regulations than those predicted in this study.

Third, we did not include inverse density-dependent catchability in our model. The existence of such a relationship could strongly affect the threshold effort that leads to severe overfishing (Hunt et al., 2011). Thus, the omission of density-dependent catchability may make our model results overly optimistic, by underestimating the risk of collapse for some species.

Fourth, other harvest regulations, such as daily bag limits, could potentially alter our study's predictions, by minimizing the disparity in fishing mortality imposed by different angler types. For example, our model may overemphasize the fishing impacts of consumptive anglers relative to other angler types, because the former are assumed to harvest all fish caught. However, this bias would only be relevant for the less vulnerable LHTs examined here, for which catch rates greatly exceed voluntary-release thresholds, and moreover, only when regulated bag limits are set low enough that catch rates can exceed them with sufficient frequency. For example, in many places anglers are allowed to harvest as many as 25 yellow perch per day, or even more (Isermann et al., 2007), while the maximum achieved catch rate in our model was 21.5 fish per day. For the more vulnerable LHTs we have examined, angler types rarely manage to catch even the most conservative daily quota (personal or regulated), resulting in harvest rates that are similar among angler types. Thus, as suggested in the literature (Cook et al., 2001), anglers are often not limited by daily bag limits: they harvest less fish than their daily bag limit would allow, either because they voluntarily choose not to harvest so many fish or because they do not manage to catch their daily limit. Nevertheless, the inclusion of daily bag limits might still alter the effort dynamics of anglers in our model, either through regulation aversions (Beard et al., 2003) or through resultant changes in fish population dynamics, which would therefore make an interesting extension for future research.

Other limitations of our model relate to fish dynamics. First, our results are based on the parameterization of a single-species system without any consideration of food-web interactions. Thus, for more realistic predictions about a specific fishery, the model will need to be calibrated appropriately. However, the purpose of this work has been to encompass a range of LHTs experienced by anglers, rather than to model any one specific population.

Second, as previously highlighted, some realistic density-dependent processes resulting from phenotypic plasticity (e.g., in maturation), which could be important for determining a LHT's compensatory (Rochet et al., 2000) potential and thus its predicted vulnerability, were not included in our model. In addition, we did not account for any harvest-induced evolutionary changes in life-history traits (e.g., Jørgensen et al., 2007) that might influence a species' response to fishing, e.g., through changes in its reproductive ecology (Enberg et al., 2010). Plastic or genetic changes that result in earlier maturation at smaller sizes, for example, could allow a fish population to withstand higher fishing pressure, especially the larger-bodied, more vulnerable LHTs. Such changes would often also influence angler behaviour, by altering the perceived quality of a fishery, e.g., if mean fish size declined.

Third, unaccounted changes in demographic structure, through juvenescence or size-dependent maternal effects, could alter reproductive potential and population stability

(Anderson et al., 2008, Arlinghaus et al., 2010, Hsieh et al., 2010). Size-dependent maternal effects would likely have more of an influence on LHTs that have lower proportions of adults in the population and fewer first-time spawners in the mature population (e.g., bull trout; Table 1), as well as on the more vulnerable LHTs. The impacts reported here are likely to be conservative if large females are preferentially removed by fishing and size-dependent maternal effects impair recruitment at low fish population abundance.

The influences of phenotypic plasticity, fisheries-induced evolution, and maternal effects on predictions about optimal regulations would be fascinating to examine, but were beyond the scope of the present study. Future research should also investigate alternative regulations, e.g., slots-length limits designed to protect large spawners (Arlinghaus et al., 2010).

Conclusions

Our study, to our knowledge, is the first to use an integrated modelling approach, based on theories from ecology, economics, and human-dimensions research, to systematically investigate how fish life history and angler types influence the vulnerabilityof fish populations to recreational overfishing and the behaviour of angler populations exploiting them. Using such an approach has revealed some unexpected results and some general patterns that could not have been exposed if the interplay among fish populations, anglers, and management measures had not been considered. We have also shown that socially optimal management generally achieves both social and biological sustainability, a result that can be taken as encouraging for recreational fisheries managers. In combination, our results demonstrate the benefit of integrating the traditionally separate fields of fisheries ecology and social sciences to facilitate the sustainable management of recreational fisheries. In this context, our results caution that managing all species according to the same rationale may result in the loss of social welfare and put fish populations at risk of overexploitation.

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References

Aas, Ø., Haider, W., Hunt, L. (2000) Angler responses to potential harvest regulations in a Norwegian sport fishery: a conjoint-based choice modeling approach. *North American Journal of Fisheries Management* **20,** 940-950.

Allen, M.S., Brown, P., Douglas, J., Fulton, W., Catalano, M. (2009) An assessment of recreational fishery harvest policies for Murray cod in southeast Australia. *Fisheries Research* **95,** 260-267.

Almodóvar, A., Nicola, G.G. (2004) Angling impact on conservation of Spanish stream-dwelling brown trout *Salmo trutta*. *Fisheries Management and Ecology* **11,** 173-182.

Anderson, C.N.K., Hsieh, C.H., Sandin, S.A., *et al.* (2008) Why fishing magnifies fluctuations in fish abundance. *Nature* **452,** 835-839.

Arlinghaus, R. (2004) *A Human Dimensions Approach Towards Sustainable Recreational Fisheries Management*. – Turnshare Ltd., London.

Arlinghaus, R., Cooke, S.J., Lyman, J., *et al.* (2007) Understanding the complexity of catch-and-release in recreational fishing: an integrative synthesis of global knowledge from historical, ethical, social and biological perspectives. *Reviews in Fisheries Science* **15,** 75-167.

Arlinghaus, R., Johnson, B.M., Wolter, C. (2008) The past, present and future role of limnology in freshwater fisheries science. *International Review of Hydrobiology* **93,** 541-549.

Arlinghaus, R., Matsumura, S., Dieckmann, U. (2009) Quantifying selection differentials caused by recreational fishing: development of modeling framework and application to reproductive investment in pike (*Esox lucius*). *Evolutionary Applications* **2,** 335-355.

Arlinghaus, R., Matsumura, S., Dieckmann, U. (2010) The conservation and fishery benefits of protecting large pike (*Esox lucius* L.) by harvest regulations in recreational fishing. *Biological Conservation* **143,** 1444-1459.

Beamesderfer, R.C.P., North, J.A. (1995) Growth, natural mortality, and predicted response to fishing for largemouth bass and smallmouth bass populations in North America. *North American Journal of Fisheries Management* **15,** 688-704.

Beard, T.D., Jr., Cox, S.P., Carpenter, S.R. (2003) Impacts of daily bag limit reductions on angler effort in Wisconsin walleye lakes. *North American Journal of Fisheries Management* **23,** 1283-1293.

Beardmore, B., Haider, W., Hunt, L.M., Arlinghaus, R. (2011) The importance of trip context for determining primary angler motivations: are more specialized anglers more catch-oriented than previously believed? *North American Journal of Fisheries Management* **31,** 861-879.

Beverton, R.J.H., Holt, S.J. (1957) On the dynamics of certain North Sea fish populations. *U.K. Ministry of Agriculture and Fisheries, Fisheries Investigations* **19,** 1-533.

Bryan, H. (1977) Leisure value systems and recreational specialization: the case of trout fishermen. *Journal of Leisure Research* **9,** 174-187.

Carpenter, S.R., Brock, W.A. (2004) Spatial complexity, resilience, and policy diversity: fishing on lake-rich landscapes. *Ecology and Society* **9,** 8 [online]. Available from www.ecologyandsociety.org/vol9/iss1/art8/.

Clark, W.G. (2002) F35% revisited ten years later. *North American Journal of Fisheries Management* **22,** 251-257.

Cochrane, K.L. (2000) Reconciling sustainability, economic efficiency and equity in fisheries: the one that got away? *Fish and Fisheries* **1,** 3-21.

Coggins, L.G., Jr., Catalano, M.J., Allen, M.S., Pine, W.E., III, Walters, C.J. (2007) Effects of cryptic mortality and the hidden costs of using length limits in fishery management. *Fish and Fisheries* **8,** 196-210.

Coleman, F.C., Figueira, W.F., Ueland, J.S., Crowder, L.B. (2004) The impact of United States recreational fisheries on marine fish populations. *Science* **305,** 1958-1960.

Cook, M.F., Goeman, T.J., Radomski, P.J., Younk, J.A., Jacobson, P.C. (2001) Creel limits in Minnesota: a proposal for change. *Fisheries* **26,** 19-26.

Cooke, S.J., Cowx, I.G. (2004) The role of recreational fisheries in global fish crises. *Bioscience* **54,** 857-859.

Cox, S., Walters, C. (2002) Maintaining quality in recreational fisheries: how success breeds failure in management of open-access sport fisheries. In: *Recreational Fisheries: Ecological, Economic and Social Evaluation.* (Eds. T.J. Pitcher, C.E. Hollingworth), Blackwell Publishing, Oxford, U.K., pp. 107-119.

Cox, S.P., Beard, T.D., Walters, C. (2002) Harvest control in open-access sport fisheries: hot rod or asleep at the reel? *Bulletin of Marine Science* **70,** 749-761.

Cox, S.P., Walters, C.J., Post, J.R. (2003) A model-based evaluation of active management of recreational fishing effort. *North American Journal of Fisheries Management* **23,** 1294-1302.

Diana, J., Smith, K. (2008) Combining ecology, human demands, and philosophy into the management of northern pike in Michigan. *Hydrobiologia* **601,** 125-135.

Dulvy, N.K., Sadovy, Y., Reynolds, J.D. (2003) Extinction vulnerability in marine populations. *Fish and Fisheries* **4,** 25-64.

Duncan, J.R., Lockwood, J.L. (2001) Extinction in a field of bullets: a search for causes in the decline of the world's freshwater fishes. *Biological Conservation* **102,** 97-105.

Enberg, K., Jørgensen, C., Mangel, M. (2010) Fishing-induced evolution and changing reproductive ecology of fish: the evolution of steepness. *Canadian Journal of Fisheries and Aquatic Sciences* **67,** 1708-1719.

Fenichel, E.P., Abbott, J.K., Huang, B. (2012) Modelling angler behaviour as a part of the management system: synthesizing a multi-disciplinary literature. *Fish and Fisheries*, doi:10.1111/j.1467-2979.2012.00456.x.

Fisher, M.R. (1997) Segmentation of the angler population by catch preference, participation, and experience: a management-oriented application of recreation specialization. *North American Journal of Fisheries Management* **17,** 1-10.

Freyhof, J. (2011) *Salmo trutta*. In: *IUCN 2011. IUCN Red List of Threatened Species. Version 2011.2*. Available from www.iucnredlist.org.

Freyhof, J., Kottelat, M. (2008a) *Esox lucius*. In: *IUCN 2011. IUCN Red List of Threatened Species. Version 2011.2*. Available from www.iucnredlist.org.

Freyhof, J., Kottelat, M. (2008b) *Perca fluviatilis*. In: *IUCN 2011. IUCN Red List of Threatened Species. Version 2011.2*. Available from www.iucnredlist.org.

Freyhof, J., Kottelat, M. (2008c) *Sander lucioperca*. In: *IUCN 2011. IUCN Red List of Threatened Species. Version 2011.2*. Available from www.iucnredlist.org.

Fulton, E.A., Smith, A.D.M., Smith, D.C., van Putten, I.E. (2011) Human behaviour: the key source of uncertainty in fisheries management. *Fish and Fisheries* **12,** 2-17.

Gabelhouse, D.W., Jr. (1984) A length-categorization system to assess fish stocks. *North American Journal of Fisheries Management* **4,** 273-285.

Gimenez Dixon, M. (1996) *Salvelinus confluentus*. In: *IUCN 2011. IUCN Red List of Threatened Species. Version 2011.2*. Available from www.iucnredlist.org.

Goodwin, N.B., Grant, A., Perry, A.L., Dulvy, N.K., Reynolds, J.D. (2006) Life history correlates of density-dependent recruitment in marine fishes. *Canadian Journal of Fisheries and Aquatic Sciences* **63,** 494-509.

Goodyear, C.P. (1993) Spawning stock biomass per recruit in fisheries management: foundation and current use. In: *Risk Evaluation and Biological Reference Points for Fisheries Management*. (Eds. S.J. Smith, J.J. Hunt, D. Rivard), Canadian Special Publication of Fisheries and Aquatic Sciences. 120, pp. 67-81.

Guy, C.S., Neumann, R.M., Willis, D.W. (2006) New terminology for proportional stock density (PSD) and relative stock density (RSD) : Proportional size structure (PSS). *Fisheries* **31,** 86-87.

Hahn, J. (1991) Angler specialization: measurement of a key sociological concept and implications for fisheries management decisions. *American Fisheries Society Symposium* **12,** 380-389.

Hilborn, R. (2007) Defining success in fisheries and conflicts in objectives. *Marine Policy* **31,** 153-158.

Hilborn, R., Stokes, K. (2010) Defining overfished stocks: have we lost the plot? *Fisheries* **35,** 113-120. [In English].

Hsieh, C.H., Yamauchi, A., Nakazawa, T., Wang, W.F. (2010) Fishing effects on age and spatial structures undermine population stability of fishes. *Aquatic Sciences* **72,** 165-178.

Hunt, L. (2005) Recreational fishing site choice models: insights and future opportunities. *Human Dimensions of Wildlife* **10,** 153-172.

Hunt, L.M., Arlinghaus, R., Lester, N., Kushneriuk, R. (2011) The effects of regional angling effort, angler behavior, and harvesting efficiency on landscape patterns of overfishing. *Ecological Applications* **21,** 2555-2575.

Isermann, D.A., Willis, D.W., Blackwell, B.G., Lucchesi, D.O. (2007) Yellow perch in South Dakota: population variability and predicted effects of creel limit reductions and minimum length Limits. *North American Journal of Fisheries Management* **27,** 918-931.

Isermann, D.A., Willis, D.W., Lucchesi, D.O., Blackwell, B.G. (2005) Seasonal harvest, exploitation, size selectivity, and catch preferences associated with winter yellow perch anglers on South Dakota lakes. *North American Journal of Fisheries Management* **25,** 827-840.

Jacobson, P.C. (1996) Trophy and consumptive value-per-recruit analysis for a walleye fishery. *North American Journal of Fisheries Management* **16,** 75-80.

Jennings, S., Reynolds, J.D., Mills, S.C. (1998) Life history correlates of responses to fisheries exploitation. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **265,** 333-339.

Johnson, B.M., Martinez, P.J. (1995) Selecting harvest regulations for recreational fisheries: opportunities for research/management cooperation. *Fisheries* **20,** 22-29.

Johnston, F.D., Arlinghaus, R., Dieckmann, U. (2010) Diversity and complexity of angler behaviour drive socially optimal input and output regulations in a bioeconomic recreational-fisheries model. *Canadian Journal of Fisheries and Aquatic Sciences* **67,** 1507-1531.

Jørgensen, C., Enberg, K., Dunlop, E.S.*, et al.* (2007) Managing evolving fish stocks. *Science* **318,** 1247-1248.

Lester, N.P., Shuter, B.J., Abrams, P.A. (2004) Interpreting the von Bertalanffy model of somatic growth in fishes: the cost of reproduction. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **271,** 1625-1631.

Lewin, W.C., Arlinghaus, R., Mehner, T. (2006) Documented and potential biological impacts of recreational fishing: insights for management and conservation. *Reviews in Fisheries Science* **14,** 305-367.

Loomis, D.K., Ditton, R.B. (1993) Distributive justice in fisheries management. *Fisheries* **18,** 14-18.

Lorenzen, K. (2008) Fish population regulation beyond stock and recruitment: the role of density-dependent growth in the recruited stock. *Bulletin of Marine Science* **83,** 181-196.

Mace, P.M. (1994) Relationships between common biological reference points used as thresholds and targets of fisheries management strategies. *Canadian Journal of Fisheries and Aquatic Sciences* **51,** 110-122.

Malvestuto, S.P., Hudgins, M.D. (1996) Optimum yield for recreational fisheries management. *Fisheries* **21,** 6-17.

McPhee, D.P., Leadbitter, D., Skilleter, G.A. (2002) Swallowing the bait: is recreational fishing in Australia ecologically sustainable? *Pacific Conservation Biology* **8,** 40-51.

Myers, R.A., Barrowman, N.J., Hutchings, J.A., Rosenberg, A.A. (1995) Population dynamics of exploited fish stocks at low population levels. *Science* **269,** 1106-1108.

Oh, C.O., Ditton, R.B. (2006) Using recreation specialization to understand multi-attribute management preferences. *Leisure Sciences* **28,** 369-384.

Ohlberger, J., Langangen, Ø., Edeline, E.*, et al.* (2011) Stage-specific biomass overcompensation by juveniles in response to increased adult mortality in a wild fish population. *Ecology* **92,** 2175-2182.

Paukert, C.P., Klammer, J.A., Pierce, R.B., Simonson, T.D. (2001) An overview of northern pike regulations in North America. *Fisheries* **26,** 6-13.

Paul, A.J., Post, J.R., Stelfox, J.D. (2003) Can anglers influence the abundance of native and nonnative salmonids in a stream from the Canadian Rocky Mountains? *North American Journal of Fisheries Management* **23,** 109-119.

Peterson, J.T., Evans, J.W. (2003) Quantitative decision analysis for sport fisheries management. *Fisheries* **28,** 10-21.

Pierce, R.B., Tomcko, C.M., Schupp, D.M. (1995) Exploitation of northern pike in seven small north-central Minnesota lakes. *North American Journal of Fisheries Management* **15,** 601-609.

Pigliucci, M. (2005) Evolution of phenotypic plasticity: where are we going now? *Trends in Ecology and Evolution* **20,** 481-486.

Post, J.R., Mushens, C., Paul, A., Sullivan, M. (2003) Assessment of alternative harvest regulations for sustaining recreational fisheries: model development and application to bull trout. *North American Journal of Fisheries Management* **23,** 22-34.

Post, J.R., Parkinson, E.A. (2012) Temporal and spatial patterns of angler effort across lake districts and policy options to sustain recreational fisheries. *Canadian Journal of Fisheries and Aquatic Sciences* **69,** 321-329.

Post, J.R., Persson, L., Parkinson, E.A., van Kooten, T. (2008) Angler numerical response across landscapes and the collapse of freshwater fisheries. *Ecological Applications* **18,** 1038-1049.

Post, J.R., Sullivan, M., Cox, S.*, et al.* (2002) Canada's recreational fisheries: the invisible collapse? *Fisheries* **27,** 6-17.

Radomski, P.J., Grant, G.C., Jacobson, P.C., Cook, M.F. (2001) Visions for recreational fishing regulations. *Fisheries* **26,** 7-18.

Reynolds, J.D., Jennings, S., Dulvy, N.K. (2001) Life histories of fishes and population response to exploitation. In: *Conservation of Exploited Species*. (Eds. J.D. Reynolds, G.M. Mace, K.H. Redford, J.G. Robinson), Cambridge University Press, Cambridge, UK, pp. 147-168.

Reynolds, J.D., Webb, T.J., Hawkins, L.A. (2005) Life history and ecological correlates of extinction risk in European freshwater fishes. *Canadian Journal of Fisheries and Aquatic Sciences* **692,** 854-862.

Ricker, W.E. (1954a) Effects of compensatory mortality upon population abundance. *Journal of Wildlife Management* **18,** 45-51.

Ricker, W.E. (1954b) Stock and recruitment. *Journal of the Fisheries Research Board of Canada* **11,** 559-623.

Rochet, M.J., Cornillon, P.A., Sabatier, R., Pontier, D. (2000) Comparative analysis of phylogenetic and fishing effects in life history patterns of teleost fishes. *Oikos* **91,** 255-270.

Roedel, P.M. (1975) A summary and critique of the symposium on optimal sustainable yield. In: *Optimum Sustainable Yield as a Concept in Fisheries Management. American Fisheries Society Special Publication*, American Fisheries Society, Bethesda, MD, pp. 79-89.

Rose, K.A. (2005) Lack of relationship between simulated fish population responses and their life history traits: inadequate models, incorrect analysis, or site-specific factors? *Canadian Journal of Fisheries and Aquatic Sciences* **62,** 886-902.

Rose, K.A., Cowan, J.H., Jr., Winemiller, K.O., Myers, R.A., Hilborn, R. (2001) Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. *Fish and Fisheries* **2,** 293-327.

U.S. Fish and Wildlife Service (2010) *Species Information: Threatened and Endangered Animals and Plants*. Washington D.C. 20240. <http://ecos.fws.gov/speciesProfile/profile/speciesProfile.action?spcode=E065

van Poorten, B.T., Post, J.R. (2005) Seasonal fishery dynamics of a previously unexploited rainbow trout population with contrasts to established fisheries. *North American Journal of Fisheries Management* **25,** 329-345.

Vila-Gispert, A., Moreno-Amich, R. (2002) Life-history patterns of 25 species from European freshwater fish communities. *Environmental Biology of Fishes* **65,** 387-400.

Wilberg, M.J., Bence, J.R., Eggold, B.T., Makauskas, D., Clapp, D.F. (2005) Yellow perch dynamics in southwestern Lake Michigan during 1986–2002. *North American Journal of Fisheries Management* **25,** 1130-1152.

Wilen, J.E., Smith, M.D., Lockwood, D., Botsford, L.W. (2002) Avoiding surprises: incorporating fisherman behavior into management models. *Bulletin of Marine Science* **70,** 553-575.

Winemiller, K.O. (2005) Life history strategies, population regulation, and implications for fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences* **62,** 872-885.

Winemiller, K.O., Rose, K.A. (1992) Patterns of life-history diversification in North American fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences* **49,** 2196-2218.

Wootton, R.J. (1984) Introduction: strategies and tactics in fish reproduction. In: *Fish reproduction: strategies and tactics*. (Eds. G.W. Poots, R.J. Wootton), Academic Press, London, pp. 1-12.

Worm, B., Hilborn, R., Baum, J.K., *et al.* (2009) Rebuilding global fisheries. *Science* **325,** 578-585.

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

* See details in Table S1

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

Figure captions

Figure 1. Fishery components and their interactions. For an overview of the corresponding integrated bioeconomic model, see Figure 2.

Figure 2. Schematic overview of the integrated bioeconomic model. Alphabetized black circles indicate model elements described in the section “Methods, Model components” Dashed lines highlight differences between model scenarios with constant vs. dynamic fishing effort.

Figure 3. Qualitative description of variation in biological characteristics among the five considered fish life-history types. Small, medium, and large circles represent low/small, intermediate, and high/large levels, respectively.

Figure 4. Qualitative description of angler type diversity in preferences for fishery attributes and fishing practices. Small, medium, and large-sized dots indicate low/small, intermediate, and high/large levels, respectively.

Figure 5. Impacts of fishing, over a range of minimum-size limits (as a percentage of $L_{\max}$) and annual fishing efforts, on the density of aged 1 year and older, on the biomass of fish aged 1 year and older, and on the spawning-potential ratio SPR (rows), across the five considered fish life-history types (columns). The shown levels correspond to fished conditions relative to unexploited conditions. Continuous contours represent relative levels smaller than 1 (greyscale bar). Dotted contours represent values relative levels greater than 1. All panels are based on considering consumptive anglers fishing with constant effort and harvesting all harvestable fish caught.

Figure 6. Impacts of fishing, over a range of minimum-size limits (as a percentage of $L_{\max}$), and license densities, on the spawning-potential ratio (grey contour areas) and on the annual fishing efforts ($h \cdot ha^{-1}$; grey contour curves), across the five considered fish life-history types (columns) and four different populations of angler types (rows); both homogeneous (rows 1-

3) and mixed angler populations (row 4; with a composition of 40%:30%:30% generic, consumptive, and trophy anglers, respectively). Grey diamonds indicate optimal regulations. All panels are based on considering anglers responding dynamically to the quality of their fishing experience.

Figure 7. Predicted optimal regulations, and biological and social conditions under these regulations, for the five considered fish life-history types. (a) Optimal minimum-size limit (as a percentage of $L_{\max}$), (b) optimal license density, (c) spawning-potential ratio SPR, (d) total utility, and (e) annual fishing effort. Grey symbols correspond to homogeneous angler populations and black symbols to mixed angler populations (with percentages as shown for generic, consumptive, and trophy anglers, respectively). In (c), a SPR below the dashed line indicates a risk of recruitment overfishing (SPR < 0.35) and a SPR below the dotted line indicates critical overfishing (SPR < 0.20).

Figure 8. Relative participation, under optimal regulations, of the three considered angler types– (a) generic, (b) consumptive, and (c) trophy anglers – in four mixed angler populations (indicated by differently shaped symbols) targeting one of the five considered fish life-history types. Here, relative participation is defined (Table A1, equation 7c) as the ratio between the proportion of the fishing effort attributed to an angler type, and the corresponding proportion of that angler type in the mixed angler population.

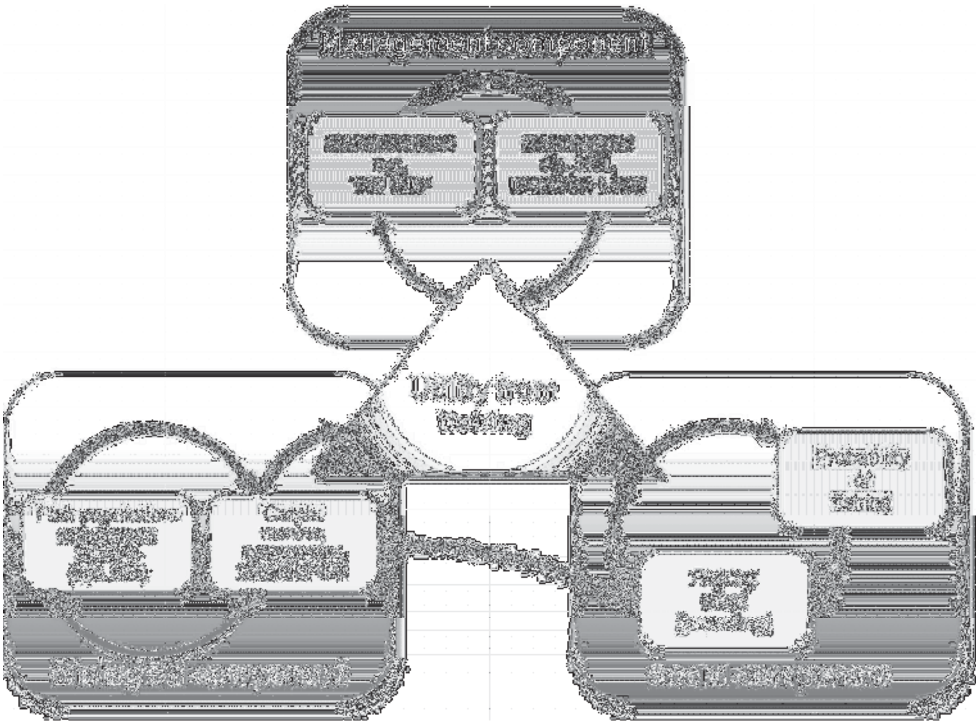
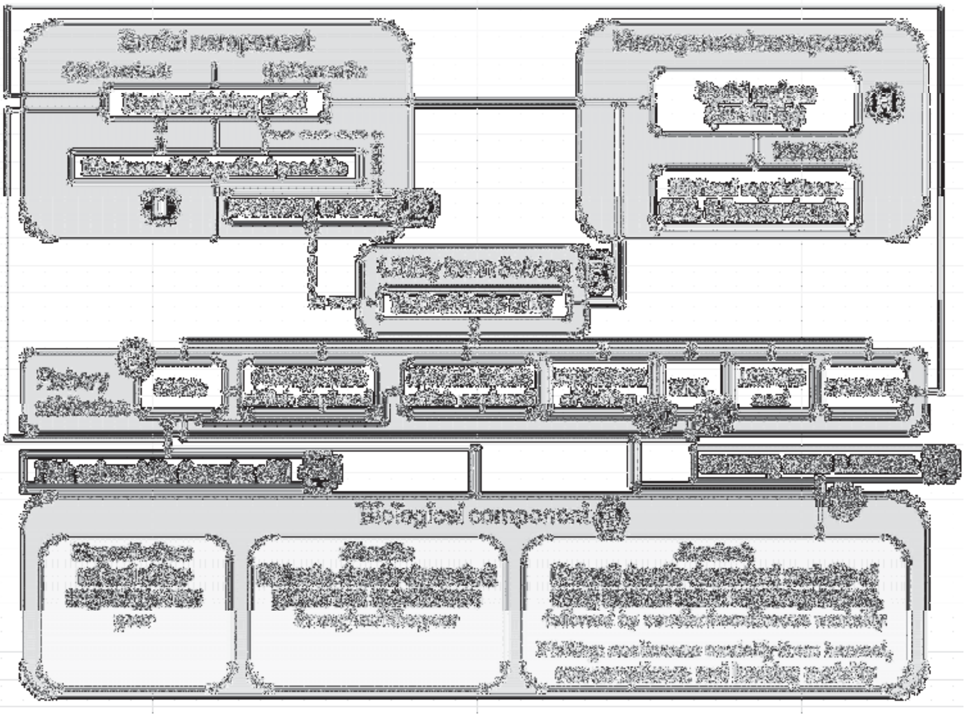

Management component
Utility from fishing
Probability
Biological component
Social component

Figure 1



Social component
Management component
Fishery
Biological component

Figure 2

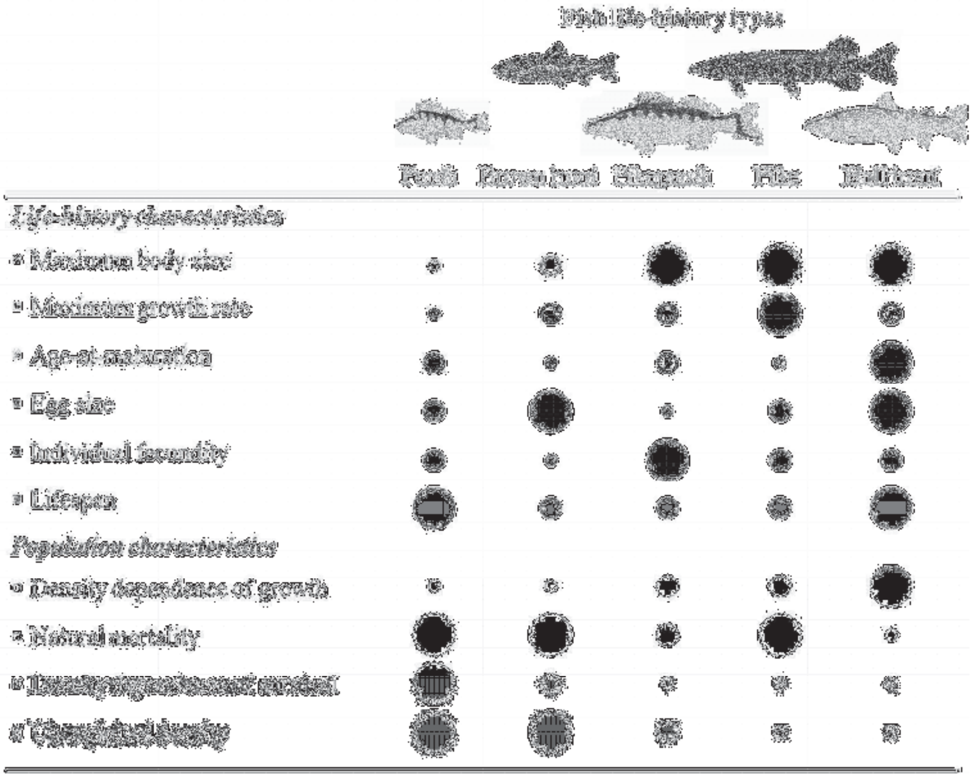

Fish life-history types
Perch
Brown trout
Pikeperch
Pike
Halibut
Life-history characteristics
Maximum body size
Maximum growth rate
Age-at-maturation
Egg size
Individual fecundity
Lifespan
Population characteristics
Density dependence of growth
Natural mortality

Figure 3

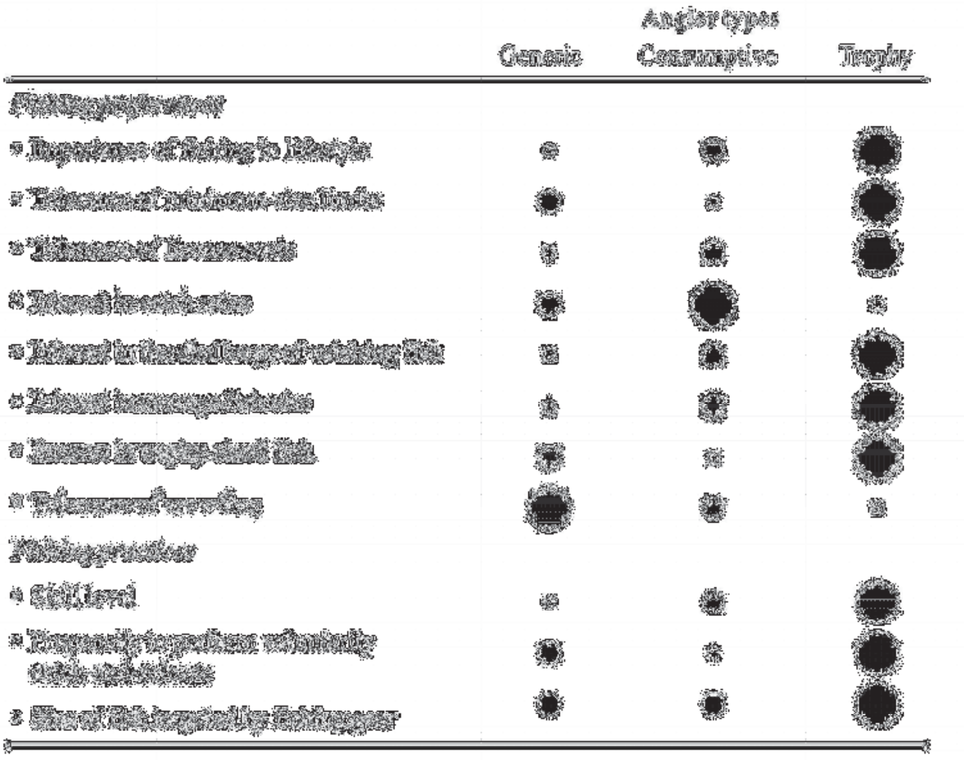

Angler types
Generic
Consumptive
Trophy
Importance of fishing in lifestyle
Interest in the challenge of catching fish
Tolerance of crowding
Fishing practices
Skill level

Figure 4

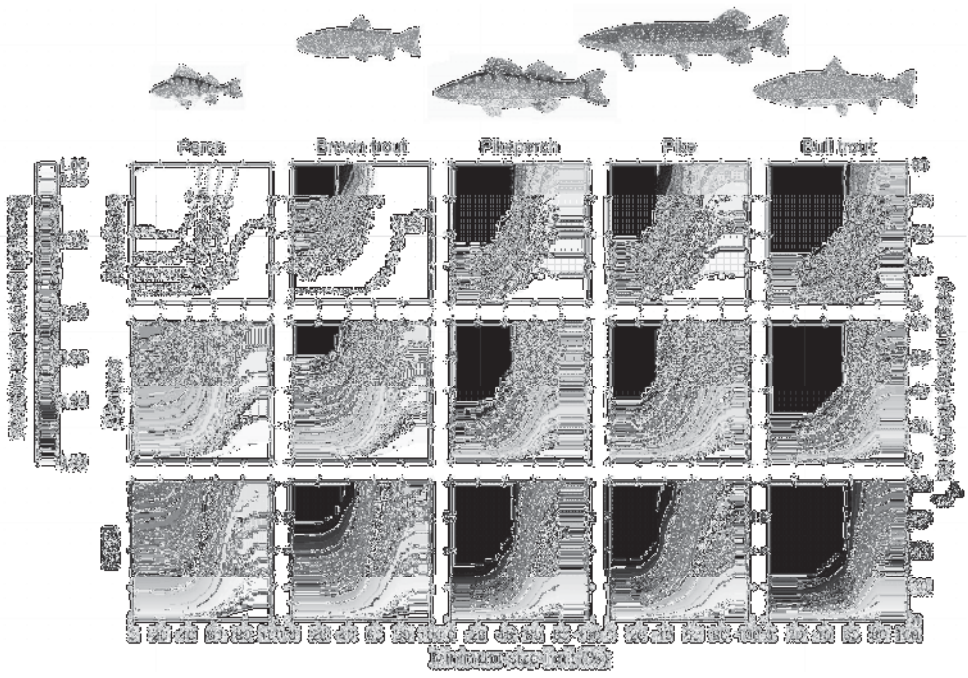

Perca
Brown trout
Pikeperch
Pike
Bull trout
1.00
0.95
0 20 40 60 80 100
Minimum size limit (%)

Figure 5

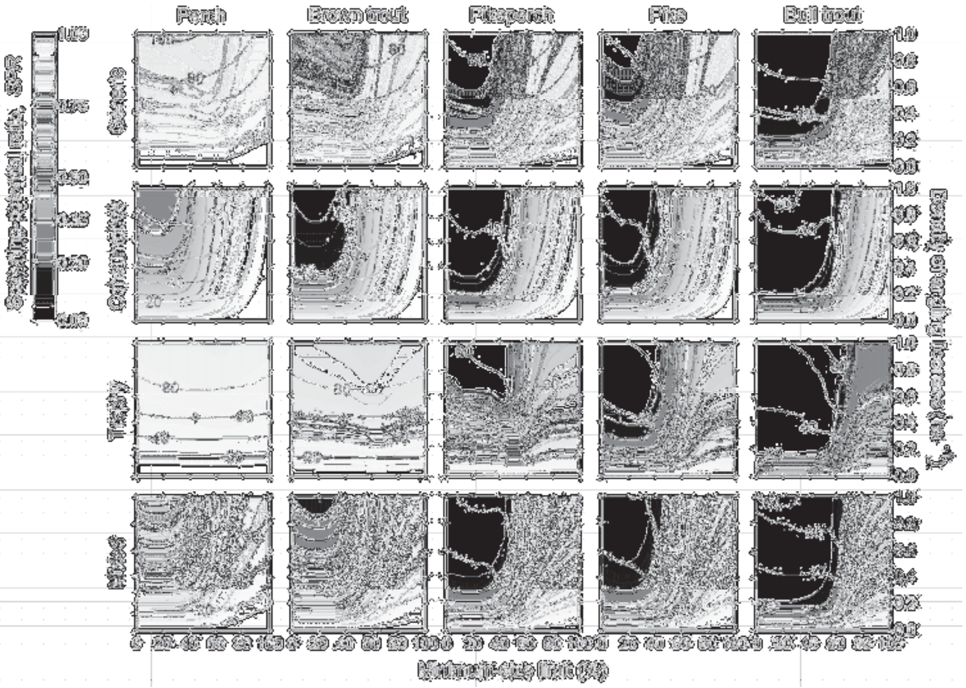

Perch
Brown trout
Pikeperch
Pike
Bull trout
Spawning potential ratio, SPR
1.00
0.75
0.50
0.00
Ontogenetic
Trophy
Mixed
1.0
0.8
0.6
0.4
0.2
0.0
0
20
40
60
80
100

Figure 6

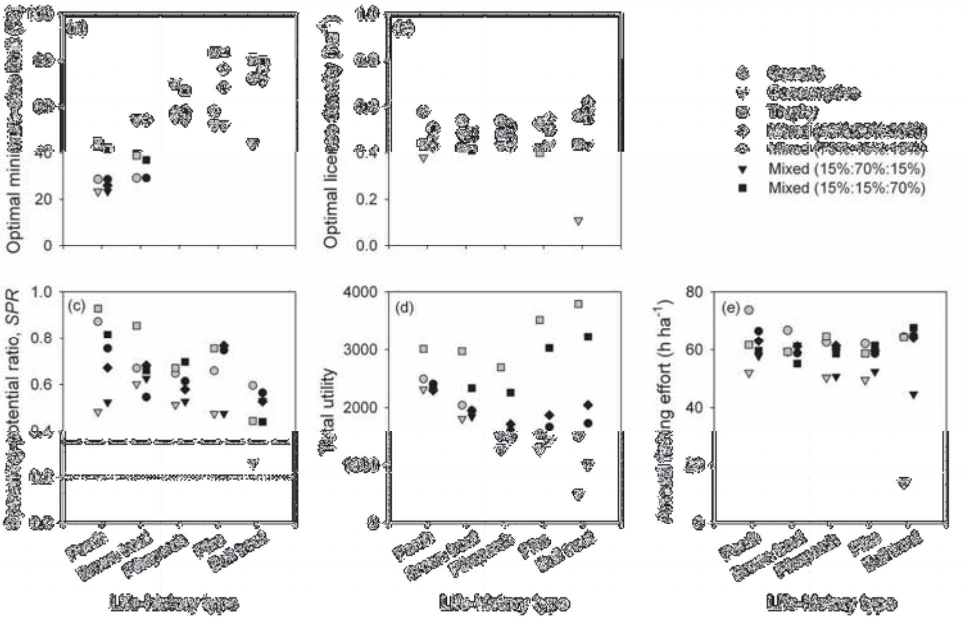

(a)
Optimal minimum-size limit (cm)
0
20
40
60
80
100
(b)
Optimal licence density (ha-1)
0.0
0.2
0.4
0.6
0.8
1.0
Casual
Consumptive
Trophy
Mixed (33%:33%:33%)
Mixed (70%:15%:15%)
Mixed (15%:70%:15%)
Mixed (15%:15%:70%)
(c)
Spawning potential ratio, SPR
0.0
0.2
0.4
0.6
0.8
1.0
(d)
Total utility
0
1000
2000
3000
4000
(e)
Annual fishing effort (h ha-1)
0
20
40
60
80
Perch
Brown trout
Pikeperch
Pike
Bull trout
Life-history type
Life-history type
Life-history type

Figure 7

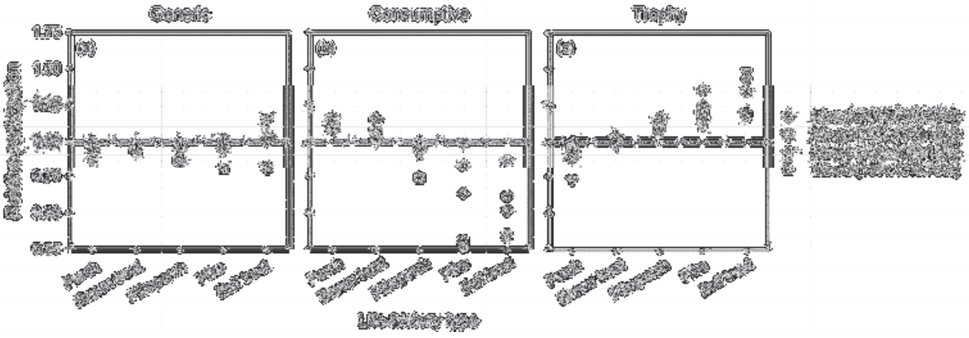

Genetic
Consumptive
Trophy
(a)
(b)
(c)
1.75
1.50
1.25
1.00
0.75
Life-history type

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	$U_{\mathrm{f}j} = U_{0j} + U_{\mathrm{c}j} + U_{\mathrm{s}j} + U_{\mathrm{x}j}$ $+ U_{\mathrm{a}j} + U_{\mathrm{r}j} + U_{\mathrm{o}j}$	Conditional indirect utility gained by an angler of type j from choosing to fish (where U_{0j} is the basic utility gained from fishing, $U_{\mathrm{c}j}$ is the PWU of daily catch, $U_{\mathrm{s}j}$ is the PWU of average size of fish caught annually, $U_{\mathrm{x}j}$ is the PWU of maximum size of fish caught annually, $U_{\mathrm{a}j}$ is the PWU of angler crowding, $U_{\mathrm{r}j}$ is the PWU of minimum-size limit, and $U_{\mathrm{o}j}$ is the PWU of annual license cost).
	Angler-effort dynamics	
2a	$p_{\mathrm{f}j} = \exp(\hat{U}_{\mathrm{f}j}) / [\exp(U_{\mathrm{n}}) + \exp(\hat{U}_{\mathrm{f}j})]$	Probability an angler of type j chooses to fish, over the alternative to not fish (where $\hat{U}_{\mathrm{f}j}$ applies to the previous year and U_{n} is the utility gained from not fishing)
2b	$p_{\mathrm{F}j} = (1-\varphi) p_{\mathrm{f}j} + \varphi \hat{p}_{\mathrm{F}j}$	Realized probability an angler of type j chooses to fish (where $\hat{p}_{\mathrm{F}j}$ applies to the previous year)

2c	$D_j = p_{\mathrm{F}j} D_{\mathrm{max}}$	Number of days an angler of type j chooses to fish during a year
2d	$A_{\mathrm{L}j} = \rho_j A_{\mathrm{L}}$	Density of licensed anglers of type j
2e	$E_j = D_j A_{\mathrm{L}j} \Psi$	Total annual realized fishing effort density by anglers of type j
2f	$e_{jt} = \begin{cases} E_j / S_{\mathrm{F}} & \text{if } t \le S_{\mathrm{F}} \\ 0 & \text{if } t > S_{\mathrm{F}} \end{cases}$	Instantaneous fishing effort density at time t by anglers of type j
	Age-structured fish population	
3a	$N_{\mathrm{total}} = \sum_{a=0}^{a_{\mathrm{max}}} N_a$	Total fish population density
3b	$B_{\mathrm{total}} = \sum_{a=0}^{a_{\mathrm{max}}} N_a W_a$	Total fish biomass density
	Growth	
4a	$h = h_{\mathrm{max}} / [1 + B_{\mathrm{total}} / B_{1/2}]$	Maximum annual growth of a fish dependent on the total fish biomass density at the beginning of the year
4b	$p_a = \begin{cases} 1 - \frac{G}{3+G}(1 + L_{a0} / h) & \text{if } a \ge a_{\mathrm{m}} - 1 \\ 1 & \text{if } a < a_{\mathrm{m}} - 1 \end{cases}$	Proportion of the growing season during which a fish of age a allocates energy to growth
4c	$g_{at} = \begin{cases} h / S_{\mathrm{G}} & \text{if } t \le p_a S_{\mathrm{G}} \\ 0 & \text{if } t > p_a S_{\mathrm{G}} \end{cases}$	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	$R_a = \begin{cases} \delta W_{at_{\mathrm{R}}} GSI / W_{\mathrm{e}} & \text{if } a \ge a_{\mathrm{m}} \\ 0 & \text{if } a < a_{\mathrm{m}} \end{cases}$	Annual fecundity of a female of age a given their

		mass at time t_R
5b	$b = \Phi \sum_{a=a_{\mathrm{m}}}^{a_{\max}} R_a N_a$	Annual population fecundity density (pulsed at the beginning of the year)
5c	Beverton-Holt: $s_0 = \alpha_{\mathrm{BH}} / (1+\beta_{\mathrm{BH}} b)$ Ricker: $s_0 = \alpha_{\mathrm{R}} \exp(-\beta_{\mathrm{R}} b)$	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	$L_{50} = z_j L_{\max} + L_{\mathrm{shift}}$	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	$H_{ajt} = \begin{cases} 1 & \text{if } L_{at} \geq MSL \\ f_{\mathrm{n}j} & \text{if } L_{at} < MSL \end{cases}$	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	$C_{\mathrm{H}jt} = \min(C_{jt}, c_{\max j} e_{jt} / \Psi)$	Instantaneous harvest rate by anglers of type j at time t
6g	$f_{\mathrm{H}jt} = \dfrac{C_{\mathrm{H}jt}}{C_{jt}} + f_{\mathrm{h}j} \dfrac{C_{jt} - C_{\mathrm{H}jt}}{C_{jt}}$	Proportion of harvestable fish killed by anglers of type j at time t
6h	$m_{\mathrm{f}ajt} = f_{\mathrm{H}jt} c_{ajt} H_{ajt} + f_{\mathrm{h}j} c_{ajt} (1 - H_{ajt})$	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	$\frac{dN_a}{dt} = -d_{at}N_a$	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	$P_{\mathrm{R}j} = \frac{E_j / \sum_i E_i}{\rho_j}$	Relative participation of anglers of type j in a mixed angler population

Table A2. Model variables. Bioeconomic model equations are listed in Table A1 and parameters for life-history types are listed in Table S1. 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)	$0 - L_{\max}$

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 ($B_{\text{total}} = 0$) (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 (†)
$B_{1/2}$	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 (†)

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

* O_{o} is the observed annual fishing license cost, C_{Do} is the observed average daily catch, $\bar{L}_{\mathrm{o}}$ is the observed average size of fish caught annually, and L_{xo} is the observed maximum size of fish caught annually (defined as the 95th percentile of the size distribution of fish caught annually).

Parameters for angler types

Table S3. Parameters, with their units and values, for the three modelled angler types (generic, consumptive, and trophy anglers). Where a single parameter value is given, it is 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
$f_{\text{h}j}$	Proportion of fish dying from hooking mortality	6g, 6h	0.05
$f_{\text{n}j}$	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

* Predicted vulnerability values are in fairly good agreement with empirical information for similar species, e.g.:, yellow perch at 27 cm is 100% vulnerable (Wilberg et al., 2005), compared with 95% for European perch in our model; rainbow trout at 30-35 cm is 100% vulnerable (van Poorten and Post, 2005), compared with 96%-99% for brown trout in our model; pike at 55 cm is 100% vulnerable (Arlinghaus et al., 2009), compared with 100% for pike in our model; bull trout at 35 cm is 100% vulnerable (Paul et al., 2003), compared with 90% for bull trout in our model.

† The intercept u_{4j}, from the PWU function of average size of fish caught annually, for trophy anglers represents a 5% increase of the average-size baseline value relative to that of generic and consumptive anglers. This reflects the fact that more specialized anglers have 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)	$\bar{L}_{\mathrm{e}}$	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)	$L_{\mathrm{x\,e}}$	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 (€) (Table S2, equation 8f)	O_e	75

Sources: (1) Almodóvar and Nicola (1998), (2) unpublished data (M. Dorow and R. Arlinghaus), (3) Gabelhouse (1984), (4) Isermann et al. (2005), (5) Paul et al. (2003), (6) Pierce et al. (1995), (7) Swales and Fish (1986).

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

To parameterize the Ricker (R) and Beverton-Holt (BH) stock-recruitment relationships (Table A1, equation 5c), empirical length-at-age and biomass-density data from various studies were used to estimate the maximum proportion of offspring surviving from spawning to post-hatch (α_{R} or α_{BH}) and the inverse population density at which offspring survival is divided by $e = 2.71$ (β_{R}) or 2 (β_{BH}).

For pike, egg density was determined using a relative fecundity relationship (Craig and Kipling, 1983), adult biomass (Kipling, 1983b), and corresponding area (1480 ha, Le Cren et al., 1977), with the density of pike aged 1 year back-calculated from natural mortality (Kipling and Frost, 1970) and the abundance of pike aged 2 years (Le Cren et al., 1977). For pikeperch, egg density was determined using the relative fecundity relationship (Schlumberger and Proteau, 1996), adult biomass, and corresponding area (19700 ha, unpublished data, H. Winkler), with adult biomass back-calculated from commercial catch (Lehtonen et al., 1996) and exploitation rate (Gröger et al., 2007), and the density of pikeperch aged 1 year back-calculated from natural mortality information (Lind, 1977) and the abundance of pikeperch aged 2 years (Gröger et al., 2007). For perch, egg density was determined using a relative fecundity relationship (Treasurer, 1981), adult biomass (Craig et al., 1979), and corresponding area (1480 ha, Le Cren et al., 1977), with the density of perch aged 1 year back-calculated from natural mortality information (Le Cren et al., 1977) and the abundance of perch aged 2 years (Le Cren et al., 1977). For brown trout, a stock-recruitment relationship for a migratory brown-trout population from England (Elliott, 1985) was scaled so that egg density and the density of brown trout aged 1 year (May/June) in the spawning stream result in a population density in line with literature values: the chosen target fish density of 300 ha^{-1} is roughly based on the density of 229 ha^{-1} observed for a British lake (Swales, 1986), although this is low compared with the density of 560-4900 ha^{-1} observed for more productive rivers in Spain (Nicola and Almodóvar, 2002). For bull trout, the stock-recruitment relationship reported by Post et al. (2003) was scaled to account for the corresponding lake area (646 ha, (Johnston et al., 2007).

The population densities predicted using these estimates under unexploited conditions generally fall within the ranges reported in the literature (although pikeperch are likely more abundant in our model than in average natural settings, whereas the densities of perch and bull trout in our model are on the low side of the reported empirical ranges): for perch, 779 ha^{-1} in our model, compared with 675-4189 ha^{-1} (Craig et al., 1979); for brown trout, 300 ha^{-1} in our model, compared with 229 ha^{-1} in a British lake (Swales, 1986) and 560-4900 ha^{-1} in more productive rivers in Spain (Nicola and Almodóvar, 2002); for pikeperch aged 3 years and older, 56 ha^{-1} in our model, compared with 26-42 ha^{-1} (Lehtonen, 1979); for pike, 23 ha^{-1} in our model, compared with 11.0-55.1 ha^{-1} (Pierce et al., 1995); for bull trout, 12 ha^{-1} in our model, and for adult bull trout, 4.4 ha^{-1} in our model, compared with, respectively, 12-38 ha^{-1} (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	Life-history parameter 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%

Trophy	-10%	-18.2%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	172.7%	9.1%	0.0%
	+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

Supplementary references

Almodóvar, A., Nicola, G.G. (1998) Assessment of a brown trout *Salmo trutta* population in the River Gallo (central Spain): angling effects and management implications (Salmonidae). *Italian Journal of Zoology* **65,** 539-539.

Almodóvar, A., Nicola, G.G. (2004) Angling impact on conservation of Spanish stream-dwelling brown trout *Salmo trutta*. *Fisheries Management and Ecology* **11,** 173-182.

Arlinghaus, R., Matsumura, S., Dieckmann, U. (2009) Quantifying selection differentials caused by recreational fishing: development of modeling framework and application to reproductive investment in pike (*Esox lucius*). *Evolutionary Applications* **2,** 335-355.

Biró, P. (1985) Dynamics of the pikeperch, *Stizostedion lucioperca* (L.), in Lake Balaton. *Internationale Revue der gesamten Hydrobiologie und Hydrographie* **70,** 471-490.

Buijse, A., Pet, J.S., van Densen, W.L.T., Machiels, M.A.M., Rabbinge, R. (1992) A size- and age-structured simulation model for evaluating management strategies in a multispecies gill net fishery. *Fisheries Research* **13,** 95-117.

Craig, J.F., Kipling, C. (1983) Reproduction effort versus the environment; case-histories of Windermere perch, *Perca fluviatilis* L., and pike, *Esox lucius* L. *Journal of Fish Biology* **22,** 713-727.

Craig, J.F., Kipling, C., Le Cren, E.D., McCormack, J.C. (1979) Estimates of the numbers, biomass and year-class strengths of perch (*Perca fluviatilis* L.) in Windermere from 1967 to 1977 and some comparisons with earlier years. *Journal of Animal Ecology* **48,** 315-325.

Crisp, D.T. (1994) Reproductive investment of female brown trout, *Salmo trutta* L., in a stream and reservoir system in northern England. *Journal of Fish Biology* **44,** 343-349.

Elliott, J.M. (1985) The choice of a stock-recruitment model for migratory trout, *Salmo trutta*, in an English Lake District stream. *Archiv für Hydrobiologie* **104,** 145-168.

Froese, R., Pauly, D. (2010) Fishbase, Version 05/2010. (Eds. R. Froese, D. Pauly), Available from www.fishbase.org.

Frost, W.E., Kipling, C. (1967) A study of reproduction, early life, weight-length relationship and growth of pike, *Esox lucius* L., in Windermere. *Journal of Animal Ecology* **36,** 651-693.

Gabelhouse, D.W., Jr. (1984) A length-categorization system to assess fish stocks. *North American Journal of Fisheries Management* **4,** 273-285.

Gould, W.R. (1987) Features in the early development of bull trout (*Salvelinus confluentus*). *Northwest Science* **61,** 264-268.

Gröger, J.P., Winkler, H., Rountree, R.A. (2007) Population dynamics of pikeperch (*Sander lucioperca*) and its linkage to fishery driven and climatic influences in a southern Baltic lagoon of the Darss-Zingst Bodden Chain. *Fisheries Research* **84,** 189-201.

Hahn, J. (1991) Angler specialization: measurement of a key sociological concept and implications for fisheries management decisions. *American Fisheries Society Symposium* **12,** 380-389.

Heibo, E., Magnhagen, C., Vøllestad, L.A. (2005) Latitudinal variation in life-history traits in Eurasian perch. *Ecology* **86,** 3377-3386.

Hubenova, T., Zaikov, A., Vasileva, P. (2007) Investigation on fecundity, follicles and free embryo size of pond-reared pike (*Esox lucius*) of different age and size. *Aquaculture International* **15,** 235-240.

Isermann, D.A., Willis, D.W., Lucchesi, D.O., Blackwell, B.G. (2005) Seasonal harvest, exploitation, size selectivity, and catch preferences associated with winter yellow perch anglers on South Dakota lakes. *North American Journal of Fisheries Management* **25,** 827-840.

Jenkins, T.M., Jr., Diehl, S., Kratz, K.W., Cooper, S.D. (1999) Effects of population density on individual growth of brown trout in streams. *Ecology* **80,** 941-956.

Johnston, F.D., Arlinghaus, R., Stelfox, J., Post, J.R. (2011) Decline in angler use despite increased catch rates:anglers' response to the implementation of a total catch-and-release regulation. *Fisheries Research* **110,** 189-197.

Johnston, F.D., Post, J.R. (2009) Density-dependent life-history compensation of an iteroparous salmonid. *Ecological Applications* **19,** 449-467.

Johnston, F.D., Post, J.R., Mushens, C.J., Stelfox, J.D., Paul, A.J., Lajeunesse, B. (2007) The demography of recovery of an overexploited bull trout, *Salvelinus confluentus*, population. *Canadian Journal of Fisheries and Aquatic Sciences* **64,** 113-126.

Joynt, A., Sullivan, M.G. (2003) *Fish of Alberta*, Lone Pine Publishing, Edmonton, AB, Canada.

Kipling, C. (1983a) Changes in the growth of pike (*Esox lucius*) in Windermere. *Journal of Animal Ecology* **52,** 647-657.

Kipling, C. (1983b) Changes in the population of pike (*Esox lucius*) in Windermere from 1944 to 1981. *Journal of Animal Ecology* **52,** 989-999.

Kipling, C., Frost, W.E. (1970) A study of mortality, population numbers, year class strengths, production and food consumption of pike, *Esox lucius* L., in Windermere from 1944 to 1962. *Journal of Animal Ecology* **39,** 115-157.

Klemetsen, A., Amundsen, P.A., Dempson, J.B*., et al.* (2003) Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecology of Freshwater Fish* **12,** 1-59.

Le Cren, E.D. (1958) Observations on the growth of perch (*Perca fluviatilis* L.) over twenty-two years with special reference to the effects of temperature and changes in population density. *Journal of Animal Ecology* **27,** 287-334.

Le Cren, E.D., Kipling, C., McCormack, J.C. (1977) A study of the numbers, biomass and year-class strengths of perch (*Perca fluviatilis* L.) in Windermere from 1941 to 1966. *Journal of Animal Ecology* **46,** 281-207.

Lehtonen, H. (1979) Stock assessment of pike-perch (*Stizostedion lucioperca* L.) in the Helsinki sea area. *Finnish Fisheries Research* **3,** 1-12.

Lehtonen, H., Hansson, S., Winkler, H. (1996) Biology and exploitation of pikeperch, *Stizostedion lucioperca* (L.), in the Baltic Sea area. *Annales Zoologici Fennici* **33,** 525-535.

Lind, E.A. (1977) A review of pikeperch (*Stizostedion lucioperca*), Eurasian perch (*Perca fluviatilis*), and ruff (*Gymnocephalus cernua*) in Finland. *Journal of the Fisheries Research Board of Canada* **34,** 1684-1695.

Lobón-Cerviá, J., Montañés, C., de Sostoa, A. (1986) Reproductive ecology and growth of a population of brown trout (*Salmo trutta* L.) in an aquifer-fed stream of Old Castile (Spain). *Hydrobiologia* **135,** 81-94.

Nicola, G.G., Almodóvar, A. (2002) Reproductive traits of stream-dwelling brown trout *Salmo trutta* in contrasting neighbouring rivers of central Spain. *Freshwater Biology* **47,** 1353-1365.

Øxnevad, S.A., Heibo, E., Vøllestad, L.A. (2002) Is there a relationship between fluctuating asymmetry and reproductive investment in perch (*Perca fluviatilis*)? *Canadian Journal of Zoology* **80,** 120-125.

Parker, B.R., Schindler, D.W., Wilhelm, F.M., Donald, D.B. (2007) Bull trout population responses to reductions in angler effort and retention limits. *North American Journal of Fisheries Management* **27,** 848-859.

Paul, A.J., Post, J.R., Stelfox, J.D. (2003) Can anglers influence the abundance of native and nonnative salmonids in a stream from the Canadian Rocky Mountains? *North American Journal of Fisheries Management* **23,** 109-119.

Pierce, R.B., Tomcko, C.M. (2003) Interrelationships among production, density, growth, and mortality of northern pike in seven north-central Minnesota lakes. *Transactions of the American Fisheries Society* **132,** 143-153.

Pierce, R.B., Tomcko, C.M. (2005) Density and biomass of native northern pike populations in relation to basin-scale characteristics of north-central Minnesota lakes. *Transactions of the American Fisheries Society* **134,** 231-241.

Pierce, R.B., Tomcko, C.M., Margenau, T.L. (2003) Density dependence in growth and size structure of northern pike populations. *North American Journal of Fisheries Management* **23,** 331-339.

Pierce, R.B., Tomcko, C.M., Schupp, D.M. (1995) Exploitation of northern pike in seven small north-central Minnesota lakes. *North American Journal of Fisheries Management* **15,** 601-609.

Post, J.R., Mushens, C., Paul, A., Sullivan, M. (2003) Assessment of alternative harvest regulations for sustaining recreational fisheries: model development and application to bull trout. *North American Journal of Fisheries Management* **23,** 22-34.

Rónyai, A. (2007) Induced out-of-season and seasonal tank spawning and stripping of pike perch (*Sander lucioperca* L.). *Aquaculture Research* **38,** 1144-1151.

Schlumberger, O., Proteau, J.P. (1996) Reproduction of pike-perch (*Stizostedion lucioperca*) in captivity. *Journal of Applied Ichthyology* **12,** 149-152.

Swales, S. (1986) Population dynamics, production and angling catch of brown trout, *Salmo trutta*, in a mature upland reservoir in mid-Wales. *Environmental Biology of Fishes* **16,** 279-293.

Swales, S., Fish, J.D. (1986) Angling catch returns as indicators of the status of upland trout lakes. *Aquaculture and Fisheries Management* **17,** 75-93.

Treasurer, J. (1993) The population biology of perch, *Perca fluviatilis* L., in simple fish communities with no top piscivore. *Ecology of Freshwater Fish* **2,** 16-22.

Treasurer, J.W. (1981) Some aspects of the reproductive biology of perch *Perca fluviatilis* L. Fecundity, maturation and spawning behaviour. *Journal of Fish Biology* **18,** 729-740.

Treasurer, J.W., Owen, R., Bowers, E. (1992) The population dynamics of pike, *Esox lucius*, and perch, *Perca fluviatilis*, in a simple predator-prey system. *Environmental Biology of Fishes* **34,** 65-78.

van Poorten, B.T., Post, J.R. (2005) Seasonal fishery dynamics of a previously unexploited rainbow trout population with contrasts to established fisheries. *North American Journal of Fisheries Management* **25,** 329-345.

Wilberg, M.J., Bence, J.R., Eggold, B.T., Makauskas, D., Clapp, D.F. (2005) Yellow perch dynamics in southwestern Lake Michigan during 1986–2002. *North American Journal of Fisheries Management* **25,** 1130-1152.

Willis, D.W. (1989) Proposed standard length-weight equation for northern pike. *North American Journal of Fisheries Management* **9,** 203-208.

Ylikarjula, J., Heino, M., Dieckmann, U., Kaitala, V. (2002) Does density-dependent individual growth simplify dynamics in age-structured populations? A general model applied to perch, *Perca fluiatilis*. *Annales Zoologici Fennici* **39,** 99-107.