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ARTICLE

Optimal management of recreational fisheries in the presence of hooking mortality and noncompliance — predictions from a bioeconomic model incorporating a mechanistic model of angler behavior

Fiona D. Johnston, Ben Beardmore, and Robert Arlinghaus

Abstract: Using a bioeconomic model, we systematically investigated how hooking mortality and regulatory noncompliance influenced management outcomes across a range of freshwater fish species exploited by diverse angler populations. The model integrated an empirically based submodel describing the behaviour of three angler types with an age-structured fish population submodel calibrated to five life-history types (LHTs). Increased hooking mortality generally undermined regulation effectiveness, decreased socially optimal input (license numbers) and output regulations (minimum-size limits), and eroded the social welfare anglers derived from the fishery. However, the results strongly varied with LHT and angler type. Noncompliance had an isolated effect, primarily affecting fish species with low compensatory reserves when hooking mortality was low. However, in the absence of regulatory constraints on effort, noncompliance facilitated recruitment overfishing and increased the minimum-size limit required to avoid it. Despite added mortality from hooking and noncompliance, the strong dependence of angler utility on catch rates usually meant socially optimal management safeguarded biological sustainability. Yet, ignoring hooking mortality and noncompliance when predicting optimal regulations often led to population collapse. To conclude, models designed to derive recommendations for recreational fisheries management must consider both hooking mortality and noncompliance. Otherwise, dissatisfied anglers or biologically overfished stocks are possible.

Résumé : En utilisant un modèle bioéconomique, nous avons systématiquement examiné l'incidence de la mortalité par hameçon et de la non-conformité aux règlements sur les résultats de gestion pour un vaste éventail d'espèces de poissons d'eau douce exploitées par différentes populations de pêcheurs sportifs. Le modèle intègre un sous-modèle à fondement empirique qui décrit le comportement de trois types de pêcheurs et un sous -modèle de population de poissons structurée par âge calibré en selon cinq types de cycle biologique (TCB). En général, l'augmentation de la mortalité par hameçon réduit l'efficacité de la réglementation, les règlements sur les entrées (nombre de permis) et sorties (limites de taille minimum) socialement optimales et le bien-être social que confère la pêche aux pêcheurs. Les résultats varient toutefois fortement selon le TCB et le type de pêcheur sportif. La non-conformité a un effet isolé, principalement sur les espèces de poissons présentant de faibles réserves compensatoires quand la mortalité par hameçon est faible. En l'absence de contrainte réglementaire concernant l'effort, la non-conformité favorise toutefois la surpêche du potentiel reproducteur et fait augmenter la limite de taille minimum nécessaire pour éviter cette surpêche. Malgré une mortalité supplémentaire par hameçon et du fait de la non-conformité, la forte dépendance de l'utilité pour les pêcheurs sur les taux de prises signifie généralement qu'une gestion socialement optimale préserve la durabilité biologique. En outre, le fait de ne pas tenir compte de la mortalité par hameçon et de la non-conformité dans les prévisions concernant la réglementation optimale mène souvent à l'effondrement de populations. En conclusion, des modèles conçus pour élaborer des recommandations pour la gestion des pêches sportives doivent prendre en considération tant la mortalité par hameçon que la non-conformité, à défaut de quoi des pêcheurs non satisfaits et la surpêche biologique des stocks sont possibles. [Traduit par la Rédaction]

Introduction

Recreational fisheries constitute the dominant user of inland fish stocks and are also becoming important in many coastal fisheries across the developed world (FAO 2012). Recreational fishing pressure has increased to such an extent in some areas that concern about the biological sustainability of exploited stocks has emerged (Post et al. 2002; Coleman et al. 2004). In response, size-based harvest regulations and daily bag limits have been widely implemented to reduce fishing mortality and to meet social objectives (Radomski et al. 2001). However, output control measures, such as minimum-size limits (MSLs), are only effective if released fish survive the catch-and-release (C&R) event (Arlinghaus et al. 2007; Coggins et al. 2007). Hooking mortality associated with C&R can be close to zero if injury is minimized and the environment is

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F.D. Johnston and R. Arlinghaus. Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany; Division of Integrative Fisheries Management, Integrative Research Institute for the Transformation of Human–Environment Systems, and Albrecht-Daniel-Thaer Institute of Agriculture and Horticulture, Faculty of Life Sciences, Humboldt-Universität zu Berlin, Philippstrasse 13, Haus 7, 10115 Berlin, Germany.
B. Beardmore. Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany; Center for Limnology, University of Wisconsin-Madison, Madison, WI 53706-1492, USA.
Corresponding author: Fiona D. Johnston (e-mail: johnston@igb-berlin.de).

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favourable (Muoneke and Childress 1994; Arlinghaus et al. 2007; Hühn and Arlinghaus 2011). However, when conditions are suboptimal, such as when water temperatures are high or when substantial injury from deep hooking or barotrauma occurs, hooking mortality rates as high as 90% can occur (Bartholomew and Bohnsack 2005; Hühn and Arlinghaus 2011). Effective management using harvest regulations demands that the downsides of C&R are considered (Post et al. 2003; Woodward and Griffin 2003; Coggins et al. 2007). Yet, in contrast with commercial fisheries models, which commonly consider discard rates and bycatch, recreational fisheries models rarely explicitly account for hooking mortality (but see Clark 1983, Post et al. 2003, Coggins et al. 2007, and Pine et al. 2008 for notable exceptions), although fishing mortality field estimates may implicitly include it.

Regulatory noncompliance is a further source of mortality that can influence the effectiveness of harvest regulations (Paragamian 1984; Post et al. 2002; Post 2013). Noncompliance is not necessarily the result of deliberate illegal harvest, but may also be due to measurement error or lack of regulation awareness (Page et al. 2004; Page and Radomski 2006). Noncompliance with daily bag limits are reportedly low (e.g., 7%; Wilberg 2009), perhaps because anglers rarely reach these limits (Baccante 1995; Radomski et al. 2001; Wilberg 2009). By contrast, noncompliance with size-based harvest regulations can be very high (e.g., >50%; Glass and Maughan 1984; Pierce and Tomcko 1998; Sullivan 2002). Moreover, if noncompliance is depensatory (Sullivan 2002; Näslund et al. 2010), it could be an important contributor to the collapse of recreational fisheries (Post et al. 2002; Post 2013) by accelerating the decline of already imperiled stocks.

How a given level of hooking mortality or noncompliance impacts the fish population, both in terms of population declines and changes in the demographic structure, will be determined by a fish populations' life-history characteristics (Coggins et al. 2007; Pine et al. 2008). Furthermore, there is an increasing recognition that accounting for angler behaviour is crucial for developing effective management strategies for recreational fisheries (Johnston et al. 2010; Abbott and Fenichel 2013; Fenichel et al. 2013). However, few studies have considered the dynamic response of anglers to changes in fishery quality in the context of hooking mortality and noncompliance impacts (but see Post et al. 2003 and Woodward and Griffin 2003 for exceptions), and none have considered the variable effort responses of diverse angler types. Thus, to systematically investigate impacts of hooking mortality and noncompliance on fish populations exploited by different types of anglers, a quantitative modelling approach that accounts for diversity in fish life history and angler behaviour seems warranted (Coggins et al. 2007; Pine et al. 2008; Johnston et al. 2013).

In fisheries science, success of management measures are often evaluated using yield-based metrics (i.e., maximum sustainable yield, MSY). This approach ignores other attributes that also influence angler utility or satisfaction and thus is not ideal for recreational fisheries (Johnston et al. 2010). Optimal social yield (OSY) incorporates the various social and economic dimensions of recreational fisheries by explicitly accounting for the contributions of a range of catch-related (e.g., trophy catch) and non-catch-related (e.g., encounters with other anglers, license fees) attributes to angler welfare (Roedel 1975; Malvestuto and Hudgins 1996; Radomski et al. 2001; Cox et al. 2003). Choice experiments are a survey tool that can be used to derive respondents' relative preferences for attributes of a fishing experience (such as catch rate) and mechanistically predict angler behaviour, particularly responses to novel scenarios such as the introduction of new management regulations (Beardmore et al. 2013; Fenichel et al. 2013; Johnston et al. 2013). By explicitly considering anglers' preferences in an mechanistic fashion in a bioeconomic modelling framework (Fenichel et al. 2013), management objectives for recreational fisheries, such as OSY, can be constructed and used to derive optimal regulations from an angler perspective.

Our study investigated the importance of hooking mortality and noncompliance using a dynamic bioeconomic model that predicted the combination of input (e.g., license number) and output (e.g., MSL) regulations that provide the greatest social welfare (i.e., OSY) to a diverse angling community exploiting a single fishery. The integrated bioeconomic model incorporated a mechanistic submodel of angler behaviour for three diverse angler types, which was linked to a biological submodel calibrated to represent five fish life-history types (LHTs). With the resulting model, we evaluated how hooking mortality and noncompliance influenced predictions about (*i*) the effectiveness of regulations for achieving biological and social sustainability, (*ii*) the potential consequences of ignoring hooking mortality and noncompliance when deriving optimal regulations, and (*iii*) the effects of hooking mortality and noncompliance on biological sustainability when the fishery cannot be managed by effort limitations, such as in open-access fisheries. Overall, the study's objective was to improve our understanding about the effects of hooking mortality and noncompliance on management outcomes. Our aim was to provide strategic insights across a range of LHTs rather than predictions for a particular fishery.

Methods

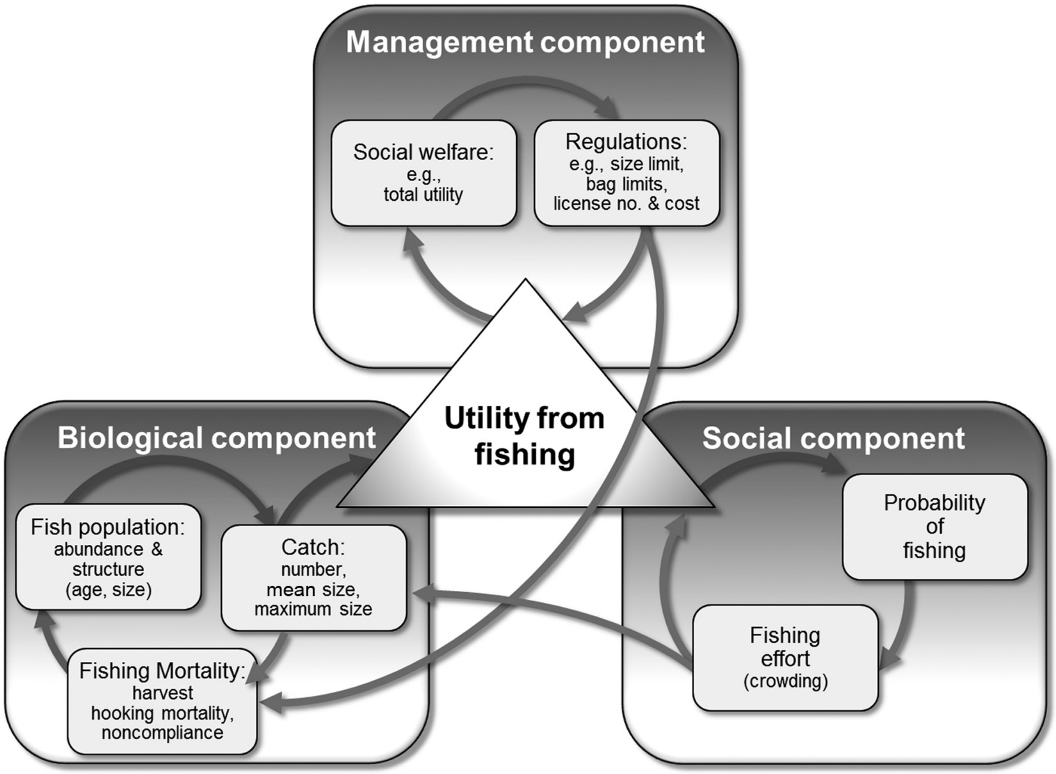
We investigated the importance of accounting for mortality from hooking and noncompliance using the bioeconomic modelling approach described by Johnston et al. (2010, 2013). To make predictions more representative, the model was adapted to include empirically described angler behaviour functions from a choice experiment conducted in northeastern Germany (Beardmore et al. 2013). The model framework included a deterministic, age-structured biological component, which described the dynamics of the fish population, a social component, which described the dynamic response of the angler population to changes in fishery attributes (e.g., catch rates, size of fish caught, crowding, regulations), and a management component, which allowed for the application of both input (e.g., license numbers) and output regulations (e.g., MSLs; Fig. 1). Model results predicted the combination of license number and MSL that provided the greatest aggregate social welfare to the angling community using the economic utility concept (Johnston et al. 2010). Model equations can be found in Table A1. Parameter values describing the fish LHTs modelled are provided in Table S1[1] of the online supplementary material.

Biological component

Details of the biological submodel can be found in Johnston et al. (2010, 2013), and we provide only a brief summary here. In short, we simulated an age-structured fish population model with two density-dependent feedbacks: (*i*) survival of the early life stage (spawning to posthatch) described by a stock–recruitment relationship and (*ii*) density-dependent somatic growth in body size, both of which are important for determining the compensatory response of fish to exploitation (Lorenzen and Enberg 2002; Lorenzen 2008). To account for the size-dependent processes inherent in a fishery, a sigmoidal vulnerability curve was used to determine vulnerability of fish to capture, and MSLs based on length were used to determine which fish were legally harvestable. Fish reproduction was assumed to occur on an annual basis at the beginning of each year, but fish mortality and somatic growth were described by continuous functions to account for

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2013-0650.

Fig. 1. Schematic of modelled fishery components and their interactions.



growth into vulnerable and legally harvestable sizes within a year and for the recapture and repeated exposure to hooking mortality of released individuals throughout the fishing season, both of which are important processes in recreational fisheries models (Coggins et al. 2007).

To examine how impacts of hooking mortality and noncompliance might differ with fish life history, we described five prototypical fish LHTs, described in detail in Johnston et al. (2013): brown trout (*Salmo trutta*), bull trout (*Salvelinus confluentus*), European perch (*Perca fluviatilis*), northern pike (*Esox lucius*), and pikeperch (also referred to as zander, *Sander lucioperca*). These LHTs were chosen because they represent the broad range of diverse life-history characteristics (see Table S1[1] and Johnston et al. 2013 for details) of species commonly targeted by freshwater recreational anglers in Europe and North America (e.g., Post et al. 2002; Almodóvar and Nicola 2004; Beardmore et al. 2011). The LHTs had different intrinsic vulnerabilities to overexploitation, being least to greatest as follows: perch, brown trout, pikeperch, northern pike, and bull trout (Johnston et al. 2013). Although bull trout is not found in Germany, where descriptions of angler behaviour were derived, it was included here to represent an extreme case of a "slow" life-history typical for slow-growing, late-maturing fish.

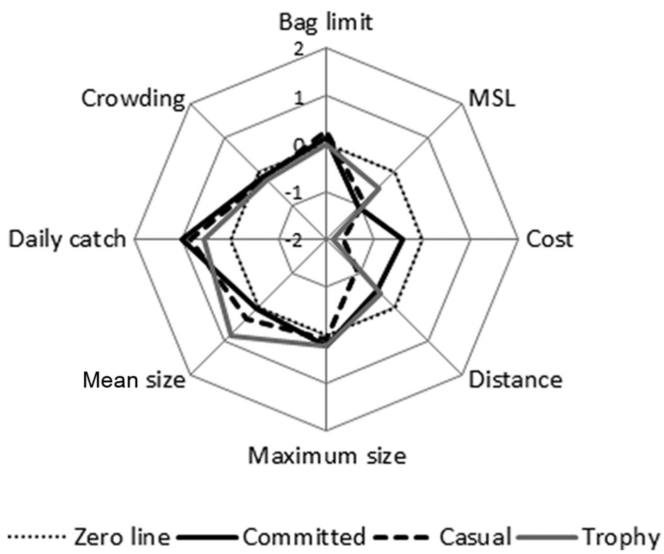
Social component

In the social submodel, annual angling effort was determined based on fishery quality experienced in the previous year. Anglers responded dynamically to the perceived quality of the fishery through the effect of utility (i.e., satisfaction) on the angler's probability of fishing (Table A1, eq. 2*a*). The following attributes determined fishery quality: expected catch, mean size and maximum size of fish caught, the number of other anglers seen while fishing (i.e., a measure of crowding), MSL, daily bag limit, license fees to fish within the region, one-way travel distance, main target species, and an attribute describing the biological status of the fish stock. The benefits anglers derived from each of these attributes, called part-worth utilities (PWUs), were summed to determine the overall utility gained from fishing. Descriptions of the functions used to determine PWUs and their parameters (Table S2[1]) were based on results from a discrete choice experiment carried out on anglers from the German state of Mecklenburg-Vorpommern (M-V) (Beardmore et al. 2013). By predicting effort, the choice model was central to evaluating the equilibrium fishing quality and hence OSY (Johnston et al. 2010). The parameters from the choice model were species-independent and thus represented the most general set of conjointly estimated angler preferences published to date (Beardmore et al. 2013). This made the PWU coefficients transferable across species, including bull trout.

Three angler types were modelled — committed, casual, and trophy anglers — which, respectively, corresponded to the class-1, class-2, and class-3 anglers described by Beardmore et al. (2013). This was in contrast with Johnston et al. (2010, 2013), who used three prototypical angler types. The three angler types used here represented differentially specialized anglers that varied in their commitment to angling and their preferences for selected fishery attributes (Fig. 2). The importance of catch rates was highest for committed anglers and lowest for trophy anglers. Trophy anglers placed the highest importance on mean size, while it was of least importance for committed anglers. Casual anglers were sensitive to MSLs, license costs, and distance. Daily bag limit, maximum size caught, and crowding were less important for determining differences among angler types. The angler types also varied in their propensity to voluntarily release fish, with committed anglers and casual anglers being similarly harvest-oriented, while trophy anglers were much less consumptive (Table S3[1]).

Incorporating the three angler types described by Beardmore et al. (2013) into the modelling framework of Johnston et al. (2010, 2013) required calibration of the PWU functions (see online supplementary material for details[1]). The resulting PWU functions are depicted in Fig. A1. While the choice model allowed for variation in distance, license cost, daily bag limit, stock status, and the relative preference for target species compared with other spe-

Fig. 2. Description of the relative preferences of the three angler types described by Beardmore et al. (2013) for various fishery attributes. Illustrated is the change in part-worth utility (PWU) from a fishery attribute across a standardized range in attribute level. Points near the zero line represent situations where the attribute has little influence on the PWU the angler type derives. Negative values suggest that increases in the attribute have a negative effect on PWU, and positive values show the opposite effect. MSL, minimum-size limit.



cies, these aspects were not investigated in this study. Thus, levels of these attributes were constant for all simulations (Table S2[1]). Our model was designed to represent a single-lake fishery, such as those run by angling clubs in central Europe, in which club managers can manipulate the fish–angler interactions by input or output regulations (Daedlow et al. 2011). However, it should be noted that similar to the conditions in North American freshwater fisheries, the mechanistic model describing angler behaviour was determined based on the conditions of an open-access regional fishery in northeastern Germany (Daedlow et al. 2011).

Range of hooking mortality and noncompliance examined

Within the management framework of a single-lake fishery, we investigated the impact of hooking mortality and noncompliance on regulation outcomes across a range of LHTs and for diverse angler types. A recent review by Hühn and Arlinghaus (2011) on hooking mortality rates of European species found that the majority (57.1%) of hooking mortality estimates were under 10% and that estimates rarely (7.9%) exceeded 50%. Reflecting this distribution, we explored five different levels of hooking mortality, f_{hj} (0%, 5%, 10%, 25%, and 50%), in the presence and absence of noncompliance mortality, f_{nj}.

The percent illegal harvest f_{nj} was modelled as a depensatory process (Fig. A2) using an empirical relationship similar to the one described by Sullivan (2002) for walleye (*Sander vitreus*) recreational fisheries in Alberta, Canada:

$$f_{nj} = \gamma\,\mathrm{CPUE}^{\varsigma}/100$$

where CPUE is the hourly catch rate of walleye protected by size limits. To account for differences in catch rates of protected fish among LHTs compared with catch rates of protected walleye from the study by Sullivan (2002), the γ parameter was customized to each LHT so that the noncompliance function was comparable across LHTs (see the online supplementary material[1] for details about this calculation). The Sullivan (2002) relationship was used as the basis in the present study, because it is the only study on noncompliance that quantitatively described a density-dependent relationship. Furthermore, we found it reasonable to assume that illegal harvest rates should increase when catch rates and the underlying population abundances of legal-sized fish declined. However, given that the Sullivan (2002) relationship represented conditions in walleye fisheries in Alberta, we examined four other noncompliance relationships (Fig. A2). In two cases, we assumed constant noncompliance at 5% and 10%, values often assumed in recreational fisheries models (e.g., Paul et al. 2003; Post et al. 2003). In the other two cases, we altered the parameters of the Sullivan (2002) relationship either by reducing the exponent ς (i.e., the strength of the density-dependent relationship) by 75% or by multiplying γ by 5 to increase the level of noncompliance that occurred under total C&R regulations from 1%, which was what Sullivan's model predicted, to 5% (see summary in Table S4[1]).

Outline of analyses

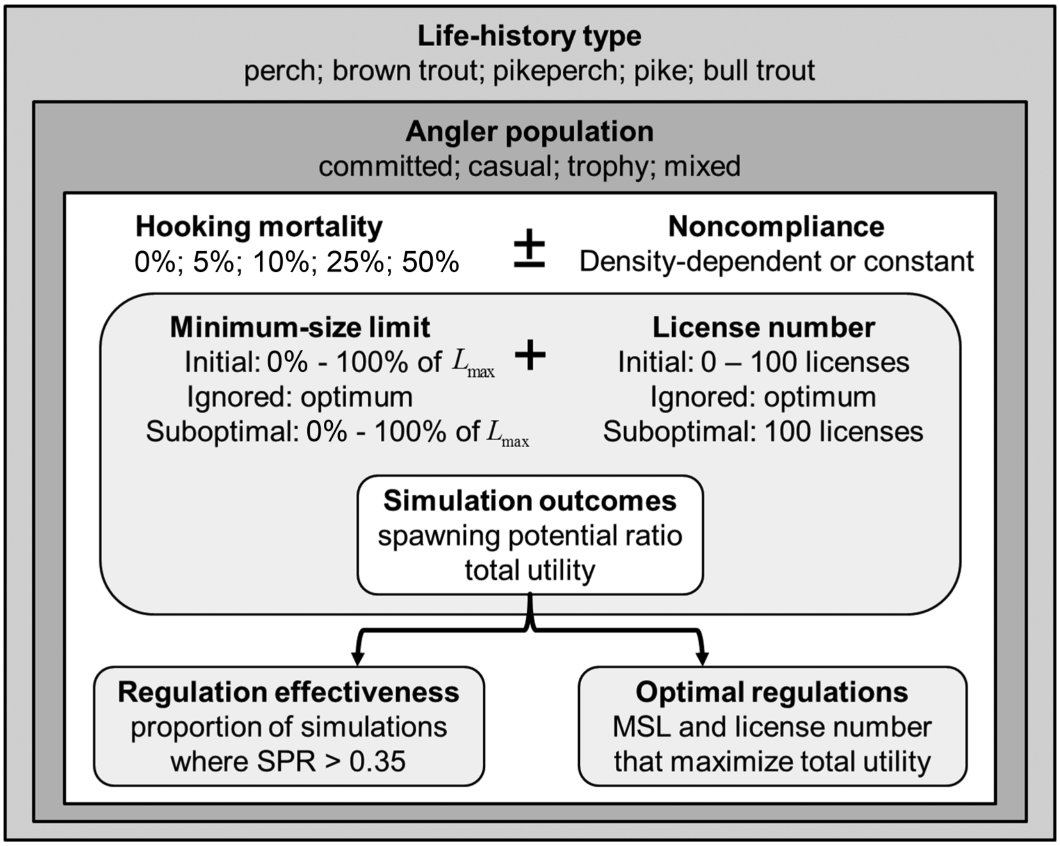
We studied three scenarios: (1) the biological and social impacts of hooking mortality and noncompliance, (2) the consequences of ignoring hooking mortality and noncompliance when setting optimal regulations, and (3) the consequences of noncompliance and hooking mortality when effort is not controlled. All three cases were run for all five LHTs independently and each LHT was tested with four angler populations (Fig. 3) — three homogeneous angler populations composed solely of committed, casual, or trophy anglers, and one mixed angler population composed of all three angler types in proportion to the relative composition reported by Beardmore et al. (2013) (Table S3[1]).

In the first set of analyses, simulations were run for a range of MSLs and license numbers, A_L (Fig. 3), for each level of hooking mortality and noncompliance (presence or absence), and the biological and social impacts at equilibrium were examined (Fig. 3). Biological impacts were evaluated using a weighted spawning-potential ratio (SPR) (Table A1, eq. 7*a*), which is commonly used to assess the likelihood of recruitment overfishing (Allen et al. 2013). SPR values below 0.35 were assumed to represent populations at risk of recruitment overfishing (Mace 1994; Clark 2002). Social impacts were assessed by changes in total utility (i.e., or individual utility aggregated across anglers; Table A1, eq. 7*b*), derived by the angling community. Similar to Johnston et al. (2010), optimal regulations were defined as the combination of MSL and license number that maximized total utility ($\mathrm{MSL}_{\mathrm{opt}}$ = optimal MSL, $A_{L\ \mathrm{opt}}$ = optimal license number). The results from this first set of analyses were used to determine the impact of hooking mortality and noncompliance on (*i*) regulation effectiveness, which was judged by changes in the proportion of simulations (i.e., regulation combinations) that resulted in biological sustainability relative to when these factors were absent, (*ii*) socially optimal regulations, and (*iii*) the biological and social conditions (SPR and total utility) under optimal regulations.

In a second set of analyses, we examined what the biological and social consequences would be if hooking mortality and noncompliance were ignored when predicting optimal regulations. This scenario mimicked an optimistic manager's assumption that hooking mortality and noncompliance were absent when in fact they were present. In this scenario, rather than testing a range of MSL and license numbers, regulations were set at those predicted to be optimal if hooking mortality was 0% and noncompliance was absent (Fig. 3). Simulations were then run for all levels of hooking mortality and noncompliance.

In a final set of analyses, we examined what happens if managers cannot directly limit angling effort, such as in open-access fisheries (Cox and Walters 2002*a*). In this so-called "suboptimal" case, license number was at the maximum possible in our model (i.e., 100 licenses, one license per hectare). We then evaluated the biological consequences of liberal input regulations at three different levels of hooking mortality (0%, 10%, and 25%) across the range

Fig. 3. Schematic diagram of the three analyses conducted: initial investigations, consequences of ignoring hooking mortality and noncompliance when setting optimal regulations, and suboptimal management when effort is not controlled. In the "ignored" case, optimal regulations were set to those that were predicted to be optimal when hooking mortality was 0% and noncompliance was absent. The different forms of noncompliance investigated are illustrated in Fig. A2; parameters are given in Table S4[1].



of MSLs modelled previously (Fig. 3) in the presence and absence of noncompliance.

Results

Influence of hooking mortality and noncompliance on biological sustainability

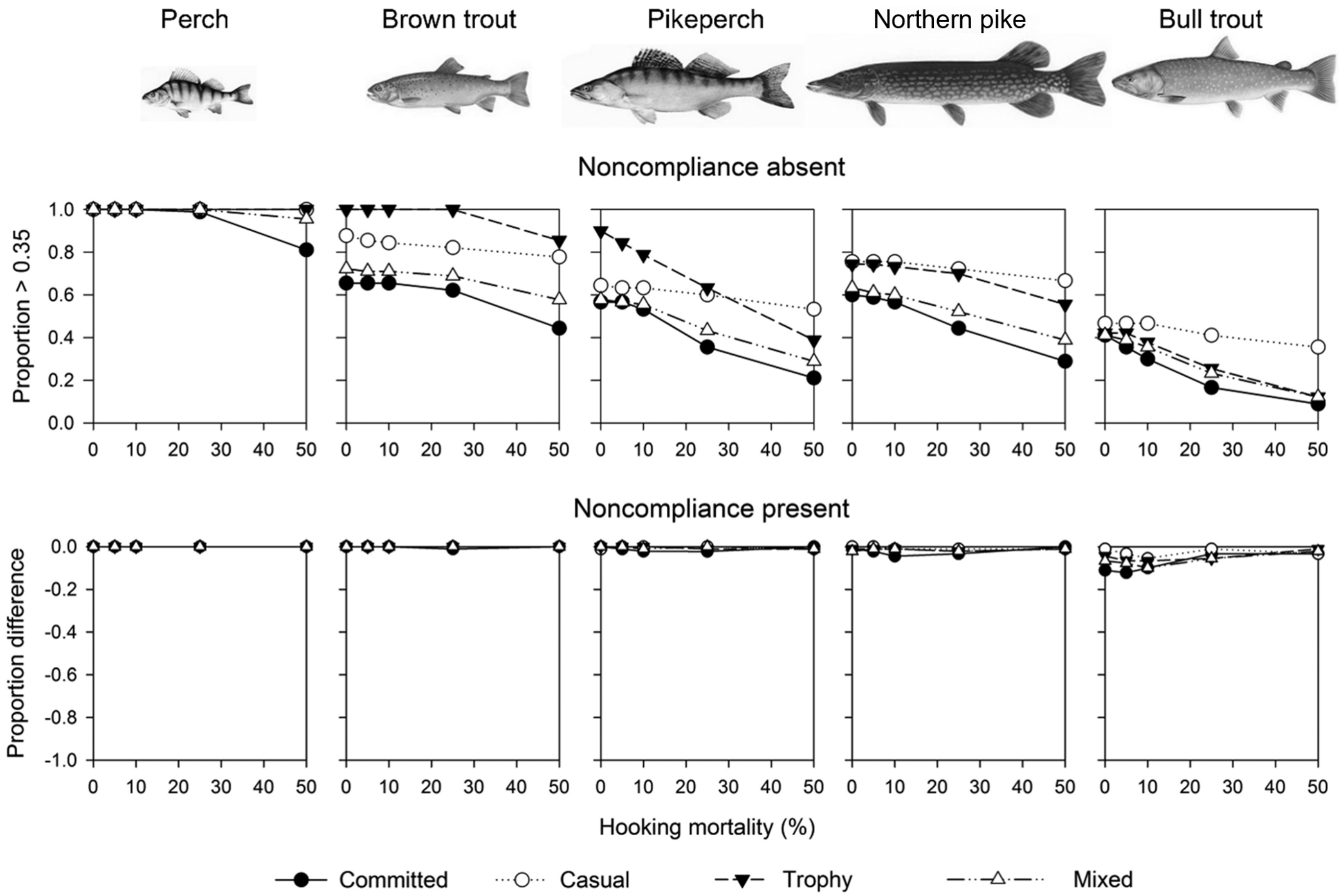
Increased hooking mortality generally reduced the range of regulations that averted recruitment overfishing, but results varied with LHT and angler type (Fig. 4). As the intrinsic vulnerability of the LHT to overexploitation increased, so did the effect of hooking mortality on regulation effectiveness. For example, for the more resilient perch and brown trout LHTs, only very high levels of hooking mortality (50%) decreased the number of regulation combinations that averted recruitment overfishing compared with situations without hooking mortality. By contrast, even low levels of hooking mortality achieved this for the intrinsically more vulnerable LHTs — pikeperch, northern pike, and bull trout. The composition of the angler population was also important for determining the biological impacts of angling on LHTs at a given level of hooking mortality (Fig. 4). Of all angler populations, committed anglers had the most severe biological impacts, whereas the angler population having the least impact differed with LHT. For example, casual anglers had the least impact on the bull trout and northern pike LHTs, but trophy anglers had the least impact on the brown trout LHT (Fig. 4).

The introduction of noncompliance had only an isolated effect on the proportion of MSL and license combinations that averted recruitment overfishing (Fig. 4). Only the more vulnerable LHTs (northern pike and bull trout and to a lesser extent pikeperch) were affected by the presence of noncompliance, and the effects were isolated to situations with low hooking mortality. Moreover, the form of the noncompliance relationship did not qualitatively alter this pattern, and only had minor effects quantitatively (Fig. S2[1]). For example, compared with the results predicted by the original density-dependent noncompliance relationship, reducing the strength of density-dependence (ς) resulted in slightly less negative effects on bull trout, and modelling noncompliance as a constant (5% or 10%) resulted in slightly more negative effects on pikeperch and slightly less negative effects on bull trout. The occurrence of only a few minor differences suggests the results were robust to alternative assumptions about noncompliance (Fig. S2[1]).

Influence of hooking mortality and noncompliance on socially optimal regulations

MSL_{opt}, in the absence of noncompliance, was generally either consistently low or declined as hooking mortality increased. However, the pattern was strongly dependent on the composition of the angler population and the LHT (Fig. 5). For example, increased hooking mortality caused small to moderate declines in MSL_{opt} (<15% of L_{max}) of angler populations composed solely, or dominated by, committed anglers, and results were similar across LHTs. By contrast, for trophy anglers the effect of hooking mortality was LHT-specific, with MSL_{opt} declining dramatically (~50% of L_{max}) at intermediate hooking mortality when bull trout, northern pike, and pikeperch were targeted, but being low (<30% of L_{max}) and unaffected by hooking mortality when more resilient LHTs (perch and brown trout) were targeted. For the casual angler population, impact of hooking mortality on MSL_{opt} was strongly

Fig. 4. The proportion of simulations across the range of minimum-size limits and license numbers tested (excluding zero licenses) that resulted in a spawning-potential ratio > 0.35 under different levels of hooking mortality in the absence of noncompliance (top row) and the proportion change in the presence of noncompliance (bottom row). Results are presented for the different angler populations and fish life-history types examined.



species-specific and less linked to the intrinsic vulnerability of a LHT.

The influence of hooking mortality on $A_{L\ opt}$, in the absence of noncompliance, was more substantial and consistent than the influence observed on MSL_{opt}. Across angler populations, $A_{L\ opt}$ generally decreased with increased hooking mortality, with the magnitude being negatively correlated with the intrinsic vulnerability of the LHT (Fig. 5). Despite these general trends, the results for casual angler populations were qualitatively different than results for the other angler types. With the exception of perch, optimal license numbers were low even when hooking mortality was absent, and consequently no large changes in $A_{L\ opt}$ for casual anglers occurred when hooking mortality increased.

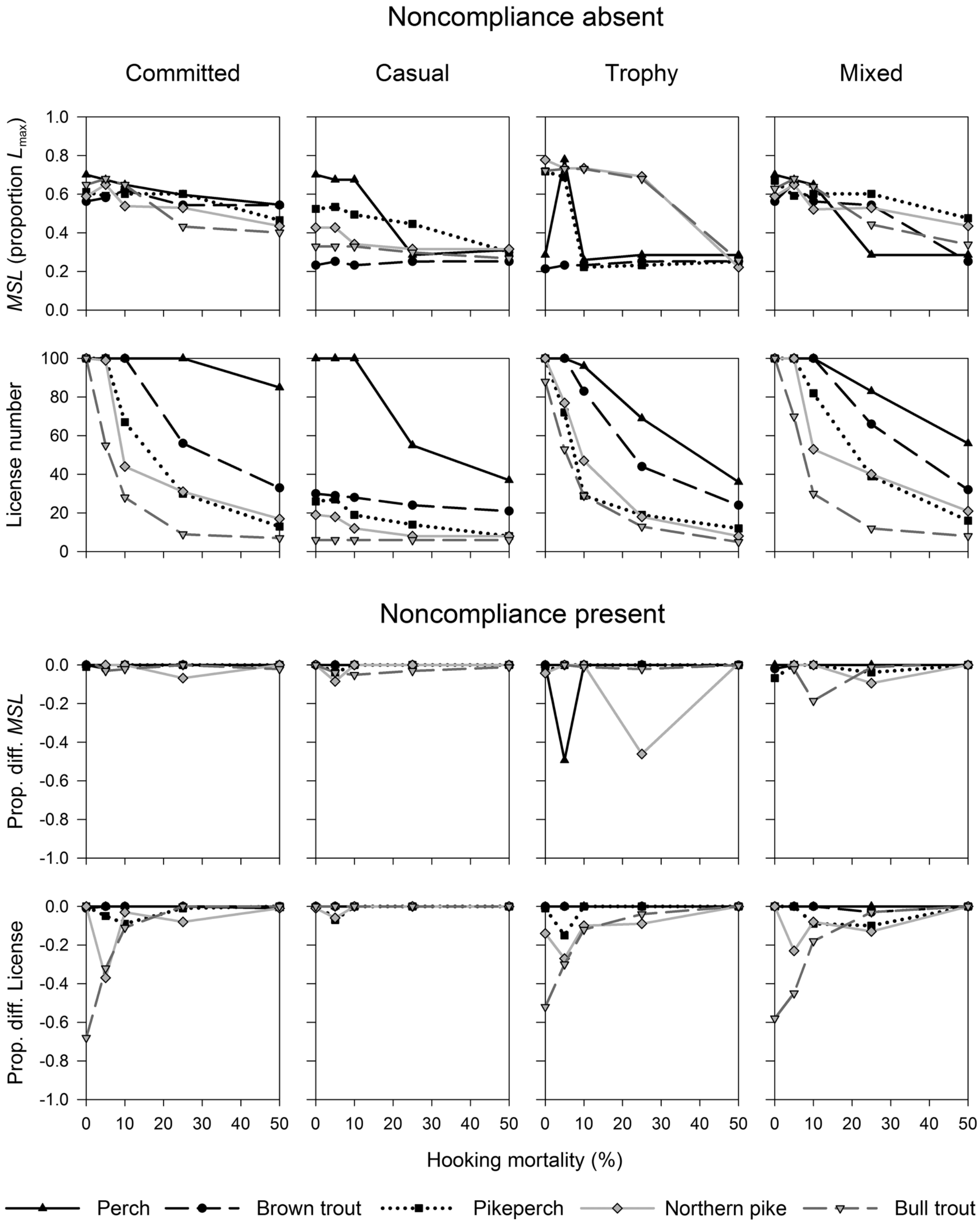
The inclusion of noncompliance mortality generally had little effect on predicted MSL_{opt} (Fig. 5). The presence of noncompliance was important, however, when predicting $A_{L\ opt}$ for the intrinsically more vulnerable LHTs, especially when hooking mortality was low. This pattern was consistent across angler populations, although the magnitude of the effect was minimal for the casual angler population, again because $A_{L\ opt}$ was low even in the absence of hooking mortality and noncompliance. Altering the noncompliance relationship rarely changed the reported trends in optimal regulations (Figs. S3 and S4[1]). There was an exception: modelling noncompliance as a constant rather than as a function of catch rate had a greater effect on the MSL_{opt} of the more resilient species and caused greater reductions in $A_{L\ opt}$ for pikeperch and northern pike (Fig. S4[1]).

Biological and social conditions under socially optimal regulations

The SPR predicted under optimal regulations declined with increased hooking mortality across all LHTs and angler populations, although increases in hooking mortality from 25% to 50% often did not decrease SPR further (Fig. 6). Despite these declines, SPR was maintained above 0.35 under socially optimal regulations except when bull trout were targeted by committed or mixed angler populations. The addition of noncompliance (in any form) did not alter findings about biological sustainability under optimal regulations, and quantitatively only slight differences in SPR occurred for the less resilient species (Figs. 6, S5, and S6[1]).

In terms of the social conditions under optimal regulations, hooking mortality systematically eroded the total utility derived by the angler population, but again the magnitude of the effect varied with fish LHT and angler population (Fig. 7). Excluding perch, declines in total utility were generally minor when LHTs were fished by a casual angler population. Reductions in total utility were often greatest for perch and least for bull trout when higher levels of hooking mortality were imposed, but this trend was much less consistent under lower levels of hooking mortality. The addition of noncompliance in any form did little to alter these trends, although quantitatively total utilities were slightly lower for the more vulnerable LHTs when hooking mortality was low (Fig. S7[1]).

Fig. 5. Optimal minimum-size limit (MSL, as a proportion of L_{max}) and optimal license number under different levels of hooking mortality, in the absence of noncompliance mortality (top two rows) and the proportion change in the presence of noncompliance (bottom two rows). Results are presented for different angler populations and fish life-history types.



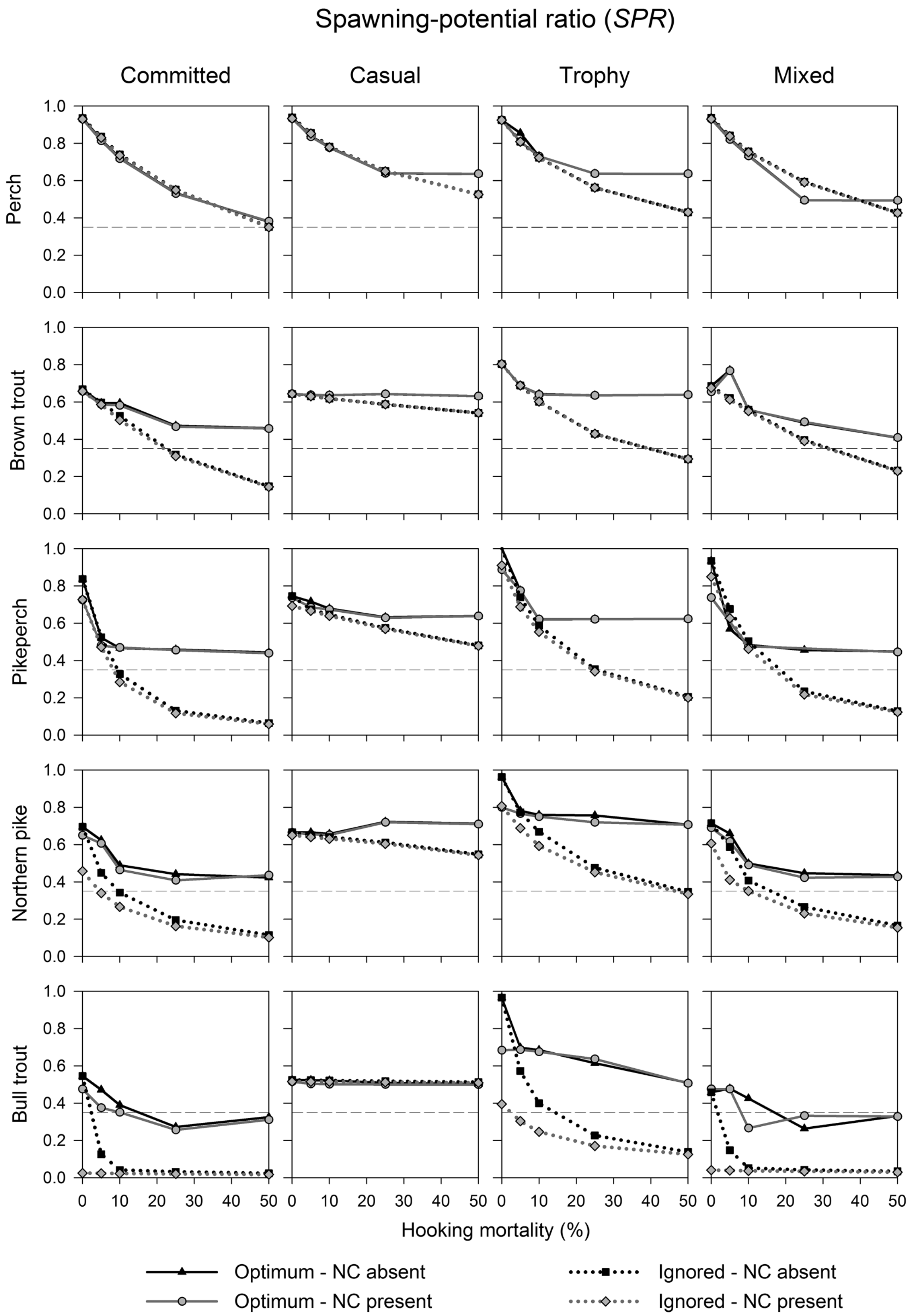
Impact of ignoring hooking mortality and noncompliance when setting optimal regulations

The consequences of ignoring hooking mortality and noncompliance when setting optimal regulations, if they were in fact present, were severe. All LHTs except perch experienced recruitment overfishing with SPRs dropping well below 0.35 at some level of hooking mortality (Fig. 6). As intrinsic LHT vulnerability increased, the hooking mortality level required to depress the SPR below 0.35 decreased (e.g., 25%–50% for brown trout compared with 5% for bull trout when fished by committed anglers). Angler type also played an important role in this context. Casual anglers never caused recruitment overfishing, and the level of hooking mortality required for trophy angler populations to cause overfishing was much higher than that for angler populations dominated by committed anglers. The patterns observed in the absence of noncompliance were reinforced by the presence of noncompliance mortality, which primarily influenced the results for the most vulnerable LHTs.

Impact of hooking mortality and noncompliance in open-access fisheries

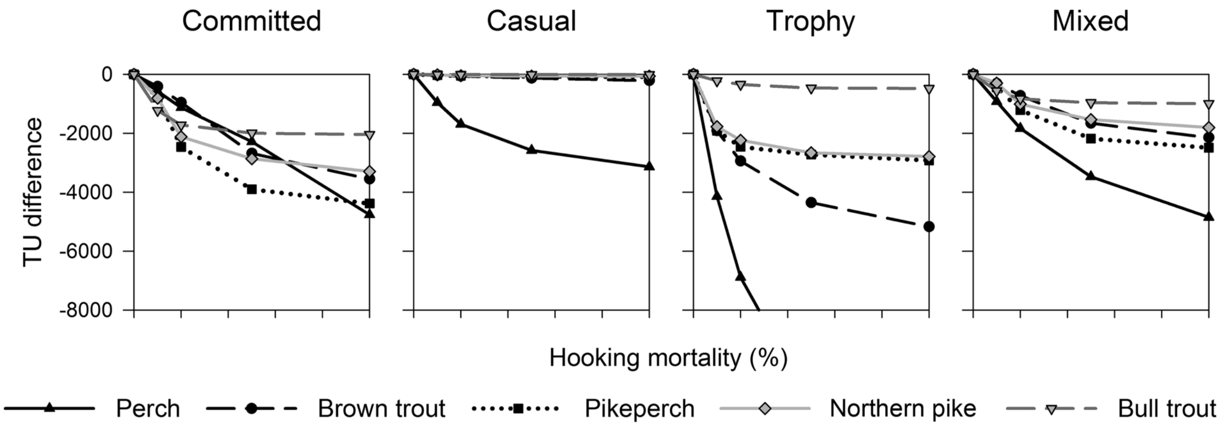
In our final analysis, which mimicked an open-access single-lake fishery, we found that at low MSLs the SPR fell below 0.35 for most LHTs except perch, regardless of whether hooking mortality or

Fig. 6. The influence of the presence (Sullivan-type relationship) and absence of noncompliance (NC) mortality, across a range of hooking mortality levels, on the spawning-potential ratio (SPR) that results under scenario optimal regulations (solid lines) and under the optimal regulations predicted when hooking mortality is ignored (i.e., 0% hooking mortality and no noncompliance; dotted lines). Results are presented for different angler populations and fish life-history types. The horizontal dashed line indicates an SPR of 0.35.



noncompliance was present or not (Fig. 8). At moderate to high MSLs approaching a total C&R fishery, recruitment overfishing was avoided across all angler types and LHTs. However, the MSL required for this to occur systematically increased as hooking mortality increased. Furthermore, for more vulnerable LHTs the minimum biologically sustainable MSLs also increased in the presence of noncompliance compared with its absence, although this disparity decreased as hooking mortality increased. Composition of the angler

Fig. 7. The change in total utility (TU) under optimal regulations at different levels of hooking mortality in the absence of noncompliance mortality. The difference presented is relative to the total utility when hooking mortality and noncompliance were absent. Results are presented for different angler populations, homogeneous and mixed, and for different fish life-history types.



population was also important, because the MSL required to avert recruitment overfishing was generally greatest for angler populations dominated by committed anglers and least for the casual angler population, particularly for the inherently more vulnerable LHTs.

Discussion

We found that the two sources of "cryptic mortality" (Coggins et al. 2007) — hooking and noncompliance mortality — strongly influenced the biological impact of recreational fishing on fish populations and the input and output measures considered to be optimal from an OSY perspective. Accounting for the diversity in both fish LHT and angler type was found to be important for determining the magnitude of the influence cryptic mortality had. Based on our results, suboptimal management of recreational fisheries is likely when hooking mortality and noncompliance are not appropriately accounted for in a species-specific and an angler-population-specific context.

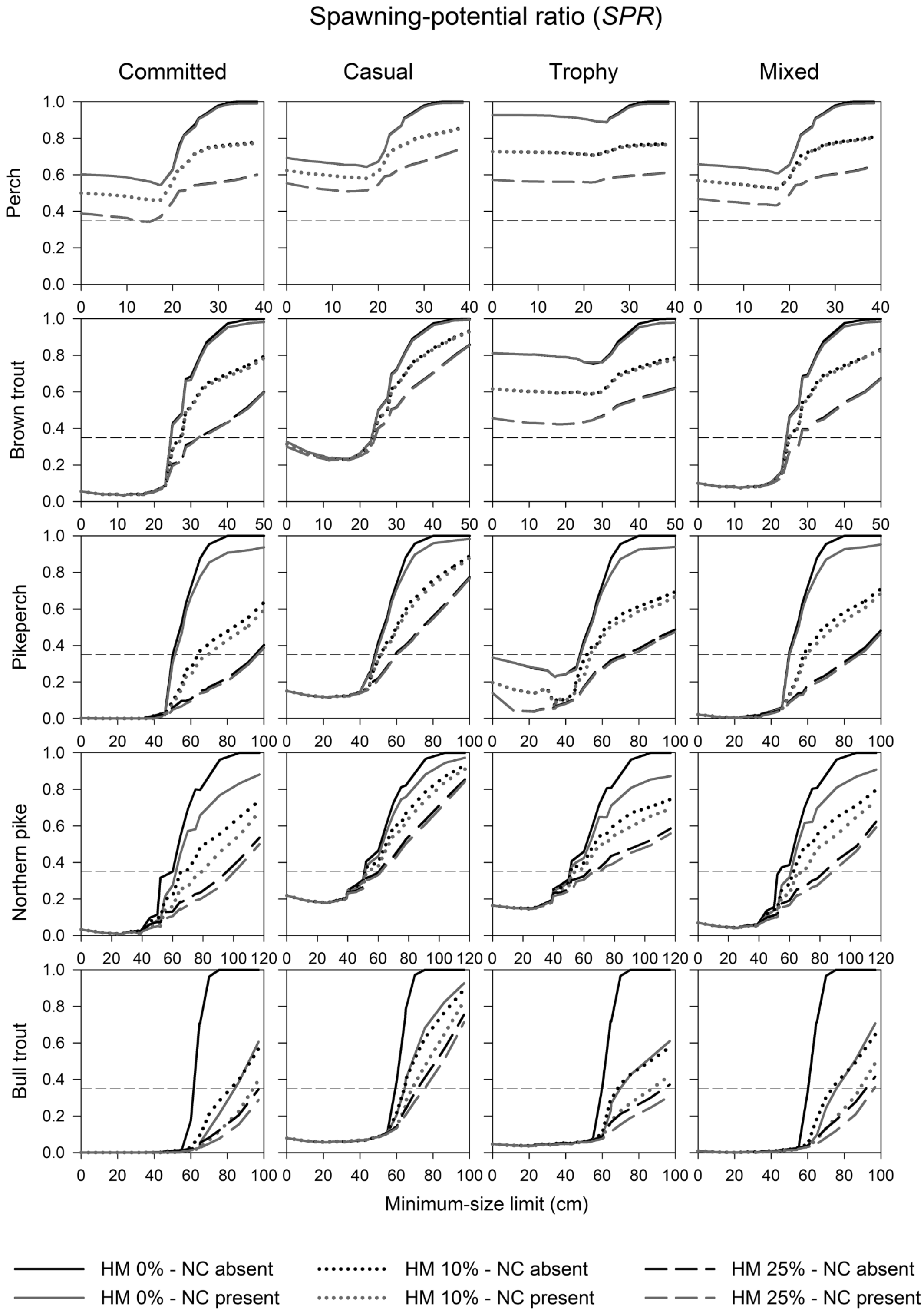
Biological impacts of hooking mortality and noncompliance

Results from our study and others (Paul et al. 2003; Coggins et al. 2007; Pine et al. 2008) reinforce the notion that understanding the impacts of hooking mortality and noncompliance on fish populations exploited by angling requires the life history of the targeted species to be explicitly considered. In this context, we found that the larger-bodied species — northern pike, bull trout, and to a lesser extent pikeperch — were intrinsically more vulnerable to additional mortality from hooking and noncompliance, corroborating previous findings that maximum body size correlates with vulnerability to overexploitation (Jennings et al. 1998; Reynolds et al. 2001; Dulvy et al. 2003; but see Pinsky et al. 2011 and Hutchings et al. 2012 for alternative findings). This trend occurred despite large differences in maturation timing and fecundity characteristics among LHTs that we modelled, characteristics that have been suggested to correlate with extinction risk of exploited species (fecundity: Jennings et al. 1998 (but see Hutchings et al. 2012 for alternative findings); age at maturation: Hutchings et al. 2012). Two factors likely determined our results. First, the low maximum recruitment rates (α, the slope at the origin of the stock–recruitment relationship) of bull trout, northern pike, and pikeperch resulted in a lower compensatory ability of these species relative to perch and brown trout (Lorenzen 2008), independent of single life-history characteristics. Second, the relatively large size-at-maturation of pikeperch, northern pike, and bull trout likely contributed to their greater vulnerability to overexploitation, because immature fish of these species were more vulnerable to capture than those of the more resilient LHTs. Our findings of the greater vulnerability of northern pike and bull trout LHTs to overexploitation were in agreement with empirical studies on northern pike (Paukert et al. 2001; Post et al. 2002) and bull trout (Johnston et al. 2007; Rodtka 2009).

A potential consequence of species having low compensatory abilities is that the effectiveness of common regulatory tools such as MSLs will be undermined by hooking mortality and noncompliance, because fish can die at a rate sufficient to put populations at risk of recruitment overfishing. In line with previous research (Post et al. 2003; Coggins et al. 2007; Allen et al. 2013), we found that even restrictive MSLs were not effective at conserving the more vulnerable LHTs at higher levels of hooking mortality or if effort was high. Compared with MSLs, we found that reductions in license numbers were much more effective at ensuring biological sustainability of the intrinsically more vulnerable LHTs. Thus, our results collectively support previous suggestions that effort regulations may be an appropriate tool for managing recreational fisheries for biological sustainability (Cox and Walters 2002*a*, 2002*b*), particularly when hooking mortality is high (Post et al. 2003; Pine et al. 2008).

A noteworthy finding from our study was that the composition of the angler population was as important as LHT for determining the biological impact of hooking mortality and noncompliance. This finding stems from angler types differing in their preferences (Hunt 2005), overall commitment to angling (Beardmore et al. 2013), and propensity to harvest (Bryan 1977; Dorow et al. 2010). In combination, these factors influenced the interplay between angling effort and fish populations (Johnston et al. 2013), resulting in nonlinear relationships between hooking mortality and regulations. For example, committed anglers had the greatest impacts on fish populations, even though their propensity to voluntarily release fish was similar to casual anglers, because committed anglers had a greater inherent propensity to fish. We also found that trophy anglers were generally more likely to cause recruitment overfishing than casual anglers when targeting intrinsically vulnerable LHTs, because these LHTs were generally not attractive to casual anglers. Our study reinforces the notion that some anglers continue fishing even when fish stocks decline and catch rates drop, because other attributes that contribute to angler utility continue to attract them (Post et al. 2002; Hunt et al. 2011; Allen et al. 2013). Thus, in the presence of avid anglers, regulations will need to be more restrictive to minimize adverse effects from hooking mortality and noncompliance than would be required for more casual anglers or anglers that are less harvest-oriented.

Fig. 8. The biological consequences in terms of spawning-potential ratio (SPR) of hooking mortality (HM) in the presence and absence of noncompliance (NC) mortality when license numbers are maximized, mimicking an open-access fishery. Three levels of hooking mortality were examined: 0%, 10%, and 25%. The horizontal dashed line indicates an SPR of 0.35.



Influence of hooking mortality and noncompliance on optimal regulations

In terms of optimal management strategies, our results were broadly similar to previous work on the topic, despite the management objective in our study (OSY) being defined by both catch- and non-catch-related fishery attributes rather than simply yield or some other catch metric as in previous research (e.g., Coggins et al. 2007; Henderson 2009). Similar to Coggins et al. (2007) and Pine et al. (2008), we found that MSL_{opt} generally declined with increased hooking mortality, because the benefits associated with a high MSL in terms of catch rates and size of fish caught were lost as fish died from hooking mortality and lower MSLs were preferred by anglers. To avoid recruitment overfishing while maximizing angler utility, a systematic decrease in $A_{L\ opt}$, and hence fishing effort, was required to ensure a biologically sustainable fishery, particularly for species that had lower compensatory ability. However, the general declines in MSL_{opt} and $A_{L\ opt}$ with increased hooking mortality were not consistent across LHTs and angler populations, because as elaborated above angler types differed in their fishing preferences and behaviour. For example, the general lack of commitment to angling of casual anglers and their correspondingly low responsiveness to changes in fishery quality, in combination with their consumptive nature, resulted in the casual anglers generally having low $A_{L\ opt}$ values for most LHTs. Only the most resilient LHT provided sufficient fishery quality to attract casual anglers. Consequently, casual anglers had minimal impacts on fish stocks, regardless of the level of hooking mortality.

Biological sustainability and social conditions under socially optimal regulations

It is encouraging that the use of an OSY approach nearly always resulted in biologically sustainable outcomes, despite the large variation in socially optimal regulations among LHTs and angler populations. This occurred because socially optimal regulations indirectly account for the underlying status of the fish population through the strong effect that large declines in the fish population have on the catch-based attributes that contribute to angler utility. Our results are good news for the fishery manager, because consistent with Johnston et al. (2010, 2013), the use of an OSY approach to management achieves the often-cited aim of recreational fisheries management to maximize the satisfaction of anglers while maintaining the biological sustainability of exploited populations (Radomski et al. 2001; Cox and Walters 2002*a*; Peterson and Evans 2003).

What is less encouraging from a management perspective is that hooking mortality systematically eroded the social welfare produced from the recreational experience. In fact, we found that hooking mortality rates as low as 5% caused large reductions in the welfare the fishery provided to the various angler types. Similar to previous studies that found a reduction in fishery yield and harvesting efficiency as hooking mortality increased (e.g., Coggins et al. 2007; Pine et al. 2008; Henderson 2009), the loss of fish to discard mortality and the reduction in license numbers required to sustain the fish population under elevated hooking mortality led to losses in angler welfare. Therefore, if maximizing angler satisfaction is a priority of recreational managers, a focus should be placed on reducing handling stress and injury through such methods as gear restrictions and education and outreach programs that are tailored to the species of interest (Cooke and Suski 2005), because these actions should increase postrelease survival and reduce the impacts of hooking mortality (Arlinghaus et al. 2007; EIFAC 2008; FAO 2012).

Consequences of ignoring hooking mortality and noncompliance when setting optimal regulations

Not explicitly considering hooking mortality and noncompliance when predicting optimal regulations was found to have negative consequences. When hooking mortality and noncompliance were present but were ignored when setting optimal regulation, all but the most resilient LHTs were at risk of recruitment overfishing, particularly if they were targeted by committed anglers. Our results suggest that a more precautionary approach should be taken that acknowledges the implementation uncertainty generated by hooking mortality and noncompliance. Otherwise, regulations might be either too stringent or too liberal, resulting in overfished stocks or socially suboptimal management, or both.

Effects of hooking mortality and noncompliance in open-access fisheries

We found that in cases where effort cannot be controlled, such as in open-access fisheries that are widespread in North America (Cox and Walters 2002*a*; Post 2013) and northern and eastern Europe (Daedlow et al. 2011), the introduction of hooking mortality and noncompliance, even low levels, undermined the output tools (MSLs) that managers are left with to regulate fisheries (Johnson and Martinez 1995; Radomski et al. 2001; Lewin et al. 2006). Of particular concern is that the range of MSLs where hooking mortality and noncompliance had their greatest effect on biological sustainability corresponded to the range of MSLs often used in many recreational fisheries: low enough to minimize the loss of potential harvest to natural mortality (Johnson and Martinez 1995), but high enough to allow most fish to spawn at least once (Noble and Jones 1999). Furthermore, our results demonstrated that noncompliance should not be ignored when managing open-access fisheries. As has been cautioned (Post et al. 2002; Post 2013), we found that noncompliance had the potential to accelerate the decline of already vulnerable species, especially at the low hooking mortality rates (≤10%), which are common in freshwater fisheries (Hühn and Arlinghaus 2011). Thus, more effort should be directed at obtaining accurate estimates of hooking mortality and noncompliance for intrinsically more vulnerable LHTs, and these estimates should be consistently integrated into models designed to predict management regulations in recreational fisheries.

The isolated effect of noncompliance on biological sustainability and optimal management

The reasons why the effects of noncompliance on biological sustainability and optimal regulations were generally isolated to the intrinsically most vulnerable LHTs and low hooking mortality rates are complex. Whether or not noncompliance had a social or biological effect was dependent on three things. First, the magnitude of noncompliance mortality was important. When the density-dependent model of Sullivan (2002) was used, noncompliance rates were very low if catch rates were high. High catch rates also meant that anglers were less likely to turn to noncompliance to harvest the number of fish they desired. High catch rates occurred if the LHT was less vulnerable to overexploitation or, for the more vulnerable LHTs, when MSLs were high. For these reasons, noncompliance rates under optimal regulations were generally less than 5% for perch and brown trout, but were generally higher (>5% and often exceeding 10%) for the intrinsically more vulnerable LHTs. However, if managed in a socially optimal manner with appropriate reductions in license numbers, we found noncompliance had negligible effects. Second, if the amount of mortality the population experienced from other sources, such as hooking mortality, was sufficient to reduce the SPR below 0.35, then the addition of noncompliance had no effect because the population was already classified as recruitment overfished. This was why the effects were isolated to low levels of hooking mortality. Third, LHT determined how much additional mortality from hooking mortality and noncompliance the population compensated for. In general agreement with Coggins et al. (2007), we found that for the more resilient LHTs, the combined mortality from hooking mortality and noncompliance needed to exceed at least 25% before reductions in regulation effectiveness occurred. By contrast, for the intrinsically more vulnerable LHTs, the greatest effects on biological sustainability were observed at a combined mortality of less than 20%. Even noncompliance rates of 5% had the potential to effect bull trout, northern pike, and to a lesser extent pikeperch. Thus, while our finding that noncompliance can undermine regulation effectiveness is consistent with other studies (Gigliotti and Taylor 1990; Post et al. 2003; Henderson and Fabrizio 2013), our results were situation-dependent.

Limitations and extensions

Like any other modelling exercise, our bioeconomic model has a number of limitations, many of which are discussed by Johnston et al. (2010, 2013). For example, by having a single-lake and single-species focus, we cannot trust our predictions will represent outcomes at the ecosystem or landscape level. However, one of the major limitations mentioned in these papers, the theoretical description of angler types, was addressed here by using empirical results from a stated discrete choice experiment to describe angler behaviour. Ironically, this brings with it a question about how general our results are. The study by Beardmore et al. (2013) was designed to remove any species-specificity in parameter estimates for angler preferences. This resulted in a general mechanistic model of angler behaviour that can be applied across species and in different contexts. However, the choice model results are still linked to the social and cultural conditions in the choice study region and the fishing experiences anglers had there. Parameter estimates from choice models might differ from a survey done in another part of the world, and consequently resulting predictions might differ. Hence, to apply the present model to a particular fishery, researchers are advised to develop choice models that will calibrate the angler model to local and regional conditions. In the absence of such calibrated models, the model by Beardmore et al. (2013) is a reasonable substitute given its generality.

Some additional limitations became apparent when the results from Beardmore et al. (2013) were applied to our model. In some cases, we needed to make assumptions about how anglers would behave at extreme attributes (e.g., at very low catch rates or at very high MSL) to "tune" some of the coefficients and functional forms of the PWU functions from Beardmore et al. (2013), because the attribute range tested in the choice experiment was not sufficiently broad. In the future, the attribute range considered in the choice experiment should reflect the range tested by the bioeconomic model. Along a similar vein, because only four attribute levels were tested for many attributes by Beardmore et al. (2013), the functional form of the PWU relationships was often limited to being linear. Testing a larger number of levels would allow for the detection of more complex relationships, such as the quadratic relationships we used in our model to describe the PWU for daily catch and the angling regulations.

The thresholds beyond which anglers voluntarily released fish can strongly influence predictions depending on the LHT in question. In this study, values used were estimated from diary data from northeast German anglers fishing for perch, and it was assumed that this threshold applied across all LHTs. However, the harvesting behaviour of anglers depends on the target species (Hunt et al. 2002; Beardmore et al. 2011). For example, an angler may be more harvest-oriented when targeting perch and more trophy-oriented when targeting northern pike (Hunt et al. 2002). Such dynamics were not accounted for in the present model. Furthermore, we assumed that angler behaviour was consistent over time, which may not be the case (Baerenklau and Provencher 2005). Likewise, hooking mortality may decrease as anglers gain experience and improve their handling practices (e.g., Diodati and Richards 1996; Meka 2004). The influence of temporal changes in angler behaviour deserves further study and should be integrated in extensions of the present work.

We chose to use the relationship from Sullivan (2002) because it was a density-dependent empirical relationship describing the change in noncompliance across a range of catch rates. By using the Sullivan relationship scaled to the catch rates of a particular species, we assumed that noncompliance rates were similar across species. However, given the lack of research on this topic, it is unknown how robust this assumption is. Anglers' species preferences may be important for determining noncompliance rates. For example, Glass and Maughan (1984) found that largemouth bass (*Micropterus salmoides*) anglers were more compliant with regulations than non-bass anglers. Compliance with regulations may also change over time (Näslund et al. 2010; but see Caroffino 2013). While Sullivan's relationship may not transfer across species, as a theoretical exercise it was valuable to see how model results differ when using depensatory rather than constant noncompliance rates. Furthermore, we found our results to be robust to alternative forms and assumptions about noncompliance. Nevertheless, more research is needed to determine if noncompliance is indeed a depensatory process, simply an additive effect, or present in some other form, and once determined what the strength of the relationship is in relation to catch rate, harvest rate, or regulation strictness across a range of species.

Implications

Hooking mortality and noncompliance were important for both determining regulation efficacy and deriving socially optimal regulations for recreational fisheries. For fish with low compensatory reserves, the effectiveness of harvest regulations was undermined sufficiently by these factors that strong effort restrictions were required to preserve the biological integrity of the stock and maintain social welfare. However, the need for such restrictions was highly dependent on the life history of the fish population and the type and number of anglers attracted to fishery. Furthermore, noncompliance had an isolated effect, affecting only the most intrinsically vulnerable species when hooking mortality rates were low, suggesting it was of less of a management concern then might be assumed. However, it is the combined mortality from hooking and noncompliance, in conjunction with resiliency of the fish population and the amount and type of fishing pressure that the fishery receives, that determines outcomes. When fish stocks are heavily exploited, such as can occur in open-access fisheries, noncompliance can drive stocks towards recruitment overfishing, as predicted by Post et al. (2002) and Post (2013). Thus, noncompliance may become a major issue if managers are unable to use optimal input and output controls, particularly when managing intrinsically vulnerable fish populations. Given that input controls are rarely used in recreational fisheries because they are often met with considerable opposition from anglers (Cox and Walters 2002*a*), noncompliance is likely of concern in most recreational fisheries worldwide.

Despite the potential negative effect of hooking mortality and noncompliance on biological sustainability, socially optimal management generally achieved biological sustainability as long as both forms of cryptic mortality were explicitly accounted for when deriving optimal regulations. This finding highlights the value of OSY as a performance measure and management objective in recreational fisheries. However, if hooking mortality and noncompliance were ignored when setting optimal regulations, or if effort controls were not feasible, we found that fish populations were often put at risk of recruitment overfishing. Accounting for hooking mortality and noncompliance is thus critical to reduce the implementation uncertainty associated with harvest regulations. Moreover, recreational fisheries managers may need to consider input controls to a greater extent than is presently the case to maintain high-quality fisheries that are also biologically sustainable.

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Appendix A

Appendix figures and table appear on the following pages.

Table A1. Bioeconomic model equations.

Equation		Description
Individual-angler utility		
(1)	$U_{\mathrm{f}\,j} = U_{\mathrm{in}\,j} + U_{\bar{c}_{\mathrm{D}}\,j} + U_{\bar{l}\,j} + U_{l_{\max}\,j} + U_{\bar{A}_{\mathrm{D}}\,j} + U_{\mathrm{MSL}\,j} + U_{\mathrm{DBL}\,j} + U_{\mathrm{Dist}\,j} + U_{\mathrm{Cost}\,j} + U_{\mathrm{Stock}\,j} + U_{\mathrm{Spp}\,j}$	Conditional indirect utility gained by an angler of type *j* from choosing to fish (where $U_{\mathrm{in}\,j}$ is the basic utility gained from fishing, $U_{\bar{c}_{\mathrm{D}}\,j}$ is the PWU of mean daily catch, $U_{\bar{l}\,j}$ is the PWU of mean size of fish caught annually, $U_{l_{\max}\,j}$ is the PWU of maximum size of fish caught annually, $U_{\bar{A}_{\mathrm{D}}\,j}$ is the PWU of angler crowding, $U_{\mathrm{MSL}\,j}$ is the PWU of minimum-size limit, $U_{\mathrm{DBL}\,j}$ is the PWU of daily bag limit, $U_{\mathrm{Dist}\,j}$ is the PWU of distance, $U_{\mathrm{Cost}\,j}$ is the PWU of annual license cost, $U_{\mathrm{Stock}\,j}$ is the PWU of stock status, and $U_{\mathrm{Spp}\,j}$ is the PWU of effort to preferred species)
Angler-effort dynamics		
(2*a*)	$p_{\mathrm{f}\,j} = \dfrac{4\exp(\hat{U}_{\mathrm{f}\,j})}{[4\exp(\hat{U}_{\mathrm{f}\,j}) + \exp(U_{\mathrm{out}\,j}) + \exp(U_{\mathrm{no}\,j})]}$	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, $U_{\mathrm{out}\,j}$ is the utility from fishing outside the region, and U_{no} is the utility gained from not fishing)
(2*b*)	$p_{\mathrm{F}\,j} = (1 - \varphi)p_{\mathrm{f}\,j} + \varphi\hat{p}_{\mathrm{F}\,j}$	Realized probability an angler of type *j* fishes (where $\hat{p}_{\mathrm{F}\,j}$ applies to the previous year)
(2*c*)	$D_j = p_{\mathrm{F}\,j} D_{\max}$	Number of days an angler of type *j* chooses to fish during a year
(2*d*)	$A_{\mathrm{L}\,j} = \rho_j A_{\mathrm{L}}$	Density of licensed anglers of type *j*
(2*e*)	$E_j = D_j A_{\mathrm{L}\,j} \Psi$	Total annual realized fishing effort density by anglers of type *j*
(2*f*)	$e_{jt} = \begin{cases} E_j/S_{\mathrm{F}} & \text{if } t \le S_{\mathrm{F}} \\ 0 & \text{if } t > S_{\mathrm{F}} \end{cases}$	Instantaneous fishing effort density at time *t* by anglers of type *j*
Age-structured fish population		
(3*a*)	$N_{\mathrm{total}} = \sum_{a=0}^{a_{\max}} N_a$	Total fish population density
(3*b*)	$B_{\mathrm{total}} = \sum_{a=0}^{a_{\max}} N_a W_a$	Total fish biomass density

Table A1 (*concluded*).

Equation	Description
Growth	
(4*a*) $h = h_{\max} /(1 + B_{\mathrm{total}}/B_{1/2})$	Maximum annual growth of a fish dependent on the total fish biomass density at the beginning of the year
(4*b*) $p_a = \begin{cases} 1 - \dfrac{G}{3+G}(1 + L_{a0}/h) & \text{if } a \geq a_{\mathrm{m}} - 1 \\ 1 & \text{if } a < a_{\mathrm{m}} - 1 \end{cases}$	Proportion of the growing season during which a fish of age *a* allocates energy to growth
(4*c*) $g_{at} = \begin{cases} h/S_{\mathrm{G}} & \text{if } t \leq p_a S_{\mathrm{G}} \\ 0 & \text{if } t > p_a S_{\mathrm{G}} \end{cases}$	Instantaneous growth rate in length of a fish of age *a* at time *t*
(4*d*) $L_{at} = L_{a\,0} + g_{at}\, t$	Length of a fish of age *a* at time *t*
(4*e*) $W_{at} = wL_{at}^{l}$	Mass of a fish of age *a* at time *t*
Reproduction	
(5*a*) $B_{♀} = \sum_{a=a_{\mathrm{m}}}^{a_{\max}} W_{at_{\mathrm{R}}} N_{a♀}$	Biomass density of female spawners at time t_{R}
(5*b*) 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 posthatch of fish of age 0 (applied at the beginning of the year)
(5*c*) $N_0 = s_0\, b$	Density of fish of age 0 at the beginning of the year
Mortality	
(6*a*) $v_{ajt} = \dfrac{1}{1 + \exp[-y(L_{at} - L_{50j})]}$	Proportion of fish of age *a* that are vulnerable to capture by anglers of type *j* at time *t*
(6*b*) $L_{50} = z_j\, L_{\max} + L_{\mathrm{shift}}$	Size at 50% vulnerability to capture
(6*c*) $c_{ajt} = q_j\, e_{\mathrm{jt}}\, v_{\mathrm{ajt}}$	Instantaneous per capita catch rate of fish of age *a* by anglers of type *j* at time *t*
(6*d*) $H_{ajt} = \begin{cases} 1 & \text{if } L_{at} \geq \mathrm{MSL} \\ f_{\mathrm{n}\,j} & \text{if } L_{at} < \mathrm{MSL} \end{cases}$	Proportion of fish of age *a* that are harvestable by anglers of type *j* at time *t*
(6*e*) $C_{jt} = \sum_{a=0}^{a_{\max}} c_{ajt} N_a H_{ajt}$	Instantaneous catch rate of fish that are harvestable by anglers of type *j* at time *t*
(6*f*) $C_{\mathrm{H}jt} = \min(C_{jt}, c_{\max\,j}\, e_{jt}/\Psi, e_{jt}\, \mathrm{DBL}/\Psi)$	Instantaneous harvest rate by anglers of type *j* at time *t*
(6*g*) $f_{\mathrm{H}jt} = \dfrac{C_{\mathrm{H}jt}}{C_{jt}} + f_{\mathrm{h}j} \dfrac{C_{jt} - C_{\mathrm{H}jt}}{C_{jt}}$	Proportion of harvestable fish killed by anglers of type *j* at time *t*
(6*h*) $m_{\mathrm{f}ajt} = f_{\mathrm{H}jt}\, c_{ajt}\, H_{ajt} + f_{\mathrm{h}j}\, c_{ajt}(1 - H_{ajt})$	Instantaneous per capita fishing mortality rate of fish of age *a* from anglers of type *j* at time *t*
(6*i*) $d_{at} = m_{\mathrm{n}a} + \sum_j m_{\mathrm{f}ajt}$	Instantaneous per capita mortality rate of fish of age *a* at time *t*
(6*j*) $\dfrac{dN_a}{dt} = -d_{at} N_a$	Instantaneous rate of change in the density of fish of age *a* at time *t*
Response variables	
(7*a*) $\mathrm{SPR} = b_{\mathrm{F}}/b_{\mathrm{U}}$	Spawning-potential ratio (= annual population fecundity density b_{F} under fishing relative to annual population fecundity density b_{U} under unfished conditions)
(7*b*) $U_{\mathrm{TU}} = \sum_j U_{\mathrm{f}\,j} D_j A_{\mathrm{L}\,j}$	Annual total utility

Note: Parameter values and their sources for the fish life-history types studied here are listed in Table S1[1] of the online supplementary material. Information for calculating part-worth utility (PWU) is given in Table S2[1]. Parameters describing fishing practices of angler types and other relevant parameters can be found in Table S3[1].

Fig. A1. Part-worth utility (PWU) functions describing the relative preferences of the three angler types described by Beardmore et al. (2013) for various fishery attributes. PWU, an economic term, is the contribution of a single fishery attribute to the utility an angler derives from fishing and was determined using the coefficients of the regression model from the choice experiment. See Table S2[1] for parameters describing these relationships. SD = standard deviation units.

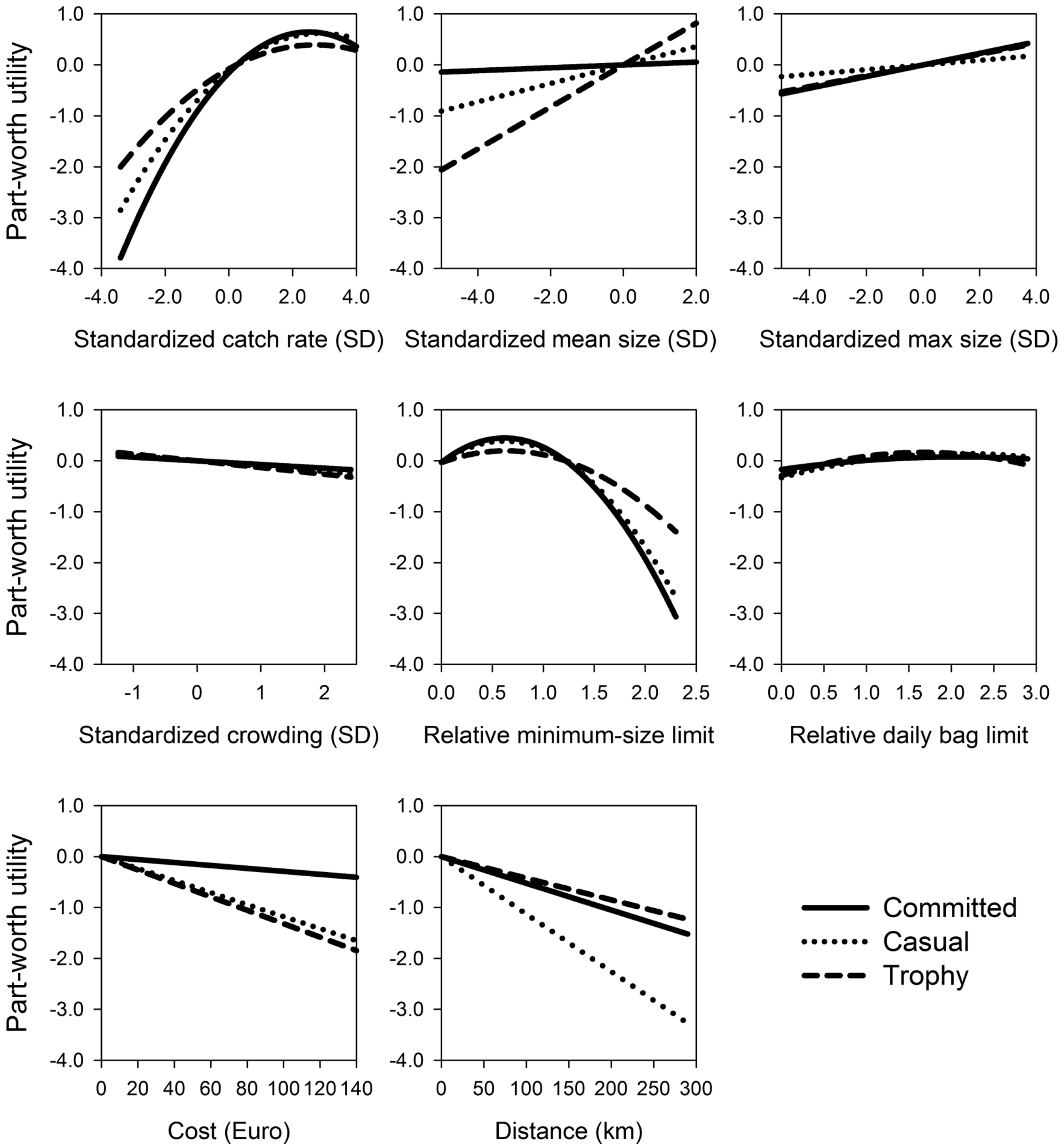

Fig. A2. Illustration of the five functions used to describe noncompliance. The solid black line describes the original depensatory relationship predicted by Sullivan (2002). The black long dashed line represents the reduction in the density-dependent parameter of this relationship, ς, by 75%. The black dotted line represents multiplication of the constant γ by 5 to increase the level of noncompliance that occurs under total catch-and-release regulations from 1% to 5%. The solid gray line represents constant noncompliance at 10%, and the dashed gray line represents constant noncompliance at 5%.