FISH and FISHERIES

Rethinking length-based fisheries regulations: the value of protecting old and large fish with harvest slots

Daniel C Gwinn[1], Micheal S Allen[1], Fiona D Johnston[2,3], Paul Brown[4], Charles R Todd[5] & Robert Arlinghaus[2,3]

[1]Program for Fisheries and Aquatic Sciences, School of Forest Resources and Conservation, The University of Florida, Gainesville, FL, 32653-3071, USA; [2]Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587, Berlin, Germany; [3]Chair for Integrative Fisheries Management, Faculty of Agriculture and Horticulture, Humboldt-Universität zu Berlin, Philippstrasse 13, 10115, Berlin, Germany; [4]Department of Environment and Primary Industries, Management and Science Branch Fisheries Victoria, Queenscliff Centre, PO Box 114, Queenscliff, Vic., 3225, Australia; [5]Department of Environment and Primary Industries, Arthur Rylah Institute for Environmental Research, 123 Brown Street, Heidelberg, Vic., 3084, Australia

Abstract

Managing fisheries using length-based harvest regulations is common, but such policies often create trade-offs among conservation (e.g. maintaining natural age-structure or spawning stock biomass) and fishery objectives (e.g. maximizing yield or harvest numbers). By focusing harvest on the larger (older) fish, minimum-length limits are thought to maximize biomass yield, but at the potential cost of severe age and size truncation at high fishing mortality. Harvest-slot-length limits (harvest slots) restrict harvest to intermediate lengths (ages), which may contribute to maintaining high harvest numbers and a more natural age-structure. However, an evaluation of minimum-length limits vs. harvest slots for jointly meeting fisheries and conservation objectives across a range of fish life-history strategies is currently lacking. We present a general age- and size-structured population model calibrated to several recreationally important fish species. Harvest slots and minimum-length limits were both effective at compromising between yield, numbers harvested and catch of trophy fish while conserving reproductive biomass. However, harvest slots consistently produced greater numbers of fish harvested and greater catches of trophy fish while conserving reproductive biomass and a more natural population age-structure. Additionally, harvest slots resulted in less waste in the presence of hooking mortality. Our results held across a range of exploitation rates, life-history strategies and fisheries objectives. Overall, we found harvest slots to represent a valuable option to meet both conservation and recreational fisheries objectives. Given the ubiquitous benefits of harvest slots across all life histories modelled, rethinking the widespread use of minimum-length limits is warranted.

Keywords Conservation, longevity overfishing, minimum-size limit, multiple objectives, open slot, recreational fishing, trade-offs

Correspondence:
Daniel C Gwinn, Fisheries and Aquatic Science Program, School of Forest Resources and Conservation, University of Florida, 7922 North West 71st Street, Gainesville, FL 32653-3071, USA
Tel.: 352-273-3624
Fax: 352-392-3672
E-mail: dgwinn@ufl.edu

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Introduction

Recreational fishing constitutes the main use of freshwater fish stocks, and many coastal ones, in all industrialized and many developing nations (Arlinghaus *et al.* 2002a; FAO 2012). To protect fish stocks from overfishing and meet ecological and social objectives, length-based management is common (Radomski *et al.* 2001; Lewin *et al.* 2006). Simple harvest regulations were already in use in mediaeval times (Redmond 1986; Welcomme 2001; Arlinghaus *et al.* 2002b), and they are widely used in freshwater recreational fisheries (Noble and Jones 1999; Paukert *et al.* 2001; Radomski *et al.* 2001). As the recreational use of fish populations in coastal zones increases (Coleman *et al.* 2004; Pawson *et al.* 2008; Ihde *et al.* 2011; Lloret and Font 2013), length-based management will likely become more prevalent in many saltwater fisheries as well (Van Poorten *et al.* 2013).

Length-based harvest regulations help achieve the maximum sustainable yield (MSY) and may contribute to the optimum social yield (OSY) in recreational fisheries (Roedel 1975; Hudgins and Malvestuto 1996). MSY was a relevant objective in recreational-fisheries management in times when subsistence motives were common (Redmond 1986; Nielsen 1999). However, consumptive motives are on the decline in many recreational fisheries (Arlinghaus *et al.* 2007; Allen *et al.* 2008; Myers *et al.* 2008). Correspondingly, the key management objective is no longer biomass-based MSY, but optimizing the quality of a multifaceted fishing experience to anglers (Crutchfield 1962; Hendee 1974; Roedel 1975; Driver 1985; Johnston *et al.* 2010).

Many factors contribute to the quality of fishing as perceived by anglers (Freudenberg and Arlinghaus 2010), and both catch-related and non-catch-related attributes of the fishing experience play a role (Hunt 2005). Although variation among cultures and fisheries exist (Bryan 1977; Fisher 1997; Dorow *et al.* 2010), non-harvest attributes of the catch-related fishing experience, such as catch rate (Anderson 1993; Cox *et al.* 2003) and size of the fish captured (Powers *et al.* 1975; Jacobson 1996; Arlinghaus 2006), are important for angler utility and satisfaction. The quality of a recreational fishery may thus be maximized at lower fishing mortality than the fishing mortality that produces MSY (Caddy 1999; Radomski *et al.* 2001). This occurs because at low fishing mortality, the degree of size and age truncation is less pronounced, in turn potentially achieving a compromise between modest harvest and improving the potential for anglers to catch large, trophy fish. Hilborn (2007) called this area left to the MSY on an inverted dome-shaped yield curve a 'zone of new consensus' because it may satisfy the interests of multiple stakeholders better than a biomass-based MSY objective.

At high fishing effort levels, length-based harvest limits are needed to prevent overfishing and meet management objectives. The most common technique is a minimum-length limit (MLL), where small, usually immature fish must be released and fish over the MLL may be harvested. Other length-based harvest regulations include maximum-length limits and combinations of minimum- and maximum-size limits that result in either harvest-slot limits (harvest of intermediate size fish, also referred to as harvest window, inverse slot or open slot) or protected slot limits (where intermediate size classes are protected from harvest) (Noble and Jones 1999; FAO 2012).[1] The majority of research on slot limits has been devoted to protected slots (e.g. Wilde 1997; Pierce and Tomcko 1998; Dotson *et al.* 2013), with no empirical assessment published on the performance of harvest slots. Despite this lack of research, harvest slots (HSs) are in use in selected fisheries such as some

[1]Note that the unqualified term 'slot limit' should not be used to avoid confusion; it is used interchangeably in the literature to mean either open or closed slot.

Florida inshore fish stocks in the Gulf of Mexico, the sturgeon fisheries on the west coast of North America and Nile perch (*Lates niloticus*, Latidae) in Lake Victoria (Law *et al.* 2012).

Some theoretical studies on the effectiveness of HSs have been conducted, but they were focused on a species-specific level (Arlinghaus *et al.* 2010 for northern pike *Esox lucius*, Esocidae, Clark *et al.* 1980; Jensen 1981; García-Asorey *et al.* 2011 for various freshwater salmonids including the anadromous steelhead *Oncorhynchus mykiss*, Salmonidae, and Koehn and Todd 2012 for Murray cod, *Maccullochella peelii*, Percichthyidae). Few generic fish population models have examined the performance of HSs, relative to alternative harvest regulations (Reed 1980; Botsford and Hobbs 1986; Law *et al.* 2012). Moreover, all these studies were strictly focused on optimizing biomass yield, and no research has compared the relative performance of HSs versus the more common MLLs across a range of fish life histories against alternative objectives to biomass yield, such as maximizing harvest numbers and the abundance of trophy fish.

The purpose of this study was to identify outcomes and trade-offs when applying HSs and MLLs to provide numerical harvest (harvest), biomass harvest (yield), trophy catch and stock conservation (using a range of indices). We performed this evaluation using a general age- and size-structured model for two prototypical fish populations that represented two extreme forms of productivities (life history). To provide a broad context to our results, we also evaluated the utility of HSs for managing several recreationally important fish species characterized by more specific life histories. The results have broad implications by calling into question the almost ‘default’ use of MLLs to manage recreational fisheries around the globe.

Conceptual background and review of length-based harvest regulations

The rationale for length-based harvest regulations involves at least four concerns. First, size limits are designed to avoid recruitment overfishing (Allen *et al.* 2013). Such arguments are common in the implementation of the popular MLLs based on the ‘spawn-at-least-once’ idea (Novinger 1984; Redmond 1986). Second, length-based harvest limits are intended to manage the size-structure of fish stocks to meet expectations of anglers (Clark *et al.* 1980; Jensen 1981; Noble and Jones 1999). Third, directing exploitation on particular size-classes can produce the MSY. Many age-structured models developed in the mid-20th century predicted an optimal age at entry into the fishery to maximize biomass yield (Ricker 1945; Allen 1953; Saila 1956; Beverton and Holt 1957). Because age and size are correlated and due to the impossibility to harvest single age classes entirely, these findings were transferred into management practice by implementing a MLL where over this size aggressive culling would maximize biomass yield or yield per recruit (Dunning *et al.* 1982; Maceina *et al.* 1998). A final reason for length-based harvest limits is convenience. Recreational fisheries are often open access, and there is a paucity of monitoring information for more complex management across the fisheries landscape (Post *et al.* 2002). In the absence of fishery-specific information, implementation of a MLL might be seen as a simple regulation intended to protect all stocks from recruitment overfishing. Correspondingly, in some countries, such as Germany, entire landscapes of spatially structured fisheries are commonly managed with one-size-fits-all MLLs (Daedlow *et al.* 2011). However, when fishing effort is intensive, a MLL severely truncates the size- and age-structure (Wilde 1997; Arlinghaus *et al.* 2010; Pierce 2010), which can affect the overall quality of the fishery by reducing the availability of trophy fish to anglers (Jacobson 1996; García-Asorey *et al.* 2011).

From a conservation perspective, there is renewed concern that the systematic removal of large fish may have ramifications for population fecundity and recruitment dynamics (e.g. Grey and Law 1987; Berkeley *et al.* 2004a,b; Birkeland and Dayton 2005). Several mechanisms have been proposed to explain why fisheries-induced demographic changes towards younger and smaller fish affect recruitment dynamics and productivity of stocks. First, a large fraction of young spawners amplifies a stock’s non-linear dynamics, hence destabilizing its abundance (Reed 1983; Anderson *et al.* 2008; Hsieh *et al.* 2010). Second, in many fish species, spawning occurs at different times and areas for fish of different size/age (Wright and Trippel 2009), providing a buffer against environmental stochasticity (Berkeley *et al.* 2004a; Hidalgo *et al.* 2011; Rouyer *et al.* 2011). Third, the existence of age- and size-dependent maternal effects on egg and larval quality could influence recruitment in some fish species (Berkeley *et al.* 2004a,b; Arlinghaus *et al.* 2010; Venturelli *et al.* 2010), but there is no agreement as to how prevalent this effect is in nature (O'Farrell and Botsford 2006; Marshall *et al.* 2010; Ottersen *et al.* 2013). Finally, in most fishes, fecundity increases exponentially with length and linearly with body mass (Wootton 1998). This is due to large fish not only having a greater body volume for holding eggs, but also because they may devote a greater fraction of surplus energy to egg production than smaller mature fish (Lester *et al.* 2004; Edeline *et al.* 2007). Thus, large fish have a greater relative reproductive value (Grey and Law 1987; Xu *et al.* 2013) and may contribute strongly to year class strength and surplus production under exploited conditions (Walters *et al.* 2008; Arlinghaus *et al.* 2010). Using length-based HSs to maintain highly fecund large individuals could thus represent a powerful strategy for managing fisheries sustainably.

The ultimate choice of the particular length-based harvest regulation depends on a range of factors such as management objective, population status, fishing mortality rate and the particular processes that govern a fish stock (FAO 2012). When the management objective is MSY, MLLs should be most useful when natural mortality and recruitment rates are low, and growth of fish is rapid (Novinger 1984; Brousseau and Armstrong 1987; FAO 2012). However, if size-related maternal effects influence recruitment (e.g. the fecundity reserve of large spawners; Venturelli *et al.* 2009, 2010), harvest-slot limits that protect both young and old fish might outperform MLLs over a range of fishing rates (Reed 1980; Arlinghaus *et al.* 2010; FAO 2012). Protected slots may perform better if people enjoy harvesting large fish, but for them to be effective recruitment must be sufficiently high (Brousseau and Armstrong 1987; FAO 2012). Protected slots are particularly advisable if competition among juvenile fish is excessive such that thinning of juvenile fish promises to relax competition, increase growth and reduce natural mortality (Brousseau and Armstrong 1987). For protected slots to work, however, people must be able and willing to harvest small fish (FAO 2012), which is often not the case (Wilde 1997; Pierce and Tomcko 1998). Thus, the applicability of protected slots may be less than for HSs and MLLs. This article therefore focused on HSs and MLLs for their utility in recreational fisheries management.

Despite the frequent use of length-based harvest limits in recreational fisheries (Radomski *et al.* 2001), most studies evaluating the effectiveness of such regulations are single-system case-studies that lack control fisheries and long time series and hence have low power to detect regulation effects (Allen and Pine 2000). In a meta-analysis, Wilde (1997) analysed MLLs and protected slots in largemouth bass (*Micropterus salmoides*, Centrachidae) fisheries in the U.S.A. He reported protected slots to be effective in increasing the proportion of large fish in the stock. However, the same regulations failed to increase angler catch rates, which is an indication that they did not elevate stock sizes. Additionally, MLLs failed to increase the proportion of large fish harvested by anglers (Wilde 1997). Based on these results and other considerations, some have questioned the usefulness of MLLs (Tesch and Wehrmann 1982; Conover and Munch 2002; Birkeland and Dayton 2005), and increasingly alternative regulations to MLLs are sought, in particular when maintaining large fish in the stock is considered important (Pierce 2010). In this context, the use of HSs has increasingly been proposed as alternative to MLLs to protect large and old as well as immature fish for reaping ecological (Berkeley *et al.* 2004a; Arlinghaus *et al.* 2010; Venturelli *et al.* 2010; Law *et al.* 2012), evolutionary (Conover and Munch 2002; Law 2007; Matsumura *et al.* 2011) and fisheries benefits (Jensen 1981; Arlinghaus *et al.* 2010). However, no theoretical research has tested the performance of HSs for a range of fish life histories relative to the much more widespread MLLs.

The model

We constructed an age- and size-structured population model to determine 'optimal' length-based fishery regulations when management objectives are to jointly consider several fishery attributes of value to anglers (harvest, yield and trophy catch), while conserving the fish stock's reproductive capacity and minimizing age and size truncation. To evaluate the performance of MLLs and HSs as fishery regulations across life histories, the model first simulated fish populations with low-productive and high-productive life histories that differed in longevity, growth and recruitment compensation levels (Myers *et al.* 1999; Goodwin *et al.*

2006). In the simulations, we accounted for natural mortality, harvest mortality, discard mortality (known in recreational fisheries as hooking mortality), length-based vulnerabilities to the fishery and density-dependent compensation in the recruitment process. We evaluated the fishery performance and conservation status for each life-history strategy, for medium and high exploitation scenarios, and across a range of MLLs and HSs to reveal regulations that provide a compromise among conservation and fishery objectives. We then modelled a series of specific fish species that commonly support recreational fisheries to provide context to our results and serve as a form of sensitivity analysis.

Model formulation

We simulated an age- and size-structured fish population with multiple growth trajectories similar in structure to Coggins *et al.* (2007). The model incorporated multiple growth trajectories to more realistically represent the effects of size-selective exploitation. The length-at-age of fish in each growth trajectory was modelled with a standard von Bertalanffy (1938) growth curve as:

$$L_{a,g} = L_{\infty,g}\left(1 - e^{-k(a-t_0)}\right), \tag{1}$$

where $L_{a,g}$ is the total length of an age a (a = 1 to A) fish in growth trajectory g (g = 1 to G), k is the metabolic parameter that determines the rate that fish attain maximum length, t_0 is the theoretical age at length zero, and $L_{\infty,g}$ represents the maximum length of fish in growth trajectory g. We simulated variability in growth by assigning each growth trajectory a unique maximum length ($L_{\infty,g}$).

Equilibrium abundance at age for each growth trajectory ($N_{a,g}$) was calculated as the product of the predicted number of age-1 recruits at equilibrium (R_{eq}) and the proportion of fish surviving to each age ($l_{a,g}$) as

$$N_{a,g} = R_{eq} l_{a,g} p_g, \tag{2}$$

where p_g is the probability of a fish belonging to a given growth trajectory. The parameter $l_{a,g}$ is the survivorship schedule that simulates the proportion of age-1 recruits surviving to each age for each growth trajectory. Survivorship to age a was calculated recursively for each growth trajectory as

$$l_{a,g} = l_{a-1,g} e^{-Z_{a,g}} \quad l_{1,g} = 1, \tag{3}$$

where $Z_{a,g}$ is the total instantaneous mortality rate for age a in growth trajectory g. The total annual instantaneous mortality rate incorporated natural mortality, harvest mortality and discard mortality as

$$Z_{a,g} = M + FV_{a,g} + (F'V_{a,g} - FV_{a,g})D, \tag{4}$$

where M is the instantaneous annual natural mortality rate, F and F' are the instantaneous annual harvest (i.e. exploitation) and catch rate of vulnerable fish, respectively, and $V_{a,g}$ and $V'_{a,g}$ are the length-specific vulnerabilities to harvest and catch, respectively. The parameter D is the discard mortality rate, which represents the proportion of caught and released fish that die due to the capture and handling process. Formulating the total mortality equation with instantaneous rates models a fishery where exploitation occurs continuously throughout each year and accounts for the competing risks of deaths due to exploitation, discard mortality and natural mortality. The vulnerability to harvest for a given age and growth trajectory ($V_{a,g}$) was expressed as a Boolean variable, where $V_{a,g}$ = 1 indicates that fish at age a in growth trajectory g are vulnerable to harvest and $V_{a,g}$ = 0 indicates that they are invulnerable to harvest. Thus, the values of $V_{a,g}$ were determined with a logical test to indicate vulnerability to the fishery as

$$\begin{aligned} &V_{a,g} = 1, \text{ when } L_{\min} < L_{a,g} < L_{\max}, \\ &V_{a,g} = 0, \text{ when } L_{\min} > L_{a,g} \text{ or } L_{\max} < L_{a,g}, \end{aligned} \tag{5}$$

where L_{min} is the minimum length where fish are vulnerable to harvest and L_{max} is the maximum length where fish are vulnerable to harvest. Thus, L_{min} and L_{max} represent the lower and upper length limit of a HS, respectively, and simulated a cohort of fish gradually becoming vulnerable to the fishery as fish in each growth trajectory grow into the legal length range for harvest. The parameter $V'_{a,g}$ is the length-based vulnerability of fish to capture, which was also determined as a Boolean variable that took the value of one when $L_{a,g}$ was greater than the minimum length vulnerable to capture (L_{cap}) and was otherwise zero.

Equilibrium recruitment R_{eq} was predicted using a Botsford modification of a Beverton and Holt (1957) stock-recruitment function (Botsford 1981a,b). This formulation predicts the number of age-1 recruits of an exploited population at equilibrium directly and is summarized in Walters and Martell (2004) as

$$R_{eq} = R_0 \frac{CR - (\Phi_0/\Phi_f)}{CR - 1}, \qquad (6)$$

where R_0 is the number of age 1 recruits in the unfished condition and CR is the Goodyear recruitment compensation ratio (Goodyear 1980), which represents the maximum increase in juvenile survival at reduced densities. The parameters Φ_0 and Φ_f are fecundity incidence functions that account for the cumulative effects of natural mortality, harvest mortality and discard mortality on the total annual fecundity of the population in the unfished and fished condition, respectively. We calculated the fecundity incidence functions per Walters and Martell (2004) as

$$\Phi = \sum_g \sum_a p_g f_{a,g} l_{a,g}, \qquad (7)$$

where $f_{a,g}$ is the average fecundity of fish of age a in growth trajectory g. Fecundity at age ($f_{a,g}$) was approximated as the difference between the mean weight-at-age and the weight-at-maturation because fecundity is usually directly proportional to weight (Walters and Martell 2004). When the mean weight-at-age was less than the weight-at-maturation, $f_{a,g}$ was set to a value of zero. This essentially modelled a 'knife-edge' transition of fish from immature to mature stages at the specified length at maturation. Weight-at-age was predicted using a standard length–weight relationship as

$$W_{a,g} = \alpha L_{a,g}^{\beta}, \qquad (8)$$

where α is the scaling parameter and β is the allometric parameter that modifies the relationship between length and weight.

Model outputs

The model was used to evaluate three standardized (scaled) measures of fishery performance at equilibrium, (i) the proportion of the maximum possible number of fish harvested (hereafter referred to as harvest); (ii) the proportion of the maximum possible number of trophy fish caught; and (iii) the proportion of maximum possible biomass yield (hereafter referred to as yield). These metrics were chosen as indicators of the social and economic value of the fishery because they are common components of the fishing experience that anglers, managers or other stakeholders value (Jensen 1981; Jacobson 1996; Arlinghaus 2006). We present all metrics on a normalized scale as proportions of total possible to allow unambiguous comparisons and elucidate possible trade-offs.

The proportion of the maximum possible harvest (H) was calculated as

$$H = \frac{\sum_g \sum_a N_{a,g}(1 - e^{-FV_{a,g}})}{H_{\max}}, \qquad (9)$$

where the term $(1 - e^{-FV_{a,g}})$ represents the proportion of age a fish harvested from each growth trajectory and $H_{\max}$ represents the maximum possible numbers harvested across the full range of both HS and MLL regulations for a given life-history/exploitation-rate scenario. Thus, the harvest obtained from each HS and MLL was compared with the maximum harvest value $H_{\max}$ obtained from any regulation.

Similarly, the proportion of the maximum possible number of trophy-sized fish caught by anglers (T) was calculated as

$$T = \frac{\sum_g \sum_a N_{a,g}\left(1 - e^{-FV'_{a,g}}\right) t_{a,g}}{T_{\max}}, \qquad (10)$$

where $t_{a,g}$ was a Boolean variable that takes the value of one when $L_{a,g}$ was greater than or equal to trophy size fish and the value of zero when $L_{a,g}$ was less than a trophy size fish. Fish were considered trophy size if they were ≥85% of the average maximum total length across growth trajectories ($\bar{L}_\infty$). The parameter $T_{\max}$ represented the maximum possible numbers of trophy fish caught across the full range of both HS and MLL regulations for a given life-history/exploitation-rate scenario.

The proportion of maximum possible biomass harvested (yield) was calculated as

$$Y = \frac{\sum_g \sum_a N_{a,g} W_{a,g}(1 - e^{-FV_{a,g}})}{Y_{\max}}, \qquad (11)$$

where $W_{a,g}$ is the weight of a fish at age a in growth trajectory g calculated with equation 8 and $Y_{\max}$ is the maximum possible yield across the full range of HS and MLL regulations for a given life-history/exploitation-rate scenario.

For simulations that included discard mortality, we calculated the harvesting efficiency (E) as a fourth performance metric. The E metric indicates the fraction of total fishery-related deaths that are due to harvest (Coggins *et al.* 2007; Arlinghaus *et al.* 2010). It was calculated as

$$E = \sum_{g}\sum_{a}\frac{N_{a,g}(1 - e^{-FV_{a,g}})}{N_{a,g}\left(1 - e^{-\left(Z_{a,g}-M\right)}\right)}, \qquad (12)$$

where the numerator is the number of harvested fish and the denominator is the total number of fishery-related mortalities (i.e. total mortalities – natural mortalities). Low values of E indicate a high proportion of fish deaths due to discard mortality after catch and release, and thus reduced harvesting efficiency.

We assessed the conservation status of all simulated life histories by calculating the spawning potential ratio (SPR) and a metric of juvenescence (J) due to fishery-induced age (and size) truncation of the stock. The SPR was applied as a measure of the reduction in per-recruit reproductive output of the fish populations and was calculated as the fecundity-per-recruit at equilibrium divided by the fecundity-per-recruit in the unfished condition (i.e. SPR = Φ_0/Φ_f). SPR is a common metric used to assess the sustainability of fisheries with values <0.35 indicating the potential for recruitment overfishing (Mace 1994; Allen *et al.* 2013). The J metric was used to index the alteration of the natural age- and size-structure and to account for the disproportional importance of old and large fish for recruitment and population stability (i.e. 'longevity overfishing', Beamish *et al.* 2006; Hsieh *et al.* 2010). The value of J was calculated as the total fecundity produced by the older half of the age classes divided by the total fecundity of the entire population ($R_{eq}\Phi_f$) at equilibrium. Thus, large J values indicated greater fecundity resulting from large, old fish, while small values indicated the loss of large fecund spawners in the population.

We defined three specific management objectives thought to be of relevance to recreational fisheries managers to evaluate the relative performance of HSs versus MLLs across the life-history types. The first objective was harvest-oriented management, the second objective was trophy catch-oriented management, and a third objective represents a compromise between harvest and trophy catch. To operationalize each objective, we drew on two normalized metrics of fishing quality, *viz.* the harvest numbers H and the catch of trophy fish T. We designed ratios between H and T to reflect underlying fishing qualities to be achieved for meeting a specific management objective. Accordingly, an objective that would aim at a ratio of the fishing quality H over T of 1.0 would reflect equal priority on both numbers of fish harvested and trophy catch. Meeting the ratio would represent identical fishing qualities for harvest and trophy catch as revealed by an identical percentage of H and T that would be present under the chosen regulation. Similarly, any ratio different from 1.0 would reflect an objective that aimed at producing a greater fishing quality on one of the two components, without entirely disregarding the other component. For illustrative purposes, we specified a harvest-oriented management objective as $H = 3T$, meaning that the harvest fishing quality H would be three times the fishing quality in terms of trophy catch T. Analogously, we defined a trophy-fish-catch-oriented management objective as one where the condition $3H = T$ is met, meaning that the fishing quality in terms of catch of trophy fish, T, would be three times that of the fishing quality for harvest H. Our compromise management objective was defined simply as $H = T$, resulting in an equal fishing quality of H and T. After identifying the specific regulation (either HS or MLL) that would meet the management objective, we calculated the fishery and conservation metrics at that regulation. Although the exact weighting of our management objectives is not likely to represent any management objective for a specific recreational fishery accurately, the specifications chosen provided a convenient reference for comparing the relative performance of MLLs and HSs for meeting conservation needs, while optimizing the fishing quality for a variety of exploited species.

Parameterization and outline of analysis

We expected that the efficacy of length-based regulations to optimize harvest, trophy catch and stock conservation would be influenced by the life-history characteristics of the fish and the level of exploitation applied by the fishery. Thus, we evaluated length-based regulations for two life-history strategies and two intensities of fishing (high and medium fishing mortality). The life-history strategies were parameterized to represent two extremes across a gradient of productivity levels, with one strategy representing a generic long-lived, low-productive species (LLLP) and the other strategy representing a generic short-lived, high-productive species (SLHP, Coggins *et al.* 2007). The LLLP represented a large-bodied fish with slow growth, late maturation and high levels of density-dependent recruitment compensation (e.g. striped bass *Morone saxatilis*, Moronidae). The SLHP represented a smaller-bodied fish with fast growth, early maturation and low levels of density-dependent recruitment compensation (e.g. spotted seatrout *Cynoscion nebulosus*, Sciaenidae). Parameter values representing these life-history strategies were taken from Coggins *et al.* (2007) with some modifications (Table 1). The maximum age of the LLLP and the SLHP was set at 30 years and 10 years, respectively. Associated mortality and growth parameter values were then determined from life-history invariants. For example, the instantaneous natural mortality rate (M) was approximated from the maximum age as 0.15 per year for the LLLP and 0.44 per years for the SLHP using Hoenig (1983). The k parameter of the von Bertalanffy growth model was approximated from M as 0.1 for the LLLP and 0.29 for the SLHP using the established relationship of $M \approx 1.5\ k$ (Jensen 1996).

We simulated a total of 101 growth trajectories for each life-history type. Maximum length in each growth trajectory was assigned by first choosing a mean asymptotic length ($\overline{L}_\infty$) and then choosing a minimum ($L_{\infty,\mathrm{min}}$) and maximum ($L_{\infty,\mathrm{max}}$) value possible. The L_∞ of each growth trajectory was then assigned a value evenly spaced between $L_{\infty,\mathrm{min}}$ and $L_{\infty,\mathrm{max}}$. The mean asymptotic length ($\overline{L}_\infty$) of the LLLP and the SLHP was set at 1000 mm and 500 mm, respectively (Table 1). The values of the minimum ($L_{\infty,\mathrm{min}}$) and maximum ($L_{\infty,\mathrm{max}}$) asymptotic length were set as ±20% of $\overline{L}_\infty$ for both life-history strategies. This range approximated the 95% probability range of a normal distribution with a mean of $\overline{L}_\infty$ and a standard deviation of 10% of the mean. The proportion of the fish recruiting to each growth trajectory (p_g) was specified as the normal probability density of $L_{\infty,g}$ given a mean equal to $\overline{L}_\infty$ and a standard deviation of 10% of $\overline{L}_\infty$. This formulation of growth trajectories and p_g mimicked common variability in growth of exploited fish populations (Walters and Martell 2004).

We simulated a medium and high exploitation fishery on each life-history strategy. The medium exploitation fishery was specified by setting the instantaneous annual harvest rate (F) to 80% of the natural mortality. This approximates a fishery harvested near MSY (Walters and Martell 2004). The high exploitation fishery was specified by setting F to twice the natural mortality rate. Exploitation rates of this level generally cause growth and recruitment overfishing indicated by yields that are less than MSY (Walters and Martell 2004). For simplicity, we assumed that there was no voluntary release of fish by anglers (i.e. $F' = F$) and that discard mortality (D) was negligible for the base simulations. However, we evaluated fishery performance and stock conservation at two levels of discard mortality rates (D = 10 and 30%) in an additional sensitivity analysis because Coggins *et al.* (2007) noted that benefits of harvest regulations are tightly related to the level of

Table 1 Parameter input values provided for a long-lived low-productive (LLLP) and short-lived, high-productive (SLHP) life-history prototype.

Parameter	Description	LLLP	SLHP
R_0	Average age 1 recruitment in the unfished state	1 000 000	1 000 000
A	Maximum age (years)	30	10
M	Natural mortality rate (per year)	0.15	0.44
CR	Compensation ratio	25	5
$\overline{L}_\infty$	Average asymptotic length (mm)	1000	500
$L_{\infty,\mathrm{min}}$	Minimum asymptotic length (mm)	800	400
$L_{\infty,\mathrm{max}}$	Maximum asymptotic length (mm)	1200	600
k	von Bertalanffy growth coefficient (years)	0.1	0.35
t_0	Theoretical age at length zero (years)	0	0
L_{mat}	Length-at-maturation (mm)	400	200
α	Length–weight constant	3.5×10^{-5}	3.5×10^{-5}
β	Allometric parameter	2.8	2.8
L_{min}	Minimum length vulnerable to harvest (mm)	400	200
L_{cap}	Minimum length vulnerable to capture (mm)	250	125
L_{troph}	Minimum total length of a trophy fish (mm)	800	400

discard mortality. The discard mortality rate of 10% was chosen because it approximates a common hooking mortality rate that represents many recreational fisheries (Bartholomew and Bohnsack 2005; Hühn and Arlinghaus 2011), while the value of 30% was chosen because it generally exceeds the rate for which fishery sustainability can be achieved through length-based harvest regulations when F is high (Coggins *et al.* 2007).

We evaluated the performance of a range of MLLs and HSs by manipulating the vulnerability to harvest (Equation 5). We considered MLLs ranging from the length-at-maturation (L_{mat}) to the maximum length possible ($L_{\infty,\max}$). A MLL equal to L_{mat} modelled a fishery where all mature fish were legal to harvest, whereas a MLL equal to $L_{\infty,\max}$ modelled a total catch-and-release fishery. Similarly, we considered HSs with a minimum legal length (L_{min}) of L_{mat} and a maximum legal length (L_{max}) ranging from L_{mat} to $L_{\infty,\max}$. A HS with L_{max} equal to $L_{\infty,\max}$ modelled a fishery where all mature fish were legal to harvest, whereas L_{max} equal to L_{mat} modelled a total catch-and-release fishery. For the base simulations, we did not consider any regulation that allowed harvest of fish shorter than length-at-maturation because harvesting fish before they reach maturity significantly increases the risk of overfishing (Myers and Mertz 1998; Froese 2004) and is usually not implemented as a recreational-fisheries regulation. We fixed the lower length vulnerable to capture (L_{cap}) at 25% of $\overline{L}_{\infty}$ to provide a realistic standard across life-history strategies and because very small fish are usually not vulnerable to recreational fishing gear (Pierce *et al.* 1995; but see Alós *et al.* 2009).

To explore how our results would transfer to specific freshwater fish species commonly targeted by recreational anglers, we evaluated MLLs and HSs for Murray cod, lake trout (*Salvelinus namaycush*, Salmonidae), Eurasian perch (*Perca fluviatilis*, Percidae), arctic grayling (*Thymallus arcticus*, Salmonidae), zander (*Sander lucioperca*, Percidae) and northern pike. Murray cod and lake trout were chosen because these species have life-history characteristics that resemble the LLLP, and Eurasian perch was chosen because its life-history characteristics resemble the SLHP. Zander, northern pike and Arctic grayling were chosen because they represent fish species that do not easily correspond to the LLLP or the SLHP prototype and represent intermediate life-history strategies. All species chosen are valued for recreational fishing with both trophy and consumption components, although cultural differences exist (e.g. pike are usually consumed by anglers in Germany and often released voluntarily in the USA). Input parameter values for each species were taken from the literature or approximated from life-history invariants (Hoenig 1983; Jensen 1996; Table 2). The Goodyear recruitment compensation parameter (CR) was taken from Myers *et al.* (1999); when species-specific values were not available, we used the average for the taxonomic family.

Fisheries managers never have perfect information about critical life-history or fishery parameters required to set appropriate regulations. Hence, identifying regulations that are robust to incorrect knowledge about the fishery is important (Walters and Martell 2004). To evaluate the relative performance of HSs and MLLs in the face of parameter uncertainty, we performed a two-step sensitivity analysis. In the first step, we determined the regulation that met the management objectives with incorrect parameter input values (mimicking the determination of regulations with imperfect knowledge). In the second step, we applied the regulations determined with incorrect parameter inputs to the simulated fishery to determine how robust the regulation performance is to the incorrect parameter inputs. Using this approach, we evaluated uncertainty about the instantaneous natural mortality rate M, the recruitment compensation ratio CR, the length at maturation L_{mat} and the instantaneous fishery exploitation rate F. These four parameters were selected because they are important determinants of the productivity of stocks and are critical for determining regulations that optimize fishery outputs and conserve stocks. Each parameter was changed by 20% in the direction that would render the population more resilient to exploitation and then we evaluated how application of regulations chosen with this optimistic scenario would play out when in reality the stock is less productive and hence, less resilient to exploitation. Hence, we evaluated the impact of basing regulation choices on an M that is 20% higher, a CR that is 20% higher, an L_{mat} that is 20% lower and an F that is 20% lower than in reality.

Results

The two life histories revealed similar patterns in terms of yield, trophy catch and harvest numbers,

Table 2 Parameter input values and information sources used for simulations of Murray cod (*Maccullochella peelii*, Percichthyidae), lake trout (*Salvelinus namaycush*, Salmonidae), Eurasian perch (*Perca fluviatilis*, Percidae), arctic grayling (*Thymallus arcticus*, Salmonidae), zander (*Sander lucioperca*, Percidae) and northern pike (*Esox lucius*, Esocidae).

Parameter	Murray cod	Lake trout	Eurasian perch	Arctic grayling	Zander	Northern pike
R_0	1 000 000	1 000 000	1 000 000	1 000 000	1 000 000	1 000 000
A	40[3]	38[3]	10[3]	16[3]	16[9]	16[3]
M	0.11[1]	0.12[7]	0.44[4]	0.27[4]	0.27[9]	0.28[4]
CR	30[1]	24[11]	9.5[11]	24[11]	9.5[11]	6.1[11]
$\bar{L}_\infty$	1200[1]	872[7]	278[8]	370[5]	818[10]	976[9]
$L_{\infty,\mathrm{min}}$	960[2]	698[2]	222[2]	296[2]	654[2]	781[4]
$L_{\infty,\mathrm{max}}$	1440[2]	1046[2]	334[2]	444[2]	982[2]	1171[4]
k	0.11[1]	0.092[7]	0.29[8]	0.18[5]	0.24[10]	0.19[9]
t_o	0[1]	0[7]	0[8]	−1.75[5]	−0.01[10]	−0.34[9]
L_{mat}	500[1]	520[7]	151[8]	230[9]	456[9]	378[9]
α	3.6×10^{-5} [1]	5.9×10^{-5} [7]	5.9×10^{-4} [8]	1.9×10^{-4} [9]	4.7×10^{-5} [10]	5.8×10^{-5} [9]
β	2.91[1]	3.18[7]	3.18[8]	2.92[9]	3.16[10]	3.07[9]
L_{min}	500	520	151	230	456	378
L_{cap}	300[12]	218[12]	70[12]	93[12]	205[12]	244[12]
L_{troph}	1020[6]	741[6]	236[6]	315[6]	695[6]	830[4]

[1]Citations in Allen *et al.* (2009).
[2]$\bar{L}_\infty \pm 0.2 * \bar{L}_\infty$.
[3]Hoenig (1983).
[4]Jensen (1996).
[5]Hughes (1997).
[6]$0.85 * L_{\infty,\mathrm{max}}$.
[7]Shuter *et al.* (1998).
[8]Heibo *et al.* (2005).
[9]Fishbase (Froese and Pauly 2006).
[10]Wysujack *et al.* (2002).
[11]Myers *et al.* (1999).
[12]$0.25 * \bar{L}_\infty$.

and corresponding trade-offs, between regulation types (Figs 1 and 2). Liberal regulations (i.e. wide HSs or low MLLs) that produced high harvest provided low trophy catch for both regulation types and fishing mortality levels. Accordingly, restricting harvest by increasing the MLL or by decreasing the upper bound of the HS resulted in an increase in the catch of trophy fish, with maximum trophy catch being realized by a full harvest closure (i.e. total catch-and-release fishery; Figs 1 and 2). Biomass yield was found to reach a maximum for both fishing exploitation level in both life-history prototypes (Figs 1c,d and 2b-d), indicating that our high fishing mortality level resulted in growth and recruitment overfishing for liberal regulations. Catches of trophy fish were eliminated for liberal regulations unless fishing mortality was low (Figs 1b,d and 2b,d). In the LLLP prototype, no dome-shaped yield curve was predicted for HSs (Fig. 1a,b), while a MLL was present that maximized yield (Fig. 1c,d). In the SLHP life-history prototype, maximum yield was predicted at the high fishing mortality for a narrow HS and a small MLL (Fig. 2b,d). This life-history prototype also revealed a very pronounced dome-shaped relationship of regulations and maximum harvest numbers for the high exploitation rate, which was not the case in the less productive LLLP life-history prototype.

In terms of management objectives, regulations that favoured trophy catch over harvest were found to result in more restrictive regulations (e.g. higher MLLs or narrower HSs), while more liberal regulations were needed to meet harvest objectives (Table 3). Regulations that met compromise objectives were always intermediate, suggesting a trade-off among trophy catch and harvest (Table 3). The HS regulations generally provided higher values of all metrics except biomass yield compared with MLLs for all management objectives (compromise, trophy and harvest) and fishing mortality rates. Values of harvest, trophy catch,

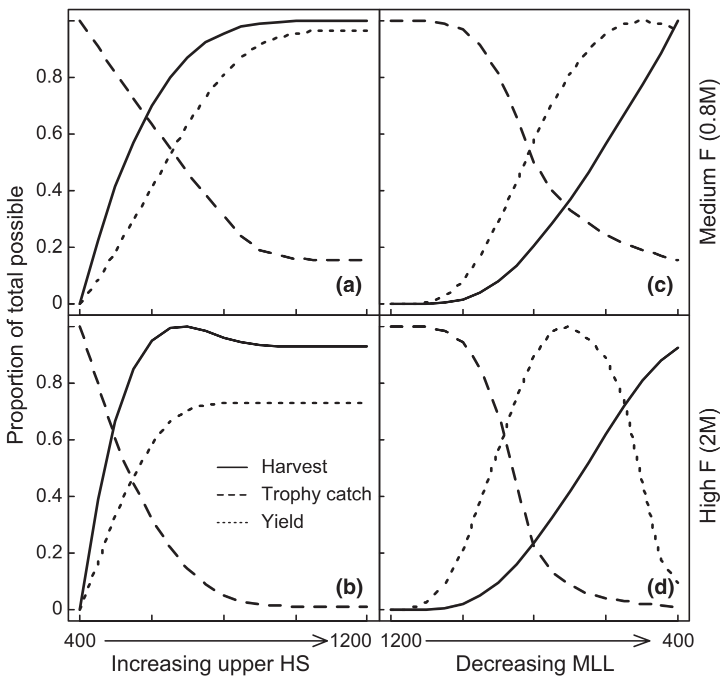

Figure 1 The proportion of the maximum possible harvest, trophy catch and biomass yield produced with a range harvest slots (left panels, a and b) and with a range of minimum-length limits (right panels, c and d) applied to a long-lived, low-productive fish population (LLLP) (Table 1). Panels a and c represent a fishery with medium exploitation (F = 0.8*M*, *M* = instantaneous annual natural mortality rate) and panels b and d represent a fishery with high exploitation (F = 2*M*). Left panels, a and b, describe a change in the upper limit of a harvest slot (HS) with a lower limit of 400 mm total length. Right panels, c and d, describe a change in the minimum-length limit (MLL).

SPR and *J* were nearly always higher with the best-performing HS regulations than for the best MLL (Table 3). This was true across life-history types, fishing mortality rates and management objectives, suggesting that improved performance of the HS regulations was a general result. The relative gains in harvest and trophy fish when applying the HS over the MLL were greater for the high exploitation fishery and for the LLLP prototype than for the medium exploitation and SLHP prototype. Biomass yield was the only metric that was nearly always higher for MLLs compared with HSs (Table 3).

High levels of fishing mortality resulted in more conservative regulations being required to meet each management objective. For example, the preferred HS narrowed and MLL increased as fishing mortality levels went from medium to high for both life-history types (Table 3). However, under conditions of high exploitation, the advantage of a HS over a MLL for meeting management objectives was particularly pronounced. For example, for the LLLP under low exploitation (0.8*M*) with a harvest-based management objective, the objective-meeting HS produced a harvest of 210 000 and trophy catch of 14 400 fish, while the objective-meeting MLL produced a harvest of 144 000 and trophy catch of 9 900 fish (Table 3). This represented a 46 and 45% increase in harvest and trophy catch, respectively, for the HS over the MLL. Under high exploitation (2*M*), the HS produced an 170 and 176% increase in harvest and trophy catch, respectively, indicating a strongly increased benefit of HSs over MLLs under high exploitation. This pattern was consistent across the two life-history strategies and the three management objectives (Table 3) and indicated that the greatest advantage of a HS over a MLL would be realized for fisheries with high exploitation rates. These general findings resulted because HSs restricted the harvest to smaller, more abundant ages (sizes) whereas the MLLs targeted larger, less abundant ages. As a result, HS regulations increased harvest while preserving old and large members of the stock to serve as trophy catch and a fecundity reserve to maintain recruitment.

Although the optimal HS for each management objective produced higher harvest and catch of

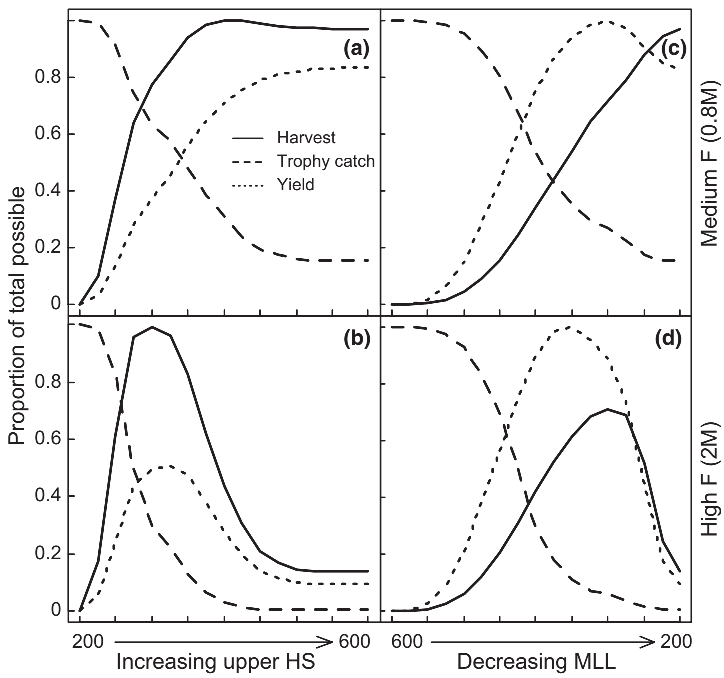

Figure 2 The proportion of the maximum possible harvest, trophy catch and biomass yield produced with a range harvest-slot limits (left panels, a and b) and with a range of minimum-length limits (right panels, c and d) applied to a short-lived, high-productive fish population (SLHP) (Table 1). Panels a and c represent a fishery with medium exploitation (F = 0.8*M*, *M* = instantaneous annual natural mortality rate) and panels b and d represent a fishery with high exploitation (F = 2*M*). Left panels, a and b, describe a change in the upper limit of a harvest slot (HS) with a lower limit of 200 mm total length. Right panels, c and d, describe a change in the minimum-length limit (MLL).

trophy fish than MLLs, this occurred at the expense of biomass yield. In fact, MLLs revealed a greater potential for yields than HSs across the full range of each regulation, particularly for the SLHP and the high exploitation fisheries (Figs 1 and 2). For example, the MLL meeting the compromise management objective produced approximately 112% greater yield than the corresponding HS for the LLLP and about 167% greater yield than the compromise HS for the SLHP at low exploitation (Table 3). The clear advantage of MLLs for producing higher biomass yields at each management objective was not noticeably influenced by the life-history strategy or the level of exploitation.

With few exceptions, both MLLs and HSs achieved conservation objectives in terms of SPR at each of the three objectives (Table 3). However, the use of the HSs resulted in a greater proportion of the total annual fecundity being produced by older fish (*J*) compared with MLLs (Table 3). This pattern was consistent across all management objectives, exploitation levels and life-history types. Thus, HSs placed on intermediate-age/size fish produced higher harvests and catches of trophy fish, while meeting conservation thresholds for SPR and for conserving the fecundity produced by older fish for nearly all scenarios simulated. The only case where this was not true was when the LLLP was managed for harvest with the optimal HS while being exploited at high rates. Under these conditions, the MLL outperformed the HS for maintaining high SPR values (Table 3). MLLs were effective at maximizing biomass yields and were similarly effective at conserving the spawning stock (SPR). Nevertheless, conservation performance was nearly always better with HS than MLL regulations.

We found the relative performance of HSs and MLLs was consistent across the five simulated fish species and mirrored the findings for the two prototypical life histories just described (Table 4). Increases in harvest, trophy catch and proportion of total annual fecundity resulting from older fish (*J*) were always realized by the application of the objective-meeting HS over the corresponding MLL for all five species (Table 4). By contrast, across all species MLLs resulted in greater biomass yield at each of the management objectives (Table 4).

Table 3 The performance of harvest slot (HS) and minimum-length limit (MLL) regulations for two different life-history prototypes, three management objectives and two fishing mortality levels *F*. The LLLP life history represents a long-lived, low-productive fish population, while the SLHP life history represents a short-lived, high-productive fish population (Table 1). Bold values indicate the best performance for each metric.

Life-history prototypes	Management objectives	*F*	Regulation (mm)	Harvest (thousands)	Trophy (thousands)	Yield (million kg)	SPR	*J*
LLLP	Compromise	0.8*M*	400–584 HS	**146**	**29.9**	0.17	**0.67**	**0.45**
		0.8*M*	712 MLL	77	15.6	**0.36**	0.69	0.28
	Compromise	2*M*	400–492 HS	**180**	**65.6**	0.16	**0.63**	**0.46**
		2*M*	802 MLL	67	23.9	**0.37**	0.71	0.27
	Trophy	0.8*M*	400–466 HS	**64**	**39.5**	0.05	**0.88**	**0.46**
		0.8*M*	816 MLL	40	24.4	**0.24**	0.62	0.36
	Trophy	2*M*	400–436 HS	**81**	**88.2**	0.06	**0.85**	**0.46**
		2*M*	854 MLL	44	48.1	**0.28**	0.80	0.34
	Harvest	0.8*M*	400–846 HS	**210**	**14.4**	0.40	0.40	**0.29**
		0.8*M*	504 MLL	144	9.9	**0.46**	**0.45**	0.22
	Harvest	2*M*	400–636 HS	**273**	**32.8**	0.35	0.29	**0.39**
		2*M*	716 MLL	101	11.9	**0.48**	**0.55**	0.15
SLHP	Compromise	0.8*M*	200–284 HS	**169**	**60.5**	0.03	**0.76**	**0.36**
		0.8*M*	376 MLL	105	37.7	**0.08**	0.75	0.21
	Compromise	2*M*	200–257 HS	**204**	**127.2**	0.03	**0.75**	**0.36**
		2*M*	411 MLL	103	63.7	**0.09**	0.73	0.17
	Trophy	0.8*M*	200–246 HS	**76**	**81.0**	0.01	**0.92**	**0.37**
		0.8*M*	429 MLL	56	60.2	**0.06**	0.86	0.28
	Trophy	2*M*	200–235 HS	**90**	**163.1**	0.01	**0.92**	**0.37**
		2*M*	446 MLL	61	113.0	**0.06**	0.84	0.26
	Harvest	0.8*M*	200–422 HS	**239**	**28.7**	0.07	0.52	**0.27**
		0.8*M*	265 MLL	180	21.7	**0.09**	**0.57**	0.15
	Harvest	2*M*	200–318 HS	**276**	**57.3**	0.05	0.48	**0.33**
		2*M*	366 MLL	146	29.8	**0.10**	**0.61**	0.10

M, instantaneous annual natural mortality rate, SPR, spawning potential ratio, *J*, proportion of fecundity produced by the older half of age classes in the population.

Additionally, SPR at the management objective was generally similar between the objective-meeting HS and MLL. Few exceptions occurred for high exploitation fisheries managed for harvest using HS, which reduced the SPR relative to MLL (Table 4). However, in all cases, the SPR was still above 0.35 (results not shown).

Discard mortality had little influence on the relative performance of HSs versus MLLs; however, it influenced the conservation objectives and the harvesting efficiency of the fishery. Moderate levels of discard mortality (10%) had minimal effects on the results, but high levels of discard mortality (30%) rendered both MLLs and HSs ineffective for maintaining SPR under conditions of high fishing mortality (Table 5). For example, both the LLLP and SLHP had SPR values ≤ 0.35 when discard mortality was 30% and exploitation was $2M$ (Table 5), with the exception of the SLHP managed for trophy catch. We found HSs to maintain harvesting efficiency (E) in the face of discard mortality, particularly when exploitation rates were high. Under high exploitation rates, the efficiency of the fishery could be doubled when applying the

Table 4 The percent change in the performance metrics when changing the regulation from the objective-meeting minimum-length limit to the objective-meeting harvest slot for a range of species (Table 2), three management objectives (compromise, trophy and harvest, Table 3) and two fishing mortality levels F.

Life history	Management objective	F	Harvest	Trophy	Yield	SPR	J
Murray cod	Compromise	0.8M	45	46	−38	6	40
		2M	76	76	−41	5	68
	Trophy	0.8M	22	25	−66	10	21
		2M	39	30	−64	13	32
	Harvest	0.8M	13	12	−10	0	23
		2M	80	80	−16	−21	109
Lake trout	Compromise	0.8M	51	52	−60	3	94
		2M	89	87	−69	1	181
	Trophy	0.8M	27	30	−83	9	48
		2M	38	40	−85	13	78
	Harvest	0.8M	17	17	−21	−2	61
		2M	90	90	−46	−26	402
Eurasian perch	Compromise	0.8M	46	43	−26	3	47
		2M	69	76	−28	3	86
	Trophy	0.8M	21	23	−57	9	26
		2M	38	30	−54	10	40
	Harvest	0.8M	11	12	−6	0	27
		2M	73	79	−3	−21	135
Arctic grayling	Compromise	0.8M	56	53	−43	0	31
		2M	88	86	−46	0	44
	Trophy	0.8M	25	32	−71	7	16
		2M	44	37	−69	8	20
	Harvest	0.8M	22	21	−13	−5	21
		2M	90	95	−24	−25	69
Zander	Compromise	0.8M	82	84	−69	2	66
		2M	133	134	−73	−2	81
	Trophy	0.8M	46	46	−86	6	30
		2M	49	48	−88	7	40
	Harvest	0.8M	52	51	−36	−13	75
		2M	138	140	−56	−28	167
Northern pike	Compromise	0.8M	40	38	−50	5	54
		2M	57	57	−57	8	98
	Trophy	0.8M	15	19	−75	8	28
		2M	21	21	−76	10	39
	Harvest	0.8M	12	13	−16	1	38
		2M	64	67	−33	−15	181

M, instantaneous annual natural mortality rate, SPR, spawning potential ratio, J, proportion of fecundity produced by the older half of age classes in the population.

objective-meeting HS over the corresponding MLL for both life-history strategies (Table 5). However, under conditions of high discard mortality, applying either a HS or MLL to meet recreational fisheries management objectives may not be an effective strategy for long-term conservation of the stock.

Results on the performance of HSs over MLLs were robust to parameter uncertainty indicating management with imperfect knowledge of key productivity parameters *M*, *CR*, *F* and L_{mat} would not alter the relative performance of HSs over MLLs (Appendix A, Tables S1–S4). In only one case did the relative performance of HSs and MLLs reverse. This reversal occurred for the trophy-oriented objective applied to the SLHP undergoing medium exploitation. In this case, the harvest numbers produced by the optimal MLL were greater than the HS; however, there were few differences among the policies (Appendix A, Tables S1–S4). The percent change of metrics in response to changing each of the parameters by 20% ranged from −92 to 55%, but in over 90% of the cases, metrics varied only between −20% and 20% indicating inelastic responses, low sensitivity and a comparatively robust model. These results inferred that HSs would outperform MLLs even with substantial uncertainty in population and fishery parameters.

Discussion

We showed that HSs produced a more favourable compromise among fishery and conservation objectives than MLLs for a range of management objectives that included harvest, compromise and trophy catches. This effect stemmed from HS regulations protecting large fecund as well as immature fish in the population from harvest, thereby

Table 5 The performance of harvest slots (HS) and minimum-length limits (MLL) regulations for two prototypical fish life histories under two levels of discard (hooking) mortality *D* with respect to three management objectives at two fishing mortality levels *F*. Long-lived, low productive (LLLP), short-lived, high productive prototype (SLHP) (Table 1).

			D = 10%			D = 30%		
Life-history prototype	Management objective	*F*	Regulation (mm)	SPR	*E*	Regulation (mm)	SPR	*E*
LLLP	Compromise	0.8*M*	400–588 HS	0.60	**0.83**	400–604 HS	**0.48**	**0.65**
		0.8*M*	698 MLL	**0.62**	0.64	646 MLL	**0.48**	0.43
	Compromise	2*M*	400–490 HS	0.46	**0.69**	400–496 HS	0.26	**0.46**
		2*M*	782 MLL	**0.53**	0.35	726 MLL	**0.30**	0.16
	Trophy	0.8*M*	400–468 HS	**0.76**	**0.60**	400–470 HS	**0.59**	**0.35**
		0.8*M*	800 MLL	0.73	0.45	766 MLL	0.56	0.23
	Trophy	2*M*	400–436 HS	**0.60**	**0.44**	400–436 HS	**0.33**	**0.22**
		2*M*	832 MLL	0.59	0.25	788 MLL	0.32	0.09
	Harvest	0.8*M*	400–794 HS	0.40	**0.92**	400–846 HS	0.35	**0.80**
		0.8*M*	540 MLL	**0.46**	0.83	464 MLL	**0.37**	0.72
	Harvest	2*M*	400–600 HS	0.27	**0.84**	400–628 HS	0.17	**0.66**
		2*M*	716 MLL	**0.44**	0.48	646 MLL	**0.24**	0.27
SLHP	Compromise	0.8*M*	200–271 HS	**0.67**	**0.77**	200–281 HS	**0.54**	**0.54**
		0.8*M*	372 MLL	**0.67**	0.64	345 MLL	0.53	0.40
	Compromise	2*M*	200–252 HS	**0.56**	**0.62**	200–249 HS	**0.34**	**0.29**
		2*M*	404 MLL	**0.56**	0.41	391 MLL	**0.34**	0.15
	Trophy	0.8*M*	200–248 HS	**0.80**	**0.52**	200–248 HS	**0.63**	**0.27**
		0.8*M*	422 MLL	0.77	0.44	407 MLL	0.60	0.21
	Trophy	2*M*	200–241 HS	**0.66**	**0.35**	200–239 HS	**0.37**	**0.12**
		2*M*	434 MLL	0.62	0.27	420 MLL	0.36	0.08
	Harvest	0.8*M*	200–391 HS	0.48	**0.90**	200–412 HS	0.41	**0.75**
		0.8*M*	272 MLL	**0.53**	0.82	254 MLL	**0.43**	0.67
	Harvest	2*M*	200–273 HS	0.39	**0.80**	200–267 HS	0.26	**0.52**
		2*M*	371 MLL	**0.49**	0.54	346 MLL	**0.30**	0.25

M, instantaneous annual natural mortality rate, SPR, spawning potential ratio, *E,* harvesting efficiency, which is the fraction of dead fish that are harvested rather than dying due to catch-and-release related hooking mortality.
Bold values indicate the regulation producing the best performance for each metric.

providing not only greater trophy catch and less size truncation, but also increasing the total number of fish harvested and improved harvesting efficiency in the context of discard mortality. These benefits of HS regulations came at a cost of biomass yields and smaller size of fish harvested (as indicated by the size of the legal length range of each regulation); however, the trade-off of biomass yield for numerical harvest when HSs are applied over MLLs is probably an attractive compromise for many recreational fisheries because it would allow more anglers to harvest fish than expected with a yield-maximizing MLL, while at the same time maintaining trophy fish catch and meeting conservation goals (Jensen 1981).

Harvest-based management objectives are often perceived to be in conflict with conservation-based objectives (Aplet *et al.* 1992; Hilborn 2007; Koehn 2010; Koehn and Todd 2012). While the shared goal of long-term sustainability can serve both conservation and human needs (but see Niesten and Rice 2004), sacrifices to exploitation goals over shorter time frames can be necessary to meet long-term conservation objectives (Secor 2000; Foley *et al.* 2005; Cheung and Sumaila 2008). Our model identified regulations where fisheries-based and conservation-based objectives are not necessarily in conflict when using appropriately narrow HSs targeting intermediate-sized mature fish. In fact, the implementation of HSs may provide necessary protection to stock age-structure and spawning stock size with little sacrifice to angler benefits, because angler satisfaction is positively related to harvest opportunities and size of fish captured for many angler types (Arlinghaus 2006). Thus, according to our model and others developed previously for specific fish species (e.g. Jensen 1981; Arlinghaus *et al.* 2010; García-Asorey *et al.* 2011; Koehn and Todd 2012), HS regulations are likely more effective at collectively meeting multiple fishery and conservation objectives than MLLs and could simultaneously improve angler satisfaction and achieve biological sustainability. Hence, HSs appear to constitute a very promising tool for many recreational fisheries because they outperform MLLs for all life histories analysed at both fishing effort levels and for all three management objectives. This statement obviously only applies when harvest numbers and number of trophy fish captured is more important to anglers than total yield or harvest of trophy fish.

We found that high discard mortality rates paired with high exploitation rates rendered both MLL and HS regulations ineffective in meeting conservation goals. These findings corroborate Coggins *et al.* (2007) who found that discard mortality could prevent sustainability of some fish stocks managed by length-based regulations. For these cases, other approaches are necessary to meet conservation goals such as temporal and/or spatial closures (Gwinn and Allen 2010) or even effort controls (Cox and Walters 2002). Alternatively, when discard mortality rates are low to moderate (e.g. <30%), the use of HSs to reduce exploitation, increase harvesting efficiency and conserve a more natural age-structure of stocks provides an option superior to MLLs that can potentially meet both long-term fishery and conservation objectives with less sacrifice to short-term fishery use. This is particularly important because fishery closures or effort controls can cause economic hardship to local communities built around recreational fisheries and will create other social costs such as stakeholder conflict (Cox and Walters 2002; Martinet *et al.* 2010).

For simplicity of presentation, we chose three management objectives that differentially weighted the social and economic value of harvest relative to trophy catch. These weightings are unlikely to represent universal objectives in recreational fisheries because angler communities vary in values and because weights attached to normative criteria will vary with managers and local culture (Fenichel *et al.* 2013). However, our model was general and we simulated the full range of size-based regulations for both MLLs and HSs. This allows the reader to choose any location on the *x*-axes of Figs 1 and 2 to trade-off among harvest, yield and trophy catch and thereby determine regulations that meet any objective along these three metrics. For example, the compromise management objective of the LLLP and high exploitation fishery was met with a narrow HS of 400–492 mm; however, the management objective of a fishery that values harvest exclusively would be met by setting the HS to 400–680 mm (Fig. 1b). Thus, our results can provide both general guidance for the application of length-based regulations and specific guidance when the weighting of specific (catch or harvest-dependent) normative criteria is known for a specific fishery.

Although protecting large and old fish with HSs is not a common fisheries regulation in practice, some previous studies have implicated the advantages of HSs over alternative regulations for managing fisheries. Froese (2004), for example, presented four indices of overfishing and recommended the use of narrow harvest windows on recently mature fish (similar to the compromise HS regulations in this study) to prevent overfishing of commercial stocks. Berkeley *et al.* (2004a) suggested that implementation of HSs when discard mortality was low could preserve natural age composition and promote sustainability of groundfish stocks. Jensen (1981) reported that HSs increase trophy trout in the catch without strongly reducing yield, and Francis *et al.* (2007) suggested that protecting old fish is required for ecosystem-based fisheries management mentioning HSs as one of three management options for achieving objectives. Additionally, HSs have been highlighted for managing recreational fisheries targeting populations that experience a range of size-dependent maternal effects on egg and larval quality (Arlinghaus *et al.* 2010; Venturelli *et al.* 2010). However, benefits of HSs over MLLs in terms of harvest numbers and catch of trophies are not contingent on maternal effects (Arlinghaus *et al.* 2010). In fact, size-dependent maternal effects on offspring quality would enhance the benefits of HSs as reported in this article. Harvest-slot regulations are currently in place for some popular freshwater (e.g. white sturgeon, *Acipenser transmontanus*, Acipenseridae) and saltwater recreational fisheries in the USA. (e.g. red drum *Sciaenops ocellatus*, Sciaenidae and common snook *Centropomus undecimalis*, Centropomidae in Florida), but are overall far less common than MLL regulations. This work represents the first synthesis of the potential benefits of HSs to meet multiple fisheries and conservation objectives for recreational fisheries exploiting stocks across a range of life histories and therefore has general implication for a wide range of recreational fisheries that value both harvest numbers and trophy catch.

Like most modelling efforts, our results are contingent on model structure and other assumptions. For example, we assumed that compliance to regulations by anglers was 100%, which may not be realistic in some cases (Pierce and Tomcko 1998; Sullivan 2002). Non-compliance at levels reported elsewhere (e.g. 29% in northern pike fishing in Minnesota, Pierce and Tomcko 1998) would likely reduce the ability of both HSs and MLLs to meet fishery objectives and conserve stocks. Additionally, reproductive senescence has been reported in some species (Reznick *et al.* 2004). Our predictions might overestimate the effects of HS limits for these species that demonstrate a loss of fecundity or egg/larval quality at very old ages. Such effects are however unlikely to be very prevalent in most exploited stocks because few fish reach maximum age under fished conditions, and reproductive senescence may not be universally present across species (e.g. Kishi *et al.* 2003). As a further limitation, we did not model density-dependent growth or survival in the post-recruited ages. How this impacts our results will depend on the range of size/age of fish that the density dependence occurs and the strength of density dependence. Lorenzen (2005) argued that density-dependent survival in the recruited stage is unlikely to be a relevant process in many fish stocks, but density-dependent growth is probably common and affect all life stages to some degree (Lorenzen and Enberg 2002). It is a safe assumption that the presence of density-dependent growth should render the stock more resilient to fishing and will thus likely widen HSs and reduce yield-maximizing MLLs (Beverton and Holt 1957). Without detailed knowledge on the density dependence in specific life stages, it is impossible to predict the relative performance of HSs and MLLs; however, HSs provide the flexibility to create ecologically sensitive regulations that target populations at the life-stage of greatest density dependence or over production. The only available study that has considered density-dependent growth comparing HSs and MLLs has been conducted in northern pike (Arlinghaus *et al.* 2010), whose results agree with the findings reported here. Future research should evaluate the performance of regulations in the presence of density-dependent growth and size-dependent survival across a range of life histories (Lorenzen 2005). Explicitly representing food-dependent growth and size-dependent predation in size-structured models may alter predictions on regulatory performance relative to more standard age-structured models (Van Kooten *et al.* 2007; Persson and de Roos 2013) like the model employed here.

In general, we believe that our predicted advantages of HSs over MLLs may be conservative for some fish species because we did not model factors, such as size-dependent maternal effects on the recruitment process, non-linear population dynamics rates or fishery-induced evolution, all of which can be affected by size-selective exploitation. For example, Venturelli *et al.* (2010) provided evidence for age-dependent maternal effects on recruitment in walleye (*Sander vitreum*, Percidae) showing that the maximum reproductive rate in Lake Erie increased by 2.75-fold as the mean age of the stock shifted from 3.03 to 4.44 years. Furthermore, they demonstrated with a simulation study that the maximum reproductive rate of walleye could be increased by 1.2-fold by managing exploitation with a HS on age 2–4 fish vs. harvest strategies that targeted older ages (e.g. MLL, see also Arlinghaus *et al.* 2010). Our simulations did not account for size-dependent maternal effects on offspring performance as demonstrated previously for a range of species (e.g. Berkeley *et al.* 2004b; Venturelli *et al.* 2009; Arlinghaus *et al.* 2010) and therefore likely produced predictions of harvest and catch lower than would be expected for HSs applied to stocks that demonstrate size-dependent maternal effects (Arlinghaus *et al.* 2010).

Because we investigated long-term equilibrium states, we also did not account for the influence of environmental or demographic stochasticity amplifying non-linear population dynamical processes on the performance of the length-based regulations evaluated. Anderson *et al.* (2008) investigated mechanisms for destabilization of fish stocks due to exploitation. The authors concluded that the mechanism with the most support was that age truncation due to size-selective exploitation causes increased fluctuations in fish abundance (see also Hidalgo *et al.* 2011; Rouyer *et al.* 2011). Hsieh *et al.* (2010) showed that this effect held across species (but see Lobón-Cervia 2011 for an alternative view for exploited brown trout, *Salmo trutta*, Salmonidae). Therefore, the current body of evidence suggests that fishery-induced age truncation can lead to higher probability of fishery crashes and local extinctions (Lande *et al.* 2003), and our results suggest that HSs may represent a regulatory option that protects age composition which may reduce the likelihood of such catastrophic outcomes.

Finally, we omitted the potential for joint evolution of life-history traits such as age- and size-at-maturation, reproductive investments and juvenile growth rate, which all affect body size at adult age and may evolve in response to size-selective recreational fisheries (Matsumura *et al.* 2011). Law (2007) suggested the conservation of large fish to reduce the effects of fisheries-induced evolution. Supporting this view, Matsumura *et al.* (2011) found that MLLs exerted the most negative impact on body size evolution due to negative selection on growth rate and size at maturation. Although intermediate HSs would not eliminate the selection pressures on all life-history traits, such regulations would lead to selection on large juvenile growth, which may increase (rather than decrease) adult fish size and yield in the long term. Therefore, the conclusion that HSs are superior to MLLs would also hold if fisheries-induced evolution would be present.

Our results suggested a greater potential for improvement in fishery performance with HSs than MLLs across a range of management objectives, life histories and fishing mortality rates. Therefore, we suggest that a new perspective on managing recreational fisheries using length-based management tools is needed in situations where both harvest numbers and trophy catch matter to stakeholders. Under these conditions, rather than relying on retention of large fish to maximize biomass yields, we contend that HS regulations will provide the most favourable compromise among multiple fisheries and conservation objectives. Because our results were robust to life history, management objective and the fishing mortality rates, HS regulations should be considered preferable over MLLs for many recreational fisheries that value harvest and size of fish in the catch. Depending on the local customs and culture, a manager can choose to meet either harvest numbers or trophy catch objectives by varying the width of the HS. We recommend empirical studies that test some of the predictions of the present model because the results promise far-reaching implications for recreational-fisheries management that is currently mainly based on MLLs.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Sensitivity test of the performance of harvest slot (HS) and minimum-length limit (MLL) regulations with incorrect estimates of the instantaneous natural mortality (M) for two different life-history prototypes (Table 1).

Table S2. Sensitivity test of the performance of harvest slot (HS) and minimum-length limit (MLL) regulations with incorrect estimates of the recruitment compensation ratio (CR) for two different life-history prototypes (Table 1).

Table S3. Sensitivity test of the performance of harvest slot (HS) and minimum-length limit (MLL) regulations with incorrect estimates of the instantaneous fisheries exploitation rate (F) for two different life-history prototypes (Table 1).

Table S4. Sensitivity test of the performance of harvest slot (HS) and minimum-length limit (MLL) regulations with incorrect estimates of the length at maturations (L_{mat}) for two different life-history prototypes (Table 1).

