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Dynamic angling effort influences the value of minimum-length limits to prevent recruitment overfishing

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Abstract Recruitment overfishing occurs when stocks are fished to a level where recruitment declines proportionally with adult abundance. Although typically considered a commercial fishery problem, recruitment overfishing can also occur in freshwater recreational fisheries. This study developed an age-structured model to determine if minimum-length limits can prevent recruitment overfishing in black crappie, *Pomoxis nigromaculatus* (LeSueur), and walleye, *Sander vitreus* (Mitchill) fisheries considering angling effort response to changes in fish abundance. Simulations showed that minimum-length limits prevented recruitment overfishing of black crappie and walleye, but larger minimum-length limits were required if angler effort showed only weak responses to changes in fish abundance. Low angler-effort responsiveness caused fishing mortality rates to remain high when stock abundance declined. By contrast, at high effort responsiveness, anglers left the fishery in response to stock declines and allowed stocks to recover. Angler effort for black crappie and walleye fisheries suggested that angler effort could be highly responsive for some fisheries and relatively stable for others, thereby increasing the risk of recruitment overfishing in real fisheries. Recruitment overfishing should be considered seriously in freshwater recreational fisheries, and more studies are needed to evaluate the responsiveness of angler effort to changes in fish abundance.

KEYWORDS: angler behaviour, black crappie, recreational fisheries, regulations, sustainability, walleye.

Introduction

Preventing overfishing is a central management goal for both recreational and commercial fisheries. Limiting fishing mortality to a level that provides maximum sustainable yield (MSY) is a common benchmark in fishery stock assessment (Hilborn & Stokes 2010). Fishing mortality rates that exceed F_{MAX} cause growth overfishing, and regulations such as minimum-length limits, daily bag limits and gear restrictions are commonly used to prevent growth overfishing in both recreational and commercial fisheries.

Recruitment overfishing is a more severe form of overfishing and occurs when spawning stock size is reduced to the point where future recruitment (or population renewal rate) declines strongly. This is the point on a stock-recruitment curve where recruitment becomes proportional to adult abundance (at small spawning stock sizes), so that further reductions in adult abundance directly reduce recruitment (Walters &

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Martell 2004). Recruitment overfishing is usually considered a greater concern than growth overfishing because it substantially impairs stock productivity and may lead to collapse. High-profile commercial fishery collapses like the northern cod, *Gadus morhua* L., in the late 1980s proved that fisheries are capable of exerting mortality rates sufficiently high to cause recruitment overfishing (Walters & Maguire 1996). Recruitment overfishing does not always lead to collapse or extinction, but recovery of the stock could be prevented by regimes shifts that accompany overfishing, as happened for northern cod (Walters & Kitchell 2001). Despite the potential for rebound, recruitment overfishing and the associated sharp age and size truncation should be avoided for precautionary reasons to reduce the potential for destabilised stock dynamics (Anderson *et al.* 2008; but see Lobón-Cervia 2011), regime shifts (Walters & Kitchell 2001; Carpenter *et al.* 2011) and collective economic and social welfare losses that may follow strong stock declines.

Most high-profile cases of recruitment overfishing have occurred in commercial marine fisheries, but it can also occur in freshwater recreational fisheries (Post *et al.* 2002). Chronic recruitment overfishing of walleye, *Sander vitreus* (Mitchill), fisheries in Alberta, Canada, were caused by recreational fishing alone in some fisheries and from joint exploitation by recreational and commercial fisheries in others (Sullivan 2003). Low-lake productivity and high regional angler density caused recreational fishing effort to remain high, despite low-walleye abundance, which caused recruitment overfishing (Sullivan 2003). Similarly, angling exploitation likely caused recruitment overfishing of a Kansas walleye population (Quist *et al.* 2010). A recreational black crappie, *Pomoxis nigromaculatus* (LeSueur), fishery exerted a 42% exploitation rate, which was near the recruitment overfishing threshold (Dotson *et al.* 2009). Bunnell *et al.* (2006) suggested that harvest restrictions would improve recruitment of white crappie *P. annularis* for some Ohio reservoirs, which indicated that some stocks were recruitment overfished. Canadian rainbow trout, *Oncorhynchus mykiss* (Walbaum), northern pike, *Esox lucius* L. and lake trout, *Salvelinus namaycush* (Walbaum), recreational fisheries near urban areas have been overfished to the point that stocks could only be sustained by stocking or highly restrictive harvest regulations (Parkinson *et al.* 2004; Post *et al.* 2008). Similarly, a Canadian bull trout, *Salvelinus confluentus* (Suckley), population collapsed in response to recreational fishing, but populations rebounded quickly after a total catch-and-release policy and a natural bait ban displaced harvest-oriented anglers away from the fishery (Johnston *et al.* 2011).

Angler effort responses to changing fishery conditions could influence the likelihood of recruitment overfishing in recreational fisheries. Changes in habitat quality and environmental stochasticity (e.g. Lobón-Cervia 2011) occasionally produce strong year classes, and periods of high fish abundance are expected to attract anglers (Cox *et al.* 2003; Carpenter & Brock 2004; Post *et al.* 2008). Temporarily aggregated angling effort may cause periodic overfishing. If anglers leave a fishery when stocks decline through year-class fluctuation, boom-and-bust cycles of effort dynamics could result. Walters and Martell (2004) and Parkinson *et al.* (2004) argued that angler movement among lakes to seek high catch rates would homogenise fishery resources as anglers seek out and sequentially deplete systems with above-average catch rates. However, Hunt *et al.* (2011) showed that this outcome is not likely if anglers seek fishing outcomes that are unrelated to catching or harvesting (e.g. close travel distance, high visual attractiveness, facilities). Therefore, understanding the potential for recruitment overfishing by recreational fisheries requires exploring interactions between angler-effort dynamics and commonly applied harvest regulations on overfishing and fishing quality (Johnston *et al.* 2010).

The objective of this article was to assess the utility of minimum-length limits to prevent recruitment overfishing and maximise angler use while accounting for angling effort responses to changes in the status of fisheries. A simulation model was built using two example species of high interest to consumptive (i.e. harvest oriented) anglers in North America, black crappie and walleye.

Methods

A simple model of dynamic recreational fisheries exploitation

A single-species fisheries simulation model was constructed to include two hypotheses about how angler effort would vary with fish abundance (i.e. responsive vs relatively unresponsive angler effort to changes in catch rates associated with stock size). The biological submodel was constructed as an age-structured population model similar to those described elsewhere (Table 1; Walters & Martell 2004, Chapter 3; Allen *et al.* 2009; Dotson *et al.* 2009). Model components that are unpublished elsewhere are described below.

The fisheries model was parameterised to simulate black crappie and walleye fisheries, both of which support popular harvest-oriented fisheries across much of North America. The walleye was chosen because the biology of this species is similar to the zander, *Sander lucioperca* (L.), a popular recreational fish species across

Table 1. Model formulation and parameter estimates for black crappie and walleye population models

		Parameter Values	
Life-history characteristics		Black crappie	Walleye
Growth (length L at age a)	$L_a = L_\infty(1 - e^{-Ka})$	L_∞ = 414 mm K = 0.258 yr^{-1}	L_∞ = 924 mm K = 0.2 yr^{-1}
Length(mm)-to-weight (kg)	$W = aL^b$	a = 2.49e-9 b = 3.345	a = 3.52e-9 b = 3.18
Fecundity	$\max\{0, (W_a - W_{mat})\}$ $f_a = 1/(1 + e^{1-*n(a-a_{mat})})W_a$	W_{mat} = 0.123	η = 1.73 a_{mat} = 4.77
Instantaneous natural mortality	M	M = 0.4	M = 0.3
Eggs-per recruit	$\varphi_e = \sum_a f_a l_a \mid l_a = e^{-M(a-1)}$		
Recruitment	$R_t = \frac{aEggs_t}{1+bEggs_t} e^{v_t} \Big\vert \begin{matrix} a = \Omega/\varphi_e \\ b = (\Omega - 1)/(R_0\varphi_e) \end{matrix}$	Ω = 15 R_0 = 1.5e5	
	$R_t = S_t e^{a-bS_t+v_t} \Bigg\vert \begin{matrix} a = ln(\Omega/\varphi_n), \varphi_n = \sum_{a=5}^{\infty} e^{-M(a-1)} \\ b = (-ln(1/\Omega))/(R_0\varphi_n) \\ S_t = \sum_{a=5}^{\infty} N_{a,t} \end{matrix}$		Ω = 26 R_0 = 2.6e3
Fishery characteristics			
Vulnerability to capture	$v_a^c = 1/\left(1 + e^{-(L_a - L_h)/\sigma}\right)$	L_{h} = 175 mm σ = 17.5	L_{h} = 300 mm σ = 30
Vulnerability to harvest	$v_a^h = 1/\left(1 + e^{-(L_a - L_h)/\sigma}\right)$	L_{h} = variable σ = 0.1*L_{h}	L_{h} = variable σ = 0.1*L_{h}
Vulnerable biomass (F = 0)	$VB_0 = \sum_a R_0 e^{-M(a-1)} W_a v_a^h$		
Vulnerable biomass	$VB_t = \sum_a N_{a,t} W_a v_a^h$		
Effort	$E_t = \left[1/\left(1 + e^{-(VB_h - VB_t)/\sigma}\right)\right] E_{total}$	VB_{h} = 0.5VB_0 $\sigma = \gamma VB_{\mathrm{h}}$ γ = 0.1 or 0.9 E_{total} = 50	VB_{h} = 0.5VB_0 $\sigma = \gamma VB_{\mathrm{h}}$ γ = 0.1 or 0.9 E_{total} = 200
Time dynamics			
Numbers-at-age	$N_{a,t} = N_{a-1,t-1} e^{-M} s_d s_h$ $s_d = \left(1 - \left(\left(v_{a-1}^c - v_{a-1}^h\right)\left(1 - e^{qE_{t-1}}\right)\right)d\right)$ $s_h = \left(1 - v_{a-1}^h\left(1 - e^{qE_{t-1}}\right)\right)$	d = 0.1 q = 0.06	d = 0.1 q = 0.01

much of Europe (Arlinghaus & Mehner 2004). Both black crappie and walleye are sought by anglers as a food fish, so recruitment overfishing is possible (Post *et al.* 2002; Sullivan 2003; Dotson *et al.* 2009). Black crappie and walleye populations also exhibit sharp recruitment fluctuations (Allen & Pine 2000; Nate *et al.* 2011) that result in large changes in adult abundance. These fluctuations would be expected to affect angling effort strongly. Therefore, black crappie and walleye are good candidate species to explore impacts of recruitment overfishing associated with recreational fishing.

The black crappie model was informed with data from Lake Lochloosa, Florida (Table 1). Beverton–Holt and Ricker stock-recruitment models were equally descriptive for crappies in Ohio (Bunnell *et al.* 2006), but the more general Beverton–Holt model was chosen for the model (Table 1). Recruitment fluctuated stochastically around the stock-recruit curve in similar magnitude to age-0 black crappie survey CPUE data at Lake Lochloosa from 1998 to 2011 (CV = 75%) using a log-normal deviate around the Beverton-Holt curve with mean of 1 and SD of 0.75. This was similar to recruitment variability for other black crappie populations in southern USA (Allen & Pine 2000).

The walleye fishery was calibrated by dynamics from Escanaba Lake, Wisconsin, where long-term data on growth, mortality and recruitment were available (Table 1, Hansen *et al.* 1998, 2011; Nate *et al.* 2011). Escanaba Lake was managed with no minimum-length limit, no bag limit and no closed season between 1946 and 2003. In 2003, a 711-mm minimum-length limit and one-fish daily bag limit was imposed on the angling fishery. The walleye model included a Ricker stock-recruitment curve for walleye in Escanaba Lake (Hansen *et al.* 1998; Table 1). Recruitment was varied around this curve according to a CV of age-0 fish of 86%, in agreement with catch-at-age estimates of age-0 abundance from 1956 to 1986 (Nate *et al.* 2011).

Analysing how angler effort might respond to changes in fish abundance and interact with minimum-length limits to cause (or prevent) recruitment overfishing was a key issue to address in this study. In general, freshwater anglers move among multiple fish populations (i.e. lakes or rivers within a fisheries landscape) in response to variation in expected catch or harvest rates and other fishing quality attributes offered by various sites (Carpenter & Brock 2004; Johnston *et al.* 2010; Hunt *et al.* 2011). For angler populations mainly interested in keeping fish for harvest, the expected harvest at a site and the possibility to keep fish should strongly determine site choice and drive angling effort dynamics (Cox *et al.* 2002; Beard *et al.* 2003; Johnston *et al.* 2010). Anglers would then be expected to change locations in response to expected catch or harvest rates, which are usually assumed to be directly proportional to fish density (Newby *et al.* 2000; Hansen *et al.* 2005). For many less harvest-oriented angler populations or angler types, factors other than expected catch or harvest rate determine site choices (Hunt *et al.* 2011), but this work assumed that harvest-based fishery utility drove angling effort for consumptive-based black crappie and walleye fisheries simulated here.

The model simulated a fishery where angler effort would respond to changes in vulnerable harvest stock biomass, as would occur if expected harvest is an important motivation of anglers choosing when and where to fish. The numerical response to angler effort in year t (E_t, h (ha yr^{-1})) was assumed to be related to vulnerable biomass using a logistic function, similar to recreational fisheries models by Post *et al.* (2003) and Arlinghaus *et al.* (2009):

$$E_t = \left[1 \middle/ \left(1 + e^{-(VB_h - VB_t)/\sigma}\right)\right] E_{total}. \qquad (1)$$

In Equation 1, VB_h is the vulnerable biomass (kg) where 50% of the total maximum angler effort (E_{total} h ha^{-1} yr^{-1}) is realised, VB_t is the annual vulnerable biomass (kg) in the fished condition (Table 1), and t represents time (yr). Total maximum angling effort is the total angling population size multiplied by a maximum potential annual investment of hours that is constrained by available leisure time. Only a fraction of this maximum angling effort potential is directed at a fishery, depending on fishing quality of the fishery. The parameter σ is a shape parameter that describes how strongly fishing effort responds to changes in vulnerable biomass to enable simulation of a range of slow to fast angling effort responses to changes in vulnerable fish biomass available for harvest. The model assumed that information about vulnerable biomass is obtained early in the season and shared instantaneously among anglers, which is likely with modern fishing information technology. Low values of σ cause fishing effort to react rapidly to changes in vulnerable biomass (i.e. high fishing effort responsiveness), and high values of σ cause fishing effort to respond slowly to vulnerable biomass (i.e. low fishing effort responsiveness). The value of σ was varied to explore how angler effort responsiveness influenced stock dynamics and the outcome of management actions (i.e. length limits designed to protect small fish from harvest).

The annual exploitation rate (U_t) was calculated in the model from annual effort as $U_\mathrm{t} = 1 - e^{qE_t}$, where q is the catchability coefficient or the fraction of the fish stock caught per unit effort. The values of E_total, VB_h and q were scaled for each species to produce fishing effort and annual exploitation estimates that were similar to those for black crappie and walleye fisheries from which model parameters were derived. The q value was held constant and did not vary with density of fish. This resulted in conservative estimates of recruitment overfishing because inverse density-dependence in catchability that is common in some recreational fish species, including walleye (Post *et al.* 2002; Hansen *et al.* 2005), would cause greater probabilities of population collapse (Post *et al.* 2008; Hunt *et al.* 2011).

Parameters were set to reflect realistic values for black crappie and walleye for each fishery. For black crappie, R_o was set at 58 age-1 recruits ha^{-1}, a scale parameter (Table 1) that resulted in an equilibrium 32 kg ha^{-1} of vulnerable black crappie biomass in the un-fished condition. The walleye model using the stock-recruitment curve for Escanaba Lake (Table 1) scaled the population to the population size in Escanaba Lake (Hansen *et al.* 1998, 2011). The value of VB_h was set at 50% of the un-fished vulnerable biomass for both walleye and black crappie fisheries, which infers that 50% of a fixed maximum fishing effort would occur at 50% of un-fished biomass (Table 1). Maximum fishing effort was set at 50 angling h ha^{-1} yr^{-1} for black crappie, and 200 h ha^{-1} yr^{-1} for walleye based on creel survey data from Florida for crappie and creel census data from Escanaba Lake, Wisconsin for walleye.

To represent two hypotheses about angler responsiveness to changes in vulnerable biomass, the value of σ was set at 10 and 90% of VB_h. Accordingly, a σ of 10% (high angler effort responsiveness) resulted in a steep, logistic relationship between fishing effort and vulnerable biomass, whereas a σ of 90% (low angler effort responsiveness) caused a weaker, linear relationship between fishing effort and vulnerable biomass (example for black crappie, Fig. 1). Therefore, changes in vulnerable biomass caused by recruitment fluctuations or regulation changes caused substantial changes in fishing effort and exploitation when σ was low, but only marginal changes in effort when σ was high.

Models were used to evaluate fishery performance, including biological sustainability and socio-economic factors indexed by attractiveness of the fishery to anglers. First, no minimum-length limit was simulated by assuming fish recruited to the fishery at 200 mm for black crappie and 300 mm for walleye. These simulated liberal harvest restrictions where size at harvest was at or above the size at maturation. Second, two more-restrictive minimum-length limits were modelled for each species, 250 and 300 mm for black crappie and 450 and 600 mm for walleye. Biological sustainability was measured with a weighted spawning potential ratio (SPR), which was computed as the population fecundity in the fished condition relative to the un-fished condition. Values of SPR below 35% are often considered recruitment overfishing in marine systems (Goodyear 1993). Socio-economic benefits generated by recreational fisheries in a region may be perceived by managers as directly related to the number of people fishing (i.e. angler effort), so the socio-economic measure of fishery performance was total annual fishing effort attracted to the fishery. The model was used to evaluate how SPR and fishing effort changed for 1000 model runs of random recruitment variation for each minimum-length limit and hypothesised level of angler responsiveness. Model estimates of fishing effort were compared to empirical estimates of fishing effort for black crappie and walleye fisheries.

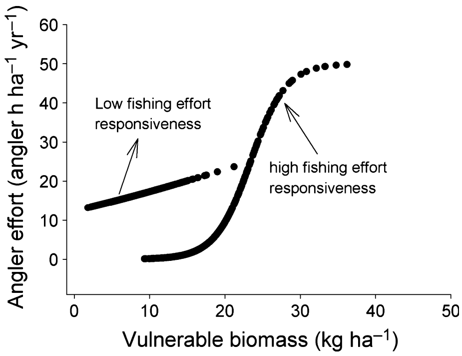

Figure 1. Example of two hypothesised angler responses to changes in vulnerable biomass. Both lines represent 1000 model runs for black crappie under a 200 mm minimum length limit. Angler effort (h ha^{-1} yr^{-1}) varied according to random recruitment fluctuations in both scenarios.

Results

Black crappie

Recruitment overfishing by recreational fishing was possible for black crappie, particularly at low minimum-length limits and low fishing-effort responsiveness (Fig. 2). The SPR increased with increases in MLL for both hypothesised values of σ, which suggests that length limits could prevent recruitment overfishing independent of angler behaviour (Fig. 2). However, if recreational-fishing effort reacted slowly to changes in expected harvest, MLLs of 250 mm or more were required to prevent recruitment overfishing for black crappie. Even at a MLL of 300 mm, some probability of recruitment overfishing remained if angler effort responsiveness was low. The SPR was generally lower at low fishing effort responsiveness than for high fishing effort responsiveness, because at low angler effort responsiveness, fishing effort stayed nearly constant regardless of vulnerable biomass (Fig. 1). Conversely, high fishing effort responsiveness caused fishing effort to decline rapidly if stock abundance declined. In black crappie, a MLL of 250 mm or more was particularly effective at preventing recruitment overfishing at high fishing effort responsiveness, but less effective if angler effort remained high, despite decreases in fish abundance.

Fishing effort was relatively stable across MLLs at low fishing effort responsiveness (σ = 90%) and highly dynamic at high fishing effort responsiveness (σ of 10%, Fig. 2). Coefficients of variation in fishing effort ranged 8–11% for low fishing effort responsiveness and 76–139% for high fishing effort responsiveness, which mimicked boom and bust cycles of effort. The MLLs produced modest increases in average fishing effort for all scenarios, and variability in fishing effort varied among MLLs. Angler effort variability was highest with a 200-mm MLL and high fishing effort responsiveness because strong or weak year classes elicited a rapid response in angler effort. Increased angler effort (boom) substantially reduced vulnerable biomass in the subsequent 1–3 years to cause periods of low effort as effort shifted away from the stock (bust). For low fishing effort responsiveness, fishing effort remained relatively constant as the MLL increased because effort did not respond strongly to changes in vulnerable biomass of the stock. Annual exploitation rates mirrored changes in angler effort.

Time-dynamic fishing effort did not always increase with vulnerable biomass of the stock. For example, vulnerable biomass declined at the 300-mm MLL under high fishing effort responsiveness because this large MLL allowed natural mortality to reduce fish biomass

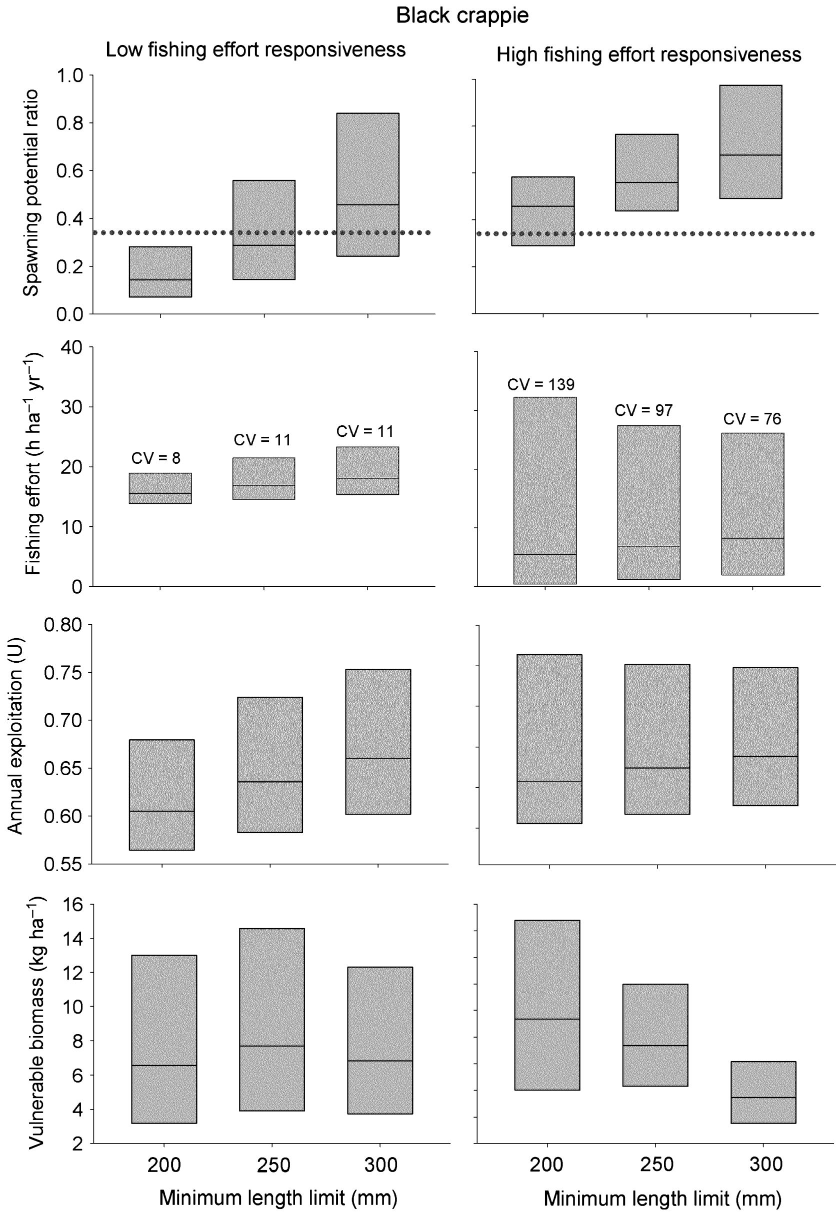

Figure 2. Model-predicted fishing effort, vulnerable biomass, annual exploitation (U) and spawning potential ratio (SPR) for black crappie. Low (left panels) and high (right panels) fishing effort responsiveness results are shown. Boxplots represent 95% confidence intervals from 1000 simulated sets of random recruitment deviations. Horizontal line within each box represents the mean. The SPR value of 35% is shown (dashed line), values below which indicate potential for recruitment overfishing.

prior to recruitment to the 300-mm MLL. However, average annual fishing effort and annual exploitation increased slightly and became more stable with a 300-mm MLL than with smaller MLLs (Fig. 2). The higher MLL prevented large declines in stock biomass and thereby allowed fishing effort and fishing mortality to be slightly higher than for the lower MLL. If fishing effort exhibited low responsiveness to changes in biomass, fishing effort increased slightly as the MLL increased. The model suggested that MLLs would increase fishing effort at both levels of effort responsiveness by preventing periodic overfishing and low stock biomass.

Roving creel survey data for black crappie fisheries in Florida lakes indicated that angling effort was highly dynamic in some lakes and relatively consistent in others. Fishing effort at Lake Lochloosa was highly variable and ranged 20-fold over the time series (Fig. 3). Lake Griffin had less variable fishing effort and Lake

Istokpoga fishing effort ranged 6–11 angler h ha^{-1} yr^{-1} over the time series. Variability in fishing effort declined with lake size, which suggests that large lakes (Istokpoga) may have more consistent fishing effort than smaller lakes (Lochloosa). Therefore, empirical data for black crappie effort indicated that fishing effort could be highly dynamic, similar to simulations with σ of 0.10 in some cases and relatively consistent (i.e. like the low effort responsiveness scenario) in others. Lakes with relatively constant fishing effort (low responsiveness of effort) had higher risk of recruitment overfishing than lakes where effort varied more strongly with stock size.

Walleye

For walleye, SPR increased with MLL for high and low fishing effort responsiveness, but remained highest under high fishing effort responsiveness because anglers left the fishery when vulnerable biomass declined (Fig. 4). Even at a high MLL of 600 mm the likelihood of recruitment overfishing did not drop to zero when walleye angling effort responded slowly to expected harvest. However, if angler effort was highly responsive, the 600 mm MLL avoided recruitment overfishing. The MLLs did not influence fishing effort for either low or high fishing effort responsiveness. Vulnerable biomass declined under a 600-mm MLL through natural mortality of the protected biomass, but average fishing effort remained similar as the MLL increased. Variability in fishing effort and annual exploitation rate increased for high angling effort responsiveness, but variability in angler effort did not decline as the MLL increased for either low or high fishing effort responsiveness.

Creel census data from Escanaba Lake showed that fishing effort was intermediate between the low and high effort responsiveness scenarios (Fig. 5). The CV of walleye angling effort since 1956 was 40%, which indicates that angler effort was higher than the low fishing effort responsiveness, (CV = 12–18%, Fig. 5) but substantially lower than the high fishing effort responsiveness. Some of the variability in angler effort was because of very high fishing effort in the 1950s and 1960s, so overall variability in more recent years was only slightly higher (i.e. 34%) than the low fishing effort responsiveness. This suggests that walleye populations would be relatively vulnerable to recruitment overfishing, if this is true for most walleye fisheries.

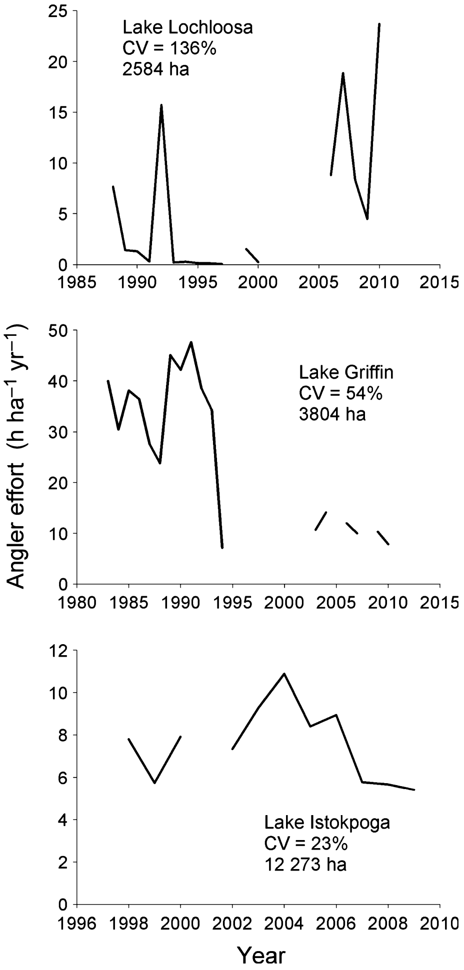

Figure 3. Fishing effort for Florida Lakes Lochloosa (top panel), Griffin (centre panel) and Istokpoga, (bottom panel) measured with roving creel surveys. The coefficient of variation (CV = $\frac{SD}{\bar{x}} \times 100\%$) of fishing effort and lake size is shown. Data were provided by the Florida Fish and Wildlife Conservation Commission.

Discussion

Angler effort dynamics strongly influenced the potential for recruitment overfishing in this study, particularly with low angler effort responsiveness predicted to cause recruitment overfishing for both black crappie and walleye. Relatively low responsiveness was found empirically for some black crappie fisheries in Florida, and the walleye fishery in Escanaba Lake, Wisconsin was not highly responsive to population density. This poses a strong challenge for management of recreational fisheries because effort will remain high even after stocks decline if anglers do not react to changes in fish abundance. Similar findings were reported in a simulation study by Johnston *et al.* (2010), who showed that overfishing was most likely where angler site choice was driven by a range of catch and catch-independent factors, rather than expected catch or harvest alone. The resulting multi-attribute utility function maintained high fishing effort even for declining catch and harvest rates associated with overfishing by angling (Johnston *et al.* 2010).

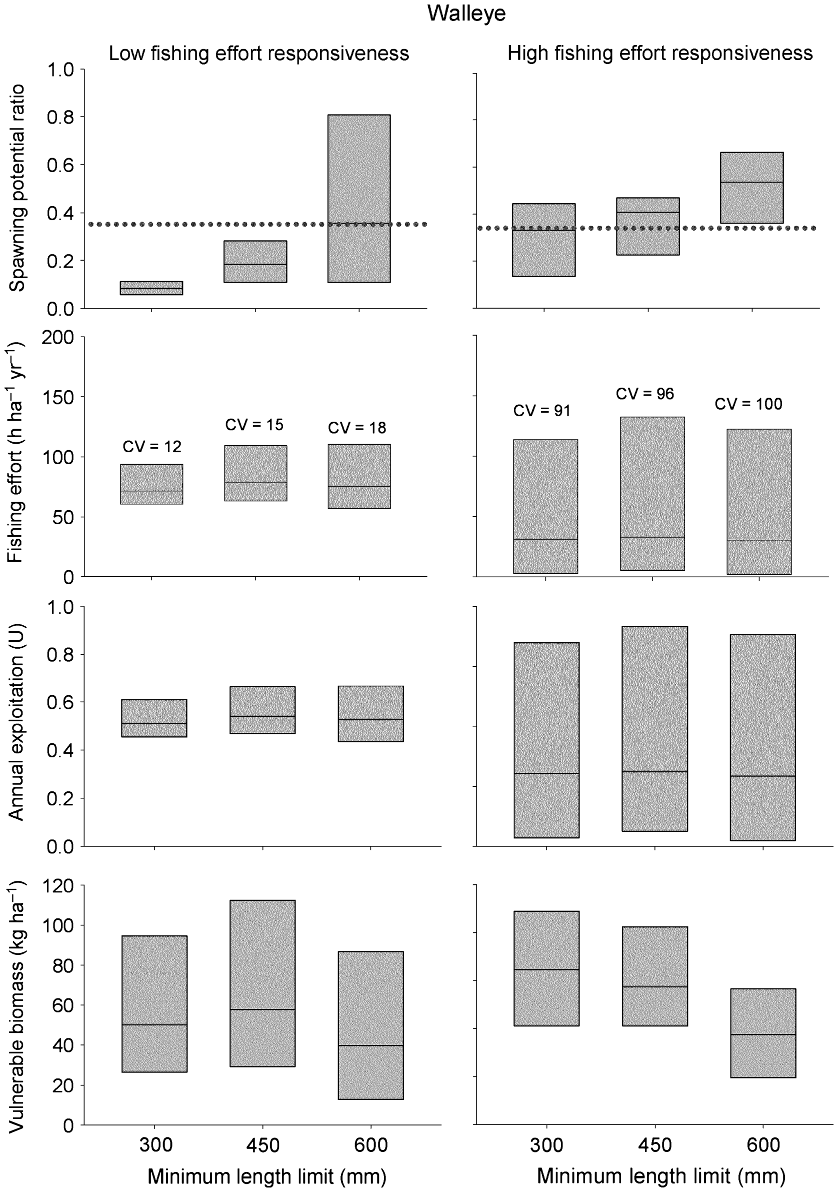

Figure 4. Model predicted fishing effort (h ha^{-1} yr^{-1}), vulnerable biomass (kg ha^{-1}), annual exploitation (U) and spawning potential ratio (SPR) for walleye. Low (left panels) and high (right panels) fishing effort responsiveness results are shown. Boxplots represent 95% confidence intervals from 1000 simulated sets of random recruitment deviations. Horizontal line within each box represents the mean. The SPR value of 35% is shown (dashed line), values below which indicate potential for recruitment overfishing.

Overfishing associated with low responsiveness of angling effort will be strongly affected by the availability of substitute angling sites and the angler density in the region. A small number of alternate fishing sites would be expected to cause low-responsiveness in angler effort to changes in fish population density (Hunt *et al.* 2011). For example, Sullivan (2003) found that a low number of available walleye lakes combined with high angler density caused fishing effort to remain high, despite low angler catch rates, thereby causing overfishing. This is similar to the results in the model results, where low angler effort responsiveness increased the likelihood of recruitment overfishing.

Creel survey/census data shown here provided evidence for both highly dynamic and relatively consistent angler effort for real black crappie and walleye fisheries, but caution is advised when generalising these patterns to other fisheries because the data represented only a small sample size of systems. More time series of fishing effort are needed for freshwater fisheries to understand

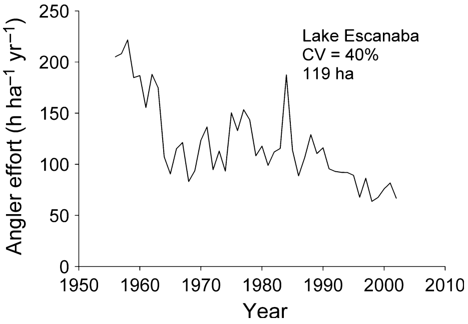

Figure 5. Fishing effort for Lake Escanaba, Wisconsin. The coefficient of variation (CV = $\frac{SD}{x}$ ×100%) of fishing effort and lake size (ha) is shown. Data were provided by the Wisconsin Department of Natural Resources.

how fishing effort varies across systems and regions. More research is needed to evaluate why angling effort dynamics vary to understand the shape of fishing effort responses to changes in fish abundance and other fishery attributes (*sensu* Carpenter *et al.* 1994; Post *et al.* 2008; Johnston *et al.* 2011; Hunt *et al.* 2011; Martin & Pope 2011). The model in this study assumed that angler effort would decline proportionally with stock abundance as anglers sought areas with higher expected catches (Carpenter *et al.* 1994; Cox *et al.* 2003; Parkinson *et al.* 2004; Post *et al.* 2008), but future research should test this hypothesis for a wide range of fish species, lake landscapes and proximities to population centres.

Fishing effort responsiveness influenced the potential for overfishing and should be considered when deliberating management actions. High fishing effort responsiveness created a greater degree of biological self-regulation than low fishing effort responsiveness. However, high catch or harvest orientation by anglers will not necessarily prevent recruitment overfishing if overall angler population density is high (Sullivan 2003; Hunt *et al.* 2011). Management actions on one system could displace the problem from one location to another, thereby resulting in domino-like overfishing patterns under high regional fishing effort (Carpenter & Brock 2004; Post *et al.* 2008; Hunt *et al.* 2011). In such situations, even highly restrictive harvest regulations may not prevent recruitment overfishing if overall effort density is sufficiently high. For example, recruitment overfishing was possible even when fishing effort was highly responsive if the MLL was too small for both black crappie and walleye. The findings and related work (e.g. Lester *et al.* 2003) require a regional perspective for modelling angling effort dynamics and a better understanding of how anglers interact with spatially structured fisheries (Hunt *et al.* 2011). In general, available evidence cautions against a one-size-fits-all policy that is applied across landscapes (Carpenter & Brock 2004). Therefore, any specific MLL from this study should not be misinterpreted as being useful to prevent overfishing across broad spatial scales. Locally existing impacts of fishing will be a function of the availability of sites in a region relative to angler density, movement patterns and culture.

The model in this study evaluated the utility of simple length-based harvest limits to prevent recruitment overfishing, but the model did not consider angler aversion to length limits. Large MLLs like 300 mm for black crappie and 600 mm for walleye could deter harvest-oriented anglers because implementation of restrictive harvest regulations can cause effort to shift in walleye fisheries (Beard *et al.* 2003; Fayram *et al.* 2006). Similarly, walleye fishery attractiveness declined despite increased catch rates because the ability to harvest was constrained (Sullivan 2003). A similar aversion to restrictive catch and release policies was evident for bull trout anglers (Johnston *et al.* 2010). Effort responses to implementation of regulations have also been reported for black crappie, where experimental use of a 300-mm MLL in Florida substantially reduced angler effort (Florida Fish and Wildlife Conservation Commission, unpublished data). The simulations showed that for black crappie fisheries angler effort could be slightly improved by use of a length limit. Effort responses to changes in size or bag limits will vary among species and regulations, and this study was not intended to infer that fishing effort will always increase or remain stable with increasing MLLs. The purpose of this work was to explore how hypotheses about angler effort dynamics could influence recreational fishing effort and biological sustainability to avoid recruitment overfishing. The results showed that if anglers are not averse to regulations, use of MLLs could maintain angler effort (despite lower vulnerable fish biomass in some cases) and improve SPR in recreational fisheries. Improvements in effort resulted from less frequent periods of very low fish biomass owing to the length limits.

The present model assumed constant catchability with changes in fish abundance, which makes the results conservative. Catchability is inversely related to population density for many recreationally important species (Post *et al.* 2002). This would cause fishing mortality rates to remain high as the population declines despite lower angler effort (Post *et al.* 2002; Hunt *et al.* 2011). Anglers would then not perceive the decline in population abundance, if fish spatial distribution contracts as abundance declines, thereby increasing or sustaining high individual angler catch rates despite low stock abundance. Further, experienced anglers with higher catchability may continue fishing as population density declines because they are able to maintain a high catch rate, thereby increasing average catchability of the angling population (but see Seekell *et al.* 2011). Incorporating density dependent catchability into the model would not alter relative changes in model output metrics across MLLs but would make recruitment overfishing more likely for all MLLs and levels of angler effort responsiveness. Therefore, the results presented should be considered conservative because recruitment overfishing would be more likely if angler site choice is determined by more than expected harvest and if catchability increases as stock size declines (Hunt *et al.* 2011).

The model used in this study evaluated only the effects of fishing and did not include other perturbations that could influence fish stocks and fishing quality. Changes in habitat quantity and quality will influence recruitment patterns and fishing quality regardless of fishing effort dynamics (Minns *et al.* 1996). Long-term changes in rainfall patterns and temperature can influence fish abundance through recruitment changes (e.g. Busch *et al.* 2011). The model included stochastic recruitment but did not simulate trends in recruitment or interactions between environmental variation and fishing effort. Future simulations should explore how long-term changes in habitat quality and quantity could interact with angler effort patterns to influence fishery sustainability.

The present study showed that recruitment overfishing can occur in recreational fisheries and is difficult to avoid if angling effort remains attracted to a fishery, despite declines in fish abundance (e.g. Sullivan 2003; Quist *et al.* 2010). However, the spatial and temporal extent of recruitment overfishing in recreational fisheries is poorly understood. The model presented here and related work (e.g. Hunt *et al.* 2011) suggests that recruitment overfishing should be evaluated more thoroughly with field studies. Management actions such as MLLs can improve fish populations and socio-economic benefits of fisheries by maintaining and increasing angler effort if angling effort is responsive to fish abundance and catchability is only weakly density dependent. However, recruitment overfishing is probably more pronounced than previously believed based on the angling responsiveness values evaluated in this modelling effort and compared with the observed creel survey data. Understanding how anglers respond to changes in fish abundance is a key need for future studies, which should quantify angler effort responsiveness to changes in fish abundance and fishery attributes across a range of fisheries to improve model predictions.

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