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Risk of Population Decline for Largemouth Bass in a Potomac River Fishery (USA): Effects from Invasive Northern Snakehead

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Abstract.—Conservation of Largemouth Bass (LMB) *Micropterus salmoides* populations requires an understanding of population dynamics that are influenced by environmental challenges, such as the spread of invasive species. We used an age-structured population model to compare population growth rates (λ) between a simulated population that included invasive Northern Snakehead (NSH) *Channa argus* as a competitor and predator and a simulated population that did not. We then assessed the sensitivity of our results to natural variation in LMB recruitment. When recruitment of LMB was already poor, there was a high risk of population decline that did not depend on whether NSH was included in the model scenario. When recruitment of LMB was high, the risk of population decline was only 40% when NSH was not included in the model scenario; however, predation by and competition with NSH caused a higher risk of LMB population decline. Regardless of the level of LMB recruitment, the size of the LMB population at equilibrium was 20% lower (on average) when including NSH in the model. We conclude that when habitat conditions do not already significantly limit recruitment, populations of LMB may be adversely affected by cohabitation with NSH. Preventing the spread of NSH will lessen ecosystem pressures that negatively affect the LMB population. We encourage continued vigilance in conserving LMB populations by encouraging actions that promote recruitment and prevent spread of invasive species.

Introduction

Population biology of Largemouth Bass (LMB) *Micropterus salmoides* has been well studied throughout the United States (Philipp and Ridgway 2002). The nationwide popularity of the fishery has led biologists to concentrate research on conservation, particularly over the past 25 years (Noble 2002). Conservation strategies for Largemouth Bass typically focus on managing fishing mortality and habitat. Intensive fishing effort coupled with naturally low population growth rates can lead to poor LMB fisheries (Gwinn and Allen 2010), which has prompted the creation of regulations (e.g., creel limits, closed seasons or areas) to protect LMB fisheries. In addition to regulation, the adoption of catch-and-release behavior by anglers has significantly reduced angling mortality (Wilde 1998; Allen et al. 2008). However, even a low probability of catch-and-release mortality may negatively affect the fishery if fishing effort is high (Gwinn and Allen 2010; Kerns et al. 2012). Moreover, protecting adults from angling mortality does not ensure good recruitment and population growth. Allen et al. (2011) found little evidence that

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the number of adults (range 6–40) influenced the number of age-0 fish collected in October. Because of the large intra- and interannual variation in recruits produced by LMB, stock–recruitment models typically do not fully explain recruitment of LMB (Jackson and Noble 2000; Garvey et al. 2002; Allen et al. 2011). Here, we used an age-structured population model to determine risks of population decline at different levels of recruitment while accounting for fishing effort and total mortality in a nationally popular fishery for the Potomac River (Chesapeake Bay watershed; Figure 1).

Fishing effort influences three aspects of LMB fishing mortality: harvest, catch-and-release mortality, and catch-and-retain mortality. Of these, catch-and-release and catch-and-retain mortality have received the most attention (Pope and Wilde 2004; Driscoll et al. 2007; reviewed in Cooke and Schramm 2007). Catch-and-retain mortality is that which occurs after fish are retained for extended periods of time during competitive sportfishing tournaments (Wilde et al. 2002). Estimates of catch-and-retain mortality can range widely from 0.3% to 64.8%, depending on water temperature and handling stress (Wilde et al. 2002; Scott et al. 2008). Thus, understanding all components of fishing mortality is important for evaluating the effects of fishing on LMB populations (Kerns et al. 2012).

Interannual recruitment varies because of juvenile natural mortality that results from nest-disruptive fishing effort on the most fit males (Sutter et al. 2012), summer water temperatures (Shuter and Ridgway 2002), prey availability (Garvey et al. 2002), and changes in habitat. Newly introduced and nonnative species may also increase natural mortality for well-established populations. Exotic and invasive species can cause habitat alterations (Bain 1993), influence extinction risk (Gurevitch and Padilla 2004), and ultimately lead to problems in managing commercial or recreational fisheries (Smith 1968). In Maryland, the exotic Northern Snakehead (NSH) *Channa argus* may pose harm to aquatic fish-

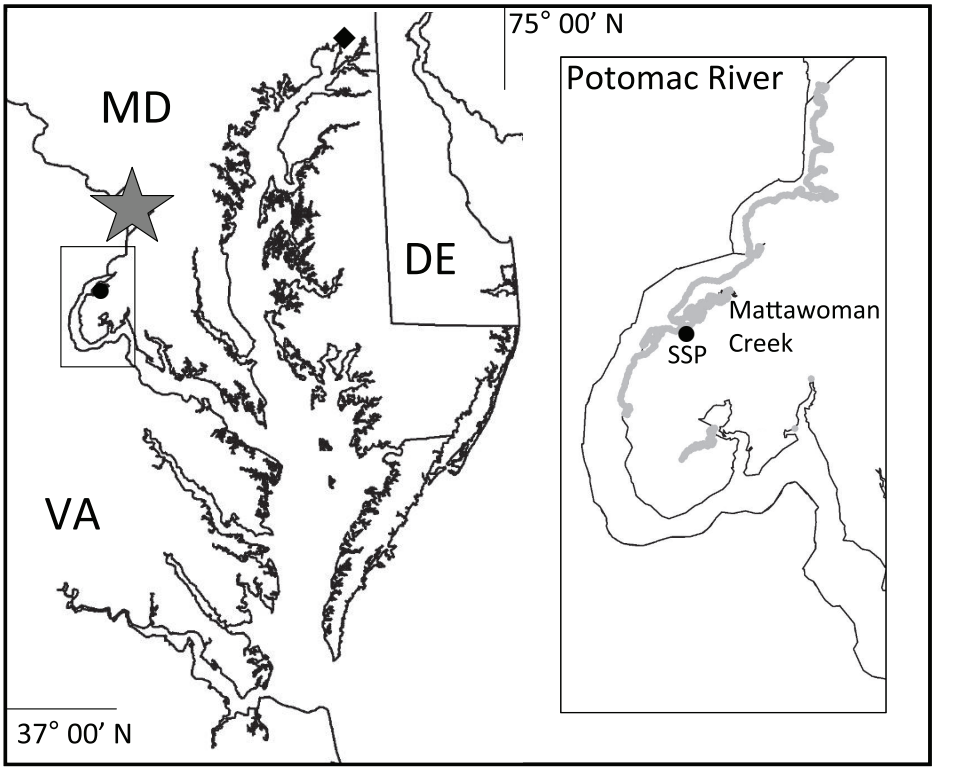

Figure 1. Map of tidal Potomac River of the Chesapeake Bay watershed (Maryland, USA), with Washington, D.C. labeled with a five-point star. Landmarks referenced in text are Smallwood State Park (SSP) and Mattawoman Creek (Potomac River).

es of Potomac River (Love and Newhard 2012; Saylor et al. 2012). The NSH is considered a predator and competitor of LMB (Saylor et al. 2012) and may adversely affect recruitment of LMB by preying on small juveniles (Love and Newhard 2012) or reducing nesting success by limiting available spawning habitats for adult LMB. Thus, there is a need to understand how NSH can influence LMB populations.

Our objectives were to (1) use estimates of fishing effort and mortality to parameterize a population model for LMB occurring in tidewater habitats of Potomac River, (2) use the population model to determine the risk of population decline and projected change in population size for fished populations and fished populations with NSH, and (3) assess the sensitivity of our findings to differences in recruitment by comparing them between good and poor recruitment simulations. We hypothesized that NSH would cause a greater risk of population decline, significantly lower population growth rate, and lower population sizes for LMB.

Methods

Population model

We created a population model to predict LMB abundance through one generation in the Potomac River (i.e., 13 years) with successive yearly time steps (t) using the equation

$$N_{(t+1)} = N_t + (R) - (A),$$

where N_t is the population size in a year, R is annual recruitment, and A is total annual mortality (for more details on aging and biology, see Appendix).

Recruitment depended on the number of sexually mature females, size of females, number of recruits produced per female (R/F), and a ratio describing density-dependent survivorship of juveniles (i.e., Goodyear compensation ratio, Goodyear 1977). The model did not include immigration or emigration because LMB has naturally restricted movements (Pribyl et al. 2005) and was not expected to commonly enter or leave the tidal freshwater region of Potomac River. The number of LMB for ages 2–6 was divided by 2 because we assumed that both males and females equally contributed to reproduction; the sex ratio of LMB is approximately 1:1 for these ages in the Potomac River (J. W. Love, unpublished data). Older ages 7–13 were dominated by females and the number of LMB was not divided by 2.

To account for differences in number of offspring produced because of differences in size, a weighting factor (ω) was calculated for average size within each age-cohort. To calculate ω, fecundity (or the number of eggs) per age-cohort was divided by fecundity at age 5, which represented the length of fish used to empirically determine R/F (see Appendix). Fecundity ($F_{a,t}$) for each age-cohort (a) in a year (t) was determined using the length–fecundity relationship published by Timmons et al. (1980) for a population in Alabama and Georgia. We did not assume senescence for older fish even though Kelley (1962) suggested that egg production diminished after age 7. Kelley (1962) utilized a small sample size ($N = 20$), and thus, we could not effectively model the level to which egg production diminished with age.

Recruitment for the unfished population was estimated for each age-cohort as

$$R_{a,t,o} = \left[\left(R/F * Fa,t,o\right) + \left(R/F * F_{a,t,o} * \omega\right)\right], \text{ and}$$
$$R_{t,o} = \sum\left(R_{a,t,o}\right),$$

where ω is a weighting factor in the model, $F_{a,t,o}$ is the number of mature females in the unfished population (o), and $R_{t,o}$ is annual recruitment for the unfished population.

Recruitment for fished populations was weighted by a density-dependent function to account for greater survivorship of juveniles and greater subsequent recruitment at lower, fished population sizes (Goodyear 1977; Barbour et al. 2011). The density-dependent R/F (R/F_k) was

$$R/F_k = \left\{\left[1 - \left(F_{a,t,f}\right)/\left(F_{a,t,o}\right)\right] * R/F\right\} * \text{CR},$$

and recruitment for each age-cohort was modified to

$$R_{a,t,f} = \left(R/F_k * F_{a,t,f}\right) + \left(R/F_k * F_{a,t,f} * \omega\right) \text{ and,}$$
$$R_{t,f} = \left(R_{a,t,f}\right),$$

where CR is Goodyear's compensation ratio (CR = 5), $F_{a,t,f}$ is the number of mature females in the fished population, and $R_{t,f}$ is annual recruitment for the fished population. We chose a CR = 5 to illustrate a well-established population (Barbour et al. 2011) and because LMB are more closely related to Percidae (CR = 8) and Percichthyidae (CR = 8.9) than other families listed in Myers et al. (1999).

Recruitment for a fished population of LMB occurring with NSH was determined as

$$R_{a,t,f} = \left\{R/F_k * \left[F_{a,t,f} - \left(F_{a,t,f} * \alpha\right)\right]\right\} \pm \left\{R/F_k * \left[F_{a,t,f} - \left(F_{a,t,f} * \alpha\right)\right] * \omega\right\},$$

where α is a reduction in the proportion of nests with females ($F_{a,t,f}$) that would not spawn because of competition for nesting sites by NSH (α). To estimate α, we estimated the relative competitive impact of NSH on LMB using a Lotka-Voltera model (Gotelli 2001). The basic form of the Lotka-Voltera model was

$$N = K_1 - \alpha K_2 / (1 - \alpha * \beta).$$

Both α and β were estimated using Solver in Microsoft Excel (version 2003). We empirically measured N, carrying capacity for LMB (K_1) and carrying capacity for NSH (K_2) (see Appendix). In Love and Newhard (2012), two additional parameters (i.e., co-occurrence and probability of being consumed) were developed to account for predation of adult NSH on juvenile LMB. Co-occurrence was defined as the percentage of sites where adult NSH existed along with juvenile LMB. The probability of being consumed depended on size of juvenile LMB and was measured with laboratory studies (Love and Newhard 2012). The product of these estimates for juvenile LMB proportionally reduced the number of juveniles surviving to age 1 (Love and Newhard 2012).

Total mortality (Z) was calculated as

$$Z = f_m + f_{cr} + f_h + f_{tx},$$

where f_m is natural mortality, f_{cr} is catch-and-release mortality, f_h is harvest mortality, and f_{tx} is tournament mortality. Fishing mortality components differed across age-classes because of size-specific vulnerability to fishing gear and harvest (Love and Newhard 2012).

Recruitment and total mortality parameters for each iteration of the model differed because parameters were randomly drawn from normal distributions determined by the mean and standard deviation of the parameter estimates. The standard deviations in parameters from the von Bertalanffy growth function (VBGF) were derived from the variation among their annual estimates obtained from empirical data. Natural mortality for age 1+ LMB varied similarly to variation in VBGF growth parameters. Variation in natural mortality for juvenile LMB was arbitrarily set at 20% of the value, which yielded a value similar to that observed for annual variation in catch of juveniles in Potomac River (J.W.L., unpublished data).

Data Analysis

Once the model was parameterized (Table 1), we compared the risk of population decline and projected change in population size resulting from the fishery (i.e., fished) with those resulting from the fishery when NSH was a competitor and predator in the ecosystem (i.e., fished with NSH). We did this for two population models that differed in recruitment, which was either good or poor in order to assess the sensitivity of our findings to the level of recruitment.

We determined the risk of population decline for each scenario by first determining the population growth rate (λ), which is the annual change in population size. The population size (N_t) for each of 13 time steps was estimated for fished populations. Initial N_t was arbitrarily set at 1,000 individuals and varied annually according to the number of survivors and the number of recruiting fish. The quotient of $\ln(N_{t+1})$ to $\ln(N_t)$ was calculated as realized λ. The λ for fished (λ_f) and fished with NSH ($\lambda_{f\text{-nsh}}$) scenarios were each averaged across the 13-year simulation period and the average was used in subsequent analyses.

The risks of population decline for both fished and fished with NSH scenarios were calculated as the proportion (p) of λ_f less than 1.0 or $\lambda_{f\text{-nsh}}$ less than 1.0, respectively. For $\lambda_{f\text{-nsh}}$ scenario, we also included parameters for competition and predation. For each scenario, a distribution of λ's was generated using a Monte Carlo simulation routine that iterated the model and recalculated values for 1,000 times. When p was greater than 0.50, the scenario was considered to have a meaningful risk of population decline. This meaningful risk of decline was compared between fished and fished with NSH scenarios. We also tested the hypothesis that $\lambda_{f\text{-nsh}}$ was significantly lower than that for λ_f by determining if $\lambda_{f\text{-nsh}}$ was included in the 95% confidence interval for λ_f, which would indicate that NSH did not influence LMB population growth for LMB populations.

We determined the level of projected change in population size by first estimating population size at equilibrium (N_{eq}). At 13 years, the change in N_t was negligible and population size reached N_{eq}. For each of the 1,000 iterations of the model, we then calculated the projected population decline as a percent change in N_{eq} due to NSH as

Table 1. Parameters used to construct the population model for Largemouth Bass from the Potomac River (Maryland).

Parameter	Value (SD)	Source
Growth constant (k)	0.389 (0.11)	MDDNR 2011
Maximum length (L_∞)	459 (27.39)	MDDNR 2011
Age at length 0 (t_o)	0	Gwinn et al. 2010
Length at age 0 (L_{init})	144.23 (25.70)	MDDNR 2011
Annual mortality (A)		
Natural (age 1+)	0.34 (0.07)	Pauly 1980
Natural (age 0)	2.25 (0.45)	Kelly 1962; Kramer and Smith 1962
Overwinter (<100 mm)	0.22 (0.04)	Love and Newhard 2012
Harvest (f_h)[a]	0.025 (0.010)	MDDNR 1995, 2006
Catch and release (f_{cr})[b]	0.084 (0.035)	Current study
Tournament (f_{tx})[a]	0.034 (0.014)	Current study

[a] Size limit for possession is 305 mm (SD = 30.5) for most of year, per Maryland Department of Natural Resources regulation.
[b] Size to gear is 200 mm (SD = 20.0), per Gablehouse 1984.

$$\Delta N_{eq} = \left[\left(N_{eq\text{-}f} - N_{eq\text{-}o}\right)/N_{eq\text{-}o}\right] - \left[\left(N_{eq\text{-}f\text{-}nsh} - N_{eq\text{-}o}\right)/N_{eq\text{-}o}\right] * 100\%,$$

where $N_{eq\text{-}o}$ is the size of the unfished population at equilibrium (see below), $N_{eq\text{-}f}$ is the size of the fished population at equilibrium, and $N_{eq\text{-}f\text{-}nsh}$ is the size of the fished population with NSH at equilibrium. These percent changes were averaged. The average was compared with a null expectation of no change (i.e., 0) using 95% confidence intervals.

The risk of population decline and projected change in population size were compared between fished and fished with NSH scenarios using *R/F* values reflecting either good or poor recruitment to assess the sensitivity of our findings to the level of recruitment. To establish levels of good and poor recruitment, the level of *R/F* for an unfished population at equilibrium was first estimated. We then arbitrarily doubled and halved that *R/F* to yield levels of good and poor recruitment, respectively (see calculation of recruitment, above). The *R/F* for an unfished population was estimated when $\lambda_o = 1.00$ (i.e., equilibrium) and was calculated from a nonlinear regression model that was fit to the relationship of λ_o's and corresponding *R/F*. The model for the unfished population was used to estimate an average λ_o (N = 1,000 Monte Carlo simulations) for various levels of *R/F*. Levels of *R/F* ranged as an increment of 5 from 5 to 165. This range was used because it included the minimum and maximum levels of *R/F* empirically measured (Table 2; see Appendix).

Results

The risk of decline in population size between fished and fished with NSH populations depended on the level of recruitment. The levels of *R/F* were 6.94 and 1.74 for good and poor recruitment simulations, respectively (*R/F* = 3.47 at $\lambda_o = 1.0$; Figure 2). Recruitment poor models led to population declines (Figure 3), with a meaningfully high risk of population decline for both the fished population and the fished with NSH population (Table 3).

When LMB recruitment was good, there was an increase in population growth (Figure 3), but a meaningful risk of decline for the scenario that included NSH (p = 0.68). There was no meaningful risk of population decline for the fished population (p = 0.40). Therefore, there was support for the hypothesis that there was a greater risk of population decline when including NSH as a competitor and predator in the scenario, but only when LMB recruitment was not already exceptionally poor.

For both recruitment levels, average $\lambda_{f\text{-}nsh}$ did not significantly differ from λ_f (Table 3). The difference between $\lambda_{f\text{-}nsh}$ and λ_f did not depend on recruitment level. For both models, λ_f was only 1% greater than $\lambda_{f\text{-}nsh}$. We therefore could not support the hypothesis that population growth rates differed significantly between a fished population and a fished population with NSH.

The projected change in population size was significantly different from 0 and was 20% lower for a fished population with NSH than for just a fished population, despite the level of recruitment (Table 3;

Table 2. The number of age 0, Largemouth Bass recruits (*R*) produced from the estimated number of likely spawning females (*F*) caught during boat electrofishing surveys of the Potomac River (Maryland) or other empirical and published data. Counts were standardized by hours (CPH) spent electrofishing.

Origin	*R* (CPH)	*F* (CPH)	*R/F*[a]
Field survey (2003–2004)	58 (10.64)	164 (19.97)	0.53
Field survey (2002–2003)	650 (79.17)	124 (18.59)	4.26
Field survey (2001–2002)	152 (22.79)	137 (17.59)	1.30
Field survey (2000–2001)	414 (53.08)	145 (23.50)	2.26
Field survey (1999–2000)	195 (31.60)	169 (21.00)	1.50
Hatchery (this study)	3,588	23	156
Allen et al. (2011)	~1,150	~20	~60

[a] Number of recruits per female, calculated as the ratio of recruit relative abundance at t+1 to female relative abundance at t, where t = year of survey.

Figure 3). There was support for the hypothesis that there was a significant decline in the projected population size for a fished population when NSH was a competitor and predator in the ecosystem. However, this projected change was less of an impact than the fishery itself because the projected reduction in population size for a fished population relative to the unfished state was 43.8% (0.6 SD) for good recruitment and 45.2% (0.6 SD) for poor recruitment models.

Discussion

Presence of NSH was predicted to increase the risk of a decline in population size for LMB because of adverse impacts on recruitment. Moreover, population size for LMB was expected to be 20% lower at equilibrium, which could lead to changes in biodiversity or community structure (Mittelbach et al. 1995). This expected reduction was much less than that observed by fisheries plagued with intensive commercial harvest and invasive species (Hansen et

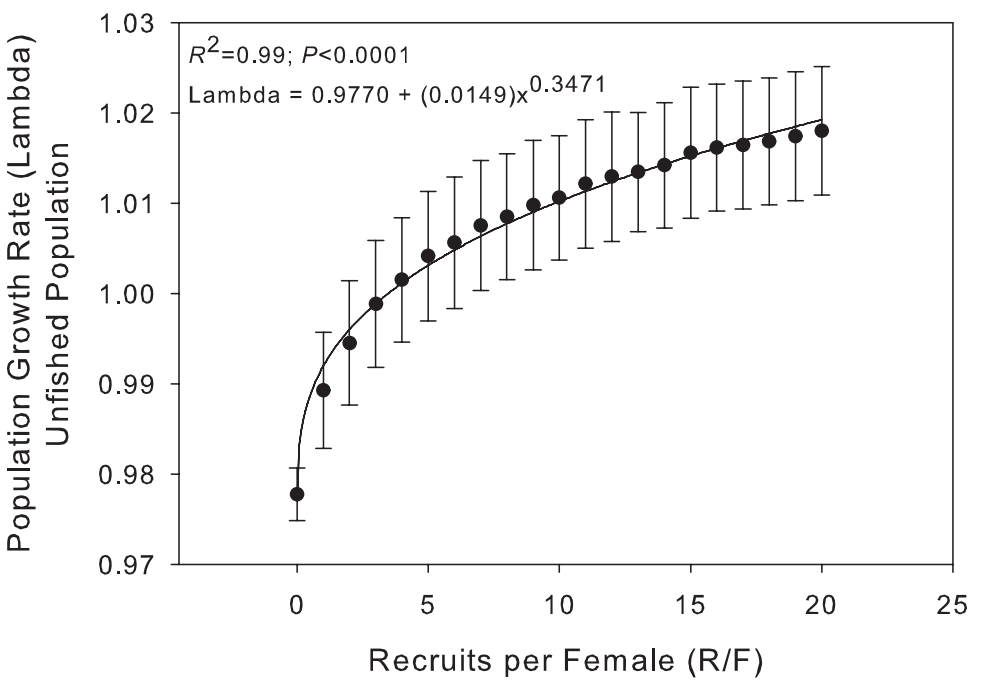

Figure 2. Population growth rates increased with the number of recruits per female (*R/F*) for an unfished population model of Largemouth Bass in the Potomac River (Maryland). Error bars represent the standard deviation of the mean.

Table 3. Predictions for recruitment poor and recruitment rich population models of Largemouth Bass of the Potomac River (Maryland). For each model, two scenarios were compared: a fishing-only scenario and a fishing with Northern Snakehead (NSH) in the ecosystem scenario. For each scenario, probability risk of population decline (p) was assumed meaningful when greater than 50% of 1,000 simulations resulted in a population growth rate (λ) less than 1.0. Average λ (SD) for fishing-only scenarios was compared with the 95% confidence interval of λ for the fishing with NSH scenario (* = $P < 0.05$; n.s. = not significant). The percent change in population size at equilibrium (ΔN_{eq}) for LMB because of NSH was determined to be significant if 0 was not included in its 95% confidence interval.

Population model	Scenario	p	λ (SD)	ΔN_{eq} (SD)
Recruitment poor	Fishing only	0.96	0.98 (0.01)	
Recruitment poor	Fishing with NSH	0.99	0.97 (0.01)$^{n.s.}$	20.0 (3.6)*
Recruitment rich	Fishing only	0.43	1.00 (0.01)	
Recruitment rich	Fishing with NSH	0.68	0.99 (0.01)$^{n.s.}$	20.4 (4.0)*

al. 1995). For species that are not targeted by commercial harvest, nonnative predator fishes can reduce distribution and abundance of native prey species by at least 50% (Hughes and Herlihy 2012). The impact of NSH on LMB may not be as significant as reported in Hansen et al. (1995) or Hughes and Herlihy (2012) because LMB is a formidable and potentially invasive predator itself (Jackson 2002). Our current expectation of reduction in population size is, however, greater than the expectation of a 3.8% reduction reported by Love and Newhard (2012). The current model differs substantially from that of Love and Newhard (2012) by including more refined estimates of LMB fishing mortality for the Potomac River, recruitment compensation, and a parameter representing competition for spawning habitat. Thus, we feel this study provided new information about the impacts of NSH on LMB populations.

Typically, to conserve black bass populations, minimizing angling mortality has been the goal of anglers and fishery managers because lowering natural mortality is often not possible. Anglers have worked with professional fish biologists to learn more about handling stress (Schramm et al. 2006; Jamison et al. 2007), catch-and-retain mortality (Seidensticker 1975; Edwards et al. 2004), and catch-and-release mortality (Pope and Wilde 2004; Wilde and Pope 2008). Catch-and-retain mortality may be tantamount to catch-and-release mortality (Driscoll et al. 2007), though exceptional cases of high angling mortality can occur during summer (Wilde et al. 2002). Fishing pressure may be low during this time, especially if tournament activity is restricted to spring and fall, which ultimately leads to overall low fishing mortality. Much of this information has been incorporated into conservation principles for black bass fisheries (Gilliland and Schramm 2009).

Natural mortality and production of juveniles vary among years because of annual differences in spawning habitat quality (Nack et al. 1993; Hoyer and Canfield 1996; Brewer and Rabeni 2011; Lawson et al. 2011; Love 2011), lake or river stage levels during the spawning and growing season (Maceina and Bettoli 1998; Peterson and Kwak 1999), and duration of the spawning season (Post et al. 1998). Long-term and progressive changes in recruitment may occur as climate changes (Rahel and Olden 2008), as development increases intensity of stream discharge (Peterson and Kwak 1999), or as development degrades water quality (Uphoff et al. 2011). In addition to these environmental factors that potentially limit recruitment, the abundance or health of males may limit recruitment. For our study, we assumed that recruitment resulted from equal and redundant contributions by males and females; however, negative effects of organic pollutants (e.g., estrogen) on males (Iwanowicz et al. 2009) or fitness differences among more-often-caught males (Sutter et al. 2012) could lead to some males playing a more important role than others in contributing to recruitment. Unfortunately, these complicated issues are not controlled by sole actions of anglers or fishery managers.

Anglers, commercial harvesters, and fishery managers have sought to control the spread of invasive species by promoting or participating in unlimited harvest of invasive species such as NSH. The expansion of NSH and other invasive species (e.g., Blue Catfish *Ictalurus furcatus*) populations in Potomac River could lead to a greater negative impact than that reported here (Love and Newhard 2012). These expansions coupled with reductions in the coverage of submerged grasses (4,441 ha in 2010 to 2,353 ha in 2012; determined using spatial data

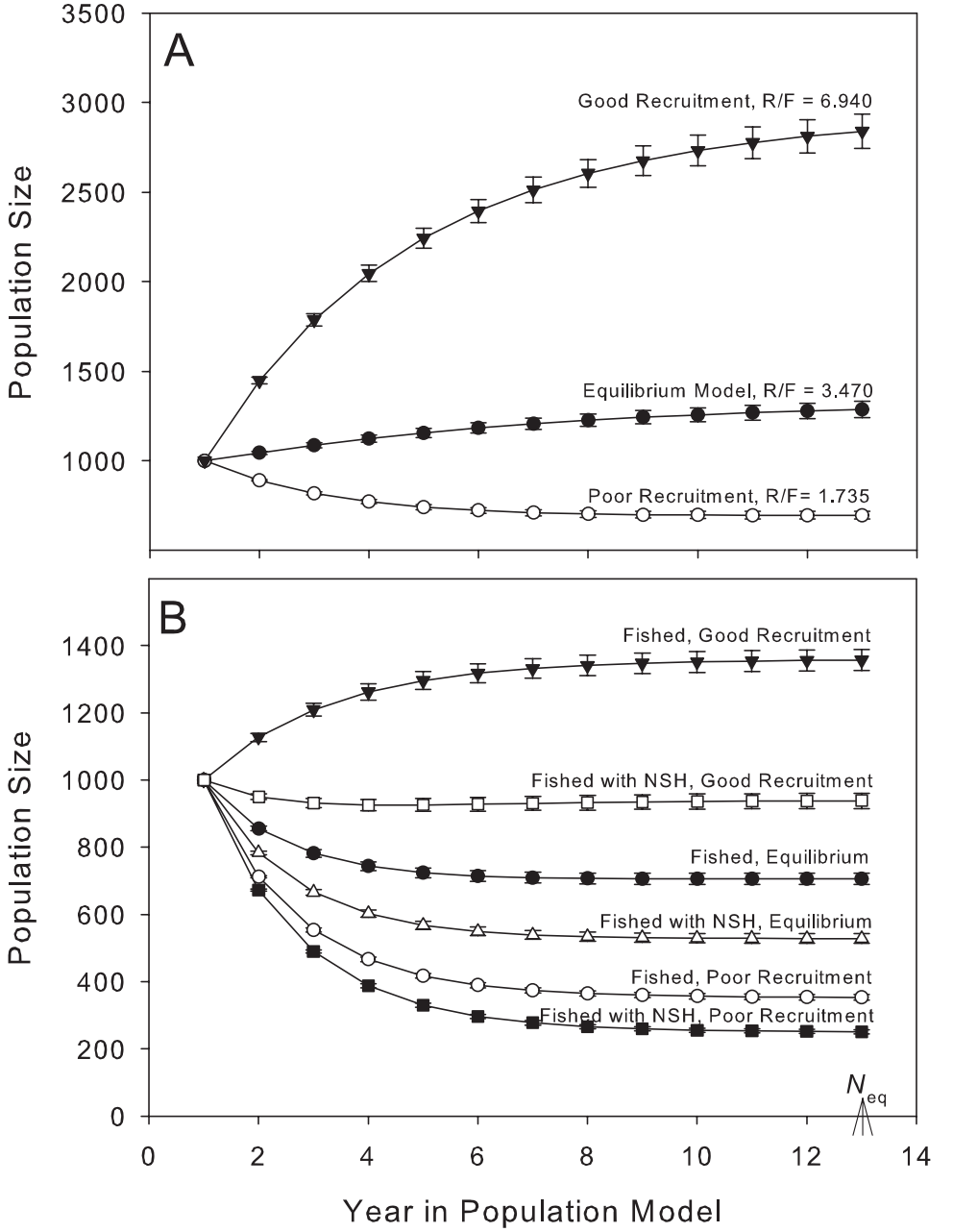

Figure 3. A. Population size changed over 13 yearly iterations for a population model of Largemouth Bass with a population growth rate of 1.0 in the Potomac River, with illustrations reflecting sensitivity of population growth to good and poor recruitment. B. Predicted population sizes for each year in the model was determined at good and poor levels of recruitment for fished and fished with Northern Snakehead (NSH) in the ecosystem.

of grasses geoprocessed by the Virginia Institute of Marine Science for 2012) may result in greater predation on juvenile LMB or greater competition for spawning habitat. From fall surveys, we have observed a steady decline in the proportion of sites occupied by juvenile LMB (since 2008), a recent reduction in the number of small LMB (<100 mm; since 2010), and a reduction in the survey's catch of

age 1+ fish by about 50% (since 2010; J.W.L., unpublished data). While such trends may be related to many factors, continued monitoring of the population and changes in the population size of NSH seem warranted. Recent trends of NSH biomass indicate a steadily increasing of distribution and biomass from 2004 until 2012 (Benson 2013). A world record NSH was caught from Potomac River in summer 2013. Our model indicates that NSH could harm LMB populations. While much uncertainty remains on the impact and spread of NSH, we strongly recommend control efforts aimed at lowering biomass and preventing spread of NSH.

We conclude that when habitat conditions do not already significantly limit recruitment, populations of black bass may be adversely affected by cohabitation with NSH. Because the number of adults may not limit juvenile production (Allen et al. 2011), environmental factors that improve recruitment may be arguably more important for protecting a population than maintaining a known quantity of females for large populations. Black bass anglers may need to expand the focus of their conservation efforts beyond minimizing angling mortality and include efforts aimed at lowering biomass of invasive species, minimizing urban impacts and informing land planners on the value of their fisheries.

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Appendix

$F_{a,t}$

The number of females for an age $F_{a,t}$ depended on growth rate between ages, as well as survivorship and recruitment (see below). Growth rate was determined using a von Bertalanffy growth function (VBGF) that modeled the relationship between length and age (Table 1). Total length was measured for Largemouth Bass (LMB) collected during fall (September–October) with electroshocking from a boat (Smith-Root 5.0 or 9.0 generator powered pulsator, pulse frequency at 60 Hz; Love 2011). Only fish collected between 1999 and 2004 (i.e., before Northern Snakehead [NSH] was discovered in Potomac River) were included in the analysis in order to lessen bias due to influence of NSH on vital rates. Among years, the number of sampled sites varied between 45 and 55 because of limited access to some sites and adverse weather conditions. Age was determined for a subsample of LMB collected from the Potomac River (spring through fall, 2005–2010) using otoliths (Buckmeier and Howells 2003) from mostly adults (≤200 mm, N = 3; 200–300 mm, N = 18; 300–350 mm, N = 31; 351–400 mm, N = 69; 400–450 mm, N = 113; 500–550 mm, N = 87; >500 mm, N = 25). Ages were used to generate a length-at-age key to predict ages from length for other surveyed LMB (Isermann and Knight 2005).

The VBGF model was modified because body growth is expected to be slower during the winter (Cloern and Nichols 1978):

$$\mathrm{TL} = L_\infty - \left(L_\infty - L_o\right) * \exp\left\{\begin{array}{l} -k*\left(x - t_o\right) - \\ \left[\left(180*k\right)/\pi\right]*\cos\left[\left(\pi*t_o\right)/180\right] - \\ \cos\left[\left(\pi*x\right)/180\right] \end{array}\right\},$$

where x = age (years), TL is total length, k is the growth constant, L_∞ is maximum asymptotic length, L_o is initial length at age 0, and t_o is age at length 0. To reduce bias of sampling gear on estimating k, we excluded small fish (<age 2) and fixed t_o at 0 (Gwinn et al. 2010). The estimated growth constant (k = 0.389, SD = 0.11) indicated that individuals grew from 60 mm/year (age 1) to 20 mm/year (age 6), which is similar to growth rates calculated from mark–recapture studies on Potomac River (55.8 mm, SD = 26; Love, unpublished data).

m

We estimated natural mortality (m) for subadult and adult ages following Pauly (1980) who used VBGF parameters and water temperature (Table 1). Natural

mortality of juveniles was determined with a combination of literature (Kelley 1962; Kramer and Smith 1962) and measuring the proportion that die in farm ponds and tanks at Maryland Department of Natural Resources' Joseph P. Manning Hatchery (Cedarville, Maryland).

f_h

Fishing mortality owed to harvest (f_h) was calculated as the proportion of fish harvested from the population in a year. Roving creel surveys of shoreline and boat anglers were conducted between May and October in 1990 and 1994 (MDDNR 1995). Monthly harvest levels ranged between 0 and 0.095 LMB per angler-hour. We calculated f_h as 0.024 (SD = 0.010) by assuming (1) a median harvest level of 0.011 LMB per angler-hour; (2) an average of 50 anglers per day (from data on angler participation in LMB tournaments, J.W.L., unpublished data); and (3) fishing 8 h/d for 180 d in a typical fishing year (April–October). The proportion of fish harvested was an average of the number harvested divided by two reported population sizes (25,137 and 46,636) that were computed using Huggins closed captures and Lincoln-Peterson models for data collected during mark–recapture studies conducted 1999–2005 for 1,071 tagged LMB from Potomac River tidewater (MDDNR 2010). This value is slightly lower than the 6% exploitation reported for reservoirs (Myers et al. 1999; Driscoll et al. 2007) but is similar to that reported for tidal rivers of the Chesapeake Bay watershed (MDDNR 2006).

f_{cr}

Fishing mortality owed to catch-and-release mortality (f_{cr}) was calculated as the proportion of fish that die from being caught and released in a year. To determine the probability that a fish will die from being caught and released, we used a combination of empirical and published data. We collected fishing data from seven average anglers of the Maryland Bass Federation Nation's youth chapter at Joseph Manning Hatchery ponds. Anglers used plastic worms with J-hooks and tallied whether the LMB adult (>305 mm) was hooked in the mouth or gut during June 2011. Of 35 LMB caught, 5 individuals were gut-hooked. The frequency of gut hooks generated a binomial distribution that represented the probability a fish would be gut hooked. This probability was multiplied by the probability of survival from gut hooking, which was estimated in Pope and Wilde (2004). Similarly, the probability of not being gut-hooked (i.e., hooked orally) was multiplied by the probability of survival from being hooked orally. The sum of these two products yielded the probability of survival if the fish is caught and released. This sum was calculated 1,000 times using a Monte-Carlo routine to determine the average probability of survival if the fish is caught and released. Using the probability of gut hooking a fish and the probability of survival from being gut-hooked, we determined that approximately 10.8% (SD = 2.9) of the LMB adults caught and released would die. This value is similar to that reported in a metanalysis of 274 species (i.e., 11%, Bartholomew and Bohnsack 2005; see also, Bettinger and Wilde 2012).

The number of LMB caught in a year was determined using a roving creel survey conducted in 1994 and current estimates from data of tournament angler participation and catches (2003–2011; MDDNR 2012). We calculated f_{cr} as 0.083 (SD = 0.035) by assuming (1) catch-and-release mortality as 0.108, (2) a catch rate of LMB as 0.35 fish/angler-hour by recreational anglers (MDDNR 1994; J.W.L., unpublished data), (3) an average of 50 anglers per day (from data on angler participation in LMB tournaments, J.W.L., unpublished data), and (4) fishing 8 h/d for 180 d in a typical fishing year (April–October). We calculated f_{cr} for estimated population sizes of 25,137 and 46,636 (MDDNR 2010) and averaged the two f_{cr} estimates. Our value of f_{cr} is similar to the upper end value reported by Driscoll et al. (2007; 2–17% of total annual mortality, $Z = -0.46$).

f_{tx}

Catch-and-retain mortality is measurable as weigh-in mortality (i.e., the average number of LMB that die throughout the fishing day) and delayed mortality (i.e., LMB that were released alive but later died). Weigh-in mortality was recorded at the end of the 1,074 fishing days by Potomac River tournament directors from 1999 to 2011. Weigh-in mortality averaged approximately 1.5% (N = 1074; average = 0.014, SD = 0.050). To estimate delayed mortality, we fin-clipped and released 264 LMB in 2011 and 215 in 2012 after they were caught and retained during a competitive sportfishing tournament on Mattawoman Creek (Smallwood State Park, Maryland; see Figure 1). Each day afterwards, an area of 0.8 km^2 was surveyed with boat electrofishing along the same survey path and using the same survey effort. The number of recovered tagged fish was converted to a natural log and plotted by day of survey. The

decline in the number of tagged fish was measured as the slope (z) of the regression of day (independent variable) and number of recovered tagged fish (dependent variable). The proportion of LMB that either died or emigrated was calculated from $1 - e^{-z}$.

The number of recovered tournament fish declined over time (Figure A1). After 72 h, that number remained relatively unchanged for the remainder of the study period. Delayed mortality was estimated as 36.9% in 2011 (z = –0.461, SE = 0.201); of these, 14.8% was observed dead and removed from the waterway. Similarly, in 2012, delayed mortality was estimated as 38.2% (z = –0.481, SE = 0.034); of these, 1.9% was observed dead and removed. We utilized a value of 37% (z = –0.431, SD = 0.035) and reduced that proportion by 40% (i.e., 15%), which may be attributed to emigration (Siebold 1991). According to telemetry work done by Siebold (1991), approximately 40% of LMB released after a competitive sportfishing tournament at Smallwood State Park emigrated within a week. Thus, a value of 22% was used to represent this portion of delayed mortality.

Fishing mortality owed to catch-and-retain mortality (f_{tx}) was calculated as 0.032 (SD = 0.014) by assuming (1) weigh-in mortality is 0.015, (2) delayed mortality is 0.220, and (3) an average of 4,536 LMB were caught each year by anglers participating in competitive sportfishing tournaments (MDDNR 2012). The proportion of tournament caught fish relative to the population was estimated using average population size of 25,137 and 46,636 (MDDNR 2010) and the f_{tx}'s calculated for each population size were averaged. Our estimate of f_{tx} is similar to those reported by Driscoll et al. (2007; 1–16% of total annual mortality, z = –0.46)

R/F estimate

For the fished population of LMB scenario, we accounted for effects due to a fishery. The recruits per female (*R/F*) was estimated from surveys of the Potomac River (1999–2004) using sampling methods described above. During each survey, we estimated the relative abundance of adults (ages 2–13) in a year and relative abundance of recruits (age 0) in the successive year. As above, relative abundance of adults (ages 2–6) was divided by 2 to estimate the relative abundance of females. Because juveniles may have a different catchability than adults,

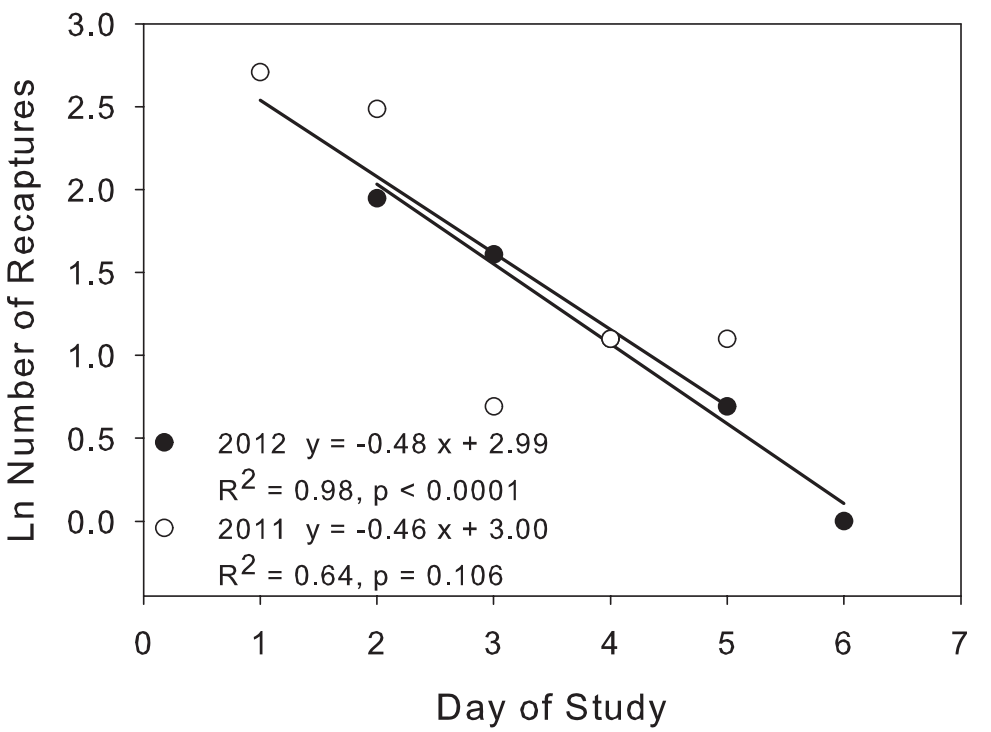

Figure A1. The number of marked and recaptured Largemouth Bass declined daily in Mattawoman Creek (Potomac River, Maryland) following competitive sportfishing tournaments (June–August, 2011–2012).

R/F was also directly estimated using hatchery pond experiments (Allen et al. 2011). A known number of spawning-ready females from the Potomac River was added with males to two 0.101-ha farm ponds in April 2012. After offspring were observed leaving their nests in June, adults were removed from ponds to limit cannibalism by parents. The number of offspring surviving from bird strikes, starvation, or intracohort cannibalism was determined by draining ponds in October and counting offspring. The *R/F* ranged between 2 and 156 (Table 2).

The *R/F* may be density-dependent, whereby recruitment may increase as population size decreases because fisheries reduce spawning stock biomass (Barbour et al. 2011). To compensate for such changes in the population model, we weighted *R/F* values used in the model with the Goodyear compensation ratio (Goodyear 1977; Barbour et al. 2011):

$$\left[1-\left(N_{t+a,f} / N_{t+a,o}\right)\right] * R/F * \mathrm{CR},$$

where $N_{t+a,f}$ and $N_{t+a,o}$ are number of age 2+ in the fished and unfished population, *R/F* is user entered for the unfished condition, and CR is *R/F* at very low population abundance relative to *R/F* in unfished condition (i.e., maximum reproductive rate, Myers et al. 1999).

α, β, K_1, K_2

In addition to accounting for the effects of a fishery on recruitment, we accounted for predation by adults on juvenile LMB and competition for spawning habitat. For an area of 0.8 km^2 in Mattawoman Creek, the population size of LMB (N = 1599) was estimated using mark–recapture data (for methods, see above). The K_1 and K_2 were the maximum number of nesting sites possible within the 0.8-km^2 area. The number of nests depended on a nest's area and the available nesting habitat. Available nesting habitat was mapped with ArcGIS (version 10.0) using spatial data of grasses geoprocessed by the Virginia Institute of Marine Science (2008–2010), submerged structure and substrate (MDDNR 2013), bathymetry from georeferenced nautical charts from the National Oceanic and Atmospheric Administration (2007), and institutional knowledge. For NSH, the available nesting habitat was defined as that which was associated with submerged structure or grasses and at depths up to 2 m (Lapointe et al. 2010). For LMB, available nesting habitat was measured as that which was associated with grasses or submerged structure, depths from 1 to 2 m, sandy substrate, and inside coves (Nack et al. 1993; Lawson et al. 2011; Love 2011).

To determine K_1 and K_2, the areas of these reproductively important habitats were divided by the area needed for defending a nest (9 m^2 for LMB and 9 m^2 for NSH). The area for LMB was calculated as 9 m^2 for a circular nest with a 1 m diameter (maximum size) built approximately 1 m from surrounding nests (assuming structure is available; Heidinger 1976). The area for NSH was based on observation (J.J.N., personal observation). The maximum number of nests for LMB predicted to occur within 0.8 km^2 (or K_1) was 82,905; that for NSH (or K_2) was 174,225. The opportunity for NSH to utilize shallow areas and more of the habitat yielded a greater carrying capacity of the environment for NSH. The associated α was 0.408 and β was 0.307. Thus, NSH was expected to be a better competitor and reduce the number of nests in the area by 40.8%.