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Strategies to Control a Common Carp Population by Pulsed Commercial Harvest

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Abstract

Commercial fisheries are commonly used to manage nuisance fishes in freshwater systems, but such efforts are often unsuccessful. Strategies for successfully controlling a nuisance population of common carp *Cyprinus carpio* by pulsed commercial harvest were evaluated with a combination of (1) field sampling, (2) population estimation and CPUE indexing, and (3) simulation using an exponential semidiscrete biomass dynamics model (SDBDM). The range of annual fishing mortalities (F) that resulted in successful control ($F = 0.244$–0.265) was narrow. Common carp biomass dynamics were sensitive to unintentional underharvest due to high rates of surplus production and a biomass doubling time of 2.7 years. Simulations indicated that biomanipulation never achieved successful control unless supplemental fishing mortality was imposed. Harvest of a majority of annual production was required to achieve successful control, as indicated by the ecotrophic coefficient (EC). Readily available biomass data and tools such as SDBDMs and ECs can be used in an adaptive management framework to successfully control common carp and other nuisance fishes by pulsed commercial fishing.

Commercial fisheries are commonly used to manage overabundant (hereafter, "nuisance") fishes in freshwater systems of the United States (Fritz 1987). However, these populations are rarely harvested at a rate that is sufficient for their control, likely due to a low landing price or the lack of a market (Wydoski and Wiley 1999). Insufficient commercial harvest can also result from a lack of information on nuisance fish population dynamics as such information is necessary to develop harvest targets that lead to population control. Formal stock assessments for

nuisance fishes in freshwater systems are scarce, likely due to their lack of significant economic value. However, assessment of nuisance fish dynamics is critically important for the success of control programs that use commercial fisheries.

Common carp *Cyprinus carpio* can dominate fish communities in North American lentic ecosystems (Cahn 1929) and can adversely affect water quality and biotic assemblages (Lougheed et al. 1998; Scheffer 1998; Chumchal et al. 2005). Common carp quickly attain large body sizes in North America

(Carlander 1969; Crivelli 1983), and their impact on aquatic systems is primarily a function of population biomass (Chumchal et al. 2005). Common carp biomass has been positively associated with chlorophyll *a*, turbidity, and total phosphorus, and high levels of these factors are symptoms of degraded water quality in aquatic systems. Significant reduction in common carp biomass can quickly (i.e., within 1 year) shift a shallow aquatic system from a degraded turbid-water state to a clear-water state with abundant macrophytes, reduced phytoplankton biomass, and increased abundance of large-bodied zooplankton (e.g., *Daphnia* spp.; Schrage and Downing 2004). Reductions in common carp biomass benefit aquatic vegetation (Threinen and Helm 1954; Tyron 1954; Bajer et al. 2009), game fish populations (Rose and Moen 1953; Jackson et al. 2010), water clarity (Schrage and Downing 2004), waterfowl production (Cahoon 1953; Bajer et al. 2009), and local economics (Cahoon 1953). Limiting common carp biomass to no more than 100 kg/ha has been identified as a potential management target that minimizes environmental degradation (Mehner et al. 2004; Bajer et al. 2009).

Common carp biomass can be reduced by using chemical, biological, and physical removal methods. Chemical removal with piscicides (e.g., rotenone) began in the 1940s (O'Donnell 1943; Weier and Starr 1950) and remains in use today (e.g., Schrage and Downing 2004). However, piscicides can be prohibitively expensive and can cause mortalities in nontarget species. Nontarget mortality associated with piscicides can require the reassembly of native fish assemblages after treatment; otherwise, common carp and other undesirable fishes will continue to dominate the system (Shapiro and Wright 2007). In systems where nontarget impacts are unlikely or negligible, chemical control methods can result in significant short-term water quality improvements (Schrage and Downing 2004). However, large-scale common carp biomass manipulations (hereafter, "biomanipulations") rarely result in long-term (>8–10 years) water quality improvements without reductions in external nutrient loadings (Hansson et al. 1998; Beklioglu 2003; Kasprzak et al. 2003; Sondergaard et al. 2007) and suppression of zooplanktivorous fishes (Sondergaard et al. 2007). Contemporary biomanipulation strategies incorporate both a top-down approach, in which piscivore biomass is manipulated (Kitchell 1992), and a bottom-up approach, in which nutrient recycling is limited by reducing benthivorous fish biomass (Schrage and Downing 2004).

Biological methods, such as the stocking of piscivores to biologically control nuisance species or to cause a trophic cascade, have been used with varying success to improve water quality. For example, northern pike *Esox lucius* have been used to control nuisance fishes; however, their success as biological control agents depends on the inclusion of nuisance fishes in their diet (Paukert et al. 2003; Ward et al. 2008), the timing of stocking events, predator biomass, and predator and prey body size (Skov and Nilsson 2007). By controlling nuisance fish populations, piscivores can induce a trophic cascade that leads to improved water quality, recovery of sport fish populations, and increased biological diversity (Carpenter et al. 1985; Kitchell 1992; Lathrop et al. 2002). Unfortunately, the biological control of common carp biomass by use of predation has not been successful without prior biomanipulation (Perrow et al. 1995; Mehner et al. 2004).

Commercial fisheries can cause nontarget impacts (e.g., bycatch); however, bycatch can be minimized by imposing size restrictions on fishing gear and identifying periods and locations of common carp aggregations (e.g., Diggle et al. 2004; Penne and Pierce 2008; Bajer et al. 2011). Additionally, harvest subsidies can replace market incentives to increase commercial harvest. Despite newer technologies that may become available in the future (e.g., "daughterless" common carp; Brown and Walker 2004), commercial harvest to control common carp is likely to continue.

Uncertainty in the minimum amount of commercial harvest needed for effective control is another problem with nuisance fish control. Identification of biomass harvest targets that reduce common carp biomass over the long term has not been attempted in a formal way (e.g., stock assessment). Biomass dynamics models (BDMs) are simpler than size- or age-structured models in that they only require estimates or indices of biomass and harvest amounts (Hilborn and Walters 1992). Harvest targets that reduce biomass to desired levels can be identified by using BDMs if sufficient time series data exist to allow fitting of a model. Simulations with a fitted BDM can then be used to evaluate potential management strategies and to identify harvest targets that result in successful control. It should be noted that harvest targets for nuisance fishes are different than harvest quotas for commercially important fishes. In particular, commercial fishing stops once a harvest quota is reached, but for nuisance species a harvest target must be equaled or exceeded for population control to be effective.

Alternative management strategies that feature different harvest targets and schedules to control common carp biomass can be evaluated by simulation modeling. Because simulations simplify the real world to a model, they provide harvest targets that do not necessarily account for real-world limitations. Practical management can potentially be limited by uncontrollable factors (e.g., weather or personnel limitations) and unintentional underharvest (i.e., missing the harvest target), among other factors. Therefore, identification of strategies that are robust to the uncertainties inherent in real-world management is necessary for successful population management and for the setting of reasonable harvest targets. Success of different scenarios can be evaluated by comparison with an objective, such as maintaining a low standing biomass (e.g., ≤100 kg/ha; Bajer et al. 2009). Potential strategies include (1) doing nothing, (2) generating market-driven commercial harvest, and (3) performing periodic large-scale removals when biomass reaches a nuisance level. Additional simulation analyses can then be used to evaluate the effect of unintentional underharvest on biomass dynamics.

The time series data that are necessary to fit BDMs can be sparse or nonexistent for nuisance fishes, thus precluding the

use of BDMs in identification of harvest targets. Ricker (1946) proposed the ecotrophic coefficient (EC) as a simple, biomass-based metric that may be useful for setting harvest targets based on a single year of data. The EC is calculated as the ratio of biomass harvested to biomass produced over an annual period and varies from 0 in the case of no harvest to greater than 1 under a scenario of very heavy harvest. The EC has been used to guide development of harvest quotas for salmonid populations in Minnesota (Waters 1992) and North Carolina (Wallace 2010), but to our knowledge the EC has never been used to develop harvest targets for nuisance fishes. An EC greater than 0.5 is considered to indicate an unsustainable level of harvest for salmonid populations (Waters 1992). However, the EC threshold for unsustainable harvest will depend on the fraction of annual production that is allocated to surplus production, and thus the threshold will vary among species.

In this study, we estimated and indexed (i.e., CPUE) common carp biomass in a shallow, eutrophic lake that was undergoing pulsed commercial harvest. Biomass estimates and CPUE were then used to fit a semidiscrete BDM (SDBDM) accommodating pulsed-harvest events. The fitted SDBDM was then used to identify the harvest targets that would be required to achieve a biomass threshold (i.e., $\leq$100 kg/ha) by using pulsed commercial fishing. Additionally, the fitted model was used to evaluate the effect of unintentional underharvest on biomass dynamics and the application of the EC to establish harvest targets in situations where data are sparse.

METHODS

Study Area

Clear Lake is a 1,464-ha, shallow (mean depth = 2.9 m) glacial lake located in the Western Corn Belt Plains ecoregion of north-central Iowa (43°08′N, 93°22′W; Figure 1). The economic value of the lake is approximately US$43 million annually, the majority of which is associated with vacation and recreational use (CARD 2008). Open-water and ice fisheries primarily target walleyes *Sander vitreus*, yellow bass *Morone mississippiensis*, and black bullheads *Ameiurus melas*, with an estimated value between $1.0 and $2.5 million annually (S. E. Grummer, unpublished data). Water quality has declined over the last half-century (Egertson et al. 2004) but has fluctuated over the past 10 years, with Secchi transparencies varying from 0.1 to 2.9 m and periodic cyanobacterial blooms during summer months (Iowa Lakes Information System 2005; Colvin et al. 2010). Reduced water transparency has been associated with the resuspension of sediment and organic material caused by the increasing biomass of common carp. Recycling of nutrients into the water column by common carp promotes production of cyanobacteria and other phytoplankton in this system (Downing et al. 2001; Wahl 2001). Water flows into the lake from Ventura Marsh, a shallow, 81-ha wetland (Figure 1). Metal grates prevent adult common carp from moving between Clear Lake and Ventura Marsh. A pump station was recently added to Ventura
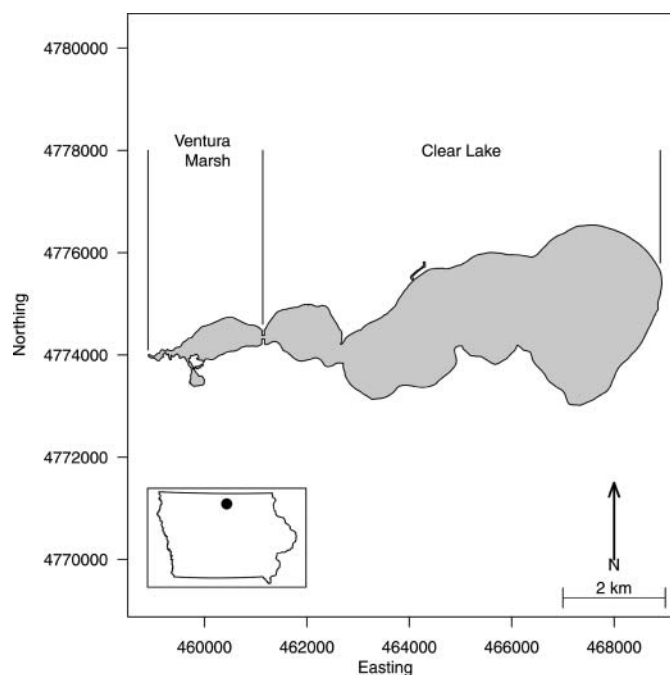

FIGURE 1. Clear Lake in north-central Iowa. Lake inflow travels east from Ventura Marsh. Adult common carp are prevented from moving between Clear Lake and Ventura Marsh by an exclusion device that is located at the inlet to the lake.

Marsh, thus allowing managers to draw down the marsh water levels under ice. These drawdowns cause low dissolved oxygen, creating winter-kill conditions and limiting common carp recruitment to the lake.

Commercial Fishery

A commercial fishery is used to limit the impacts of common carp on the Clear Lake ecosystem, and more than 1 million kg of biomass have been harvested from the system over the past 70 years (Wahl 2001; Colvin et al. 2010). In contrast to commercial fisheries for economically valuable species, which occur over much longer time periods, a pulsed commercial fishery for common carp operates only for short periods of time (<2 weeks) on Clear Lake. Pulsed harvests occur during the common carp spawning season beginning in late May or early June, and an additional fall harvest period of similar duration occurs between late October and early November. A period of high common carp biomass (~540 kg/ha) in Clear Lake during the early 2000s corresponded with severely reduced water quality, prompting the Iowa Department of Natural Resources (IADNR) to augment the commercial fishery with a $0.22-per-kilogram subsidy in an attempt to increase harvest (Wahl 2001; Larscheid 2005). Common carp biomass has fluctuated over the past 10 years despite continued intense commercial fishing (Larscheid 2005; Colvin et al. 2010). However, the identification of common carp aggregations, both spatially and temporally (Penne and Pierce 2008), has led to more efficient fishing and an overall reduction in fishing effort over the past 4 years.

Common Carp Biomass Estimation

Marking and recapture.—Annual common carp abundance was estimated by mark–recapture. Between 2,840 and 3,515 common carp were captured by commercial fisherman during spring harvest events from 2007 to 2010, and these fish were marked with a year-specific fin clip. Marked fish were released alive, were allowed to mix with the unmarked population over the summer, and were then recaptured during fall commercial harvest. The entire fall harvest was sorted, and the marked and unmarked fish were enumerated. Individual total lengths (nearest 1 mm) and weights (nearest 200 g) were measured for a representative subset of captured common carp. The population was assumed to be closed to immigration, emigration, and mortality during the summer mixing period.

Abundance estimation.—Annual common carp abundance was estimated by using closed-population mark–recapture models. Abundance was estimated by fitting binomial, hypergeometric, and multinomial (M_t) models to mark–recapture data by maximum likelihood (Otis et al. 1978; White et al. 1982; Hayes et al. 2007). Annual abundance estimates ($\hat{N}$) were determined by maximizing model-specific log-likelihoods with a quasi-Newton nonlinear search algorithm (for specific likelihood functions for mark–recapture models, see Otis et al. 1978; Amstrup et al. 2005; Hayes et al. 2007) via the optim function in R software (R Development Core Team 2010). The variance of $\hat{N}$ was calculated by solving the inverse of the numerically derived Hessian matrix (Bolker 2008).

Model selection.—An information theoretic approach was used to select between competing mark–recapture models. Akaike's information criterion (AIC) was calculated for each model using the maximized log-likelihood and the number of model parameters for each year (Akaike 1974). The AIC difference (ΔAIC) for each model was calculated as the within-year difference between the model-specific AIC and the minimum AIC. Model-specific likelihood was calculated as $e^{-0.5(\Delta AIC)}$ and was relatively weighted (w_{model}) to sum to 1 (Burnham and Anderson 2002). Abundance estimates from the best-approximating model or from models that were within one-tenth of the maximum w_{model} (i.e., $w_{model} > 0.9$) were used for subsequent annual biomass estimates (Royall 1997).

Common carp biomass estimates.—Whole-lake biomass ($\hat{B}$) of common carp was estimated as the annual mean common carp weight at capture ($\bar{w}$) multiplied by $\hat{N}$. The variance of $\hat{B}$ was calculated as $var(\hat{B}) = [\bar{w}^2 var(\hat{N})] + [\hat{N}^2 var(\bar{w})] - [var(\hat{N})var(\bar{w})]$, where $var(\hat{N})$ is the variance of estimated abundance and $var(\bar{w})$ is the variance of mean weight (Hayes et al. 2007). The 95% CIs were calculated by assuming that $\hat{B}$ was normally distributed. The estimated $\hat{B}$ and 95% CIs were divided by lake area (1,464 ha) to standardize to area (i.e., kg/ha). Date of initial capture was converted to the nearest 0.001 year for subsequent BDM fitting.

Biomass indices.—Common carp biomass was indexed by daytime (0800–1900 hours) trawling during September and October of 2007–2010. A semiballoon otter trawl with an 8-m headrope, a 3.8-cm stretch-mesh body, and a 6.3-mm-mesh cod end was used to sample the offshore zone of the lake. Trawling locations were allocated proportionally to the area of the lake's three basins, with starting location and trawling direction selected at random. Routes were constrained to be greater than 100 m from shore and 400 m from the nearest trawling location. Each trawling sample was conducted at a speed of 3.2–4.0 km/h for a period of 5 min to maintain comparability with previous trawling efforts (Larscheid 2005). Captured common carp were enumerated, measured (nearest 1 mm), and weighed (nearest 200 g). The CPUE (I) was calculated as the total biomass of common carp captured per trawl sample. Annual mean CPUE ($\bar{I}$) was calculated as the mean among-sample CPUE within a year. Bootstrap resampling was used to estimate the variance and CV of annual $\bar{I}$ (Efron and Tibshirani 1991). Median date of trawling was converted to the nearest 0.001 year for subsequent BDM fitting.

Biomass dynamics model.—An exponential SDBDM was fitted to annual $\hat{B}$ and $\bar{I}$ data for 2007–2010. Semidiscrete BDMs extend continuous BDMs to accommodate discrete harvest events (Colvin et al. 2012). An exponential model was used because only 4 years of data were available to fit the model, thus precluding the use of more complex BDMs that include parameters for limiting production (e.g., Schaefer or Fox). Because common carp biomass as high as 540 kg/ha had been estimated as recently as 2002 (Larscheid 2005), the biomass estimates for 2007–2010 (100–200 kg/ha) were assumed to be well below carrying capacity. The exponential SDBDM used to model $\hat{B}$ and $\bar{I}$ dynamics was

$$\left.\begin{aligned} \frac{dB(t)}{dt} &= r \cdot B(t), & t \neq \tau_k \\ B(\tau_k^+) &= B(\tau_k) - C(\tau_k), & t = \tau_k \end{aligned}\right\},$$

$$\bar{I}(t) = q \cdot B(t)$$

where r is the intrinsic growth rate; $B(t)$ is common carp biomass at time t; $B(\tau_k^+)$ is the biomass occurring instantaneously after the pulsed-harvest event at time τ_k; $C(\tau_k)$ is the biomass harvested during event τ_k; $\bar{I}(t)$ is mean CPUE at time t; q is catchability; t is continuous time; τ_k is the time of the pulsed-harvest event; and k indexes the pulsed-harvest events. The SDBDM was solved by numerical integration for $t = 2007$–2011 by using a time step of 0.001. Livermore numerical integration routines are the most accurate and thus were used for all numerical integration by using the deSolve package in R (Stevens 2009; Soetaert et al. 2010).

Data and model fitting.—Exponential SDBDM parameters were estimated by maximum likelihood. The log-likelihood was modified to account for uncertainties by including year-specific variance estimates for $\hat{B}$ and $\bar{I}$. The log-likelihood of the model

was calculated as

$$
\begin{aligned}
&\ell[r, B_0, q, \sigma \,|\, y(t)_i\,, \bar{I}(t)_j\,, \sigma_i, \sigma_j] \\
&= \sum_1^i \log_e \left(\frac{1}{\sqrt{2 \cdot \pi \cdot \sigma_i^2}} e^{-\left\{ \frac{[y(t)_i - \hat{y}(t)_i]^2}{2 \cdot \sigma^2 + 2 \cdot \sigma_i^2} \right\}} \right) \\
&\quad + \sum_1^j \log_e \left(\frac{1}{\bar{I}(t)_j \sqrt{2 \cdot \pi \cdot \sigma_j^2}} e^{-\left\{ \frac{\log_e\left[\bar{I}(t)_j / \hat{I}(t)_j\right]^2}{2 \cdot \sigma_j^2} \right\}} \right),
\end{aligned}
$$

where r is the intrinsic growth rate; B_0 is the initial common carp biomass; q is catchability; $y(t)_i$ is the mark–recapture biomass estimate at time t; σ is the interyear residual SD of $y(t)_i$; $\hat{y}(t)$ is the SDBDM-predicted biomass at time t; σ_i is the year-specific SD of each biomass estimate; $\bar{I}(t)_j$ is mean CPUE at time t; $\hat{I}(t)$ is the SDBDM-predicted mean CPUE at time t; and σ_j is the year-specific CV of CPUE. Model-predicted biomass and mean CPUE values corresponding to estimated values of $\hat{B}$ and $\bar{I}$ based on fractional year were extracted from the predicted time series to calculate the log-likelihood. We assumed that $\bar{I}$ was multiplicative and lognormally distributed; therefore, year-specific CV was used for σ_j. Parameter estimates that maximize the log-likelihood were obtained by using a bounded, nonlinear quasi-Newton search algorithm via the optim function in R (Stevens 2009; R Development Core Team 2010). All parameters were constrained to be positive. Parameter estimate variances were calculated by solving the inverse of the numerically derived Hessian matrix (Bolker 2008). The fitted

SDBDM was used for all subsequent simulations to evaluate common carp management strategies.

Simulation of Management Strategies

Scenarios.—Alternative harvest strategies to reduce common carp biomass were evaluated by simulation using the fitted SDBDM. Scenarios are model-based implementations of management strategies that are formalized as mathematical functions. Hereafter, the term "scenario" will refer to management strategies that were simulated by using the fitted SDBDM. Scenario 1 evaluated the continued use of conventional, seasonally pulsed commercial fishing as currently practiced. We evaluated two additional scenarios representing biomanipulation management strategies in which common carp biomass was significantly reduced when biomass exceeded a nuisance level ($B_{nuisance}$) ranging from 220 to 550 kg/ha (Table 1). The $B_{nuisance}$ was bounded between 220 and 550 kg/ha so that the biomanipulation events did not occur too frequently (i.e., every year); the upper bound represented the maximum of recent biomass estimates. Scenario 2 (the first biomanipulation scenario) used a pulsed proportional reduction of 0.75 when biomass exceeded $B_{nuisance}$ (Perrow et al. 1995; Hansson et al. 1998). Scenario 3 (the second biomanipulation scenario) employed a pulsed reduction of biomass to 100 kg/ha (Mehner et al. 2004; Bajer et al. 2009) when $B_{nuisance}$ was exceeded. Commercial fishing can also be utilized to maintain biomass levels during the years after a biomanipulation event. For example, after common carp biomass is reduced to 100 kg/ha, supplemental smaller harvests in the subsequent years can be used to keep biomass at reduced levels. Therefore, supplemental fishing mortality

TABLE 1. Common carp management scenarios and parameter intervals that were evaluated by using the fitted semidiscrete biomass dynamics model ($F =$ fishing mortality; $B =$ biomass; $C(\tau_k) =$ biomass harvested during pulsed-harvest event τ_k; $\tau_{k,spring} = \{0.2, 1.2, \ldots 50.2\}$; $\tau_{k,fall} = \{0.8, 1.8, \ldots 50.8\}$; $t =$ continuous time; see Methods for definitions of other parameters).

Harvest type	Harvest functions	Management parameter intervals
Scenario 1: conventional commercial harvest	$C(\tau_k) = \begin{cases} F_{spring}B(t), & t = \tau_{k,spring} \\ F_{fall}B(t), & t = \tau_{k,fall} \end{cases}$	$F_{spring} = [0.00, 0.3]$ $F_{fall} = [0.00, 0.3]$
Scenario 2: proportional biomass reduction by 0.75,[a] with supplemental fishing	$C(\tau_k) = \begin{cases} 0, & t \leq 3 \\ 0.75B(t), & B(t) \geq B_{nuisance}, & t > 3, & t = \tau_{k,spring} \\ F_{supplemental}B(t), & B(t) < B_{nuisance}, & t > 3, & t = \tau_{k,spring} \end{cases}$	$B_{nuisance} = [220, 550]$ $F_{supplemental} = [0.00, 0.3]$
Scenario 3: biomass reduction to 100 kg/ha,[b] with supplemental fishing	$C(\tau_k) = \begin{cases} 0, & t \leq 3 \\ B(t) - 100, & B(t) \geq B_{nuisance}, & t > 3, & t = \tau_{k,spring} \\ F_{supplemental}B(t), & B(t) < B_{nuisance}, & t > 3, & t = \tau_{k,spring} \end{cases}$	$B_{nuisance} = [220, 550]$ $F_{supplemental} = [0.00, 0.3]$

[a] Perrow et al. 1995; Hansson et al. 1998.
[b] Bajer et al. 2009.

($F_{supplemental}$) occurring in the years after a biomanipulation event was also evaluated in the two biomanipulation scenarios. See Table 1 for mathematical formalizations of the scenarios used in simulations.

Simulation.—Common carp biomass was forecasted by using the fitted SDBDM to evaluate harvest scenarios. A 50-year time period was used because current lake restoration legislation in Iowa (HF2782, Section 26; 2006) requires restoration efforts to be sustainable over this time period. The evaluated parameters included F_{spring}, F_{fall}, $B_{nuisance}$, and $F_{supplemental}$ for harvest functions of scenarios in Table 1. All F-parameters (i.e., F_{spring}, F_{fall}, and $F_{supplemental}$) from 0.00 to 0.30 (in increments of 0.01) were evaluated. Values of F were limited to 0.30 to reflect the maximum F observed for this common carp population. The $B_{nuisance}$ was evaluated over the interval of 220–550 kg/ha in increments of 10. The lower limit of $B_{nuisance}$ was set as the biomass after a 3-year period, assuming that the initial biomass was 100 kg/ha. Spring harvest pulses occurred at 0.2 of each year (~day 72), and fall pulses occurred at 0.8 of each year (~day 292). All harvest pulses in biomanipulation scenarios occurred at 0.2 of each year, simulating the typical timing of annual harvest pulses observed for Clear Lake. Every parameter combination for each scenario in Table 1 was evaluated to identify a set of parameter combinations that resulted in a mean common carp biomass of no more than 100 kg/ha over the simulation period. In total, 961 parameter combinations were evaluated for the conventional commercial fishing scenario, and 1,023 combinations were evaluated for the biomanipulation scenarios.

Effect of unintentional underharvest.—The effect of unintentional underharvest on management strategies was evaluated by simulation. A mean simulation biomass of 100 kg/ha or less was achieved by 602, 192, and 187 parameter combinations for the three scenarios evaluated. Therefore, a single set of parameter values was selected for each scenario and was used to evaluate the effect of unintentional underharvest on biomass dynamics. Conventional commercial fishing was evaluated by using an F_{spring} of 0.22 and an F_{fall} of 0.03, thereby replicating recent patterns in Clear Lake harvest wherein 86% and 14% of F_{annual} occurred in the spring and fall, respectively (Colvin et al. 2012). Mean F_{spring} was 0.245 for 2007–2010, and $B_{nuisance}$ was evaluated by using values of 335.2 kg/ha for scenario 2 (75% reduction in biomass) and 335.5 kg/ha for scenario 3 (biomass reduction to 100 kg/ha). Values of $B_{nuisance}$ corresponded to the highest level of $B_{nuisance}$ and an F_{spring} of 0.245 from the solution parameter set for the biomanipulation scenarios. Selecting a high level of $B_{nuisance}$ minimized the number of large-scale removals over time.

Underharvest was simulated by randomly reducing fishing mortality in all three scenarios. Underharvest F-values were calculated as $F_{under} = F_i \cdot (1 - \varepsilon)$, where F_i is the scenario-specific fishing mortality (i.e., F_{spring}, F_{fall}, $F_{biomanipulation}$, or $F_{supplemental}$) and ε is a random, uniformly distributed value between 0 and η (η = the upper bound of underharvest). The $F_{biomanipulation}$ was

0.75 for scenario 2 and was calculated as $[B \cdot (\tau_k) - 100]/B(t)$ for scenario 3. Stochastic simulation was used to evaluate forecasted biomass dynamics for 100 replicates of η equal to 0.1, 0.2, and 0.3. Values of η were selected to represent a reasonable range of underharvest (i.e., 10–30%). Effects of η on biomass dynamics were graphically assessed. For biomanipulation scenarios, the number of biomanipulation pulses was summarized for each level of η to assess the effect of η on the frequency of pulses.

Calculation and Evaluation of the Ecotrophic Coefficient

Annual population summary.—Annual values for the common carp population were summarized to calculate EC. Annual fishery harvest (C) was calculated as the annual sum of harvested common carp biomass. Maximum individual weight (w_{max}) in kilograms was identified as the maximum weight of individuals captured during spring marking, fall trawling, or fall recapture efforts for each year. Mean annual biomass ($\bar{B}$) in kilograms per hectare was calculated as the annual mean of model-estimated biomass from the fitted SDBDM. Annual production (P; $kg \cdot ha^{-1} \cdot year^{-1}$) was estimated as $\log_{10}(P) = 0.32 + 0.94 \cdot \log_{10}(\bar{B}) - 0.17 \cdot \log_{10}(w_{max})$, where $\bar{B}$ is the mean standing biomass (kg/ha) and w_{max} is the maximum individual weight observed (Downing and Plante 1993). The F_{annual} was calculated for each time step as the within-year sum of $C(t)/\bar{B}(t)$, where $C(t)$ is harvest at time t and $\bar{B}(t)$ is model-estimated biomass at time t. Year-specific production-to-biomass ratios were calculated as $P/\bar{B}$; the EC was calculated as C/P (Ricker 1946).

Evaluating the ecotrophic coefficient.—The EC was evaluated as a potential tool for setting harvest targets in situations where data are sparse by simulating biomass dynamics using the fitted SDBDM over a 10-year period. The mean among-year $P/\bar{B}$ was used to calculate production and harvest levels for EC values varying from 0.0 to 1.3 in increments of 0.01. The evaluated values of EC reflect the observed EC values for the common carp population in Clear Lake. Harvest amounts were calculated as $C(\tau_k) = EC \cdot (P/\bar{B}) \cdot B(\tau_k)$, where $C(\tau_k)$ is the amount of harvest that is instantaneously removed at pulse time τ_k, $P/\bar{B}$ is the mean among-year production-to-biomass ratio, and $B(\tau_k)$ is the biomass at time t. Pulsed-harvest events occurred every year at 0.2 of the year. Instantaneous rate of change (γ) for annual mean biomass ($\bar{B}$) was calculated as $\gamma = \log_e(\bar{B}_{Y+1}/\bar{B}_Y)$ for years 9 and 10 of the simulation to identify EC values that resulted in decreasing ($\gamma < 1$) biomass over time.

RESULTS

Biomass and Catch per Unit Effort

Common carp abundance and mean weight were variable over the study period. Mean weight of common carp captured during spring marking efforts varied from 3.8 to 5.7 kg (Table 2). A mark–recapture model that allowed for heterogeneous capture efficiency (multinomial model M_t) best approximated the data for all study years ($w_{model} > 0.9$; Table 3). Annual abundance

TABLE 2. Summary of common carp mark–recapture efforts, mean weight at capture, mean CPUE, and estimated biomass in Clear Lake, Iowa. Numbers in parentheses are estimated SDs.

Year	Marked fish	Captured fish	Recaptured fish	Mean weight (kg)	Mean CPUE (kg/trawl)	Biomass estimate (kg/ha)
2007	3,515	1,387	136	3.8 (1.20)	7.82 (0.0966)	92.6 (8.50)
2008	2,959	1,702	89	5.2 (1.88)	7.74 (0.0976)	211.9 (28.86)
2009	3,367	819	76	5.7 (1.82)	7.57 (0.0999)	126.9 (15.06)
2010	2,840	2,450	172	5.5 (1.59)	9.98 (0.0757)	159.5 (10.13)

estimates from model M_t varied from 35,738 individuals (95% CI = 29,756–41,694) in 2007 to 62,003 individuals (95% CI = 54,133–69,872) in 2010. Common carp biomass estimates varied from 93 kg/ha (95% CI = 86–99) in 2007 to 233 kg/ha (95% CI = 203–263) in 2010 (Table 2). Annual biomass estimates were variable over the study period (Figure 2). Mean CPUE varied from 7.57 kg/trawl (95% CI = 4.9–12.6) to 9.98 kg/trawl (95% CI = 6.6–15.8; Table 2) over the same period (Figure 2).

Commercial Harvest

Commercial fishery harvest was variable over the study period, with the largest within-year harvests occurring in the spring. Annual harvest generally decreased over time, from 56.06 kg/ha in 2007 to 8.82 kg/ha in 2010 (Table 4; Figure 2). Spring harvest was typically higher than fall harvest (mean spring harvest = 30 kg/ha; mean fall harvest = 5.7 kg/ha; Figure 2). Spring harvest varied from 0.39 to 51.5 kg/ha, and fall harvest varied from 2.58 to 8.45 kg/ha.

Semidiscrete Biomass Dynamics Model

Visual inspection of model predictions indicated that the SDBDM fit the biomass and $\bar{I}$ data well (Figure 3). Estimated intrinsic growth rate (r) was 0.27 (95% CI = 0.18–0.36), and
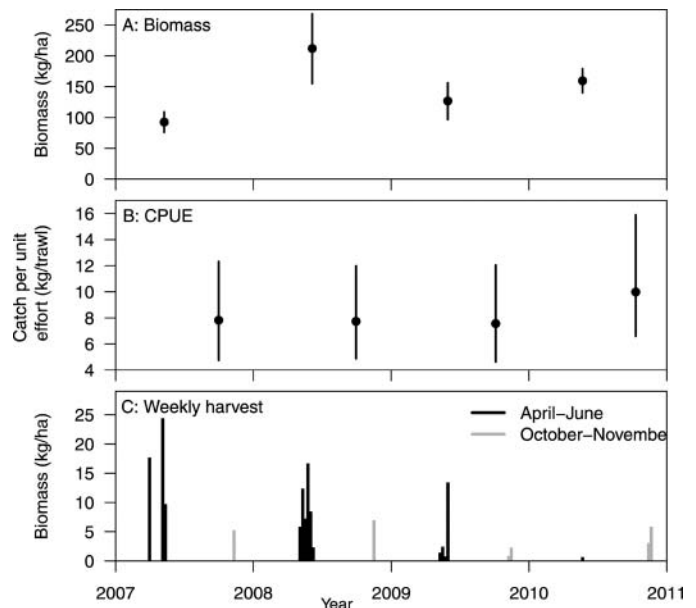

FIGURE 2. Common carp (A) biomass, (B) CPUE, and (C) commercial harvest over a 4-year period in Clear Lake, Iowa. Vertical lines in panels A and B represent 95% CIs.

TABLE 3. Selection of mark–recapture models (assuming a closed population) fitted by maximum likelihood. Based on Akaike's information criterion (AIC), there was substantial support for a model that allowed for heterogeneous capture probabilities (multinomial model M_t), with a relative model weight (w_{model}) greater than 0.9 (SE = estimated SE; ΔAIC = AIC difference; l[model] = model-specific likelihood, calculated as $e^{-0.5[\Delta AIC]}$).

Year	Model	$\hat{N}$	SE	AIC	ΔAIC	l(model)	w_{model}
2007	M_t	35,725	3,045	−64,553	0.00	1	1
	Bailey's binomial	35,848	2,919	−31,111	3,341.93	0	0
	Hypergeometric	35,848	2,499	3,107	67,660.26	0	0
2008	M_t	59,330	4,723	−61,178	0.00	1	1
	Bailey's binomial	56,587	5,816	−18,135	43,043.16	0	0
	Hypergeometric	56,587	4,144	2,121	63,298.37	0	0
2009	M_t	32,615	3,432	−54,566	0.00	1	1
	Bailey's binomial	32,917	3,618	−38,617	15,949	0	0
	Hypergeometric	32,917	2,931	1,725	56,292	0	0
2010	M_t	62,003	4,015	−76,957	0.00	1	1
	Bailey's binomial	61,948	5,251	−7,240	69,717	0	0
	Hypergeometric	61,948	5,862	3,167	80,124	0	0

TABLE 4. Estimates of annual commercial fishery harvest (C), maximum individual weight (w_{max}), mean annual standing biomass ($\bar{B}$), fishing mortality (F), production (P), production-to-biomass ratio ($P/\bar{B}$), and ecotrophic coefficient (EC) for common carp in Clear Lake. The $\bar{B}$ was calculated as the annual mean of model-estimated biomass.

Year	C (kg/ha)	w_{max} (kg)	$\bar{B}$ (kg/ha)	F	P (kg·ha^{-1}·year^{-1})	$P/\bar{B}$	EC
2007	56.06	10.0	152.3	0.368	42.8	0.323	1.14
2008	58.05	12.8	138.7	0.419	38.1	0.311	1.34
2009	19.54	12.8	138.9	0.141	39.4	0.311	0.45
2010	8.82	16.0	169.3	0.052	48.6	0.296	0.18
Mean	35.62	12.9	149.8	0.245	42.2	0.311	0.78

estimated q was 0.06 (95% CI = 0.041–0.070). The B_0 was estimated at 142 kg/ha (95% CI = 102–182). Time required to double biomass was 2.7 years. Simulated termination of commercial harvest resulted in common carp biomass exceeding the previous maximum biomass estimate (i.e., 540 kg/ha) by the year 2014.

Evaluation of Management Scenarios

Conventional commercial fishing (scenario 1).—Mean simulated biomass varied with F_{spring} and F_{fall} for the scenario evaluating the use of conventional spring and fall commercial harvests. A narrow range of annual commercial fishing mortality ($F_{annual} = F_{spring} + F_{fall}$) varying from 0.244 to 0.265 was needed to achieve biomass objectives. Increased F_{annual} was required to achieve biomass objectives when F_{spring} and F_{fall} were similar in magnitude (e.g., $F_{spring} = 0.12$ and $F_{fall} = 0.14$). Lower F_{annual} was required to achieve biomass objectives when

F_{spring} was substantially higher than F_{fall} or vice versa (e.g., $F_{spring} = 0.24$ and $F_{fall} = 0$; or $F_{spring} = 0$ and $F_{fall} = 0.25$; Figure 4). Based on adequate harvest (i.e., no underharvest), spring and fall harvest targets over 10 years decreased from 33 to 32 kg/ha and from 4.1 to 3.9 kg/ha, respectively, to achieve biomass objectives (Table 5). Over the first 10 years of the simulation, spring and fall harvest targets totaled 314 and 39 kg/ha, respectively, to achieve biomass objectives (Table 5). Common carp biomass increased quickly for all levels of η, indicating that underharvest in either spring or fall can have a strong effect on common carp biomass dynamics (Figure 5).

Biomanipulation reducing biomass by 75% with supplemental fishing (scenario 2).—Mean simulated biomass varied for the scenario evaluating a biomass reduction of 75% once $B_{nuisance}$ was reached, with the addition of $F_{supplemental}$ in subsequent years. Biomass objectives could not be achieved unless $F_{supplemental}$ values exceeded 0.227. As $B_{nuisance}$ increased, increasing values of $F_{supplemental}$ were needed to reach biomass objectives (Figure 4). Harvest targets based on the
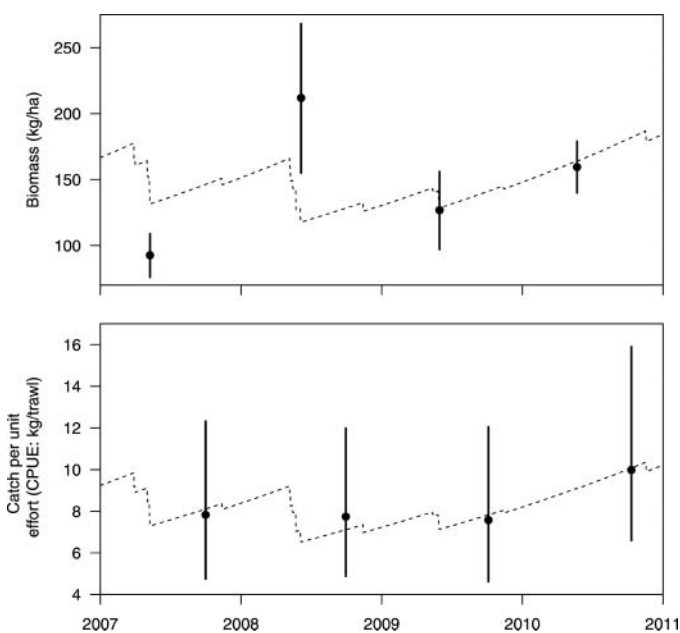

FIGURE 3. Observed (circles; ±95% CI) and predicted (dotted line) levels of common carp biomass (top panel) and trawling CPUE (bottom panel) over a 4-year period in Clear Lake, Iowa. Predicted biomass and CPUE are from the fitted semidiscrete biomass dynamics model.

TABLE 5. Common carp harvest targets (kg/ha) required to achieve biomass objectives for the three harvest scenarios evaluated. Harvest amounts calculated by using the parameter combinations for scenarios 1–3 are indicated by black circles in Figure 4.

Year	Scenario 1[a] Spring	Scenario 1[a] Fall	Scenario 2[b] Spring	Scenario 3[c] Spring
2011	33.0	4.1	0	0
2012	32.6	4.1	0	0
2013	32.3	4.0	0	0
2014	31.9	4.0	0	0
2015	31.6	3.9	328.5	338.0
2016	31.2	3.9	35.1	32.0
2017	30.9	3.9	34.6	31.6
2018	30.6	3.8	34.2	31.2
2019	30.2	3.8	33.7	30.8
2020	29.9	3.7	33.3	30.4
Total	314.2	39.2	499.4	494

[a]Conventional commercial fishing.
[b]Biomanipulation reducing biomass by 75%, with supplemental fishing.
[c]Biomanipulation reducing biomass to 100 kg/ha, with supplemental fishing.
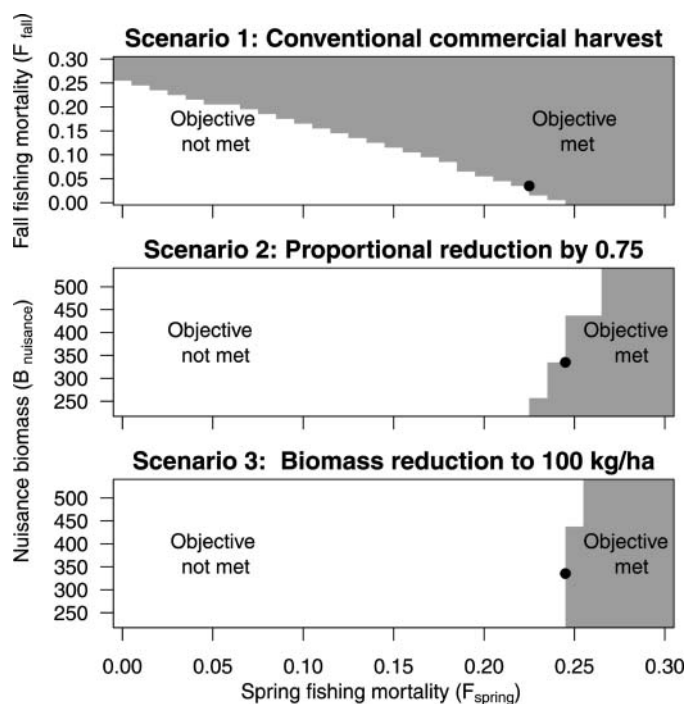
FIGURE 4. Plot of parameter combinations that were evaluated for three common carp management scenarios. Every combination of *x*- and *y*-axis parameters was used to calculate the mean 50-year simulation biomass. The gray area highlights parameter combinations for which the mean simulation biomass was 100 kg/ha or less. The black dot in each panel denotes the parameter value combination that was used to evaluate the potential consequences of unintentional underharvest in each scenario.

fitted SDBDM evaluated at a $B_{nuisance}$ of 335.5 kg/ha and an $F_{supplemental}$ of 0.245 required no harvest in the first 4 years and an initial biomass reduction of 328.5 kg/ha (in the fifth year) when $B_{nuisance}$ was exceeded, followed by supplemental harvest of 35.1 kg/ha in the sixth year (Table 5). In total, a harvest of 499.4 kg/ha was required over the initial 10-year period to achieve biomass objectives. Scenario 2 was relatively insensitive to the level of η, with slight biomass increases for all η values (Figure 5). Mean number of biomanipulation pulses increased with increasing η, varying from 1.0 pulse for an η value of 0.1 to 2.72 pulses for an η value of 0.3 (Table 6).

Biomanipulation reducing biomass to 100 kg/ha with supplemental fishing (scenario 3).—Mean simulated biomass varied for the scenario evaluating a reduction in biomass to 100 kg/ha once $B_{nuisance}$ was reached, with the addition of $F_{supplemental}$ in subsequent years. Biomass objectives could not be achieved unless $F_{supplemental}$ exceeded 0.241. With increasing values of $B_{nuisance}$, increases in $F_{supplemental}$ were required to achieve biomass objectives (Figure 4). Harvest targets based on the fitted SDBDM evaluated at a $B_{nuisance}$ of 335 kg/ha and an $F_{supplemental}$ of 0.25 required no harvest in the first 4 years and an initial biomass reduction of 338 kg/ha in the fifth year, followed by supplemental harvest of 32 kg/ha in the sixth year (Table 5). In total, a harvest of 494 kg/ha was required over the initial 10-year

TABLE 6. Summary of common carp biomanipulation events (mean, median, range, and SD of the number of biomanipulation pulses) for 100 replicate stochastic simulations of the two biomanipulation scenarios (scenario 2: biomanipulation reducing biomass by 75%; scenario 3: biomanipulation reducing biomass to 100 kg/ha; η = the upper bound of underharvest). The simulated biomanipulations also included supplemental fishing. Harvest amounts calculated using the parameter combinations for scenarios 2 and 3 are indicated by black circles in Figure 4.

η	Mean	Median	Range	SD
		Scenario 2		
0.1	1.00	1	(1, 1)	0.00
0.2	1.86	2	(1, 2)	0.35
0.3	2.72	3	(2, 4)	0.55
		Scenario 3		
0.1	1.00	1	(1, 1)	0.00
0.2	1.68	2	(1, 2)	0.46
0.3	2.84	3	(2, 4)	0.52

period to achieve biomass objectives. Scenario 3 was relatively insensitive to the level of η, with slight increases in biomass for all η values (Figure 5). Mean number of biomanipulation pulses increased from 1.00 pulse at an η of 0.1 to 2.84 pulses at an η of 0.3 (Table 6).

Ecotrophic Coefficient

Maximum individual weights (w_{max}) of common carp varied from 10.0 to 16.0 kg over the study period (Table 4), $\bar{B}$ varied from 138 to 169 kg/ha, and F varied from 0.05 to 0.48. Production estimates varied from 38.1 to 48.6 kg·ha^{-1}·year^{-1}. The $P/\bar{B}$ values were consistent among years, varying from 0.296 to 0.323. The EC generally decreased over the study period, from 1.14 in 2007 to 0.18 in 2010 (maximum EC = 1.34 in 2008; Table 4). Based on model simulations, the harvest of a majority of annual production (EC = 0.76) was required to achieve zero change in population biomass. Simulated harvest at EC values greater than 0.76 resulted in biomass declines.

DISCUSSION

Formal stock assessments of common carp in North America are rare despite the widespread distribution of this species and despite the fact that commercial fisheries are commonly used to control common carp biomass. The present study contributes to the relatively small pool of published common carp stock assessments (Li and Mosman 1977; Linfield 1980; Pinto et al. 2005). Common carp biomass was identified as increasing in our study system, while harvest has been variable; sufficiently high annual commercial fishing mortality (i.e., $F_{annual} > r$) only occurred during 2 years (2007 and 2008) of our 4-year study. Biomass doubling time was estimated to be 2.7 years based on an r of 0.27; this doubling time estimate is less than the current 3-year commercial fishery contracts utilized by the state of
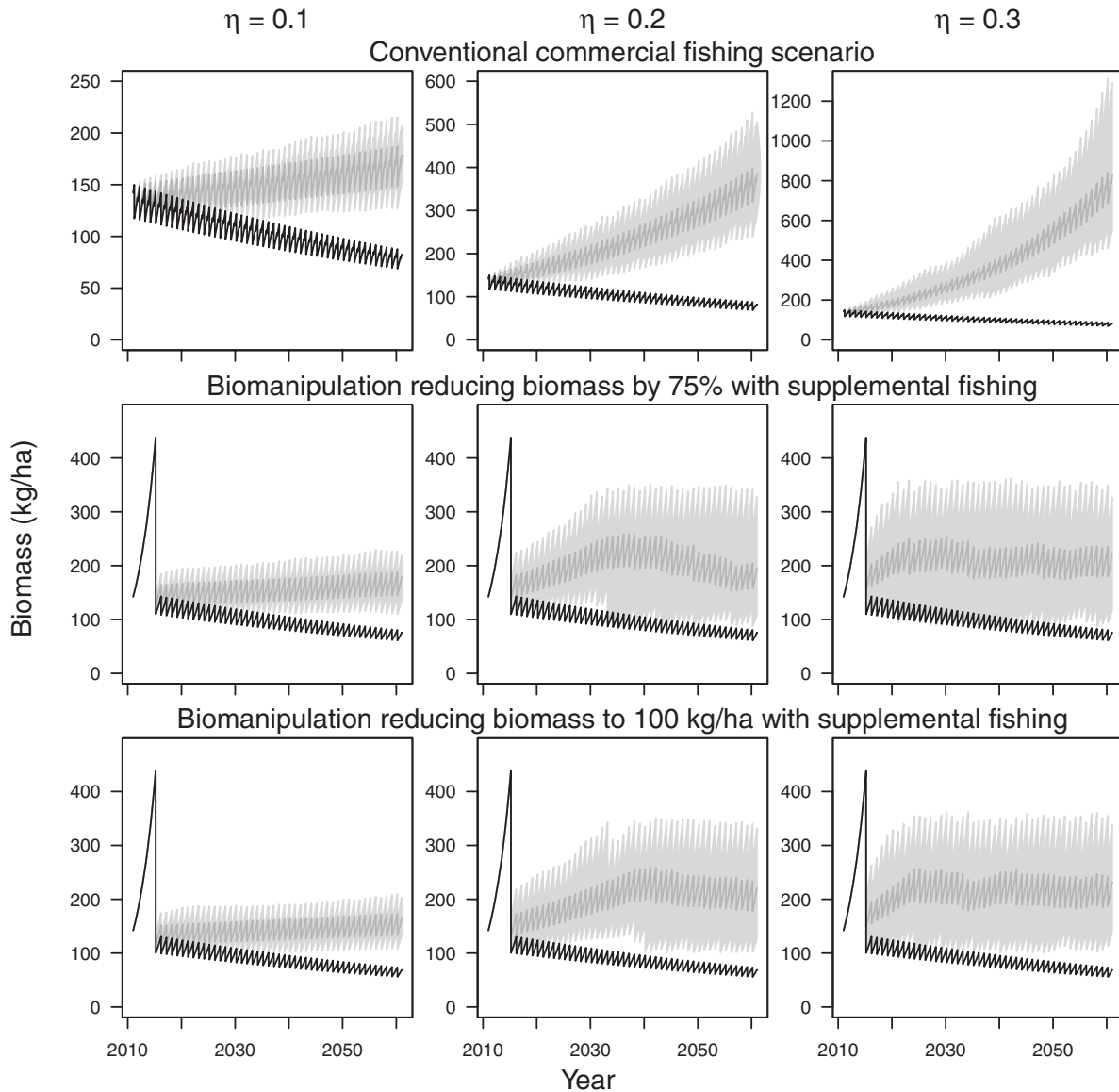
FIGURE 5. Effect of varying levels of underharvest on common carp biomass dynamics (η = the upper bound of underharvest; mild underharvest: $\eta = 0.1$; moderate underharvest: $\eta = 0.2$; severe underharvest: $\eta = 0.3$). Black lines denote the biomass dynamics for baseline harvest (with no underharvest) and are shown for reference. Dark-gray lines denote mean biomass with assumed underharvest, and the gray area denotes the simulation envelopes (i.e., simulation bounds) of 100 replicate stochastic simulations for three common carp management scenarios.

Iowa. Contract commercial fishing can play a key role in controlling common carp, but consecutive years of underharvest may result in a doubling of biomass during the contract period. The contract bidding process can result in different commercial fishers—each with varying efficiencies and system-specific knowledge—working in different time periods. Together, such factors may limit the efficacy of commercial fishing in controlling common carp biomass over time. The possibility that harvest amounts could vary over time, the apparent sensitivity of common carp biomass dynamics to unintentional underharvest, and the relatively short doubling time we documented in

Clear Lake may go a long way toward explaining why commercial fisheries in inland waters have rarely succeeded in the long-term control of common carp biomass (Wydoski and Wiley 1999).

Analysis Assumptions

Recruitment and migration.—Our mark–recapture analysis assumed that the population was closed to recruitment and migration. Recruitment is believed to be negligible in Clear Lake given the lack of small common carp (<270 mm) captured in yearly fall index seining (S. E. Grummer, unpublished

data). However, migration of juvenile common carp from Ventura Marsh through the exclusion barrier is believed to be a recruitment source for Clear Lake, which potentially violates the assumption of population closure. However, juvenile immigrants are typically too small to be captured by commercial fishery gear during the year in which they enter the lake; thus, immigrating juveniles had no effect on our abundance estimates. If juvenile common carp immigrants are captured in commercial fishing gear, then abundance will be overestimated, positively biasing biomass estimates. Systematic overestimation of biomass should result in an overestimate of B_0, which in turn would positively bias harvest targets.

Mortality.—Mortality (i.e., due to predation, senescence, and other sources) over the mark–recapture period can negatively bias abundance estimates by decreasing the number of fish that are captured during recapture efforts. Common carp can be larger than 300 mm by age 2 (Larscheid 2005; Colvin et al. 2010), rapidly exceeding the gape sizes of the majority of piscivorous predators in Clear Lake (Sammons et al. 1994). Common carp can be found in littoral areas of the lake during the summer (Penne and Pierce 2008) and may be susceptible to avian predation. Large avian predators that are capable of preying on common carp (e.g., bald eagles *Haliaeetus leucocephalus* and American white pelicans *Pelecanus erythrorhynchos*) are present and may pose a predation risk (Knopf and Kennedy 1981; Findholt and Anderson 1995). However, American white pelicans generally occupy the adjacent Ventura Marsh (M. E. Colvin, personal observation), and predation by piscivorous birds is probably limited due to the large size of common carp (mean length $\sim$ 603 mm) and the low water transparency. Common carp can tolerate low dissolved oxygen levels and are resistant to summerkills and winterkills (Edwards and Twomey 1982; Panek 1987). Early studies of common carp dynamics found that mean monthly mortality rates were 0.06% (over 4 months) and 0.045% (over 19 months), with mortality rates being lower in summer than in winter (Neess et al. 1957). Common carp mortality over the mark–recapture mixing period should be minimal or nonexistent; however, if mortality did occur, then abundance would be underestimated.

Biomass dynamics.—Biomass dynamics models require several assumptions to approximate true biomass dynamics. Water temperature is a major factor affecting production (Jobling 1994). The assumption that r is constant over time (i.e., that biomass production does not vary with seasonal changes in temperature) may bias parameters estimated for BDMs since it does not incorporate variation in biomass production due to thermal variability. Maximum water temperature in Clear Lake during the summer is approximately 30°C (M. E. Colvin, unpublished data), which is also the thermal optimum for growth of common carp (Goolish and Adelman 1984). However, water temperature is below 30°C for the majority of the year, and ice covers the lake during December through late March or early April (Jacobsen 1968; Penne and Pierce 2008). Incorporating temperature would likely result in increased biomass

production (i.e., higher r) when water temperatures are warmest. The fitted SDBDM applies a constant r over an annual period, which ignores temperature-related variation in biomass production; however, based on the data fit, we believe our analysis provides predictions and fit that are adequate for setting harvest targets.

Immigration was not explicitly accounted for in the SDBDM, and this can potentially affect harvest targets. In particular, harvest would have to be higher if significant levels of biomass are immigrating to Clear Lake from Ventura Marsh. However, the area of Ventura Marsh equals only a fraction of the area of Clear Lake ($\sim$5%); therefore, a very large and biologically unrealistic flux of biomass from the marsh to the lake would be required for an order-of-magnitude change in results. Although the marsh is not amenable to sampling, the barrier generally precludes large common carp from contributing to the standing biomass of Clear Lake. However, juvenile immigrants may preclude the complete eradication of common carp in Clear Lake. It should be recognized, though, that the objective of this analysis was to provide harvest targets and guidance to reach a biomass level that may minimize common carp impacts.

Fitting of the model required the assumptions that (1) CPUE is proportional to biomass (i.e., constant q) and (2) production is density independent. Assuming that CPUE is proportional to B is a common assumption in analyses of inland fish species and provides the basis for several published studies that relate common carp to water quality (e.g., Egertson and Downing 2004; Jackson et al. 2010; Weber et al. 2010). Whether common carp q exhibits hyperstability (i.e., high catches at low abundance) or hyperdepletion (i.e., low catches at high abundance) behavior is unknown and should be further examined (Harley et al. 2001). The SDBDM assumes that production is density independent, which overestimates production at high levels of biomass. Ideally, production should be limited at high biomass, as is the case for models that include a carrying capacity term (e.g., logistic; Schaefer 1954). However, given our limited data and low biomass levels relative to a previous maximum biomass estimate (540 kg/ha; Larscheid 2005), we believe that it is reasonable to fit an exponential BDM to these data. As more data are accumulated, more complex models (e.g., Schaefer or Fox) can be fitted to evaluate density-dependent production constraints under an assumption of constant q, potential immigration, and overall model structural uncertainty in a multimodel framework (Burnham and Anderson 2002).

Assimilation of data from multiple sources is often necessary to make informed management decisions. The inclusion of CPUE as a biomass index, with q estimated simultaneously with the exponential SDBDM parameters, provides a tool for managers to make informed decisions in the absence of annual biomass estimates. Mark–recapture abundance estimates are invaluable for estimating biomass and fitting models, but mark–recapture studies are not always accepted by the public. The public's perception that returning large numbers of live common carp back into the ecosystem will cause further environmental

degradation can potentially create a public relations backlash. Biomass dynamics models that utilize CPUE provide a tool for using CPUE data in a way that may minimize the need for annual mark–recapture population estimates. Essentially, CPUE data can be used to supplement BDMs with biomass indexes during years when mark–recapture studies are not conducted.

Management Scenarios

Model simulations indicated that biomanipulations (scenarios 2 and 3) never achieve biomass objectives unless supplemental fishing mortality is imposed. The majority of biomanipulation projects in which common carp biomass has been reduced by 75% or more have been unsuccessful in the long term (Meijer et al. 1998), consistent with our simulation results. For biomanipulation to be successful without supplemental fishing mortality, a reduction in r is required. However, the biological processes (e.g., predation) that are necessary to reduce r may be delayed until the fish assemblage responds to the biomanipulation and subsequent change in water quality. In the period after biomanipulation, common carp production likely remains unchanged, thus allowing this species to potentially dominate the fish assemblage again. Fish assemblage changes after biomanipulation may take several years (Rose and Moen 1953); this may result in delayed predation on common carp by native piscivores, thus requiring supplemental fishing mortality to compensate for the delay. Predation mortality can be a significant mechanism regulating biomass dynamics if increases in piscivorous fishes occur after biomanipulation. In disturbance-limited systems (e.g., winterkills), native centrarchids can prey heavily on common carp eggs, potentially regulating common carp populations (P. Bajer, University of Minnesota, personal communication).

Biomanipulation scenarios were relatively robust to unintentional underharvest. Setting a system-specific $B_{nuisance}$ simulates an active management feedback. To evaluate whether a biomanipulation is required, a manager needs to know the biomass level at which to make a decision. When underharvest occurs, the manager can respond with appropriate biomass reductions. Feedback provided to the manager by evaluating $B_{nuisance}$ is important, as common carp biomass can rapidly increase with only a few years of underharvest (i.e., biomass can double in ~2.7 years). Management in light of probable underharvest is difficult; however, continued monitoring through biomass estimates or calibrated CPUE can provide information on population biomass and whether or not management actions may be required. Additionally, a precautionary approach can be used in which harvest targets are arbitrarily increased to compensate for the possibility of underharvest.

Annual Metrics and Ecotrophic Coefficient

Common carp $P/\bar{B}$ calculated from production estimates and mean biomass was greater than r. The $P/\bar{B}$ is expected to be slightly higher than r when predation and other mortality sources are small components of annual production (i.e., high surplus production). This is supported by our analysis, in which r was

approximately 83% of mean $P/\bar{B}$. Fast-growing common carp escape predation by rapidly exceeding the gape limitations of predators (Sammons et al. 1994; Ward et al. 2008). Additionally, the long life span of common carp in Clear Lake (maximum age = 13 years; Colvin et al. 2010) indicates that other sources of mortality (e.g., senescence) represent a small percentage of production.

The EC provided a simple, production-based method for setting biomass harvest targets based on data that can be collected within a single year. The EC value that was required to cause declines in common carp biomass was higher than the EC of 0.5 that was recommended for application to salmonids in Minnesota (Waters 1992). Due to their long life span, common carp are generally less productive in terms of biomass turnover (i.e., lower P/B) than salmonid stocks (Carlander 1969; Colvin et al. 2010). However, rapid growth and low predation rates result in greater production of common carp relative to salmonids. We expected that EC would be higher than the guidelines presented by Waters (1992) because the majority of annual production in common carp is surplus production. Harvest targets can be based on data from a single year by multiplying the estimated annual production by EC. Monitoring in the next year can determine whether or not the biomass removals were sufficient for decreasing biomass, and EC can then be adjusted accordingly in an adaptive management framework (Walters 1986). The EC levels established in our analysis (EC $\geq$ 0.76) can provide a management tool for determining harvest targets that can be applied to nuisance common carp in data-sparse situations. Additionally, the EC may be used to establish or provide supplemental harvest targets in existing common carp commercial fisheries that lack time series data.

Management Implications

Managers seeking to reduce common carp biomass can choose among several strategies. They can take a "wait and see" approach, collect more data, or embrace uncertainty in an adaptive management framework (Walters 1986; Starfield 1997). Doing nothing would likely lead to a return of common carp biomass to previous nuisance levels (~540 kg/ha) within just a few years. In some studies, delaying conservation or restoration efforts to collect additional data beyond 2 years did not increase the ultimate effectiveness of the restoration efforts (Grantham et al. 2009). Tools like BDMs and the EC can be used to set annual harvest targets that can be revised each year as more data are accumulated in an adaptive management framework (Walters 1986). Singular biomanipulation events are likely to be unsuccessful over the long term unless common carp production is reduced through changes in biological processes (i.e., increased predation) or unless supplemental harvest is utilized to compensate for delays in biological processes after biomanipulation.

Semidiscrete BDMs provide a flexible approach for utilizing a variety of data to establish the harvest targets that are required to control nuisance populations through commercial fishing. Overall, BDMs require simpler data than existing age-structured

approaches (e.g., Brown and Walker 2004; Weber et al. 2011). Although age-structured models (e.g., yield per recruit or dynamic pool) are potentially useful, harvest targets cannot be directly set without knowledge of biomass. Ideally, a combination of biomass and age-structured models would be used to develop harvest targets for nuisance common carp. However, obtaining both catch data and age-structure data is a tall order for most inland fisheries—especially nuisance fisheries. Due to the realities of ever-increasing limitation on personnel and budgets, biomass-based frameworks are likely to be the only realistic approach for identifying commercial harvest targets to control common carp.

ACKNOWLEDGMENTS

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