

Semidiscrete biomass dynamic modeling: an improved approach for assessing fish stock responses to pulsed harvest events

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Abstract: Continuous harvest over an annual period is a common assumption of continuous biomass dynamics models (CBDMs); however, fish are frequently harvested in a discrete manner. We developed semidiscrete biomass dynamics models (SDBDMs) that allow discrete harvest events and evaluated differences between CBDMs and SDBDMs using an equilibrium yield analysis with varying levels of fishing mortality (F). Equilibrium fishery yields for CBDMs and SDBDMs were similar at low fishing mortalities and diverged as F approached and exceeded maximum sustained yield (F_{MSY}). Discrete harvest resulted in lower equilibrium yields at high levels of F relative to continuous harvest. The effect of applying harvest continuously when it was in fact discrete was evaluated by fitting CBDMs and SDBDMs to time series data generated from a hypothetical fish stock undergoing discrete harvest and evaluating parameter estimates bias. Violating the assumption of continuous harvest resulted in biased parameter estimates for CBDM while SDBDM parameter estimates were unbiased. Biased parameter estimates resulted in biased biological reference points derived from CBDMs. Semidiscrete BDMs outperformed continuous BDMs and should be used when harvest is discrete, when the time and magnitude of harvest are known, and when F is greater than F_{MSY} .

Résumé : Si les modèles continus de dynamique de la biomasse (CBDM) partent souvent du principe que la capture est continue au cours d'une période annuelle, les prises de poissons s'effectuent fréquemment de manière discrète. Nous avons mis au point des modèles semidiscrets de dynamique de la biomasse (SDBDM) qui permettent l'intégration d'événements de prise discrets et avons évalué les différences entre les CBDM et les SDBDM à la lumière d'une analyse du rendement équilibré à différents taux de mortalité par pêche (F). À de faibles F , les CBDM et les SDBDM ont donné des rendements équilibrés semblables, l'écart entre ces derniers augmentant à mesure que F s'approche puis dépasse le rendement maximum durable (F_{MSY}). L'intégration de prises discrètes s'est traduite par des rendements équilibrés plus faibles à des F élevés que ceux obtenus pour des prises continues. L'incidence de l'utilisation de prises continues dans des cas où les prises sont en fait discrètes a été évaluée en ajustant les CBDM et les SDBDM aux données de séries chronologiques générées pour un stock hypothétique de poissons faisant l'objet de prises discrètes et en évaluant le biais des estimations de paramètre. L'intégration de prises discrètes a fait en sorte que les CBDM ont donné des estimations de paramètre biaisées alors que les estimations de paramètre découlant de SDBDM n'étaient pas biaisées. Les estimations de paramètre biaisées se sont traduites par des points de référence biologiques biaisés découlant des CBDM. Les SDBDM ont donné de meilleurs résultats que les CBDM et devraient être utilisés dans les cas où la capture est discrète, où le moment et la magnitude des prises sont connus et où F est supérieur à F_{MSY} .

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Introduction

Biomass dynamics models (BDMs) are the simplest stock assessment models used to manage fish stocks when stock data are limited to biomass harvested and biomass estimates or indices. Compared with more complex stock assessment models, biological realism is simplified with BDMs because population structure data (e.g., age, length) are not consid-

ered (National Research Council 1998). Despite simplified biological realism, BDMs are a convenient assessment approach, which in some cases have outperformed more sophisticated age- or stage-structured assessments (Ludwig and Walters 1985, 1989).

Continuous biomass dynamics models (CBDMs) predict biomass at any time and take the form of an ordinary differential equation (ODE): $dB/dt = f(B) - C$, where dB/dt is the

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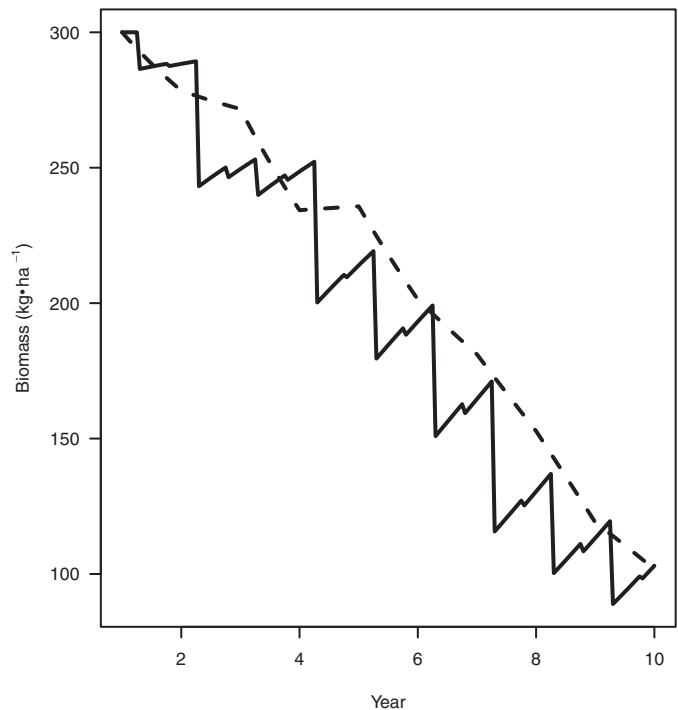
change in biomass (B) over time, $f(B)$ is the biomass production function, and C is the amount of biomass harvested (Polacheck et al. 1993). Biomass production is a function of biomass, representing the net effect of population processes (e.g., somatic growth, recruitment, mortality) on change in biomass over time (Schaefer 1954; Hilborn and Walters 1992; Prager 1994). The exponential model is the simplest CBDM producing a range of biomass dynamics (i.e., increasing, decreasing, no change) using the production function $f(B) = r \cdot B$. The exponential model provides a way to represent biomass dynamics in situations where there are insufficient data to resolve more complex models that require additional parameters (e.g., B_{\max}). However, since the exponential model does not limit biomass production, unrealistically high biomass predictions can result. Therefore, it provides limited utility and predictive ability for fisheries management.

The flexible trajectory of the exponential model provides a foundation for more complex BDMs that include density-dependent constraints to limit production. The Schaefer (Schaefer 1954), Fox (Fox 1970), and Pella–Tomlinson (Pella and Tomlinson 1969) models are common BDMs used to assess fish stocks that include a carrying capacity parameter, but vary in underlying assumptions of how production is related to biomass. In addition to continuously operating population processes, a common assumption of all CBDMs is continuous application of harvest over an annual period, which has been identified as a shortcoming of CBDMs (National Research Council 1998).

Accurate assessment of parameters representing stock biomass dynamics is important for managing fisheries. Parameter estimates from CBDMs are used to calculate biological reference points (i.e., MSY , B_{MSY} , F_{MSY} , $F_{0.1}$) used to manage fish stocks, where maximum sustainable yield (MSY) is a function of stock productivity, F_{MSY} is the fishing mortality (F) that maximizes sustained yield, and B_{MSY} is the resulting standing biomass of a stock being harvested at MSY (Cadima 2003). To prevent overfishing, harvesting at MSY has been reduced by finding the fishing mortality that is 10% of the slope of the production curve at the origin ($F_{0.1}$) and using that value to set harvest limits. Violating model assumptions can bias parameter estimates, resulting in biased biological reference points, which may have consequences for fish stock management. For example, Polacheck et al. (1993) found that incorrectly assuming a population was in equilibrium prior to fishing resulted in overestimating potential yield and optimum effort. The effect of assuming continuous harvest of fish stocks actually undergoing discrete harvest on parameter estimates and biological reference points is uncertain and worthy of examination.

Inland freshwater commercial fisheries intended to reduce overabundant (hereafter referred to as nuisance) fish species represent an extreme discrete application of harvest within an annual period. Commercial fisheries are commonly used to minimize the effects of common carp (*Cyprinus carpio*) on water quality in aquatic systems (Cahoon 1953; Arlinghaus and Mehner 2003; Chumchal et al. 2005). Commercial fisheries for common carp are unique because they can occur over a range of aquatic system areas (100 ha to more than 10 000 ha) with short duration (<5 days) harvests, often during spring and fall to minimize thermal-related mortality of

Fig. 1. Hypothetical fish stock biomass dynamics illustrating continuous (dotted line) and discrete (solid line) commercial harvest. Model parameters and annual harvest are the same for both models, but harvested biomass is removed continuously in the continuous model and discretely in the semidiscrete model.



sport fish bycatch (Rose and Moen 1953). Infrequent but intense harvest events of common carp contrast sharply with the continuous assumptions of CBDMs. Biomass dynamics characterized by large instantaneous decreases rather than smooth gradual changes over time are an ideal situation to evaluate the assumption of continuous harvest (Fig. 1).

Discrete fishery harvest is not limited to nuisance fishes. There are several conditions where fish are harvested over a very short period of time within a year and therefore should be treated as a pulsed harvest. Many species are harvested during migration periods. For example, white sucker (*Catostomus commersonii*) commercial fisheries in Maine typically occur in the spring where traps intercept sexually mature fish for use as lobster bait (M. Colvin, personal observation). Additionally, anadromous fishes are harvested over a short season (i.e., 1–2 weeks) in coastal river systems when excesses allow. Flesh and caviar fisheries can occur over a relative short period of time when mature females are abundant. For example, a paddlefish (*Polyodon spathula*) snagging fisheries on the Missouri River occur over a 2-week span while fish are sexually mature and vulnerable to exploitation (Jennings and Zigler 2000; Mestl and Sorensen 2009). Additionally, some fish stocks can experience a combination of discrete and continuous fishing mortality. For example, tribal walleye (*Sander vitreus*) harvest by spearing occurs within a few weeks in the spring, while traditional recreational angling occurs over the annual period in the ceded territories of Wisconsin (Hansen et al. 2010). Additionally, Da-Rocha et al. (2012) found that optimal fishing strategies for European

Table 1. Continuous and semidiscrete biomass dynamics models used in this paper.

Model	Continuous	Semidiscrete
Exponential	$\frac{dB(t)}{dt} = rnB(t) - CC(t)$	$\left. \begin{aligned} \frac{dB(t)}{dt} &= rnB(t), & t \neq \tau_k \\ B(\tau_k^+) &= B(\tau_k) - DC(\tau_k), & t = \tau_k \end{aligned} \right\}$
Schaefer	$\frac{dB(t)}{dt} = rnB(t)n \left[\frac{B_{\max} - B(t)}{B_{\max}} \right] - CC(t)$	$\left. \begin{aligned} \frac{dB(t)}{dt} &= rnB(t)n \left[\frac{B_{\max} - B(t)}{B_{\max}} \right], & t \neq \tau_k \\ B(\tau_k^+) &= B(\tau_k) - DC(\tau_k), & t = \tau_k \end{aligned} \right\}$
Fox	$\frac{dB(t)}{dt} = rnB(t)n \left[1 - \log_e \frac{B(t)}{B_{\max}} \right] - CC(t)$	$\left. \begin{aligned} \frac{dB(t)}{dt} &= rnB(t)n \left[1 - \log_e \frac{B(t)}{B_{\max}} \right], & t \neq \tau_k \\ B(\tau_k^+) &= B(\tau_k) - DC(\tau_k), & t = \tau_k \end{aligned} \right\}$
Pella–Tomlinson ^a	$\frac{dB(t)}{dt} = \frac{r}{p}nB(t)n \left[1 - \frac{B(t)}{B_{\max}} \right]^{p-1} - CC(t)$	$\left. \begin{aligned} \frac{dB(t)}{dt} &= \frac{r}{p}nB(t)n \left[1 - \frac{B(t)}{B_{\max}} \right]^{p-1}, & t \neq \tau_k \\ B(\tau_k^+) &= B(\tau_k) - DC(\tau_k), & t = \tau_k \end{aligned} \right\}$
Schaefer _{CPUE}	$\frac{dB(t)}{dt} = rnB(t)n \left[\frac{B_{\max} - B(t)}{B_{\max}} \right] - CC(t)$	$\left. \begin{aligned} \frac{dB(t)}{dt} &= rnB(t)n \left[\frac{B_{\max} - B(t)}{B_{\max}} \right], & t \neq \tau_k \\ B(\tau_k^+) &= B(\tau_k) - DC(\tau_k), & t = \tau_k \end{aligned} \right\}$
	$I(t) = q \cdot B(t)$	$I(t) = q \cdot B(t)$

^aThe term r/p is eliminated when $p = 0$.

hake (*Merluccius merluccius*) were dependent on whether fishing occurred continuously or in periodic pulses.

Difference models can be used to represent discrete biomass dynamics phenomena (Hilborn and Walters 1992), but small time steps (e.g., daily, weekly) are needed to realistically model infrequent, intense bouts of harvest associated with nuisance species. Altering model time step to days or weeks results in parameters that may be difficult to interpret and apply, as the majority of inland fisheries statistics are primarily available as annual values (Allen and Hightower 2010). Even with sufficiently short discrete time steps, the net effects of processes such as predation, growth, recruitment, and senescence on production may be more realistically modeled continuously rather than discretely. Neither continuous nor discrete (i.e., difference) BDMs adequately accommodate discrete harvest in a way that would result in useful biological reference points. A framework allowing for a combination of continuous and discrete biomass dynamics would increase biological realism by representing discrete harvest within continuous population processes governing biomass production.

Semidiscrete models are a hybrid class of models that can be used to simultaneously represent continuous processes and discrete events (Mailleret and Lemesle 2009). However, semidiscrete models have rarely been used in biological modeling or applied management settings because solving these models requires complex algebra and calculus to integrate equations over time and derive analytical solutions, if they exist at all (Mailleret and Lemesle 2009). Advanced computer-based numerical integration has facilitated continuous ODE solutions to accommodate discrete events (e.g., harvest) and semidiscrete modeling approaches (e.g., R package deSolve Soetaert et al. 2010).

We developed semidiscrete biomass dynamics models (SDBDMs) to evaluate the consequences of assuming continuous harvest when harvest was occurring discretely by fitting

CBDMs and SDBDMs to a simulated common carp stock. We simulated fishery yield for 9999 years for CBDMs and SDBDMs to compare yield in year 10 000 (i.e., approximate equilibrium, year to year equilibrium) and biological reference points at varying levels of F . Consequences of estimated parameter bias on biological reference points were evaluated by comparing biological reference points calculated from parameter estimates for CBDMs with numerically derived reference points from the equilibrium analysis. Specific objectives of this study were to (i) develop semidiscrete BDMs (i.e., exponential, Schaefer, Fox, Pella–Tomlinson, Schaefer model with an index of biomass and catch per unit effort), (ii) evaluate differences in equilibrium yield and biological reference points between continuous and semidiscrete Schaefer, Fox, and Pella–Tomlinson BDMs, (iii) evaluate how assuming continuous harvest when it was actually discrete biases parameter estimates of BDMs, and (iv) evaluate consequences of incorrectly assuming continuous harvest on biological reference points (i.e., MSY , F_{MSY} , B_{MSY}) when harvest is in fact discrete.

Materials and methods

BDMs

Five CBDMs were extended to accommodate discrete commercial fishery harvest (Table 1). The simplest was an exponential model that is used in cases of introduced species or where sufficiently long time series of biomass observations are not available to fit more complex models. Schaefer, Fox, and Pella–Tomlinson models, used in systems where a carrying capacity parameter (B_{\max}) limits production, were also used. A Schaefer model including an additional index of biomass, catch per unit effort (CPUE), was also developed (hereafter Schaefer_{CPUE}). Continuous models are presented as ODEs of the general form $dB(t)/dt = f[B(t)] - F \cdot B(t)$, where $dB(t)/dt$ is the change in biomass ($\text{kg} \cdot \text{ha}^{-1}$) over the time step

Table 2. List of symbols, descriptions, and units.

Symbol	Description
τ_k^+	Time when instantaneous harvest occurs (year)
t	Continuous time (year)
τ_k	Discrete time (year)
i	Index of biomass observations
j	Index of CPUE observations
k	Index of events
l	Index of model parameters
$B(t)$	Biomass at time t (kg·ha ⁻¹)
$I(t)$	Observed CPUE at time t (kg·effort ⁻¹)
$\hat{I}(t)$	Predicted CPUE at time (kg·effort ⁻¹)
$y(t)$	Observed biomass at time t (kg·ha ⁻¹)
$\hat{y}(t)$	Predicted biomass at time t (kg·ha ⁻¹)
$CC(t)$	Continuous catch at time t (kg·ha ⁻¹ ·year ⁻¹)
$DC(\tau_k)$	Discrete catch at harvest event τ_k (kg·ha ⁻¹)
r	Intrinsic growth rate (kg·ha ⁻¹ ·year ⁻¹)
B_{\max}	Maximum biomass (kg·ha ⁻¹)
q	Catchability (kg·ha ⁻¹ ·effort ⁻¹)
p	Asymmetry parameter (dimensionless)
F	Fishing mortality (year ⁻¹)

dt , $f[B(t)]$ is the function relating production to biomass at time t less the instantaneous rate of fishing mortality (F ; year⁻¹) times biomass at time t ($B(t)$; kg·ha⁻¹) (Table 1). However, SDBDMs are presented as the base ODE in the form $dB(t)/dt = f[B(t)]$ and an additional equation accounting for losses due to pulsed harvest occurring at discrete times. Semidiscrete model notation used in this paper is based on Mailleret and Lemesle (2009) and Zhang et al. (2006). (CBDMs and SDBDMs used in these analyses are detailed in Table 1, and an explanation of symbols is in Table 2.)

Solving BDMs

Numerical integration was required to solve CBDMs and SDBDMs for given values of rates (r), parameters (B_{\max} , p), scalars (q), and initial biomass (B_0). Among numerical integrators (e.g., Euler, Runge–Kutta), the Livermore integration routine is the most accurate (Stevens 2009) and was used to solve BDMs in this study. Numerical integration was performed using the deSolve package (Soetaert and Herman 2009; Soetaert et al. 2010) for the R program (R Development Core Team 2010). Values of initial biomass (B_0), rates (r), scalars (q), and parameters (B_{\max} , p) are required to solve the ODEs by numerical integration, and values used in all subsequent analyses will be presented in the following sections.

A hypothetical common carp stock

A hypothetical stock of common carp was simulated to evaluate CBDMs and SDBDMs, based on a real stock of common carp in Clear Lake, Iowa, undergoing discrete commercial harvest (Colvin et al. 2010). Clear Lake has supported a commercial fishery for nuisance common carp since the early 1930s (Bailey and Harrison 1945). Dates and amounts of commercial fishery harvest have been reported since 1980. Harvest amounts have varied from 0.1 to 51 kg·ha⁻¹ during spring and 0 to 19 kg·ha⁻¹ during fall events. Identification of common carp aggregation areas in

space and time by Penne and Pierce (2008) has increased harvest and reduced the number of within-year harvests over the past 4 years. Therefore, data from 2007 to 2010 were used to set up harvest timing and amount of commercial harvest in this simulation study. Annual commercial common carp harvest averaged 35.6 kg·ha⁻¹ (minimum = 8.8 kg·ha⁻¹, maximum = 58.1 kg·ha⁻¹), with an average of 86% (minimum = 4%, maximum = 91%) occurring in the spring and 14% (minimum = 8%, maximum = 95%) of harvest occurring in fall. In both seasons, harvest occurred over short periods of time (<5 days). Timing of actual harvest was used to establish temporal harvest structure for simulations and subsequent analyses. Simulated spring and fall harvest events occurred every 0.2 and 0.8 years, respectively. In semidiscrete model notation, time of harvest is represented by τ_k , where k indexes when harvest occurred (i.e., $\tau_k \in \{0.2, 0.8, 1.2, 1.8, \dots, 9.2, 9.8\}$). In simulations, 86% of harvest occurred in the spring and 14% during the fall.

Values for r , B_{\max} , p , and q were selected to generate hypothetical common carp biomass dynamics similar to the real population in Clear Lake. Common carp biomass in Clear Lake between 1999 and 2010 varied from 124 to 540 kg·ha⁻¹ (Larscheid 2005; Colvin et al. 2010), therefore, a midrange value of 300 kg·ha⁻¹ was used to approximate average maximum biomass (B_{\max}). Preliminary estimates of intrinsic growth rate (r) and catchability (q) of the Clear Lake common carp stock are approximately 0.3 and 0.07 (M. Colvin, unpublished data), respectively, and were used in all models containing parameters r and q . A value of 1.3 for p in the Pella–Tomlinson model was arbitrarily selected to cause peak surplus production to occur at a biomass less than half B_{\max} . A value of 115 kg·ha⁻¹ was used for B_0 in the exponential model, and 300 kg·ha⁻¹ was the value of B_0 in all other models. The same values for B_0 , B_{\max} , r , p , and q were used for subsequent equilibrium yield analysis and to generate biomass dynamics for the hypothetical carp stock undergoing discrete harvest.

Equilibrium yield analysis

An equilibrium analysis was performed to compare the relationship of fishing mortality (F) to equilibrium fishing yield for continuous and semidiscrete Schaefer, Fox, and Pella–Tomlinson models. Analysis was limited to BDMs where a dome-shaped relationship of yield and fishing mortality exists. Equilibrium fishery yields of continuous and semidiscrete Schaefer and Pella–Tomlinson BDMs for F ranging from 0 to 0.30 by 0.01 increments were calculated by running each scenario until equilibrium was reached. Since F_{MSY} occurs at the value of r for the Fox model (Cadima 2003), equilibrium yields were evaluated for F ranging from 0 to 1.4. In SDBDMs, F occurred every 0.2 (86% of F) and 0.8 years (14% of F), simulating previously described seasonal commercial harvests in Clear Lake. The annual fishery yield for year 9999 was related to annual F to evaluate differences in equilibrium yield between continuous and semidiscrete Schaefer, Fox, and Pella–Tomlinson BDMs. Biological reference points (MSY , B_{MSY} , F_{MSY} , $F_{0.1}$) were calculated using equations in Cadima (2003) for CBDMs. A grid search was used to find MSY , B_{MSY} , and F_{MSY} for SDBDMs. Analytical solutions for $F_{0.1}$ are unavailable and therefore not calculated.

Parameter bias

Generating known biomass dynamics

The effect of assuming continuous harvest when it is actually discrete was assessed by fitting each CBDM and SDBDM (Table 1) to a simulated common carp stock experiencing discrete harvest events. Underlying (true) biomass time series were generated from each SDBDM using previously described parameter values and four values of F to calculate amount of harvest ($C_{\text{spring}} = 0.86F \cdot B$, $C_{\text{fall}} = 0.14F \cdot B$). The exponential model used F values equal to $0.5r$, r , $1.5r$, and $1.75r$. Values of F for remaining BDMs were calculated as $0.5F_{\text{MSY}}$, F_{MSY} , $1.5F_{\text{MSY}}$, and $1.75F_{\text{MSY}}$, where F_{MSY} is semidiscrete F_{MSY} . Harvest amounts were calculated as $C(\tau_k) = (\gamma_{\text{season}} \cdot F) \cdot B(\tau_k)$, where $C(\tau_k)$ is the harvested biomass in $\text{kg} \cdot \text{ha}^{-1}$ at event τ_k , γ_{season} is the fraction of annual fishing mortality in a season, F is the annual fishing mortality, and $B(\tau_k)$ is the biomass at the time of harvest event. Harvested biomass was summed within year for CBDM inputs.

Simulating observations of biomass and CPUE

A Monte Carlo simulation was used to simulate time series of biomass and CPUE observations that were fit to BDMs. Biomass sampling occurred every 0.3 year ($t = 0.3, 1.3, \dots, 9.3$), mimicking the common practice of batch marking common carp captured during spring commercial fishing in Clear Lake and returning those fish to the lake for mark-recapture population estimates (Colvin et al. 2010). Observed CPUE occurred every 0.7 year ($t = 0.7, 1.7, \dots, 9.7$), simulating fall indexing of biomass by CPUE. For each generated biomass time series (20 combinations in total, five models, four values of F), 50 replicated time series of biomass observations (10 observations per time series) were simulated using the equation $y(t)_i = B(t) \cdot e^\varepsilon$, where $y(t)_i$ is observed biomass at time t , $B(t)$ is biomass at sampling time t , and ε is a random, multiplicative, lognormally distributed observation-only error with $\log_e(\text{mean}) = 0$ and constant coefficient of varia-

tion (CV). An additional 50 replicate time series of CPUE (10 observations per time series) were generated for the Schaefer_{CPUE} BDM by $I(t)_j = q \cdot B(t) \cdot e^\varepsilon$, where $I(t)_j$ is the observed CPUE at time t , and q , $B(t)$, and ε are as previously described. Only the Schaefer_{CPUE} model was evaluated because of the common use of the model and to simplify the analysis. The level of CV used in all analyses was 20% and was selected to represent the level of certainty recommended for management (Van Den Avyle and Hayward 1999).

Parameter estimation

CBDMs and SDBDMs were fit to each time series of biomass estimates and CPUE to compare bias in parameter estimates for increasing harvest. Harvest amount was instantaneously removed in SDBDMs during model fitting. Total annual harvest was continuously removed over the annual period during model fitting for CBDMs. Model parameters (e.g., r , B_{max} , p , q) were estimated by maximum likelihood assuming a multiplicative lognormal observation-error structure (Polacheck et al. 1993; Hilborn and Mangel 1997; Walters and Martell 2004). Maximum likelihood estimates of model parameters were found using the optim function in R to maximize the following log likelihood:

$$\ell[\theta_l | y(t)_i] = \sum_1^i \log_e \left(\frac{1}{y(t)_i n \sqrt{2\pi\sigma_y^2}} n e^{-\left\{ \frac{\log \{y(t)_i / \hat{y}(t)_i\}}{2\sigma_y^2} \right\}^2} \right)^2$$

where θ_l is the vector of model parameters (e.g., r , B_{max}), $y(t)_i$ is observed biomass at time t , $\hat{y}(t)_i$ is model-estimated biomass at time t , and σ_y is the standard deviation of the residuals. The previous log likelihood was used to find values of model parameters that maximize the log likelihood for the exponential, Schaefer, Fox, and Pella–Tomlinson models. To include CPUE (I), the log likelihood was modified to

$$\ell[\theta_l | y(t)_i, I(t)_j] = \sum_1^i \log_e \left(\frac{1}{y(t)_i n \sqrt{2\pi\sigma_y^2}} n e^{-\left\{ \frac{\log \{y(t)_i / \hat{y}(t)_i\}}{2\sigma_y^2} \right\}^2} \right)^2 + \sum_1^i \log_e \left(\frac{1}{I(t)_j n \sqrt{2\pi\sigma_I^2}} n e^{-\left\{ \frac{\log \{I(t)_j / \hat{I}(t)_j\}}{2\sigma_I^2} \right\}^2} \right)^2$$

where θ_l is the vector of model parameters (i.e., r , B_{max} , q , σ_y , σ_I), $\hat{I}(t)_j$ is model-estimated CPUE at time t , σ_y , and σ_I are standard deviations of biomass and CPUE residuals, respectively, and $y(t)_i$, $\hat{y}(t)_i$, and $I(t)_j$ are as defined previously. The initial biomass (B_0) was constrained to be equal to B_{max} in models containing B_{max} for estimation purposes. This constraint was used since it is possible for B_0 to exceed B_{max} in numerical optimization (Prager 1994), and this constraint performed well for estimating biological reference points even when discrepancies in B_0 and B_{max} exist (Punt 1990). Quasi-Newton (BFGS) nonlinear search algorithm was used for all maximizations.

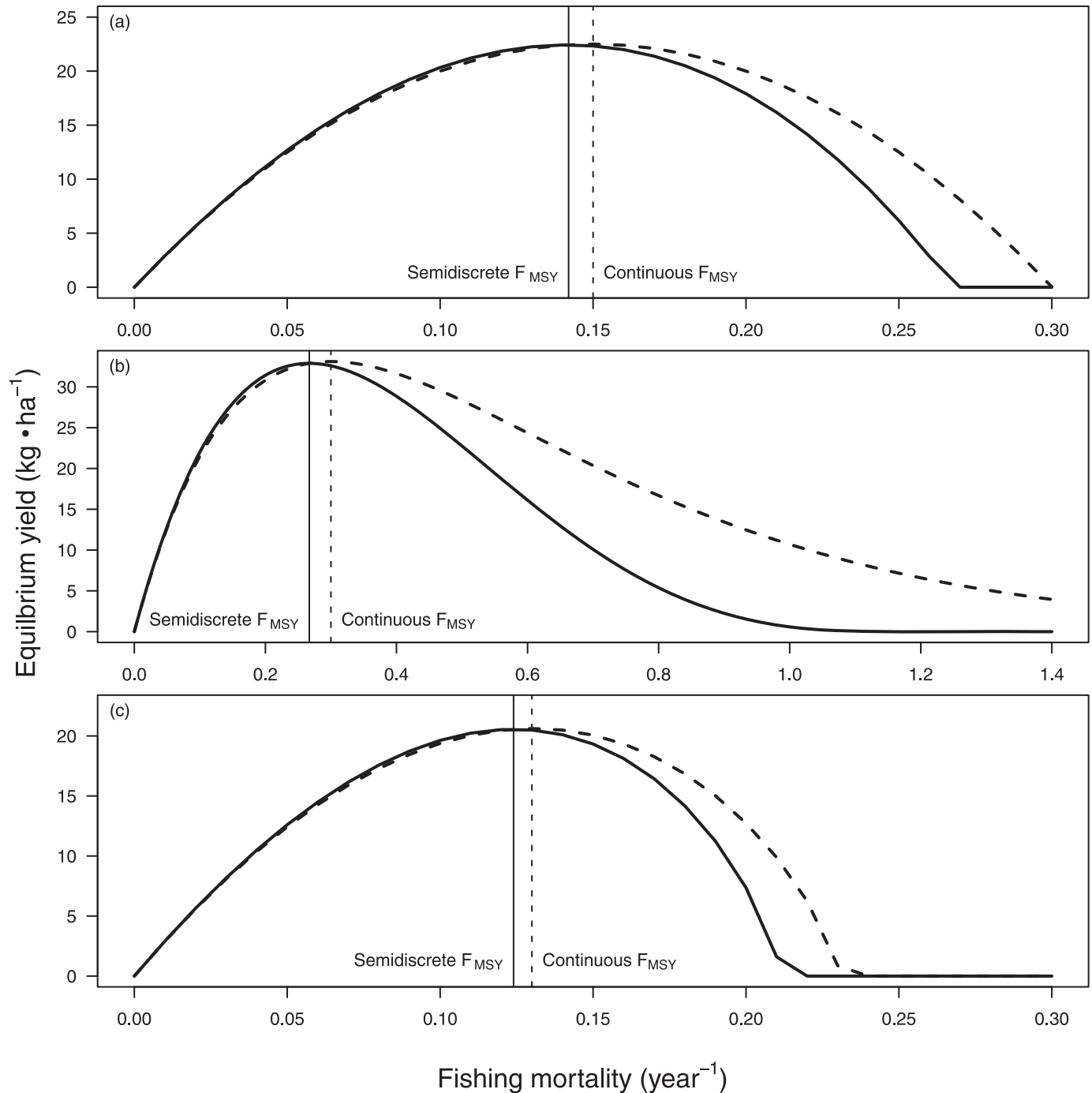
Parameter estimate bias was used to evaluate consequences of applying discrete harvest continuously. Proportional parameter bias was calculated by subtracting the estimated parameter by the true parameter and dividing by the true

parameter used to generate the underlying true biomass dynamics for each BDM. A parameter was considered unbiased if Monte Carlo replicates were centered on 0. Parameter bias was graphically assessed.

Biological reference points

Consequences of assuming continuous fishing mortality on biological reference points were evaluated by comparing reference points derived from CBDMs with true values used to generate hypothetical common carp stock biomass dynamics. Biological reference points were calculated from maximum likelihood estimates for parameters of continuous Schaefer, Fox, Pella–Tomlinson, and Schaefer_{CPUE} BDMs using equations in Cadima (2003). Proportional bias of biological reference points were calculated as $(\hat{\theta} - \theta)/\theta$, where θ is the true biological reference point from the equilibrium anal-

Fig. 2. Equilibrium fishing yield over a range of fishing mortalities for continuous (broken line) and semidiscrete (solid line) Schaefer (a), Fox (b), and Pella–Tomlinson (c) biomass dynamics models.



ysis, and $\hat{\theta}$ is the biological reference point calculated from estimated parameters for CBDMs. A parameter was considered unbiased if Monte Carlo replicates were centered on 0. Bias of biological reference points was graphically assessed.

Results

Equilibrium yield

Equilibrium yield results of continuous and semidiscrete

Schaefer, Fox, and Pella–Tomlinson BDMs provided different biological reference points despite sharing the same annual fishing mortality and parameter values (Fig. 2; Table 3). Equilibrium yields for CBDMs and SDBDMs were similar at low levels of F and became increasingly divergent as F approached and exceeded F_{MSY} (Fig. 2). Equilibrium yield at high levels of F ($F \gg F_{MSY}$) was reduced for SDBDMs relative to CBDMs (Fig. 2). F_{MSY} was slightly reduced when F occurred discretely compared with continuous

Table 3. Biological reference points for CBDMs and SDBDMs.

Model	Model type	MSY	B_{MSY}	F_{MSY}	$F_{0.1}$
Schaefer	Continuous	22.50	150.0	0.150	0.136
	Semidiscrete	22.42	151.3	0.142	
Fox	Continuous	33.11	110.5	0.300	0.236
	Semidiscrete	32.88	112.8	0.267	
Pella–Tomlinson	Continuous	20.62	158.1	0.130	0.120
	Semidiscrete	20.56	159.2	0.124	

Note: Values of $F_{0.1}$ for SDBDMs are not available and therefore not calculated.

application of F for all three BDMs (Table 3). MSY and B_{MSY} were slightly higher when F was applied discretely relative to continuous application.

Parameter bias

Proportional bias varied with harvest amount and type of BDM. Median absolute parameter bias was within ± 0.1 for the majority of parameters estimated by semidiscrete exponential, Schaefer, Fox, and Schaefer_{CPUE} BDMs (Figs. 3 and 4). Exceptions were negative biases in estimates of r and B_{max} in semidiscrete Schaefer and Schaefer_{CPUE} models. Negative bias increased for r and B_0 with increasing harvest for the continuous exponential model (Fig. 3). Median parameter bias of CBDMs was minimized at low values of F (Figs. 3 and 4). The magnitude of median parameter bias (negative or positive) increased with F for continuous exponential, Schaefer, Fox, and Schaefer_{CPUE}. Median bias of q was less than 0.1 but increased systematically with F . Median bias of r did not exhibit systematic pattern for either continuous or semidiscrete Pella–Tomlinson models. B_{max} was unbiased (median bias < 0.1) at low levels of F for continuous and all levels of F for semidiscrete Pella–Tomlinson BDM. Both continuous and semidiscrete Pella–Tomlinson BDMs overestimated p , but this bias was minimized at low F levels.

Biological reference points

Proportional bias of biological reference points varied with F and among CBDMs (Fig. 5). Negative median proportional bias of B_{MSY} and MSY increased with increasing F for all CBDMs. Bias of F_{MSY} did not vary systematically with F , but the range of proportional bias declined with increasing F .

Discussion

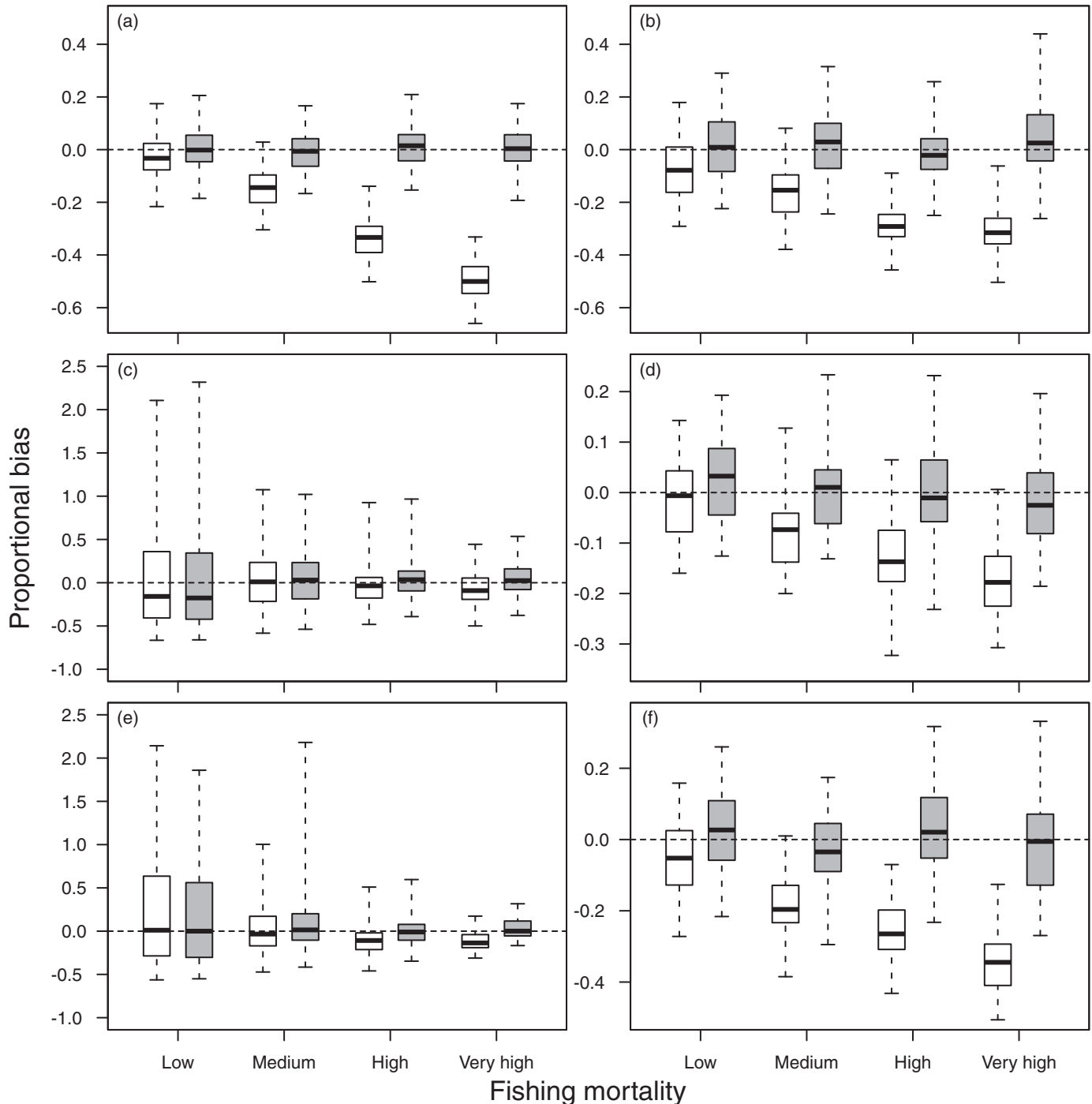
Results of our analyses demonstrate that assuming continuous fishing mortality when it is occurring discretely has potential management consequences. The SDBDMs we evaluated reduced parameter estimate bias at high values of F relative to CBDMs for stocks experiencing discrete harvest. Additional biological realism provided by SDBDMs did not come at the expense of greater computer time required to fit models. Maximum likelihood solutions were achieved for both continuous and semidiscrete BDMs in less than 2–3 min for even the most complex models. Explicitly accounting for discrete harvest structure (date and amount) using SDBDMs outperformed CBDMs when F approaches and exceeds F_{MSY} . It should be noted that SDBDMs are not more complex in terms of number of parameters, but add biological realism by explicitly accounting for amount and timing of biomass harvest. Knowing when and how much biomass is

removed imposes an informative physical constraint when fitting models to time series, since a stock must have sufficient biomass and production to support discrete harvest events (i.e., discrete harvest must be less than standing biomass).

Equilibrium analysis of the Schaefer, Fox, and Pella–Tomlinson BDMs provided insight into differences in effect of fishing mortality on equilibrium yield in continuous and discrete fishing systems. Under low values of F , the differences between CBDMs and SDBDMs were negligible, indicating that use of either model type would yield similar management results. Equilibrium yield at F approaching or greater than F_{MSY} were increasingly different between CBDMs and SDBDMs, indicating that applying harvest continuously when it is actually discrete can influence management recommendations. Equilibrium yield predicted for high levels of F (i.e., greater than F_{MSY}) was lower for SDBDMs, which could have management consequences when a fish stock is experiencing heavy discrete harvest but harvest is modeled continuously in BDMs. Production over an annual period is less when discrete harvest reduces biomass levels over a short period, since production is dependent on biomass. In other words, biomass is reduced by a discrete harvest and the population cannot “catch up” and equal production of a population where the same amount of biomass is continuously harvested. Applying F continuously when it occurs discretely overestimated equilibrium yield at high values of F based on our equilibrium analyses. Overestimating equilibrium yield is obviously problematic for managing sustainable fisheries and is potentially part of the reason for the long-standing discontent with MSY as a biological reference point for managing fish stocks (Larkin 1977; Punt and Smith 2001). Harvest objectives identified using equilibrium approximations of continuous biomass dynamics models should result in overharvest if harvests are satisfied using discrete commercial fishing efforts. Overestimating sustained yield is not necessarily a problem with nuisance commercial fisheries, where the objective is to overfish a stock to reduce biomass-dependent impacts.

F_{MSY} was slightly lower when fishing effort was modeled as discrete events rather than on a continuous basis. This result was observed for all BDMs exhibiting a dome-shaped relationship of equilibrium yield and F used in this study. These discrepancies in F_{MSY} between CBDMs and SDBDMs are notable in providing a potential basis for use of $F_{0.1}$ as a biological reference point. The use of $F_{0.1}$ has emerged as a useful “rule of thumb” for managing fisheries, but according to Hilborn and Walters (1992) this is an arbitrary, ad hoc strategy with no theoretical basis. It is unlikely that fishery harvest is truly continuous over an annual period, so reducing F_{MSY} cal-

Fig. 3. Boxplots of proportional bias for parameters estimated for exponential (r , panel (a); B_0 , panel (b)), Schaefer (r , panel (c); B_{\max} , panel (d)), and Fox (r , panel (e); B_{\max} , panel (f)) CBDMs (no shade) and SDBDMs (shaded). The solid horizontal line in the boxes represents the medians. Boxes represent the bounds of the 25th and 75th quartiles of the data. Whiskers represent the lower and upper bounds of the data. The horizontal dotted line denotes a proportional bias value of zero.

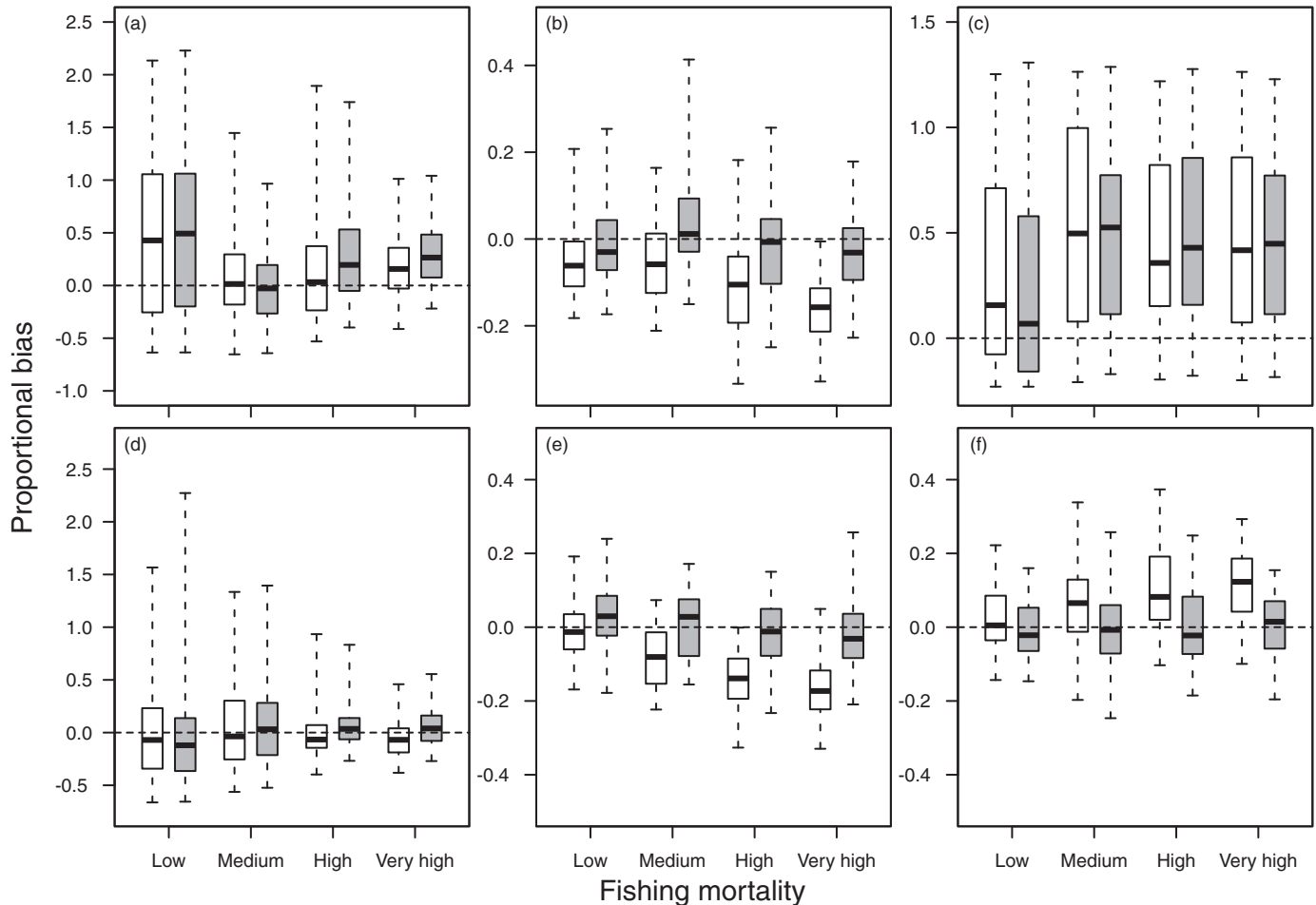


culated from CDBDM parameter estimates compensates for violating the assumption of continuous fishing mortality.

Time series are the recommended method for fitting BDMs (Hilborn and Walters 1992). Accurate estimates of parameters such as r and B_{\max} based on time series are critical for establishing biological reference points used to manage fish stocks using output controls (e.g., total allowable catch). Bias in parameter estimates can result in biased estimates of

MSY and F_{MSY} , potentially leading to stock mismanagement. On average, parameter bias was negative for most biological reference points, which indicates that reference points may be conservative when fishing harvest is applied discretely but modeled continuously because of underestimating B_{\max} . Parameter bias in CBDMs was dependent on how much biomass was harvested. In particular, bias in B_{\max} was consistently more severe at higher harvest levels among all

Fig. 4. Boxplots of proportional bias for parameters estimated for Pella–Tomlinson (r , panel (a); B_{\max} , panel (b); p , panel (c)) and Schaefer_{CPUE} (r , panel (d); B_{\max} , panel (e); q , panel (f)) CBDMs (no shade) and SDBDMs (shaded). The solid horizontal line in the boxes represents the medians. Boxes represent the bounds of the 25th and 75th quartiles of the data. Whiskers represent the lower and upper bounds of the data. The horizontal dotted line denotes a proportional bias value of zero.



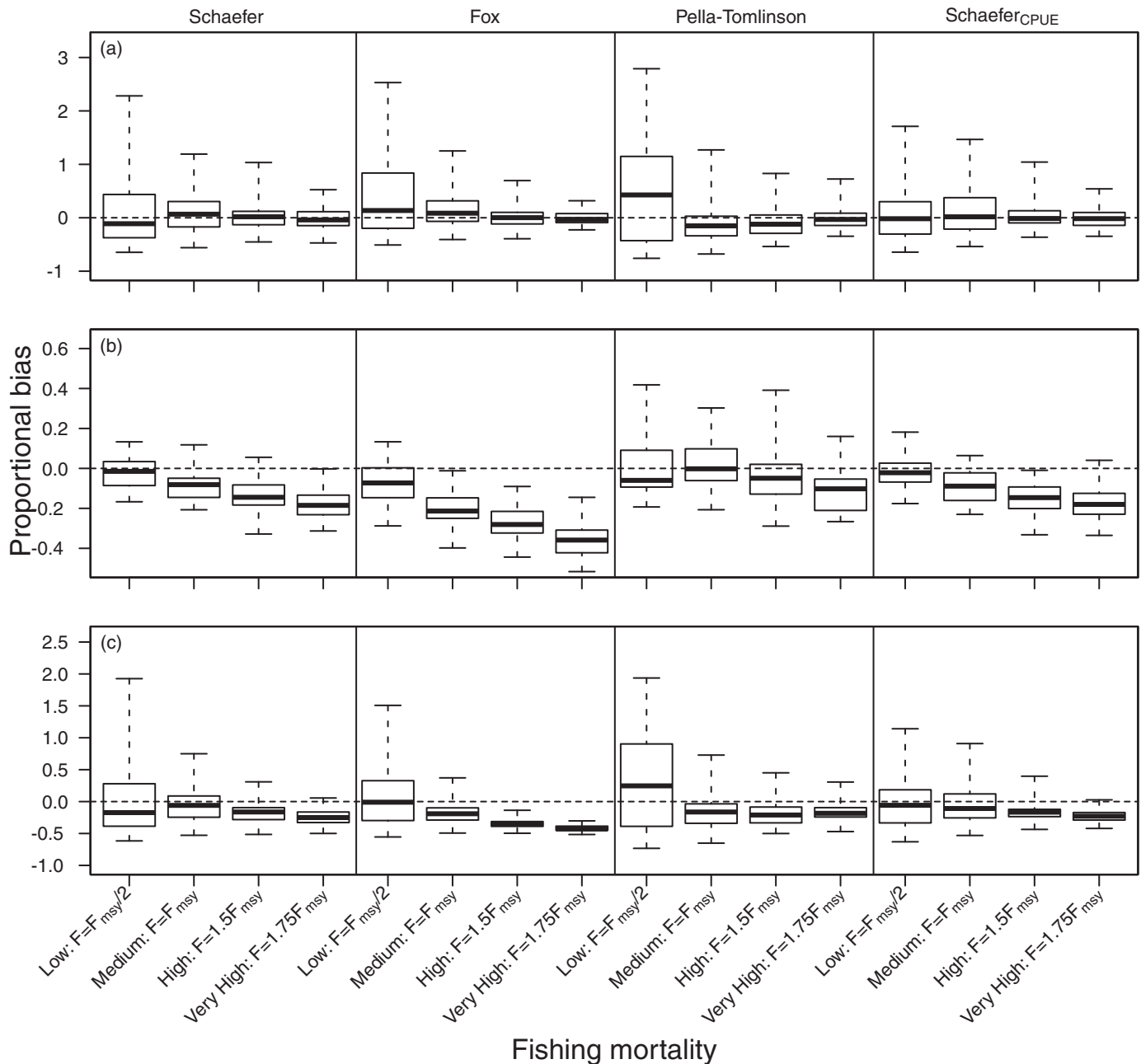
CBDMs. In hypothetical biomass dynamics of SDBDMs, biomass is instantaneously reduced then increases thereafter. Failure to incorporate information on magnitude or timing of large biomass harvests in relation to biomass observation results in negative bias in B_{\max} in CBDMs. It should be noted that neither CBDMs nor SDBDMs did a good job of estimating model parameters for the Pella–Tomlinson model, where fitting an additional parameter (four parameters in total) relative to the other models resulted in poor fits and the possibility that additional data or reparameterizing may be required.

Fishery harvest dynamics likely exhibit a combination of discrete and continuous fishing mortality. For example, an “opening day” phenomenon can occur when a recreational or commercial fishery opens resulting in eager fishers and greater fishing mortality during the opening day compared with the remaining season. Greater fishing mortality likely occurs on opening day since the amount of fishing effort is high owing to the number of casual (i.e., only fish opening day) fishers exploiting vulnerable fish over a short period of time. It is likely that after opening day, fishing effort is dominated by serious fishers. For example, commercial harvest of Caribbean spiny lobster (*Panulirus argus*) fisheries of Bahia de la Ascension, Mexico, was found to be greatest on open-

ing day and subsequently decreased over time (Lozanoalvarez et al. 1991). In an inland recreational fishery, the majority of fish were harvested during the first 2 days of opening on a previously unfished lake in Wisconsin (Goedde and Coble 1981). Events such as free fishing days and tournaments could be viewed as discrete harvest events because of angler behavior that occurs in addition to ongoing licensed recreational fishing (i.e., continuous harvest). Overfishing may result if discrete fishing mortality events are not accounted for in assessments of recreational fisheries because of overestimation of harvest when F exceeds F_{MSY} . SDBDMs accommodate the potential for biomass dynamics to be modeled as a mixture of discrete and continuous harvest and therefore may provide a more realistic and accurate stock assessment.

Discrete events influencing aquatic animal biomass frequently occur in aquatic systems. One example is the stocking of fish into aquatic systems to serve as biological controls (Lathrop et al. 2002), provide additional fishing opportunities (Pine et al. 2007), or promote species conservation (Oosterhout et al. 2005). This discrete input of fish biomass can have major food web impacts through an instantaneous increase in the consumption required to support these newly stocked fish. For example, Pope et al. (2009) found

Fig. 5. Boxplots of proportional bias for biological reference points F_{MSY} (a), B_{MSY} (b), and MSY (c) calculated for CBDMs. The solid horizontal line in the boxes represents the medians. Boxes represent the bounds of the 25th and 75th quartiles of the data. Whiskers represent the lower and upper bounds of the data. The horizontal dotted line denotes a proportional bias value of zero.



that trout stocked in alpine lakes altered the alpine lake ecosystem by preying on emerging insects that would otherwise be a terrestrial subsidy. SDBDMs could be used to more realistically explore the consequences of stocking timing and amount on prey dynamics in food web and ecosystem models.

Our analysis shows that the use of semidiscrete models to represent discrete phenomena such as pulsed harvest within the context of continuous mortality and other population processes can have important management implications. Discrete phenomena can result in complex population dynamics that continuous models may not adequately represent. Periodic (i.e., seasonal, disturbance) mortality events can have a major influence on population dynamics. For example, large

snow events can cause mortality in ring-necked pheasant hens (*Phasianus colchicus*; Perkins et al. 1997) or high flow events can cause mortality in juvenile coho salmon (*Oncorhynchus kisutch*; Ebersole et al. 2006). Winter- and summer-fish kills where large mortality occurs over a short period of time owing to decreased dissolved oxygen levels (Hurst 2007) could be accommodated in BDMs as discrete events. Biomanipulation is a common restoration technique to restore water quality (e.g., Schrage and Downing 2004), and removal of common carp by rotenone would be more realistically modeled using SDBDMs than CBDMs. Other disturbances such as reproductive failure within a year (e.g., Carlander 1958) or disease epidemics represent discrete

events that could have large influences on biomass dynamics over short periods of time. Additionally, conservation and supplementation stocking can be discrete efforts occurring for a number of aquatic and terrestrial species. The present study focuses on a nuisance population of common carp as an example; however, this approach could also be applied to pest suppression occurring in agroecosystems (i.e., predator releases, pesticides) (Lu et al. 2003; Nundloll et al. 2010). Accounting for these events occurring over a short period of time relative to the annual period using semidiscrete models can potentially improve understanding and management of population dynamics in a variety of systems and circumstances.

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