



Abstract—Yield-per-recruit and spawning-biomass-per-recruit models, are commonly used for evaluating the status of a fishery. In practice, model parameters are themselves usually estimates that are subject to both bias (uncertainty in the mean) and imprecision (uncertainty in the standard deviation). Using Monte Carlo simulation with data for female Japanese eel (*Anguilla japonica*) from the Kao-Ping River in Taiwan, we examined the sensitivity of such models to different degrees of bias and imprecision in the life history parameters. Positive biases in natural mortality and the von Bertalanffy growth coefficient led to larger relative changes in the mean and standard deviation of estimated fishing-mortality-based biological reference points (F_{BRPs}) than did changes under negative biases. Higher degrees of imprecision in parameters did not affect the means of F_{BRPs} , but their standard deviations increased. Composite risks of overfishing depended mainly on the changes in the means of F_{BRPs} rather than on their standard deviations. Therefore, reducing the biases in key life history parameters, as well as the bias and imprecision in the current rate of fishing mortality, may be the most relevant approach for obtaining correct estimates of the risks of overfishing.

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Sensitivity of yield-per-recruit and spawning-biomass-per-recruit models to bias and imprecision in life history parameters: an example based on life history parameters of Japanese eel (*Anguilla japonica*)

Yu-Jia Lin¹

Chi-Lu Sun (contact author)¹

Yi-Jay Chang¹

Wann-Nian Tzeng²

Email for contact author: chilu@ntu.edu.tw

¹ Institute of Oceanography
National Taiwan University
No.1, Sec.4, Roosevelt Road
Taipei 10617, Taiwan

² Department of Environmental Biology and Fisheries Science
National Taiwan Ocean University
No. 2, Beining Road
Keelung 20224, Taiwan

Yield-per-recruit (YPR) and spawning-biomass-per-recruit (SPR) models, in which the total yield or spawning biomass of a cohort is standardized for the numbers of recruits, are commonly used in fisheries assessment (Beverton and Holt, 1957; Quinn and Deriso, 1999). They can be used to infer the total yield and spawning biomass of an entire population composed of different cohorts with an assumption of a steady state and with knowledge of equilibrium recruitment (King, 2007). Several fishing-mortality-based biological reference points (F_{BRPs}) derived from YPR and SPR models can be used to evaluate whether the yield per recruit is optimal or the spawning biomass per recruit is sufficient for the population to persist under current fishing pressure.

Uncertainties in the parameters of such models are inevitable and result from observation and process error (Charles, 1998). Ignoring uncertainties in parameters can lead to incor-

rect estimation of F_{BRPs} , and consequently the examination of fishery status could be misleading, given the cases of the American lobster (*Homarus americanus*) (Chen and Wilson, 2002), green sea urchin (*Strongylocentrotus droebachiensis*) (Grabowski and Chen, 2004), Atlantic cod (*Gadus morhua*) (Jiao et al., 2005), pronghorn spiny lobster (*Panulirus penicillatus*) (Chang et al., 2009), and Japanese eel (*Anguilla japonica*) (Lin et al., 2010a).

Estimation of natural mortality (M) is challenging (Vetter, 1988) because both its mean and variance are prone to considerable uncertainty. For example, the estimates of M have varied among different empirical methods (Pascual and Iribarne, 1993; Lin and Sun, 2013). The variances of M estimates also have differed among approaches (e.g., Cubillos et al., 1999, versus Hall et al., 2004; Lin et al., 2012). It is easier to obtain growth information. The von Bertalanffy growth function is an

often used growth model, but different estimation approaches (e.g., length-frequency methods versus readings of rings in calcified structures; see Lin and Tzeng, 2009, versus Lin and Tzeng, 2010), different regions of study (Helser and Lai, 2004; Keller et al., 2012), and aging errors from annuli readings (Lai and Gunderson, 1987; Cope and Punt, 2007) may lead to biases in the von Bertalanffy growth coefficient (K).

In another example of the potential for uncertainty, biases in the asymptotic length (L_∞) may result from the regional variation in growth potential in different habitats (Beverton and Holt, 1957), from a latitudinal trend (Helser and Lai, 2004; Keller et al., 2012), or from sampling schemes unrepresentative of the population size structure, because of its high dependency of maximum size in the sample (Formacion et al., 1991; Froese and Binohlan, 2000). In addition, the uncertainty (or multiplicative error) in the growth curve (ε_{GR}) is related to the imprecision in the lengths-at-age scatter at a given age. The current fishing mortality rate (F_{cur}) can be estimated from various methods (e.g., Seber, 1982; Quinn and Deriso, 1999; King, 2007) with both the mean and variance of high uncertainty (Chen and Wilson, 2002).

It is essential to incorporate and quantify these uncertainties in the assessment of population dynamics (Hilborn and Walters, 1992; Peterman, 2004). Further, parameter uncertainties can be categorized into bias uncertainty and precision uncertainty. The influence of parameter bias on YPR and SPR models has been investigated since the 1950s (e.g., Beverton and Holt, 1957; Goodyear, 1993; Mace, 1994), but the effects of precision uncertainty have seldom been addressed. The effects of parameter imprecision with a limited number of comparisons (i.e., high or low variation) that were inadequate to reveal a full picture of the sensitivity to bias and imprecision in the parameters have been examined in a few studies (e.g., Restrepo and Fox, 1988; Chen and Wilson, 2002; Chang et al., 2009). Systematic examinations of different degrees of parameter bias and imprecision with a wider range and finer resolution could provide detailed information about their effects on model outputs (e.g., Goodyear, 1993), but few such examinations exist for per-recruit models.

It is difficult to elucidate the sensitivity of per-recruit models to parameter bias and imprecision through analysis of the formulae because the effects of the parameters on F_{BRPs} are nonlinear with complicated forms (Schnute and Richard, 1998). Alternatively, a sensitivity analysis through the use of a Monte Carlo simulation can be used to examine their effects on the estimation of F_{BRPs} , on fishery status, and on management implications (Jiao et al., 2005). Therefore, the objective of this study was to evaluate the effects of different degrees of bias, represented by the differences in parameter means, and of imprecision, represented by the differences in parameter standard deviations (SDs), in the YPR and SPR model results, specifically in the F_{BRPs} and the resultant composite risks of overfishing.

Materials and methods

To better understand the sensitivity of outputs from the YPR and SPR models, we changed the mean or SD of selected parameters one at a time over large ranges with fine increments (from 5% to 95% with increments of 5% for cases of under-specification and from 150% to 1000% with increments of 50% for cases of over-specification). The following parameters were selected: 1) M ; 2) von Bertalanffy growth coefficients of K and L_∞ ; and 3) F_{cur} . In addition, the multiplicative error in the growth curve (ε_{GR}) and length-weight relationship (ε_{LW}) were selected as well. In this study, we used information on the mean and SD values of these parameters from previous studies conducted during 1998–2006 on the life history and fishery of the Japanese eel in the Kao-Ping River in Taiwan (Lin and Tzeng 2009; Lin et al. 2010a, 2010b) to examine the sensitivity of model results to effects of parameter bias and imprecision with a Monte Carlo simulation.

We used wide ranges for the parameters for 3 reasons: 1) the scale of boundaries used; a factor of 10 was applied in a classical study (figure 4 in Goodyear, 1993); 2) a wide range is more general because it can include all likely ranges; and 3) in our previous study (Lin and Sun, 2013), we found that the variation in estimates of M from several different indirect methods can vary from 0.10/year to 2.13/year. Also, the difference in K can be large, especially when different approaches are involved. For the same region, for example, in Kao-Ping River, K has varied from 0.12/year to 0.38/year, depending on whether methods based on otoliths or length frequencies were applied (Lin and Tzeng, 2009, 2010).

YPR and SPR models

The YPR and SPR models were calculated according to the formulae in Quinn and Deriso (1999):

$$YPR = e^{-M(t_c - t_r)} \int_{t_c}^{t_{max}} F(t)N(t)W(t)dt \quad \text{and} \quad (1)$$

$$SPR = \int_{t_c}^{t_{max}} N(t)W(t)S(t)dt, \quad (2)$$

where $F(t)$ = the fishing mortality at age t ;
 $N(t)$ = population size in numbers at age t ;
 $W(t)$ = the weight at age t ;
 $S(t)$ = the maturation proportion at age t ;
 t_r = the age at recruitment;
 t_c = the age at first capture; and
 t_{max} = the maximum age (the formulae for $F(t)$, $N(t)$, $W(t)$, and $S(t)$ are shown in Table 1).

Because, in Kao-Ping River, females were 4 times more abundant than males (Han and Tzeng, 2006) and because females contribute more directly to spawning biomass, the parameters of female Japanese eels were used in this study; they were also used in Lin et al. (2010a). Estimates of means and corresponding SDs of the parameters were derived from our previous works (Lin and Tzeng, 2009; Lin et al., 2010b).

Table 1

Formulae, estimates of model parameters, and corresponding simulated random errors for the length–weight relationship (a and b are coefficients, and ε_{LW} =the corresponding multiplicative error), N =the population size in numbers; von Bertalanffy growth function (K =the growth coefficient (/year), L_∞ =the asymptotic length (mm), t_0 =the theoretical age at length of zero (year), and ε_{GR} =the multiplicative error of the growth curve), M =the natural mortality (/year); ε_M =the standard deviation of M ; F_{cur} =current fishing mortality (/year); fishing process under gear selection (α_0 and α_1 =selection curve coefficients), and maturation process of female Japanese eel (*Anguilla japonica*) in the lower reach of the Kao-Ping River in southern Taiwan (β_0 and β_1 =the maturation curve coefficients, and ε_{β_0} and ε_{β_1} =the standard error for β_0 and β_1 , respectively). The means and standard deviations of the parameters are from previous studies conducted in 1998–2006 on life history parameters and the fishery of Japanese eel in the Kao-Ping River, Taiwan (Lin and Tzeng 2009, Lin et al. 2010a, 2010b).

Formula	Parameter
Weight at age t , $W(t)$	
$W(t) = aL(t)^b e^{\varepsilon_{LW}}$	$a, b = 4.56 \times 10^{-8}, 3.55$ $\varepsilon_{LW} \sim N(0, 3.93 \times 10^{-4})$
$L(t) = L_\infty [1 - e^{-K(t-t_0)}] e^{\varepsilon_{GR}}$	$L_\infty, K, t_0 = 1024, 0.12, -0.69$ $\varepsilon_{GR} \sim N(0, 3.10 \times 10^{-2})$
Population size in number at age t , $N(t)$	
$N(t) = e^{-[F(t)+(M+\varepsilon_M)](t-t_r)}$	$M = 0.18/\text{year}$ $\varepsilon_M \sim N(0, 1.98 \times 10^{-5})$
Fishing process under logistic gear selection, $F(t)$	
$F(t) = F_{cur} \times \frac{e[\alpha_0 + \alpha_1 L(t)]}{1 + e[\alpha_0 + \alpha_1 L(t)]}$	$F_{cur} \sim \text{Gamma}$ with mean of 0.12 and variance of 1.06×10^{-2} , $\alpha_0, \alpha_1 = -4, 0.02$
Maturation (silvering) proportion at age t , $S(t)$	
$S(t) = \frac{e^{[(\beta_0 + \varepsilon_{\beta_0}) + (\beta_1 + \varepsilon_{\beta_1})L(t)]}}{1 + e^{[(\beta_0 + \varepsilon_{\beta_0}) + (\beta_1 + \varepsilon_{\beta_1})L(t)]}}$	$\beta_0, \beta_1 = -13.31, 0.02$ $\varepsilon_{\beta_0} \sim N(0, 1.36)$ and $\varepsilon_{\beta_1} \sim N(0, 4.04 \times 10^{-6})$
Others	
Maximum observed age, t_{max}	16 years
Length and age at recruitment, L_r, t_r	55 mm, 0.489 year
Length and age at first capture, L_c, t_c	200 mm, 1.15 year

Four F_{BRPs} were calculated to compare with F_{cur} (0.120/year, Lin et al., 2010b): F_{max} , the fishing mortality at which yield per recruit is at its maximum; $F_{0.1}$, the fishing mortality at which the increase of yield per recruit is only 10% of the increase of yield per recruit when fishing mortality is zero (King, 2007); and $F_{30\%}$ and $F_{50\%}$, the fishing mortality rates at which the SPR is 30% and 50% of the SPR when fishing mortality is zero (Goodyear, 1993).

The reference points F_{max} and $F_{0.1}$ can be regarded as boundaries in order to constrain harvesting below the level within which the fish population can produce maximum sustainable yield (United Nations, 1995), and they usually are used as limiting and precautionary indicators of growth overfishing, respectively; fishing mortality rates above F_{max} indicate that fish are caught before they reach optimal size given the rate of natural mortality and their growth rate (Gabriel and Mace, 1999; Quinn and Deriso, 1999). Fishing mortalities at 30% and 50% of SPR, compared with SPR at $F=0$, are considered to be the limiting and precaution-

ary levels for anguillid eels (ICES¹). Therefore, $F_{30\%}$ and $F_{50\%}$ were considered the limiting and precautionary reference points for recruitment overfishing, where the spawners are insufficient in numbers to produce enough offspring to replace themselves (Sissenwine and Shepherd, 1987).

Incorporation of uncertainties in parameters

We used Monte Carlo simulation, which has been widely applied to other species (e.g., Chen and Wilson, 2002; Grabowski and Chen, 2004; Chang et al., 2009; Lin et al., 2010a) to incorporate the uncertainties of the parameters into the models. In each run, random errors for natural mortality (ε_M) and for coefficients in the logistic maturation curve (ε_{β_0} and ε_{β_1}), as well as ε_{LW}

¹ ICES (International Council for the Exploration of the Sea). 2002. Report of the ICES/EIFAC Working Group on Eels. ICES Council Meeting (C.M.) Documents 2002/ACFM:03, 55 p. [Available at [website](#).]

Table 2

Summary of the 9 scenarios for evaluation of the sensitivity of the results from models of yield per recruit and spawning biomass per recruit to different degrees of bias and imprecision in several parameters: natural mortality (M), von Bertalanffy growth coefficient (K), asymptotic length (L_∞), and current fishing mortality rate (F_{cur}). Also the multiplicative error in the growth curve (ϵ_{GR}) and the length-weight (LW) relationship (ϵ_{LW}) are modeled. In each scenario, the mean or standard deviation (SD) of only one parameter was changed.

Scenario	Description	Parameter	Range
1	Standard scenario	Unchanged	100%
2	Mean of M	M	10–1000%
3	SD of M	ϵ_M	10–1000%
4	Mean of K	K	10–1000%
5	Mean of L_∞	L_∞	50–200%
6	Error in growth curve	ϵ_{GR}	10–1000%
7	Error in LW relationship	ϵ_{LW}	10–1000%
8	Mean of F_{cur}	F_{cur}	10–1000%
9	SD of F_{cur}	$\epsilon_{F_{cur}}$	10–1000%

and ϵ_{GR} , were generated from normal distribution with the means and variances listed in Table 1. These random errors were incorporated into the YPR and SPR formulae provided in Table 1, and then 4 F_{BRPs} (F_{max} , $F_{0.1}$, $F_{30\%}$, and $F_{50\%}$) were calculated. For each simulation scenario, this process was repeated 5000 times to produce 5000 corresponding sets of F_{BRP} values from which the empirical distributions of the 4 F_{BRPs} were generated and composite risks were calculated.

Calculation of composite risks

Because F_{cur} and the F_{BRPs} are not fixed constants, we applied composite risk analysis that allowed for the incorporation of the uncertainty in both indicator and management reference points (Prager et al., 2003; Jiao et al., 2005). By the discrete approach proposed by Jiao et al. (2005), the composite risks were calculated as the expected probability of one random variable being larger than another. Let $f(x)$ be the empirical probability density function of the F_{BRP} of interest (e.g., F_{max}) and $g(y)$ be the empirical probability density function of F_{cur} with a corresponding cumulative density function of $G(y)$ and then, let Δx be a small increase in x (i.e., the F_{BRP}), and by summing x over its range, the composite risk of F_{cur} exceeding F_{BRP} is calculated with the following equation:

$$P(F_{cur} > F_{BRP}) = 1 - \sum_{-\infty}^{\infty} [G(x)f(x)]\Delta x \tag{3}$$

Here, we assume a gamma distribution for F_{cur} because 1) our previous study (Lin and Tzeng, 2008) indicated that gamma distribution fitted better for the distribution of fishing efforts, 2) it produces nonnegative values, and 3) it is flexible in shape. For details in cal-

culatation of composite risks in discrete approach, refer to Jiao et al. (2005).

Sensitivity analysis

For the sensitivity analysis, the parameter values in Table 1 were set as the standard scenario (scenario 1; Table 2). The parameters for which mean and SD values may potentially affect results of YPR and SPR models were investigated in 9 scenarios, in which the mean or SD of only one parameter was changed (Table 2): the mean of M (scenario 2) and its SD (ϵ_M , scenario 3), the mean of K (scenario 4), and the mean of L_∞ (scenario 5). In practice, the bias in K can result from aging error and the use of different estimation approaches, and the bias in L_∞ often results from unrepresentative sampling schemes. Therefore, we assumed that the sources of biases in K and L_∞ are unrelated and they were modeled

independently. Because modeling the estimation errors in the coefficients K and L_∞ can lead to underestimation of the actual uncertainty in the data (Lin et al., 2012), the error was modeled on the growth curve (ϵ_{GR}) rather than coefficients (scenario 6). The remaining scenarios are ϵ_{LW} (scenario 7) and the mean and SD values of F_{cur} and $\epsilon_{F_{cur}}$ (scenarios 8 and 9).

For scenarios 1–7, the mean and SD values of the parameters, except for L_∞ , were decreased to 10% with an increment of 5% or were increased to 1000% with an increment of 50% to cover the possible magnitudes of biological variation (as applied in Goodyear, 1993). Because information about L_∞ can be obtained from the maximum observed length in the data, that parameter may be subject to less bias and imprecision and was set from 50% to 100% with an increment of 5% and from 100% to 200% with an increment of 10% (Table 2). For scenarios 8 and 9, because of less computational load (calculation of an F_{BRP} is independent of F_{cur} , and, therefore, we needed to compute only composite risks of overfishing), we used finer increments: the mean and SD of F_{cur} were decreased to 10% with an increment of 1% or increased to 1000% with an increment of 10%.

The relative change (RC) between the mean or SD of one F_{BRP} for increment i in scenario j ($RC_{F_{BRP}}^{ij}$) and the mean or SD of that F_{BRP} in the standard scenario was used to quantify the sensitivity of a given F_{BRP} for all scenarios except 8 and 9. RC is defined with the following equation:

$$RC_{F_{BRP}}^{ij} = 100 \times T_{F_{BRP}}^{ij} \times (T_{F_{BRP}}^S)^{-1}, \tag{4}$$

Where $T_{F_{BRP}}^{ij}$ = the statistic (mean or SD) of the F_{BRP} of interest (e.g., F_{max}) for increment i in scenario j ; and

Table 3

Mean and standard deviation (SD) per year of 4 fishery-mortality-based reference points (F_{BRP} s)—the fishing mortality at which yield per recruit is at its maximum (F_{max}), the fishing mortality at which the increase of yield per recruit is only 10% of the increase of yield per recruit when fishing mortality is zero ($F_{0.1}$), and the fishing mortality rates at which the spawning biomass per recruit (SPR) is 30% and 50% of the SPR when fishing mortality is zero ($F_{30\%}$ and $F_{50\%}$)—and the composite risks, $P(F_{cur} > F_{BRP})$, calculated as percentages, of current fishing mortality, F_{cur} (0.120/year), exceeding F_{BRP} s after repeating the standard scenario 1000 times. Numbers in the parentheses provide the ranges of relative changes in means and SDs from random Monte Carlo simulation with data for female Japanese eel (*Anguilla japonica*) in the Kao-Ping River in southern Taiwan.

F_{BRP}	Mean	SD
F_{max}	0.156 (99.95–100.04%)	1.6×10^{-3} (97.23–103.89%)
$F_{0.1}$	0.111 (99.96–100.03%)	9.2×10^{-4} (97.24–103.90%)
$F_{30\%}$	0.129 (99.97–100.03%)	8.7×10^{-4} (97.32–104.44%)
$F_{50\%}$	0.073 (99.97–100.03%)	4.6×10^{-4} (97.31–104.43%)
$P(F_{cur} > F_{max})$	13.44	0.47
$P(F_{cur} > F_{0.1})$	56.44	0.70
$P(F_{cur} > F_{30\%})$	35.48	0.65
$P(F_{cur} > F_{50\%})$	94.31	0.32

$T_{F_{BRP}}^S$ = the same statistic of the same F_{BRP} from the standard scenario.

The sensitivity of an F_{BRP} also has to be distinguished from the random variation that results from Monte Carlo simulation, namely the variation that results from the incorporation of random errors in M , length-weight relationship, and maturation process. To understand the scale of this random variation, the standard scenario (scenario 1, without any biases or imprecision in parameters) was repeated 1000 times, producing 1000 corresponding RC values for the means and SDs of F_{BRP} s. The minimum and maximum values of RC from these 1000 repetitions of scenario 1 were used as the lower and upper limits of random variation from the Monte Carlo simulation. The effect of changes in the mean or SD of a parameter was considered significant only when its RC is lower than the minimum or larger than the maximum RC. All the computations and simulations were completed in R, vers. 3.1.0 (R Core Team, 2014).

Results

Magnitude of the random variation from Monte Carlo simulation

Running the Monte Carlo simulation of the standard scenario 1000 times produced RC values for the means of F_{max} , $F_{0.1}$, $F_{30\%}$, and $F_{50\%}$ that ranged

from 99.95% to 100.04%, from 99.96% to 100.03, from 99.97% to 100.03, and from 99.99% to 100.03%, respectively (Table 3). The SD values of the F_{BRP} s had larger RC values that ranged from 97.23% to 103.89% for F_{max} , from 97.24% to 103.90% for $F_{0.1}$, from 97.32% to 104.44% for $F_{30\%}$, and from 97.31% to 104.43% for $F_{50\%}$ (Table 3). Therefore, variation of RC within 0.05% for the mean and within 4.50% for the SD of the F_{BRP} was applied as the criterion for significance of effects; that is, we considered the effect of changing one parameter on the F_{BRP} to be significant when the resultant RC was wider than this criterion.

Sensitivity of reference points from the YPR model

The means of F_{BRP} s from the YPR model, namely F_{max} and $F_{0.1}$, were sensitive to both the means of M and K , which had similar trends but different magnitudes (Fig. 1, left panels). The RC values for the means of F_{max} and $F_{0.1}$ decreased slowly to 75–80% when M and K decreased to 5%. As M and K increased to 1000%, their RC values rose with an accelerating trend, especially for F_{max} , to more than 12,000% and 1100%, respectively. However, the means of F_{max} and $F_{0.1}$ were not sensitive to changes in L_{∞} and ϵ_{GR} because their RC varied less than 0.05%. The ϵ_M had marginal effects on the mean of F_{max} and $F_{0.1}$, given that the RC was around 100.6% when ϵ_M became 1000% (Fig. 1, left panels). The SD values of F_{max} and $F_{0.1}$ were also sensitive to the means of M and K with similar accelerating trends. The SD of F_{max} was more sensitive to changes in M and K than was the SD of $F_{0.1}$ (Fig. 1, right panels). In addition, the SD values of F_{max} and $F_{0.1}$ were nearly related linearly to ϵ_M . Similar to the means, the SD values of F_{max} and $F_{0.1}$ did not show significant sensitivity to L_{∞} and ϵ_{GR} , and their RC values did not exceed the significance level of 4.50%.

Sensitivity of reference points from the SPR model

The means of F_{BRP} s from the SPR model, $F_{30\%}$, and $F_{50\%}$, were sensitive to the mean of M , but their RC values (from 90% to 170%; Fig. 2, left panels) were smaller than those of F_{max} and $F_{0.1}$. When K decreased to 40%, the RC for the mean of $F_{30\%}$ and $F_{50\%}$ reached a minimum of around 80%. As K increased to 1000%, the RC of the means of $F_{30\%}$ and $F_{50\%}$ increased to 300% and 400%. They also were affected by L_{∞} such that the RC was around 85–125% as L_{∞} increased from 50% to 200%. Neither ϵ_M nor ϵ_{GR} affected the means of $F_{30\%}$ and $F_{50\%}$. The SD values of $F_{30\%}$ and $F_{50\%}$ showed the highest sensitivity to the mean of M , with

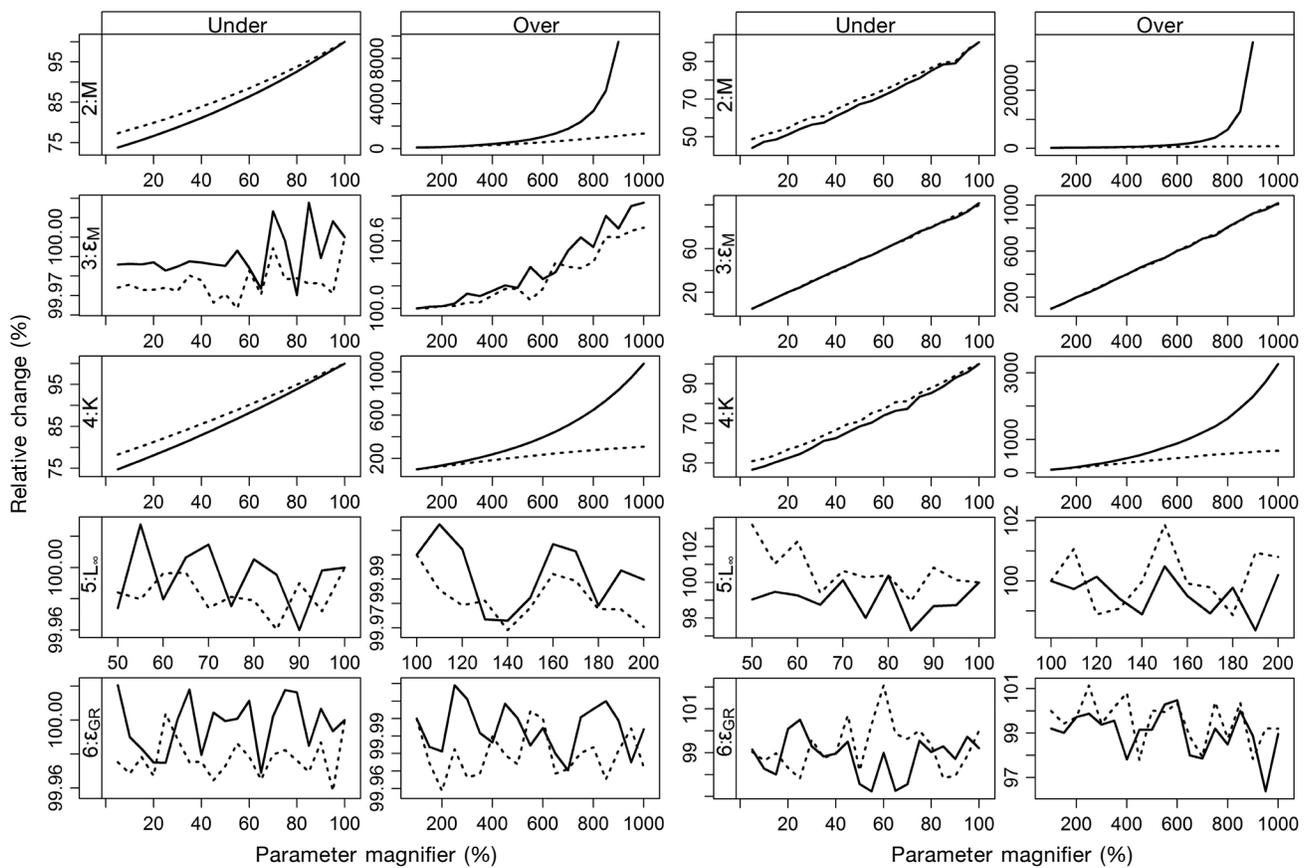


Figure 1

Relative changes determined from Monte Carlo simulation with data collected during 1998–2006 for female Japanese eel (*Anguilla japonica*) in the Kao-Ping River in southern Taiwan. The relative changes are measured as percentages for the means (shown in the left panels) and standard deviations (SD; shown in the right panels) of fishery-mortality-based reference points (F_{BRPs}) in scenarios 2–6 of the yield-per-recruit model, where the mean and SD of the natural mortality (M and ϵ_M), the von Bertalanffy growth coefficient (K), the asymptotic length (L_∞), and the multiplicative error in the growth curve (ϵ_{GR}) were under-specified from 5% to 95% and over-specified from 150% to 1000% (except for values of L_∞ that went from 50% to 200%). In each graph, the solid line indicates fishing mortality at which yield per recruit is at its maximum, and the dashed line indicates fishing mortality at which the increase of yield per recruit is only 10% of the increase of yield per recruit when fishing mortality is zero. Because of the large variation in RC values for the different scenarios, the scales of the y-axes differ greatly to allow changes to be seen. Under=underspecified parameters; Over=overspecified parameters; ϵ_M =the SD of M ; F_{cur} =current fishing mortality and; $\epsilon_{F_{cur}}$ =SD of F_{cur} .

the RC changing from 70% to around 4000%. The parameter K had high influence on the SD values of $F_{30\%}$ and $F_{50\%}$, with RC changing from 20% to 1500% (Fig. 2, right panels). The parameters ϵ_M and L_∞ had considerable effects on the SD values of $F_{30\%}$ and $F_{50\%}$, with RC ranging from 90% to 400% and from 40% to 150%, respectively. The SDs of $F_{30\%}$ and $F_{50\%}$ were not affected by ϵ_{GR} .

Sensitivity of the composite risks of overfishing

The composite risks of growth overfishing (F_{cur} exceeding F_{max} and $F_{0.1}$) decreased with increasing

means of M and K and did not depend on changes in L_∞ , ϵ_{GR} , and ϵ_M (Fig. 3). The risks of recruitment overfishing (F_{cur} exceeding $F_{30\%}$ and $F_{50\%}$) showed the greatest sensitivity to K followed by M . The risk of recruitment overfishing was affected also by changes in L_∞ but with less sensitivity. The parameters ϵ_M and ϵ_{GR} did not contribute to noticeable changes in the risks of overfishing. The risks of both growth and recruitment overfishing showed strong sensitivity to both the mean and SD of F_{cur} . As the mean of F_{cur} increased from around 150% to 225%, the risks approached 100%. The risks of overfishing decreased with increasing SD for F_{cur} .

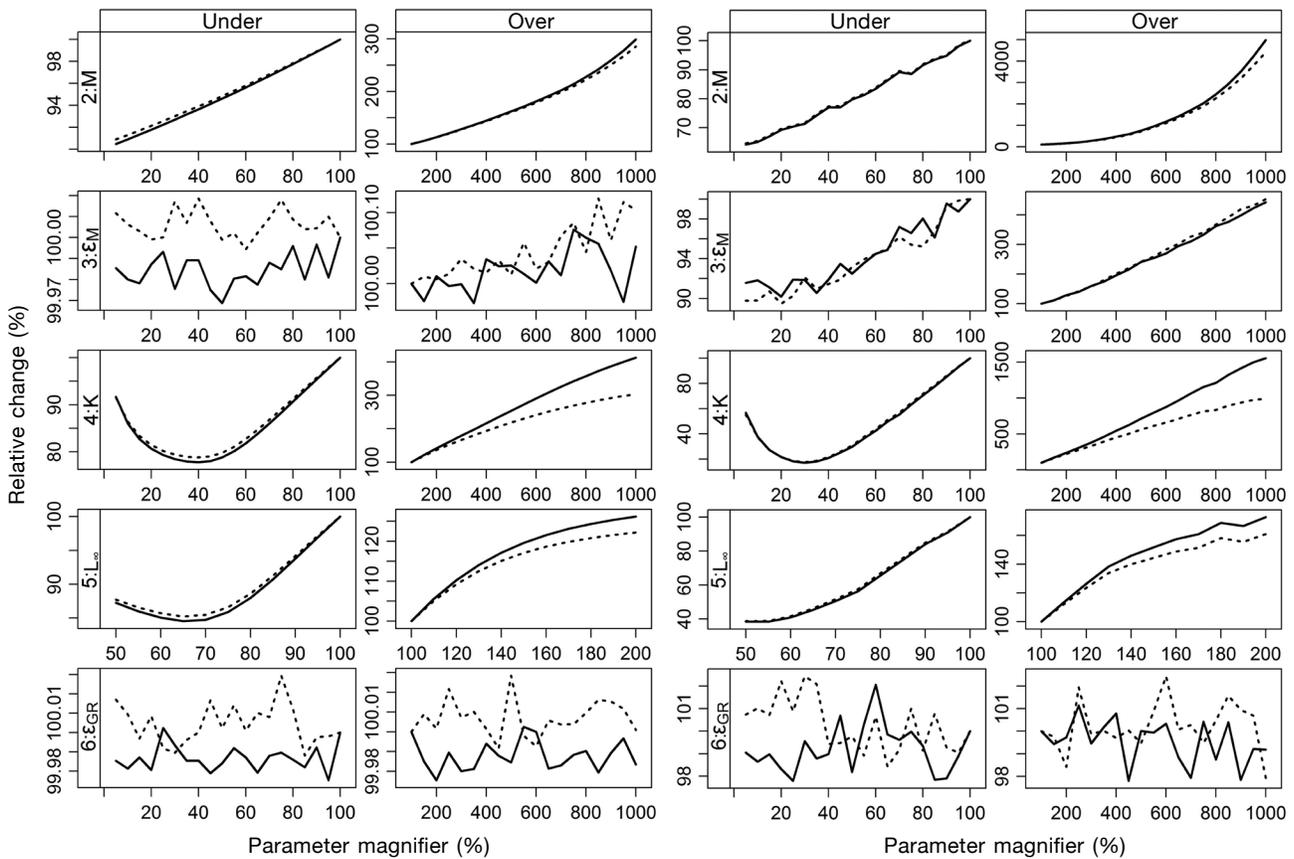


Figure 2

Relative changes from the Monte Carlo simulation with data collected during 1998–2006 for female Japanese eel (*Anguilla japonica*) in the Kao-Ping River in southern Taiwan. The relative changes are measured as percentages, for the means (shown in the left panels) and SDs (shown in the right panels) of fishery-mortality-based reference points (F_{BRPs}) in scenarios 2–6 of the spawning-biomass-per-recruit model, where the mean and SD of the natural mortality (M and ϵ_M), the von Bertalanffy growth coefficient (K), the asymptotic length (L_∞), and the multiplicative error in the growth curve (ϵ_{GR}) were under-specified from 5% to 95% and over-specified from 150% to 1000% (except for values of L_∞ that went from 50% to 200%). In each graph, the solid line indicates the fishing mortality rate at which the spawning biomass per recruit (SPR) is 30% of the SPR when fishing mortality is zero, and the dashed line indicates the fishing mortality rate at which the SPR is 50% of the SPR when fishing mortality is zero. Because of the large variation in RC values for the different scenarios, the scales of the y-axes differ greatly to allow changes to be seen. Under=underspecified parameters; Over=overspecified parameters.

Effects of multiplicative error in the length–weight relationship

The changes in ϵ_{LW} resulted in nonsignificant changes in the mean and SD of the 4 F_{BRPs} . They also did not affect the composite risks of exceeding these F_{BRPs} .

Discussion

Effects of uncertainty in mean and SD of natural mortality

Estimates of the mean of M are usually highly uncertain, possibly because of the lack of appropriate data

for direct estimation, data such as those from tag–capture experiments (Vetter, 1988). As M increases, the YPR curve becomes flatter with a decreasing maximum value and decreasing slope at the origin (fig. 17.18 in Beverton and Holt, 1957). This change in the shape of YPR curve accounts for the nonlinear accelerating trend of F_{max} and $F_{0.1}$ found in our study. Uncertainty in the mean (bias) of M can also cause significant biases in results of the model for SPR, particularly at a high level of fishing mortality (Goodyear, 1993). A higher mean of M led to a steeper SPR curve, but the general shape of the curve was not altered, explaining the lower sensitivity of $F_{30\%}$ and $F_{50\%}$ to M . On the other hand, the SD (imprecision) of M resulted

in significant changes only in the SDs of the 4 F_{BRPs} examined. Therefore, as indicated in the Appendix Figure, the risks of both growth and recruitment overfishing were affected more by the changes in the mean of M than by changes in the SD. The bias in M seems to be more important than the imprecision in M in influencing the risks of overfishing.

Effects of uncertainty in growth parameters

The shape of the YPR curve also was altered by K (fig. 17.22 in Beverton and Holt, 1957). The flattening of the YPR curve with decreasing K accounts for the accelerating increase in the mean and SD of F_{max} . On the other hand, Beverton and Holt (1957) found that the changes in W_{∞} (equivalent to L_{∞} under the same length-weight relationship) did not affect the shape of the YPR curve. This insensitivity of the YPR shape on L_{∞} explains our finding that changes in L_{∞} did not affect the mean and SD of F_{max} and $F_{0.1}$ or the corresponding risk of growth overfishing.

The peaks in the values of RC in the means and SDs of $F_{30\%}$ and $F_{50\%}$ when K and L_{∞} were around 40–60% possibly resulted from the use of a length-dependent maturation curve for anguillids (Davey and Jellyman, 2003) in the calculation of SPR. In the cases with extremely small values of K or L_{∞} , the proportion of mature eels was close to zero even at the maximum age (16 years). A very small part of the spawning biomass was lost because of fishing, consequently resulting in higher $F_{30\%}$ and $F_{50\%}$ values.

Effects of current fishing mortality

The bias and imprecision in F_{cur} played an important role in determining risks of overfishing. Greater effects due to changes in the mean of F_{cur} on the risks of both growth and recruitment overfishing were expected because differences in the mean played an important part in influencing the composite risk, as in the example of 2 standard normal random variables (Appdx Fig.). Given the same difference in the means, a larger SD leads to lower composite risks (Appendix. Figure, panels B and D), accounting for the observed decreasing risks of overfishing with increasing $\epsilon_{F_{cur}}$. Given that F_{cur} is from the gamma distribution, decreasing composite risks with increasing $\epsilon_{F_{cur}}$ also resulted in the convergence of 4 risks of overfishing. This finding indicates that a high $\epsilon_{F_{cur}}$ value may mask the distinction between target (usually $F_{0.1}$ or $F_{50\%}$) and threshold (F_{max} or $F_{30\%}$) F_{BRPs} because the risks of target and threshold F_{brp} are similar.

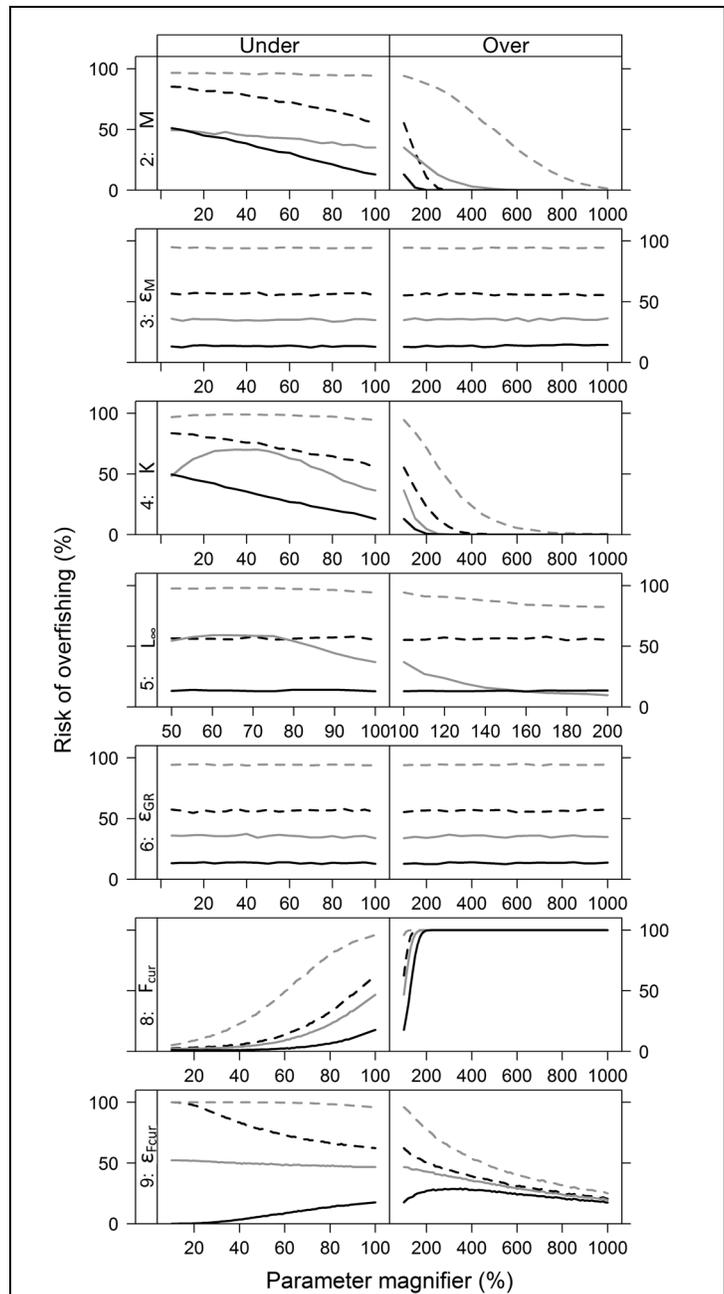


Figure 3

The composite risks of overfishing in scenarios 2–6, 8, and 9, where the mean and standard deviation (SD) of the natural mortality (M and ϵ_M), the von Bertalanffy growth coefficient (K), the asymptotic length (L_{∞}), the multiplicative error in the growth curve (ϵ_{GR}), and the mean and SD of current fishing mortality (F_{cur} and $\epsilon_{F_{cur}}$) were under-specified from 5% to 95% and over-specified from 150% to 1000% (except for values of L_{∞} that went from 50% to 200%). The black solid line indicates the composite risk of F_{cur} exceeding the fishing mortality at which yield per recruit is at its maximum, the black dashed line indicates the composite risk of F_{cur} exceeding the fishing mortality at which the increase of yield per recruit is only 10% of the increase of yield per recruit $F=0$, and the gray solid and dashed lines indicate the composite risk of F_{cur} exceeding the fishing mortality rates at which the spawning biomass per recruit (SPR) is 30% and 50% of the SPR when $F=0$.

The assumption of a gamma distribution of F_{cur} may be the reason for increasing risks of exceeding F_{max} when $\varepsilon_{F_{\text{cur}}}$ lies between 5% and 200%. When $\varepsilon_{F_{\text{cur}}}$ was 50% or less, the gamma distribution of F_{cur} resembled the normal distribution with density highly concentrated around its mean. Because F_{max} (0.151) was much larger than F_{cur} (0.120), the area of the distribution of F_{cur} that exceeded F_{max} became smaller and smaller as $\varepsilon_{F_{\text{cur}}}$ decreased, resulting in lower risks.

Asymmetry in the sensitivities of reference points

The responses of the means and SDs of 4 F_{BRPs} to the changes in the means of M or K showed disproportionate increases, indicating that the means and SDs of F_{BRPs} were more sensitive to over-specification. This accelerating trend, arising from the nonlinear relationship between these parameters and F_{BRPs} (Schnute and Richards, 1998), indicates that under the same degree of misspecification (e.g., 50%) an over-specified mean of M or K could result in seriously overestimated values of F_{BRPs} . Consequently, the risks of overfishing would be underestimated, potentially leading to overexploitation.

In summary, bias in life history parameters, such as M , F_{cur} , K , and L_{∞} , resulted in considerable changes in the means and SDs of 4 selected F_{BRPs} : F_{max} , $F_{0.1}$, $F_{30\%}$, and $F_{50\%}$. Different degrees of the imprecision in the life history parameters did not affect the means of F_{BRPs} but substantially influenced their SDs. Over-specification of the mean of M and K led to larger values of RC in the means and SDs of F_{BRPs} than did under-specification of the means of M and K .

The composite risks of F_{cur} exceeding these 4 F_{BRPs} were affected mainly by bias in the life history parameters rather than by their imprecision. Both bias and imprecision in F_{cur} played crucial roles in determining the risks of F_{cur} exceeding these 4 F_{BRPs} . The variation in growth curves and length-weight relationships did not affect results of the per-recruit models. Our results agreed with those of previous studies without consideration of parameter uncertainty, indicating that they can apply to YPR and SPR models for other species. We recommend 1) minimizing the bias in the life history parameters, especially bias in M , K , and F_{cur} , and 2) maximizing the precision in F_{cur} as the most relevant approaches for development of correct estimates of F_{BRPs} and determining risks of overfishing.

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Appendix

This appendix presents changes in composite risks of 2 random variables, X and Y , under different means and standard deviations.

