Incorporating uncertainty into the estimation of biological reference points for a spiny lobster (*Panulirus penicillatus*) fishery

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Abstract   The status of a fishery is often defined as the probability of fishing mortality rate exceeding a perilous level for long-term sustainability. Lobster stock assessments are often subject to large uncertainty in input data and high levels of natural variability in lobster life history processes, which calls for incorporating uncertainty associated with both indicator and management reference points in an evaluation of biological risk of overfishing. Using a Monte Carlo simulation approach, we evaluated the impacts of uncertainty in modelling on the determination of the status of the Taitung spiny lobster (*Panulirus penicillatus*) fishery (Taiwan), which has not been quantitatively determined despite its commercial importance. The commonly used biological reference points derived from the per recruit model ($F_{0.1}$, the fishing mortality rate where the slope of the curve of yield-per-recruit model is 10% of the maximum slope and $F_{40\%}$, the fishing mortality rate that reduces the expected egg production for a cohort of female lobsters to 40% of that produced in the absence of a fishery of the egg-per-recruit model) were influenced by uncertainties associated with lobster life history and fishery parameters. A large uncertainty in the current fishing mortality rate (F_{cur}) and estimates of biological reference points (F_{BRPs}) increased the uncertainty in determining the risk of overexploitation throughout the confidence levels of the stochastic decision-making framework. This simulation study suggests that the target reference point of $F_{40\%}$ is less sensitive to the input parameters' uncertainty than $F_{0.1}$. We suggest a further evaluation of other F-based references points and development of biomass-based reference points before final selection and implementation for the management of the Taitung lobster fishery.

INTRODUCTION

Exploited marine fish and invertebrate populations characteristically exhibit high levels of variability in abundance as a result of variations in their ecosystems (Forgarty et al. 1996). The importance of incorporating uncertainty into fisheries stock assessments has been well documented in the literature (Hilborn & Walters 1992; Restrepo 1999; Mace 2001; Helser et al. 2001). Per recruit analysis is commonly used to estimate yield, spawning biomass or egg production (Fogarty & Idoine 1988) an average recruit may contribute over its life span (Beverton & Holt 1957). Per recruit analysis is primarily dependent on growth, mortality, and maturation parameters (Restrepo & Fox 1988). Uncertainty in these parameters can lead to uncertainty in per recruit analysis, resulting in uncertainty in stock assessment. Recent studies were specifically focused on the investigation of the effects of uncertainty of life history and fisheries parameters on the estimation

of biological reference points in per recruit analysis (Chen & Wilson 2002; Grabowski & Chen 2004; Jiao et al. 2005).

Biological reference points (BRPs), such as F_{max} and $F_{0.1}$, estimated in the yield-per-recruit (YPR) analysis, are widely used in finfish fisheries management (Hilborn & Walters 1992). F_{max} is defined as the instantaneous rate of fishing mortality that results in the highest YPR and was historically considered a management target (Ricker 1975). More recently $F_{0.1}$, corresponding to a fishing mortality rate where the slope of the YPR curve is 10% of the maximum slope, is regarded as a more appropriate management target (Mace 1994; Quinn & Deriso 1999; Restrepo 1999). The $F_{10\%}$ of the egg-per-recruit (EPR) model is the fishing mortality rate that reduces the expected egg production for a cohort of female lobsters to 10% of that produced in the absence of a fishery (Fogarty & Idoine 1988) and was used to evaluate the stock status for the American lobster (*Homarus americanus*) in the United States (ASMFC 2000). Per recruit models are often treated as deterministic, and results of such analyses only include point estimates (Restrepo & Fox 1988). However, uncertainty in biological reference points is not always considered in stock assessments, possibly resulting in erroneous conclusions about the stock status (Helser et al. 2001).

The pronghorn spiny lobster, *Panulirus penicillatus* (Olivier 1791), is a widely distributed species commonly found in the Indo-West Pacific (Fischer & Bianchi 1984). Its main habitat is in the upper 4–5 m on outer reef slopes in the tropical Pacific (George 1972). The spiny lobster is an important commercial species in the southeastern coastal waters off Taiwan (Taitung County), that is caught by skin-diving or trammel nets throughout the year (Chang et al. 2007). The spiny lobster fishery in Taiwan is managed with a minimum size limit of 20 cm total length (76.62 ± 0.34 mm carapace length, CL; mean ± SE) for all species along the coast of Taiwan. However, the minimum size limit is not strictly enforced, and small lobsters and non-protected berried (egg-bearing) females are common in local fish markets (Chang et al. 2007). There are no other regulations for the lobster fishery and Chang et al. (2007) suggested that lack of protection of spawners and young lobster might lead to recruitment- and growth-overfishing of the spiny lobster stock in Taiwan.

Despite its importance, no quantitative stock assessment has been conducted for spiny lobster in Taitung to date. Developing BRPs for the Taitung lobster fishery must consider the substantial natural variability in the spiny lobster stock, as well as uncertainty resulting from the lack of understanding of the species. In this study, we present a Monte Carlo method to investigate how uncertainties associated with fisheries parameters might affect fishing-mortality-based BRPs (F_{BRPs}) of the per recruit models and to determine the relative importance of uncertainty associated with different life history parameters. We also evaluate the impacts of uncertainty in BRPs in assessing the biological risk of overfishing following a stochastic decision-making framework (Helser et al. 2001; Chen & Wilson 2002).

MATERIALS AND METHODS

YPR model

The commonly used discrete YPR model (Chen 1997), described below, was used for the YPR analysis:

$$Y/R = \sum_{t=t_R}^{t_\lambda} \left[\frac{\alpha_1 [CL_\infty (1 - e^{-K(t-t_0)})]^{\beta_1} S_t F}{S_t F + M} \right. $$

$$\left. (1 - e^{-S_t F - M}) \times e^{-\sum_{j=t_R}^{t-1}(S_j F + M)} \right] \tag{1}$$

where Y is the yield, R is the number of recruits, t_R is the age of entry into the fishery, t_0 is the maximum age of fish in the fishery, CL_∞, K, and t_0 are parameters in the von Bertalanffy growth function (VBGF), α_1 and β_1 are parameters in the weight-length relationship (Ricker 1975), F is the fishing mortality rate, M is the natural mortality rate, and S_t (S_j) the selectivity coefficient for fish of age t (j), which was set to a "knife edge" at the size of 47 mm CL.

We calculated the derivative of Y/R with respect to fishing mortality rate,

$$\frac{\partial(Y/R)}{\partial F}$$

to estimate $F_{0.1}$ and F_{max} iteratively from the following equations:

$$\frac{\partial(Y/R)}{\partial F}\Big|_{F=F_{0.1}} = 0.1 \times \frac{\partial(Y/R)}{\partial F}\Big|_{F=0} \tag{2}$$

$$\frac{\partial(Y/R)}{\partial F}\Big|_{F=F_{max}} = 0 \tag{3}$$

The estimations described above are deterministic and do not consider the possible uncertainty

associated with the model parameters. We used a Monte Carlo simulation approach to evaluate the impacts of parameter uncertainty on the estimation of F_{max} and $F_{0.1}$.

Two approaches were used for quantifying uncertainties for the YPR model parameters. The first approach was to simulate uncertainty in model parameters independently. This approach was used for natural mortality M for YPR and EPR (described below). The uncertainty of M for each sex was assumed to follow a log-normal distribution. Thus we have:

$$B_i = x\exp(\varepsilon_i - \frac{\sigma_M^2}{2})\qquad(4)$$

where B_i is the simulated natural mortality value in the ith simulation run, ε_i is an error term following the normal distribution of $N(0, \alpha_M^2)$, x is the mean value of M estimations (Table 1, and detailed in the natural mortality estimation), and α_M is the standard deviation of M (Hilborn & Mangel 1997) (defined in Table 2). These values were, however, determined somewhat arbitrarily to facilitate the simulation study.

The second approach we used included simulation of the uncertainty for parameters that are likely to be highly correlated (Chen 1996). High correlations usually exist among CL_∞, K, and t_0 in the VBGF and between two parameters (α_1 and β_1) describing the weight-length relationship (W-CL). We used the mean parameter values (Table 1) to calculate the "true" values of the dependent variable (i.e., size-at-age and weight-at-length), and then added random errors of log-normal distribution to the "true" values to yield simulated data (Table 2). The simulated data were then used to estimate simulated VBGF and W-CL parameters using the nonlinear least squares method (Bard 1974). By repeating this procedure 2000 times, a probability distribution was generated for each parameter. We then jointly and randomly sampled parameters (i.e., VBGF and W-CL parameters, and natural mortality) from the generated distributions of parameters in estimating $F_{0.1}$ and F_{max} (Chen 1996). More specifically, we used the following procedure to simulate CL_∞, K, and t_0 in this study: (1) using the average values of CL_∞, K, and t_0 (Table 1) to calculate "true" size at age CL_t based on the VBGF; (2) simulating size at age as $CL_t = CL_t e^{\varepsilon_t}$, where $\varepsilon_t \in N(0, \alpha_{CL}^2)$ and α_{CL} are defined in Table 2; (3) fitting the VBGF to size-at-age data simulated in step (2) to estimate three parameters (CL_∞, K, and t_0) using the nonlinear least squares method; and (4) repeating steps (2) and (3) 2000 times to yield 2000 sets of simulated parameters.

Table 1 Models and their parameters for which uncertainties were considered in this study. The estimates of parameters are from Chen (2005), CL_i is the carapace length (mm) of lobster at a given age t, and CL_∞, K and t_0 are parameters of the von Bertalanffy growth function. BW_i is the body weight (g) of lobster at a given size i, α_1 and β_1 are parameters, M is natural mortality, α_{CL}^2 and α_M^2 are the variances of carapace length-at-age and natural mortality, Fec_i is the fecundity of lobster at a given size i, α_2 and β_2 are parameters. P_{mat_i} is the percentage of berried (egg-bearing) females at a given size i, α_3 and β_4 are parameters. ε_i denotes the error term for each stochastic model i.

Model description	Model	Mean parameters
Model for carapace length of lobster at a given age t	$CL_t = CL_\infty\{1 - \exp[-K(t - t_0)]\}\cdot\exp(\varepsilon_1 - \sigma_{CL}^2/2)$	Male: $CL_\infty = 135.2$, $K = 0.192$ and $t_0 = 0.014$ Female: $CL_\infty = 104.7$, $K = 0.259$ and $t_0 = 0.0015$
Model for body weight of lobster at a given size i	$BW_i = \alpha_1\,CL^{\beta_1}\cdot\exp(\varepsilon_2)$	Male: $\alpha_1 = 1.2\times10^{-3}$ and $\beta_1 = 2.90$ Female: $\alpha_1 = 1.3\times10^{-3}$ and $\beta_1 = 2.92$
Natural mortality rate	$M = M\cdot\exp(\varepsilon_3 - \sigma_M^2/2)$	Male: $M = 0.49$ Female: $M = 0.46$
Model for fecundity of lobster at a given size i	$Fec_i = \alpha_2\,CL^{\beta_2}\cdot\exp(\varepsilon_4)$	$\alpha_2 = 2.4\times10^{-3}$ and $\beta_2 = 4.18$
Model for the fraction of berried female at a given size i	$P_{mat_i} = 1/\{1 + \exp[\alpha_3(CL - \beta_3)]\} + \varepsilon_5$	$\alpha_3 = 0.28$ and $\beta_3 = 56.46$

This approach considers the covariance of three parameters in the VBGF (Sullivan et al. 1990; Chen & Hunter 2003) in simulating uncertainty of size-at-age data. The same approach was also applied to simulating parameters (α_1 and β_1) of the *W-CL* relationship. To ensure that the simulated growth parameters are biologically realistic for spiny lobster, changes in simulated parameters were constrained to ± 40% of their mean values in the simulation.

The mean length-at-age values and their associated uncertainty were estimated based on multiple length frequency analyses (MULTIFAN; Fournier et al. 1990). Eight modes in length distribution were separated, and the estimates of CL_∞ and K tended to be more biologically realistic when the sampling duration was 15 months. The first month was set in June, and the choice of length interval was set at 3 mm CL for females (twice log-likelihood, $2L = 5985$) and males ($2L = 6461$; Chen 2005). Eight scenarios with different standard deviations were considered for each sex (Table 2). The first three scenarios had medium, high, and low levels of variations for model parameters, respectively. *W-CL* data varied less than length-at-age data, and the standard deviations of *W-CL* data were set lower than those for length-at-age data (Table 2). Scenarios 4 to 6 included high variations for growth, *W-CL* length parameters, and natural mortality, respectively, for testing the impacts of uncertainty of different life history parameters on the estimation of reference points, while variations for other parameters were the same as those for the median variation scenario (scenario 1). High and low natural mortality scenarios (scenario 7 and 8) were used to investigate the impacts of different natural mortality rates upon the reference point estimates.

EPR model

The total egg production for a cohort throughout its lifespan was calculated by EPR model as follows:

$$E/R = \sum_{t=t_R}^{t_\lambda} P_{CL_i} \times Egg_{CL_i} \times e^{-\sum_{j=t_R}^{t-1}(S_j F + M)} \quad (5)$$

$$CL_i = CL_\infty(1 - e^{-K(t-t_0)})$$

where t_R is the age of entry into the fishery, t_λ the maximum age of fish in the fishery, P_{CL_i} the fraction of berried lobster at size CL_i, Egg_{CL_i} is the fecundity of lobster at size CL_i and S_t (S_j) the selectivity coefficient for fish of age t (j). The $F_{10\%}$ can be estimated as:

$$\frac{E}{R}\bigg|_{F=F_{10\%}} = 0.1 \times \frac{E}{R}\bigg|_{F=0} \quad (6)$$

The uncertainties of natural mortality, VBGF parameters and of the fecundity-length relationship (Table 1) in the EPR model were simulated according to the procedure described above. Uncertainty associated with maturation by size (Table 1) was assumed to follow a multinomial distribution. A subsampling approach (Chen 1996) was used to generate the multinomial errors.

Similar to the YPR analysis, nine scenarios were considered to cover the possible range of uncertainty for each parameter in the EPR model (Table 3). In particular, scenarios 5 and 6 with high variation for the percentage of mature female by size (P_{mat}-CL) and the fecundity-length relationship (*Fec-CL*), respectively, were used to evaluate the relative importance of variation in maturation and fecundity parameters in assessing the uncertainty of $F_{10\%}$.

For each scenario in YPR and EPR analyses, 1000 Monte Carlo simulations with parameters randomly drawn from 2000 sets of simulated parameters were used to estimate the probability distributions of F_{max}, $F_{0.1}$, $F_{10\%}$, $F_{20\%}$, $F_{30\%}$, and $F_{40\%}$. The coefficient of variation (CV) of each F_{BRP} from the YPR and EPR

Table 2 Uncertainty considered in the estimation of biological reference points of the yield-per-recruit model under different simulation scenarios. α_M, α_{CL} and α_{BW} denote the SDs of natural mortality, carapace length-at-age and body weight-at-size, respectively. M is natural mortality.

	SD of the parameters		
Scenario	α_M (year^{-1})	α_{CL} (cm)	α_{BW} (g)
1 Medium-variation scenario (most realistic scenario)	0.2	0.2	0.1
2 High-variation scenario	0.4	0.4	0.2
3 Low-variation scenario	0.1	0.1	0.05
4 High growth-variation scenario	0.2	0.4	0.1
5 High weight-length-variation scenario	0.2	0.2	0.2
6 High *M*-variation scenario	0.4	0.2	0.1
7 High *M* scenario (mean = 0.6)	0.2	0.2	0.1
8 Low *M* scenario (mean = 0.2)	0.2	0.2	0.1

analysis was used to evaluate the variation of F_{BRP} under different scenarios. During the simulation, the randomly drawn values of parameters may generate flat YPR and EPR curves. We pre-specified that the F_{BRPs} must be between 0.0001 and 10. Per recruit models may yield poorly-defined BRPs when

$$(\frac{\partial(Y/R)}{\partial F}|_{F=0.0001} \times \frac{\partial(Y/R)}{\partial F}|_{F=10}) > 0$$

for the YPR model and

$$(E/R|_{F=0.0001} - E/R|_{F=F_{BRPs}}) \times$$

$$(E/R|_{F=10} - E/R|_{F=F_{BRPs}}) > 0$$

for the EPR model. We considered the out-of-bounds values as "poorly-defined results". The estimation of the percentage of poorly-defined results was as:

[poorly-defined /(poorly-defined + well-defined)] × 100 (7)

For the uncertainty of current fishing mortality (F_{cur}), 1000 sets bootstrapped size distributions were used to estimate total mortality rates by length-converted curves (Pauly 1983), then the distribution of F_{cur} was derived independently from total mortality rates minus median natural mortality estimates derived from three life history empirical formulae (Pauly 1980; Beverton & Holt 1959; Rikhter & Efanov 1976) of Chen (2005). The status of a fish stock is often determined by comparing an indicator reference point (e.g., F_{cur}) with a management reference point (e.g., $F_{0.1}$). In this study, the stock status was determined by including the uncertainty in both the estimates of F_{cur} and F_{BRPs}. We determined the probability of F_{cur} larger than F_{BRPs}, $P(F_{cur} > F_{BRPs})$, for each confidence level from the empirical distributions of F_{cur} and F_{BRPs} using the stochastic decision-making

framework proposed by Helser et al. (2001) and Chen & Wilson (2002).

RESULTS

YPR model and biological reference points

The relationship between Y/R and fishing mortality rate varied with the uncertainty in model parameters for each sex (Fig. 1). High percentages of the poorly-defined results suggested that F_{max} was not well defined when uncertainty was low (i.e., scenario 3) and only a few individual simulation runs could be estimated for females when uncertainty was high (Fig. 2), suggesting that F_{max} is not well defined and may not be appropriate to be used as a BRP in managing the lobster fishery.

In contrast to F_{max}, $F_{0.1}$ was well defined for each scenario. The uncertainty in model parameters yielded considerable variability in the $F_{0.1}$ estimation (Fig. 3). The median of $F_{0.1}$ estimates for the medium-variation scenario (scenario 1) was 0.46 for females and 0.42 for males (Table 4). The mode of the F_{cur} distribution had a lower value than that of $F_{0.1}$ derived for scenario 1. The distributions for $F_{0.1}$ and F_{cur} did, however, overlap (Fig. 3). The probability profile suggested that the probability of current fishing mortality rate being higher than $F_{0.1}$ changed with the decision confidence level (Fig. 4).

When comparing the low-, median and high scenarios (Fig. 3), the result suggests that the uncertainty of the $F_{0.1}$ estimate increases with the variation in input parameters. The CV of the distribution of $F_{0.1}$ in the high-variation scenario (scenario 2) was 0.44 and 0.43 for females and males, respectively. The Y/R curves tended to have higher variation for

Table 3 Uncertainty considered in the estimation of the biological reference points of egg-per-recruit model under different simulation scenarios. α_M, α_{CL} and α_{Fec} denote the SDs of natural mortality, carapace length-at-age and fecundity-at-size (number of eggs). n is the sample size used to control the variation associated with proportional data (Chen 1996). M is natural mortality.

| Scenario	SD of the parameters			
	α_M (year^{-1})	α_{CL} (cm)	α_{Fec} (eggs)	n
1 Medium-variation scenario (most realistic scenario)	0.2	0.2	0.1	100
2 High-variation scenario	0.4	0.4	0.2	10
3 Low-variation scenario	0.1	0.1	0.05	200
4 High growth-variation scenario	0.2	0.4	0.1	100
5 High mature(%)-variation scenario	0.2	0.2	0.1	10
6 High fecundity-variation scenario	0.2	0.2	0.2	100
7 High M-variation scenario	0.4	0.2	0.1	100
8 High M scenario (mean = 0.6)	0.2	0.2	0.1	100
9 Low M scenario (mean = 0.2)	0.2	0.2	0.1	100
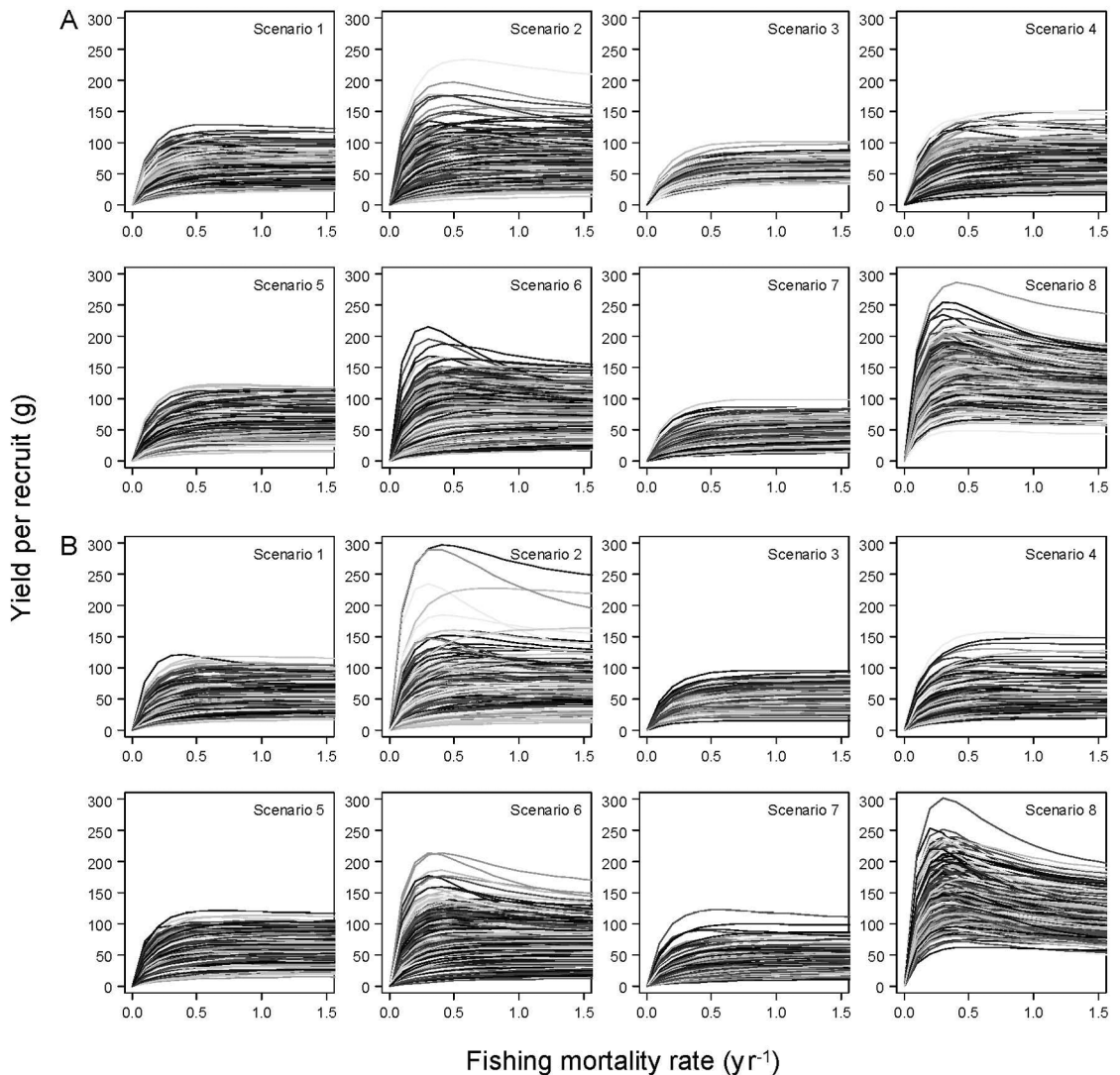
Fig. 1   Variations in yield-per-recruit analyses of eight simulated scenarios for **A**, female and **B**, male spiny lobster, *Panulirus penicillatu*s, in the Taitung fishery, Taiwan.

the high-variation scenario (scenario 2; Fig. 1A and 2B). The comparison of the probability profiles among the first three scenarios (Fig. 4) suggested that at high (>50%) and low (<50%) confidence levels, $P(F_{cur} > F_{0.1})$ tended to decrease and increase, respectively, with uncertainty in the parameters.

The $F_{0.1}$ distributions of the high-growth variation scenario (scenario 4) and the high *W-CL* variation scenario (scenario 5) were similar to that for the medium-variation scenario (scenario 1) for each sex (Fig. 3). However, variation in growth had

larger influences on the $F_{0.1}$ distributions than *W-CL* variations (Table 4) and $F_{0.1}$ distributions had different variations in the high *W-CL* variation scenario between males (CV 0.30) and females (CV 0.28). The profile plots of probability that F_{cur} is larger than $F_{0.1}$ for scenarios 4 and 5 were similar to those for scenario 1 for both sexes (Fig. 4).

For the first six scenarios, the *Y/R* curve and $F_{0.1}$ distribution for scenario 6 were different from those for all other scenarios except for scenario 2 (Fig. 1, 3). Furthermore, $P(F_{cur} > F_{0.1})$ was relatively high

over most confidence levels in the high mortality-variation scenario (scenario 6), compared with other scenarios (Fig. 4). These findings suggest that uncertainty in $F_{0.1}$ was mainly influenced by the uncertainty of natural mortality.

For the high-mortality (scenario 7) and the low-mortality scenario (scenario 8), the distributions of $F_{0.1}$ were significantly different from those of the other scenarios (Fig. 3). For example, for scenario 7, the estimated median $F_{0.1}$ was 0.62 and 0.53 for females and males, respectively. These values were about 1.5 times greater than those of the medium-scenario (0.46 for females and 0.42 for males; Table 4). The $P(F_{cur} > F_{0.1})$ values for scenarios 7 and 8 were also significantly different from those of other scenarios with increasing decision confidence levels (Fig. 4). The estimated mean and median of $F_{0.1}$ for females tended to be higher than that for males for each scenario (Table 4). However, males had a lower probability of F_{cur} being larger than $F_{0.1}$ with increasing confidence intervals than females (Fig. 4).

EPR model and biological reference points

The relationships between E/R and fishing mortality rate (F) varied with uncertainties in model parameters (Fig. 5). High percentages of poorly-defined results suggested that the $F_{10\%}$ was not well defined in comparison with $F_{20\%}$, $F_{30\%}$, and $F_{40\%}$ (Fig. 6). This finding suggests that $F_{10\%}$ may be inappropriate to be used as a BRP in managing the Taitung lobster fishery.
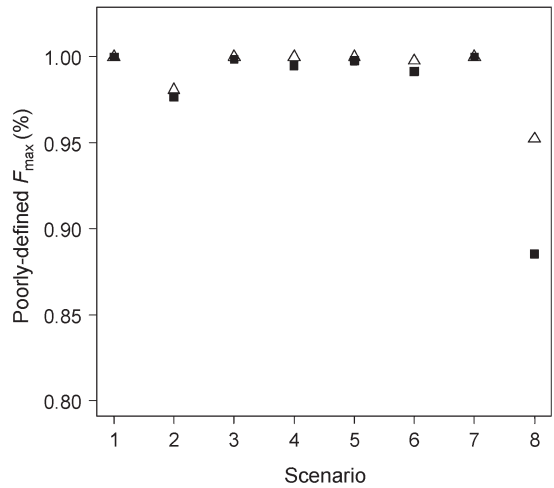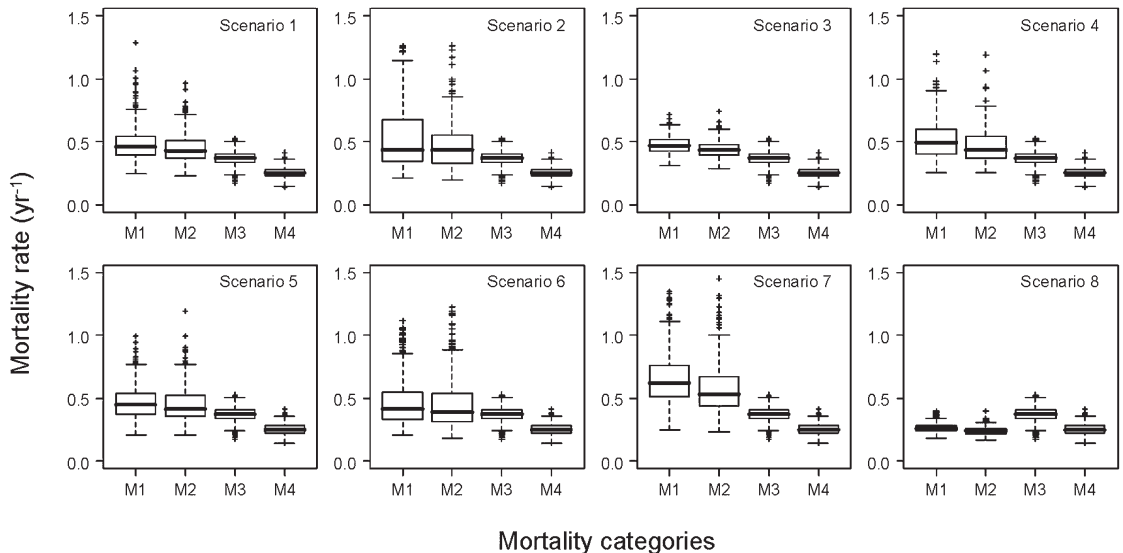

Fig. 2 Percentage of poorly-defined estimates for the biological reference point, F_{max}, in the yield-per-recruit model under different simulation scenarios for female (open triangles) and male (closed squares) *Panulirus penicillatus*. (Note that *y* axis is truncated from 0.80 to 1.00.)

Fig. 3 (*below*) Boxplots of the estimated biological reference point of the yield-per-recruit model ($F_{0.1}$) and the current fishing mortality rate (F_{cur}) in the simulation study under eight different scenarios. M1 and M2 denote $F_{0.1}$ estimates of females and males, respectively. M3 and M4 denote F_{cur} estimates of females and males, respectively.
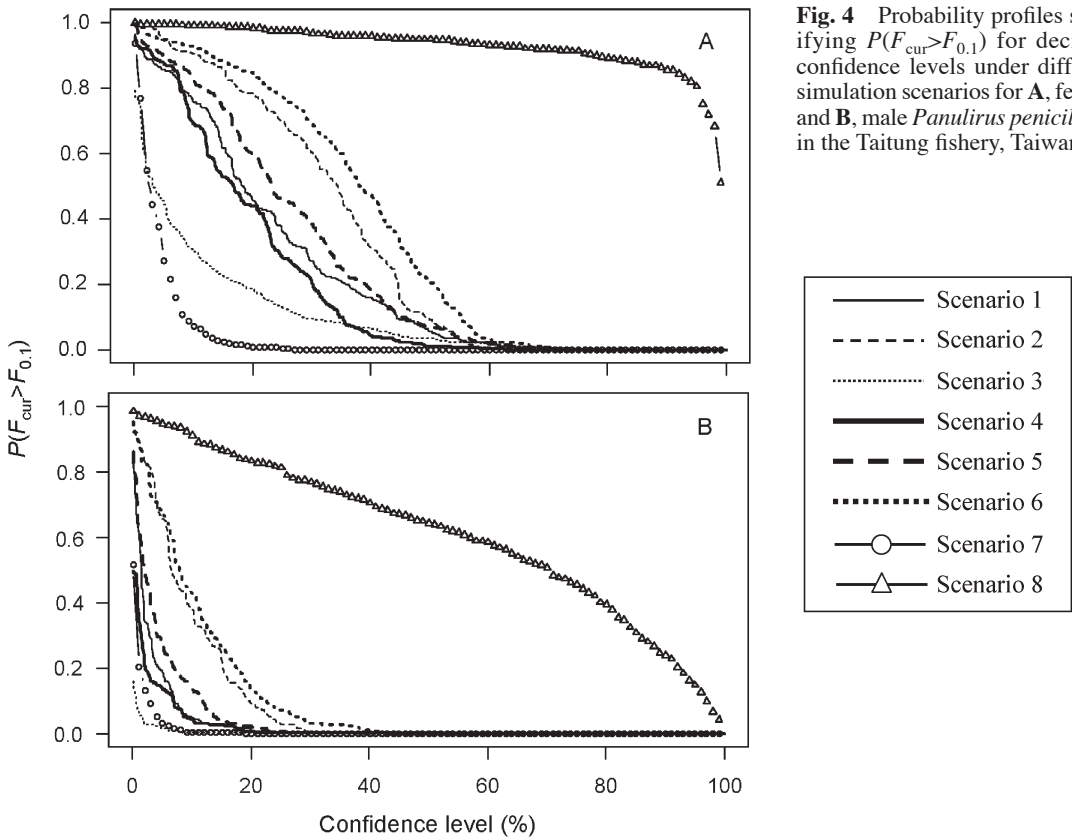
Fig. 4 Probability profiles specifying $P(F_{cur}>F_{0.1})$ for decision confidence levels under different simulation scenarios for **A**, female and **B**, male *Panulirus penicillatus* in the Taitung fishery, Taiwan.

Table 4 Estimates of the mean, median and coefficient of variation (CV) for the biological reference point ($F_{0.1}$) of the yield-per-recruit model under different scenarios and current fishing mortality rate (F_{cur}), for female and male lobster *Panulirus penicillatus*.

Scenario	Sex	Mean	Median	CV
1	M	0.44	0.42	0.26
	F	0.48	0.46	0.26
2	M	0.48	0.44	0.43
	F	0.52	0.44	0.44
3	M	0.44	0.44	0.15
	F	0.47	0.47	0.13
4	M	0.47	0.44	0.31
	F	0.51	0.49	0.31
5	M	0.45	0.42	0.30
	F	0.47	0.45	0.28
6	M	0.46	0.39	0.46
	F	0.46	0.42	0.38
7	M	0.57	0.53	0.34
	F	0.66	0.62	0.31
8	M	0.24	0.24	0.13
	F	0.27	0.26	0.13
F_{cur}	M	0.25	0.25	0.16
	F	0.37	0.37	0.16

The variations of $F_{20\%}$, $F_{30\%}$, and $F_{40\%}$ estimates increased with the uncertainty of parameters (Fig. 7). For example, for scenarios 1, 2, and 3, the CV of $F_{40\%}$ was 0.21, 0.36, and 0.13, respectively. Similar to the YPR results, the probability profile suggested that $P(F_{cur}>F_{BRPs})$ in EPR models tended to increase and decrease with increasing uncertainty of EPR parameters at lower (<50%) and higher (>50%) confidence levels, respectively (Fig. 8).

The distributions of $F_{40\%}$, $F_{30\%}$, and $F_{20\%}$ of the high-growth variation scenario (scenario 4), the high maturity percentage variation scenario (scenario 5), and the high fecundity-variation scenario (scenario 6) were similar to those of the medium-variation scenario (scenario 1; Fig. 7). Scenario 6 (CV 0.24) had larger influences on the F_{BRPs} distributions than scenarios 4 (CV 0.19) and 5 (CV 0.22). Furthermore, the probability profiles of $P(F_{cur}>F_{BRPs})$ in the EPR analysis for scenarios 4, 5 and 6 were also similar to that of scenario 1 (Fig. 8), suggesting that uncertainties of other parameters (i.e., growth-related parameters) had limited effects on the uncertainty of
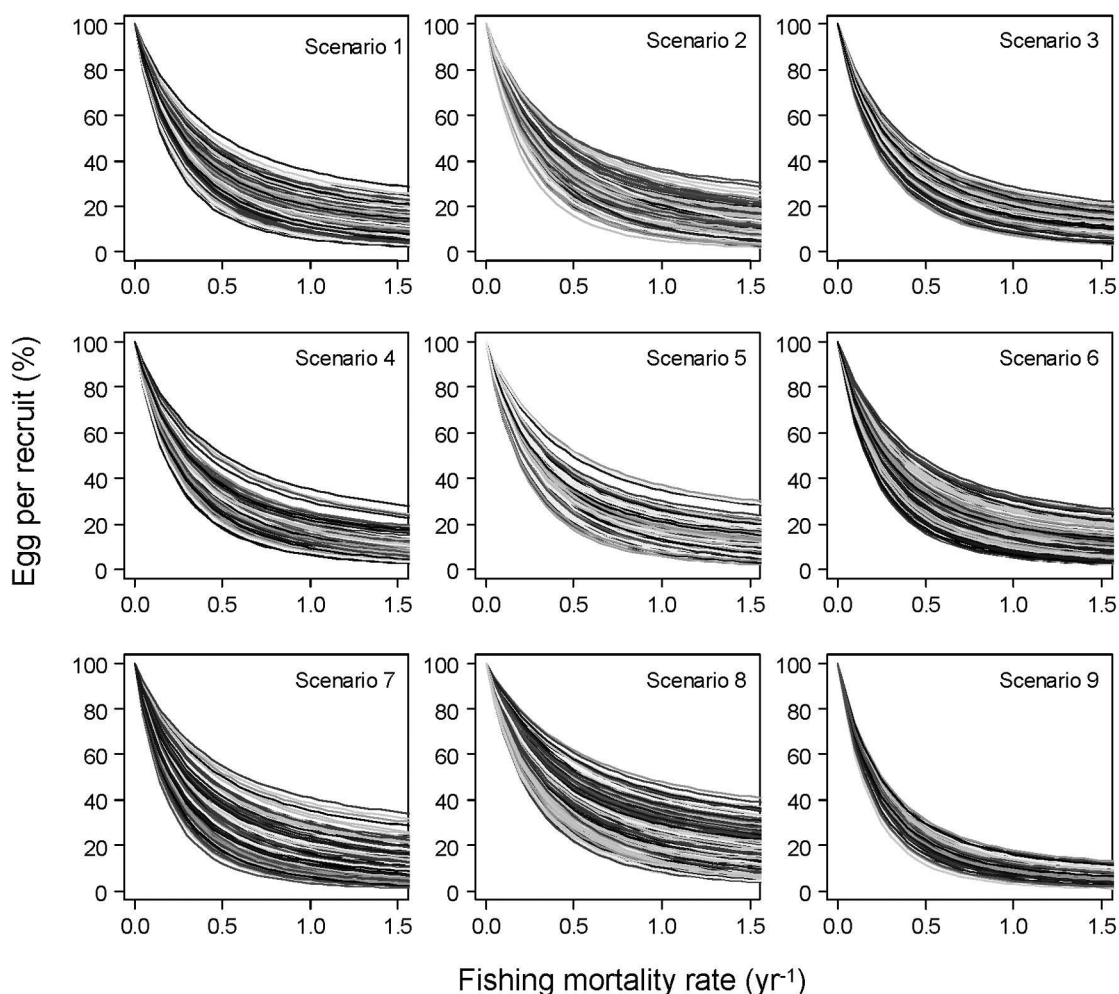
Fig. 5 Variations in egg-per-recruit analyses under nine simulated scenarios for *Panulirus penicillatus* in the Taitung fishery, Taiwan. Egg-per-recruit is expressed as a percentage of the egg-per-recruit when the stock is in a pristine state.

F_{BRPs} estimated from the EPR model.

For the high-mortality (scenario 8) and the low-mortality scenario (scenario 9), either the E/R-F relationships or the F_{BRPs} distributions or the probability profile of $P(F_{cur}>F_{BRPs})$ over confidence levels differed greatly from those of other scenarios (Fig. 5, 7 and 8), suggesting that the uncertainty in natural mortality was the main contributor to the estimated uncertainty for F_{BRPs} in the EPR analysis.

Comparing the probability distributions of $F_{20\%}$, $F_{30\%}$, and $F_{40\%}$ among different scenarios suggested that the impacts of parameter uncertainty on the uncertainty of $F_{10\%}$ tended to be larger than those on the other reference points (Table 5). The CVs of

the $F_{0.1}$ probability distribution in the YPR analyses were similar to those for $F_{20\%}$ and $F_{30\%}$, but not as high as that for $F_{10\%}$ or as low as that for $F_{40\%}$ (Tables 4 and 5).

DISCUSSION

This per recruit analysis is a preliminary investigation into developing BRPs for the Taitung lobster fishery. A BRP derived from per recruit analysis has often been used as a proxy for reference points derived from a stock assessment model (e.g., spawner-recruit reference points), because it is relatively simple and
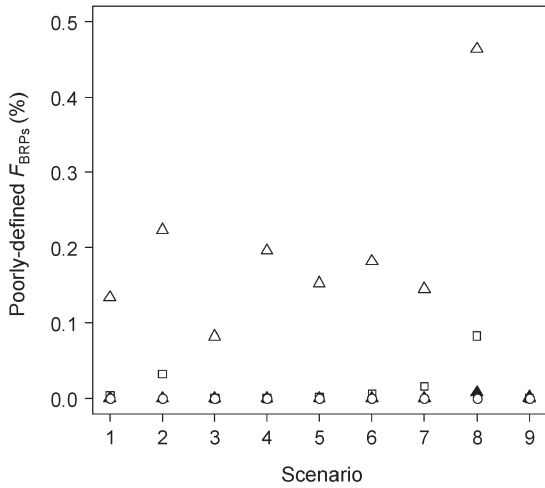
Fig. 6 (*left*) Percentage of poorly-defined estimates for the biological reference points, F_{BRPs}, in the egg-per-recruit model under different simulation scenarios. $F_{40\%}$, open circles; $F_{30\%}$, closed triangles; $F_{20\%}$, open squares; $F_{10\%}$, open triangles.

Fig. 7 (*below*) Boxplots of the estimated biological reference points (F_{BRPs}) and current fishing mortality rate (F_{cur}) in the simulation study under nine different scenarios for the egg-per-recruit analysis. M1, M2, M3 and M4 denote the estimations of F_{BRPs} ($F_{40\%}$, $F_{30\%}$ and $F_{20\%}$) and F_{cur}, respectively.
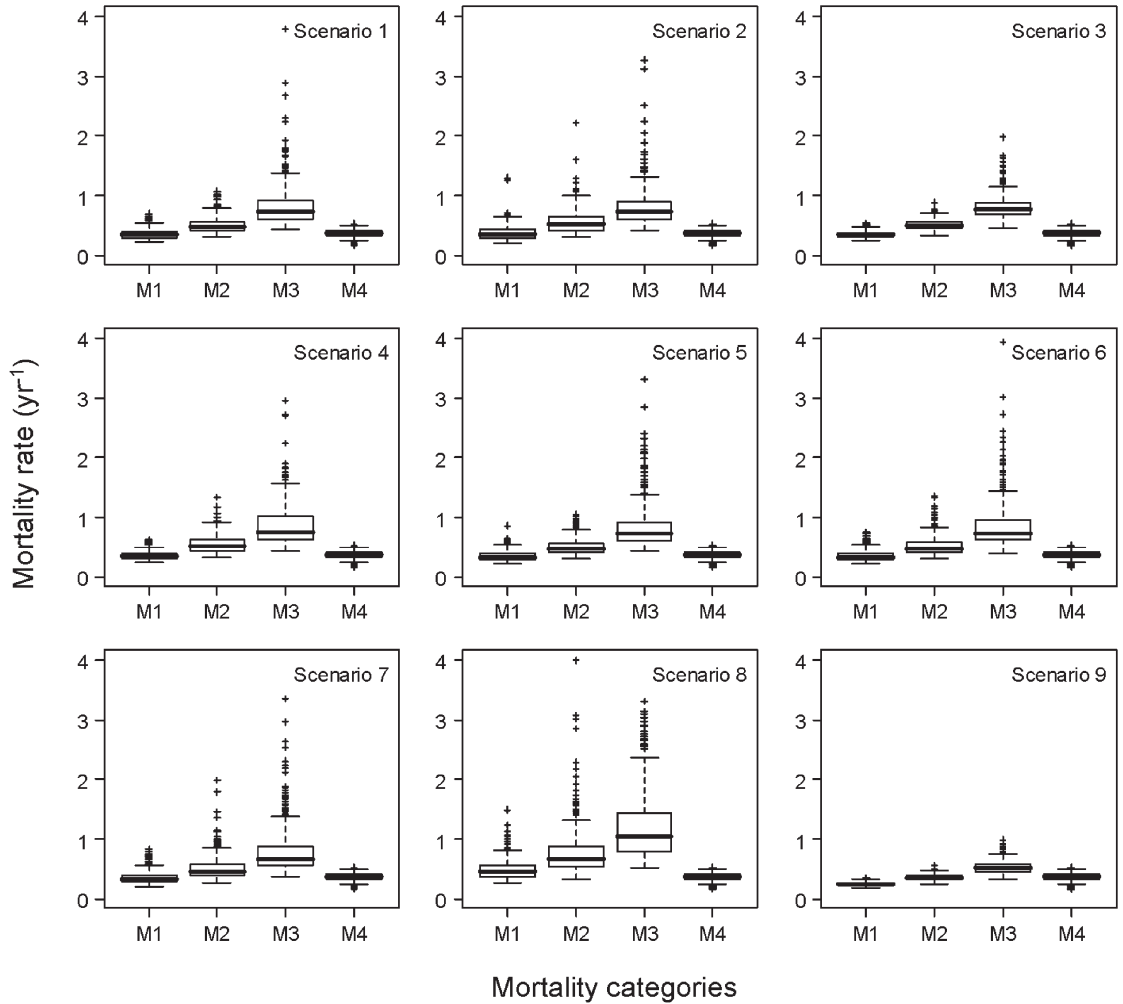
Fig. 8 Probability profiles specifying the probability of the current fishing mortality rate (F_{cur}) being larger than the biological reference points, **A**, $F_{20\%}$; **B**, $F_{30\%}$; and **C**, $F_{40\%}$; for decision confidence levels under different simulation scenarios of the egg-per-recruit analysis for *Panulirus penicillatus* in the Taitung fishery, Taiwan.
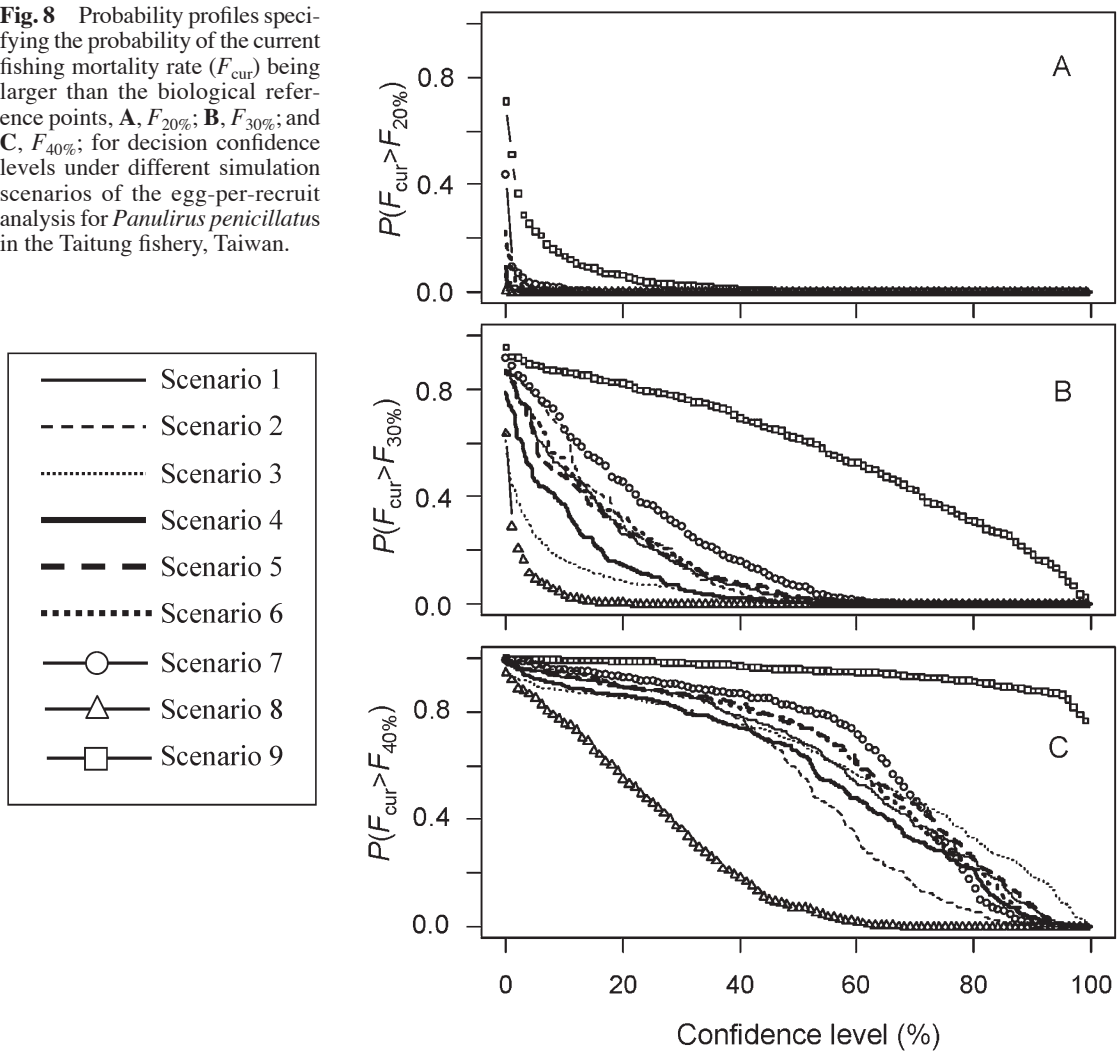

Table 5 Estimates of CV for the distribution of biological reference points (F_{BRPs}: $F_{10\%}$, $F_{20\%}$, $F_{30\%}$, and $F_{40\%}$) in egg-per-recruit analyses under different scenarios. (Numbers in the parentheses denote the median of F_{BRPs} estimates.)

Scenario	$F_{10\%}$	$F_{20\%}$	$F_{30\%}$	$F_{40\%}$
1	0.45 (1.32)	0.40 (0.73)	0.25 (0.48)	0.21 (0.35)
2	0.49 (1.33)	0.51 (0.73)	0.43 (0.51)	0.36 (0.36)
3	0.41 (1.56)	0.23 (0.77)	0.15 (0.50)	0.13 (0.35)
4	0.46 (1.33)	0.44 (0.75)	0.30 (0.51)	0.19 (0.35)
5	0.47 (1.32)	0.41 (0.74)	0.26 (0.47)	0.22 (0.34)
6	0.43 (1.34)	0.44 (0.74)	0.29 (0.48)	0.24 (0.34)
7	0.42 (1.22)	0.48 (0.67)	0.38 (0.45)	0.31 (0.32)
8	0.42 (1.66)	0.48 (1.04)	0.48 (0.47)	0.32 (0.45)
9	0.27 (0.92)	0.18 (0.52)	0.12 (0.36)	0.12 (0.25)

easy to implement for data poor fisheries (Restrepo 1999). In general, there are two sources of uncertainty common to most life history and fisheries parameter estimations: variation in the statistical estimation of the parameter (i.e., the parameter was not estimated without error as is assumed) and natural variability in fish life history process (i.e., different geographic data). For example, the divergent estimates of the growth parameter of *P. penicillatus* might result from both of these sources (Chen 2005). The Monte Carlo simulation approach enabled us to incorporate uncertainty into the model parameters. The sensitivity study demonstrated that uncertainty of different parameters can have different impacts on estimating F_{BRPs} and determining stock status. The high uncertainty in F_{BRPs} resulting from high uncertainty in life history parameters can be translated into a decreasing $P(F_{cur} > F_{BRPs})$ at high (>50%) and low (<50%) confidence levels, leading to an increase in uncertainty in the determination of stock status.

The comparison of scenario 1 with scenarios 4 and 5 in the YPR analysis suggests that growth-variation and *W-CL* variation have some influence on the $F_{0.1}$ distributions. The $F_{0.1}$ distribution for the high-mortality variation scenario was significantly different from that for scenario 1 and similar to that for scenario 2. Furthermore, $F_{0.1}$ distributions for high-mortality and low-mortality scenarios were different from those for the other scenarios. Similar results were observed in the EPR analysis, suggesting that the uncertainty in natural mortality is a main contributor to the uncertainty for F_{BRPs}. In general, natural mortality is the most difficult parameter to estimate in fish population dynamics, and especially for crustacean species that have complex multistage life history patterns (i.e., moult and long larval duration, Smith & Addison 2003).

The uncertainty of current fishing mortality rate was derived from the bootstrapped total mortalities minus the median of natural mortality estimates (Chen 2005). The size-converted catch curve is strongly influenced by population structure such as size at recruitment, gear selectivity, sample size and range, and outliers, which influenced the goodness of fit and the slope of the regression line. Given the sensitivity of the total mortality estimation, it is likely that the estimated total mortality for Taitung lobster has large uncertainty. The variation associated with the current fishing mortality rate F_{cur} is also important in determining the status of a fish stock using the method proposed in this study (Chen & Wilson 2002; Jiao et al. 2005). The distributions of F_{cur} and F_{BRPs} were estimated independently from

two models for comparison. It would be preferable to use one model for estimating F_{BRPs} and F_{cur} under the same set of parameters to incorporate the covariance between F_{BRPs} and F_{cur} (Chen & Wilson 2002). Thus, we need to develop a model in the future that can estimate both F_{BRPs} and F_{cur} within the same modelling framework.

F_{max} is often used as a proxy for fishing mortality rate at maximum sustainable yield (F_{MSY}), but is believed to be an overestimate of F_{MSY} because it does not account for recruitment-dependent factors (Gabriel & Mace 1999). In this study, the Monte Carlo simulation suggests that F_{max} cannot be well defined in most scenarios for this lobster fishery, suggesting that F_{max} is not a good BRP candidate for the management of the fishery (Fig. 2). $F_{0.1}$ is often considered more suitable as a management target than F_{max} (Deriso 1987; Hilborn & Walters 1992). Although $F_{0.1}$ is commonly interpreted as a conservative estimate of F_{MSY}, this approximation is not always so (Mace 1994). It is, however, well defined for the lobster fishery in this study.

Mace & Sissenwine (1993) advocated $F_{20\%}$ as a recruitment overfishing threshold for well-known stocks with at least average resilience and $F_{30\%}$ as a recruitment overfishing threshold for less well-known stocks or those considered to have low resilience. For American lobster, EPR reference points have formally been adopted in the United States and the stock status is determined based on a comparison of F_{cur} and $F_{10\%}$ (limit BRP) (ASMFC 2000). The choice of $F_{10\%}$ as the limit BRP was based on the meta-analysis of the slope of the recruitment curve at origin for a number of marine species, with further qualitative consideration of lobster life history features (Fogarty & Gendron 2004). Ennis & Fogarty (1997) indicated a steep ascending limb near the origin of the recruits and egg production curve for American lobster and suggested that the population would be resilient to a high level of exploitation. For this study, however, we had no biological information about the population recruitment dynamics for Taitung lobster. Although adapting F_{BRPs} by extrapolating data from other species is common, it introduces considerable uncertainty and may lead to mistakes in developing BRPs for a particular fishery (Hilborn 2002). In the present study, $F_{10\%}$ was not well defined in comparison with other F_{BRPs} in the EPR model (Fig. 6), which may have resulted from the high parameter of natural mortality.

In general, $F_{0.1}$ and $F_{40\%}$ were reference points that gained prominence as proxies of target reference

points. In this study, the variation estimates of F_{BRPs} for the EPR model (i.e., CV) suggest that uncertainty of F_{BRPs} in the EPR analysis increased with exploitation level. Furthermore, comparing the CVs of the distributions of $F_{0.1}$ and F_{BRPs} of the EPR analysis suggests that $F_{40\%}$ is less sensitive to the parameters' uncertainty than $F_{0.1}$ (Tables 4 and 5). This study demonstrates the impact of uncertainty of different parameters on F_{BRPs} in per recruit analysis. However, detailed evaluation of the appropriateness of F_{BRPs} for the Taitung lobster stock was outside the scope of this study and further studies are necessary to assess the effectiveness and appropriateness of using $F_{40\%}$ as target reference points for this stock.

In this study, knife-edge recruitment was assumed for the Taitung fishery. However, the unenforced minimum size regulation may lead to smaller functional age at recruitment, which in turn is likely to give lower F_{BRPs} than the present estimates. Furthermore, changes in both biotic and abiotic conditions may also affect the specifications of limit and target reference points in the future (Fogarty & Gendron 2004). We suggest the establishing of a realistic population dynamics simulator that mimics the lobster life history and fishery process and incorporates uncertainties from other sources (e.g., moulting, discarding, gear selectivity) in estimating biological reference points. It is currently unknown if there are additional larvae inputs from adjacent waters (e.g., waters near Philippine Islands) through the Kuroshio Current for the Taitung lobster fishery. If large numbers of larvae are from outside areas, we might need to consider developing spatially explicit management BRPs.

ACKNOWLEDGMENTS

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