

Linking fishing mortality reference points to life history traits: an empirical study

Shijie Zhou, Shaowu Yin, James T. Thorson, Anthony D.M. Smith, and Michael Fuller

Abstract: The rule of thumb that fishing mortality to achieve maximum sustainable yield (F_{MSY}) equals natural mortality (M) has been both criticised and supported by theoretical arguments. However, the relationship has been rarely investigated using empirical data. We carried out a meta-analysis on 245 fish species worldwide and linked three types of reference points (F_{BRP} : F_{MSY} , F_{proxy} , and $F_{0.5r}$) to M and other life history parameters (LHP). We used Bayesian hierarchical errors-in-variables models to investigate the relationships and included the effect of taxonomic class and order. We compared various models and found that natural mortality is the most important LHP affecting F_{BRP} . Other covariates, such as von Bertalanffy growth coefficient, asymptotic length, maximum age, and habitat types, add little to the relationship, partially because of correlation and large measurement and process errors. The best model results in $F_{MSY} = 0.87M$ (standard deviation (SD) = 0.05) for teleosts and $F_{MSY} = 0.41M$ (SD = 0.09) for chondrichthyans. F_{proxy} based on per-recruit analysis is about 15% smaller than F_{MSY} . Results could be used to estimate F_{BRP} from LHP in data-poor situations.

Résumé : Des arguments théoriques ont été utilisés tant pour critiquer que pour appuyer la règle généralement évoquée voulant que la mortalité du poisson nécessaire à l'atteinte du rendement équilibré maximum (F_{MSY}) soit égale à la mortalité naturelle (M). Cependant, cette relation a rarement été examinée à la lumière de données empiriques. Nous avons effectué une méta-analyse de 245 espèces de poissons à l'échelle planétaire et relié trois types de points de référence (F_{BRP} : F_{MSY} , F_{proxy} , et $F_{0.5r}$) à M ainsi qu'à d'autres paramètres du cycle biologique (LHP). Nous avons utilisé des modèles hiérarchiques bayésiens d'erreurs sur les variables pour étudier ces relations et y avons intégré l'effet de la classe et de l'ordre taxinomiques. Nous avons comparé divers modèles et déterminé que la mortalité naturelle est le LHP ayant la plus grande incidence sur les F_{BRP} . D'autres covariables, telles que le coefficient de croissance de von Bertalanffy, la longueur asymptotique, l'âge maximum et les types d'habitat, n'ont que peu d'incidence sur la relation, en raison notamment de la corrélation et d'importantes erreurs de mesure et de traitement. Le meilleur modèle donne une valeur de $F_{MSY} = 0,87M$ (écart-type (SD) = 0,05) pour les téléostéens et de $F_{MSY} = 0,41M$ (SD = 0,09) pour les chondrichthyens. La valeur de F_{proxy} basée sur l'analyse du rendement par recrue est d'environ 15 % inférieure à F_{MSY} . Les résultats pourraient être utilisés pour l'estimation de F_{BRP} à partir de LHP dans les cas où peu de données sont disponibles.

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Introduction

Biological reference points (BRPs) are used both as targets and limits in stock status assessment, harvest control rules, and tactical fisheries management. Generally, BRPs may be based either on fishing mortality (F_{BRP}) or biomass (B_{BRP}). There are also two general approaches to calculating F_{BRP} and B_{BRP} . F_{MSY} and B_{MSY} are calculated from population dynamics models (e.g., stock–recruitment or biomass dynamic models) and include estimated compensatory effects (e.g., recruitment compensation). Alternatively, $F_{0.1}$, $F_{x\%}$, $B_{0.1}$, and $B_{x\%}$ are based on per-recruit analysis (e.g., yield-per-recruit or spawner-per-recruit). The per-recruit approach requires fishery

selectivity and individual growth and mortality parameters and does not use data to estimate recruitment processes or density-dependent mechanisms, although the numeric target for each per-recruit proxy (e.g., $F_{35\%}$ vs. $F_{25\%}$) implies an assumed value for steepness (see Quinn and Deriso 1999 for more details). Data required for deriving these BRPs vary widely, and maximum sustainable yield (MSY)-based BRPs may be preferred over per-recruit BRPs when data are available to estimate recruitment compensation, recognizing that the precision of MSY-based reference points depends on the specific model and the quality of the data.

Estimating BRPs for fishery management can be difficult. Reliable estimation requires parameters derived from quanti-

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S. Zhou. CSIRO Marine and Atmospheric Research and Wealth from Oceans Flagship, P.O. Box 2583, Brisbane, Qld 4001, Australia.

S. Yin. School of Life Sciences, Nanjing Normal University, 1 Wenyuan Road, Nanjing, Jiangsu 210046, P.R. China.

J.T. Thorson. School of Aquatic & Fishery Sciences, Box 355020, University of Washington, Seattle, WA 98195-5020, USA.

A.D.M. Smith and M. Fuller. CSIRO Marine and Atmospheric Research and Wealth from Oceans Flagship, Castray Esplanade, Hobart, Tas 7001, Australia.

Corresponding author: Shijie Zhou (e-mail: shijie.zhou@csiro.au).

Table 1. Examples of theoretical studies on biological reference points with life history traits.

Reference	Formula	Note
Francis 1974	$F_{MSY} = M$	If recruitment was constant
Deriso 1982	$F_{MSY} = (\alpha - M)/2$	α : parameter of logistic spawner–recruit model
Deriso 1987	$F_{0.1} = 0.88 \sim 1.25M$	For a wide range of M/κ
Clark 1991	$F_{mmy} \approx F_{0.1} \approx M$	In most cases; F_{mmy} is the maximum of the minimum yields at each level of spawning biomass per recruit
Thompson 1992	$F_{MSY} > \text{or} < M$	Depending on the power parameter in a power function of stock–recruitment relationship
Thompson 1993	$F \leq 0.8 M$	Would prevent stock from overfishing
Mace 1994	$F_{0.1} \approx F_{35\%} \approx M$	For each M – κ combination
Kirkwood et al. 1994	$F_{MSY} \propto M$	For given length at first exploitation l_c and M/κ
Siddeek 2003	$F_{MSY} = \left(\frac{W(F_{MSY})R(F_{MSY})\{1 - \exp[-Z_{MSY}(\lambda - t_r)]\}}{XW(0)R(0)\{1 - \exp[-Z_{MSY}(\lambda - t_r)]\}} \right) M$	Based on general growth and mortality assumptions
Beddington and Kirkwood 2005	$F_{max} = a(L_c, h)\kappa$	$a(L_c, h)$ is a constant depending on the length at first exploitation and steepness

tative stock assessments (e.g., selectivity at age) and often requires time series data and considerable biological information. Unfortunately, most commercial species worldwide do not have sufficient data to use quantitative stock assessment methods. This is particularly the case for small fisheries with low economic value, new fisheries in exploratory or developmental phases, species fished opportunistically because of sporadic availability, by-product species, etc. Furthermore, the goals of maintaining biodiversity and ecosystem structure in fishery management require that all species impacted by fishing be sustainable in the long term. The ecosystem approach to fishery management calls for sustainability evaluation for both target and nontarget species (Food and Agriculture Organization of the United Nations 2003). However, it would be impossible to develop BRPs using formal stock assessment methods for hundreds of nontarget bycatch species that have little data.

One possible approach to identifying F_{BRP} for data-poor stocks is to identify a relationship between F_{BRP} and commonly available estimates of life history traits. There has been a long history of interest in using life history traits as a surrogate for optimal fishing mortality. Early studies included Alverson and Pereyra (1969), who suggested using natural mortality as a proxy for sustainable fishing mortality, and Gulland (1970, 1971), who used natural mortality and pristine biomass to derive an estimate for MSY. These early works resulted in the well-known approximation $F_{MSY} = M$.

Since the 1970s, numerous theoretical studies (Table 1) have tried to prove, improve, or disprove this relationship between F_{BRP} and M . Francis (1974) showed that optimal fishing mortality $F_{MSY} = M$ held if recruitment was constant using Schaeffer surplus production model, but that density-dependent recruitment would affect this relationship. Deriso (1982) included the von Bertalanffy growth coefficient (κ) and reproductive parameters using a delay-difference model and found that F_{MSY} could be equal to, less than, or greater than M depending on other variables. Deriso (1987) explored the impact of life history parameters (LHPs) and concluded that $F_{0.1}/M$ ranged from 0.88 to 1.25 over a wide range of M/κ (i.e., ratio between natural mortality and growth parameter). Through simulation with a range of LHP values typical of demersal fish and a range of realistic spawner–recruit relationships, Clark (1991) showed that yield will be at least 75% of MSY so long as the spawning biomass was maintained in

the range of about 20%–60% of the unfished level, regardless of the form of the spawner–recruit relationship. A relative spawning biomass in this range can be achieved by choosing a fishing mortality rate that will reduce the spawning biomass per recruit (SPR) to about 35% of the unfished level. This is the level of fishing mortality that maximizes the minimum yield among all of the spawner–recruit relationships. Clark (1993) revised the recommendation of 35% SPR to 40% because of serial correlation in recruitment and even higher for species with low levels of resiliency (Clark 2002). Similarly, Thompson (1992) found that F_{MSY} could be greater or less than M depending on the power parameter in a stock–recruitment relationship, while Thompson (1993) concluded that setting a maximum fishing mortality rate at 80% of the natural mortality rate would in general prevent overfishing.

Other studies have used age-structured and multispecies models to explore the relationship between F_{BRP} and M . Mace (1994) used age-structured population models and assumed forms for recruitment compensation and showed that $F_{0.1}$, F_{max} , $F_{20\%}$, and $F_{35\%}$ all increased with both M and κ . For each M – κ combination, $F_{0.1}$, $F_{35\%}$, and $F = M$ were of similar magnitude. Using a fully age-structured model, Kirkwood et al. (1994) showed that when recruitment was constant and independent of mature stock size, the yield as a proportion of unexploited biomass was directly proportional to the natural mortality rate. When recruitment was allowed to vary deterministically with mature stock size, this proportional relationship held approximately, at least for biologically feasible parameter combinations. Collie and Gislason (2001) tested a suite of F_{BRP} types for their robustness to observed changes in natural mortality and growth rates in a multispecies context and found that F_{BRP} was much more sensitive to the changes in natural mortality rates than to growth variation. Siddeek (2003) developed a general formulation of the F_{MSY} to M relationship and found that F_{MSY} exceeded M for most cases. Using life history invariants, Beddington and Kirkwood (2005) estimated F_{MSY} from growth parameters, length at first capture, and recruitment steepness and concluded that F_{MSY}/M increased with higher levels of steepness, but that $F_{MSY} < M$ for most stocks.

In contrast with these theoretical and simulation modelling studies, few studies have empirically investigated the relationship between F_{BRP} and LHPs. Such a relationship from data-rich stocks would be extremely valuable for data-poor stocks.

Patterson (1992) related change in stock biomass to exploitation rate using data from 28 stocks of 11 small pelagic species. He concluded that fishing at exploitation rate $F/Z = 0.4$ would keep biomass from declining. This is equivalent to $F = \frac{2}{3}M$. Mertz and Myers (1998) compiled data for a broad range of taxa and found that the long-term ratio of biomass-averaged fishing mortality to the biomass-averaged total mortality (F/Z) was around 0.8 for piscivore ground fish and near 0.5 for prey species, which means $F = 4M$ and $F = M$, respectively.

In this paper, we compiled F_{BRP} data for more than 200 species and stocks worldwide that have been assessed with different methods. We conducted a meta-analysis and linked fishing mortality based reference points to natural mortality and other commonly available LHPs by taking errors in variables into account. Our goals were (i) to estimate the ratio of F_{BRP} to M ; (ii) to estimate the differences among F_{MSY} , F_{proxy} , and $F_{0.5r}$; (iii) to explore the impact of other LHPs on F_{BRP} ; and (iv) to explore differences in productivity (e.g., F_{BRP}/M) by taxonomic class and order. The results aim to provide management guidance for data-poor and bycatch species (Smith et al. 2009; Zhou et al. 2009a) that do not have sufficient data for quantitative stock assessment.

Materials and methods

Data

We collected F_{BRP} data from a variety of sources, including published research papers, reports, and unpublished documents. Fishing mortality has often been expressed in two ways: the instantaneous fishing mortality rate (F) and exploitation rate (E). The majority of data we collected were based on F_{BRP} . For the literature that reported exploitation rates, we converted E_{BRP} into F_{BRP} by incorporating natural mortality (Quinn and Deriso 1999). When available, we recorded LHPs from the same paper, report, or document as used to provide the F_{BRP} . When LHPs were not listed in the original material, we collected these data from FishBase (<http://www.fishbase.org>). Considering potential large uncertainty in FishBase, we avoided using data flagged as “questionable”. Data from FishBase may not be deemed to be accurate by local practitioners, but represents a data source that is generally available for data-poor assessments. We therefore believe that sourcing data from FishBase allows model estimates of error-in-variables that will be immediately applicable for future data-poor assessments. A total of 245 species with 333 F_{BRP} points were included in the analysis (Table 2; Supplementary Table S1¹).

Fishing mortality-based biological reference points (F_{BRP})

We distinguish between three broad categories of F_{BRP} when compiling and analysing these data. Within each category, definitions and methods used to derive the reference points may differ, but we do not distinguish them further. For example, F_{MSY} can be defined from an age-structured model or a biomass dynamics model. This broad grouping is to increase the sample size in each category while allowing the models to capture the uncertainty.

The first category, F_{MSY} from formal stock assessments, includes age-structured stock assessment models fit to time-

Table 2. Number of species and data points included in the analysis.

Type	Chondrichthyes		Teleostei	
	Species	Data points	Species	Data points
F_{MSY}	10	12	73	88
F_{proxy}	4	4	99	131
$F_{0.5r}$	52	87	7	11
Total	66	103	179	230

Note: Type is the methods used to derive the three types of reference points.

series data for estimating fishing mortality rate that will result in MSY. It also includes biomass-dynamic (a.k.a. surplus production) models fitted to survey or annual catch-effort data. The resulting estimate of F_{MSY} accounts for compensatory processes (recruitment compensation for age-structured models or aggregate compensation for surplus production models) and is currently the standard for single-species stock assessment F_{BRP} . It should be noted that the values of F_{MSY} depend on the methodologies, assumptions, and data being used to estimate them and thus represent a summary of current stock assessment estimates of F_{MSY} with any inaccuracies or biases this may imply.

The second category, F_{proxy} from per-recruit methods, includes BRPs derived from yield-per-recruit (e.g., $F_{0.1}$) and spawner-per-recruit ($F_{x\%}$) analyses. Per-recruit analysis incorporates information about individual growth and fishery selectivity parameters and is generally less data-intensive than assessment estimates of F_{MSY} . When multiple proxies were available, we chose to use $F_{0.1}$ (i.e., the fishing mortality where marginal yield-per-recruit is 10% of its level for an unexploited population).

The third category is $F_{0.5r}$ from demographic analyses of intrinsic growth rate. Population growth rate r for a given population can be derived from life history tables and or Leslie matrices (e.g., Smith et al. 1998; Cortes 2002). The resulting estimate r has often been interpreted as the intrinsic growth rate in the fisheries literature (Smith et al. 1998; Cortes 2002, 2006), although this is only true where the demographic parameters are estimated while the population is severely depleted (Gedamke et al. 2007). Resulting estimates of r can then be transformed to an estimate of F_{MSY} , given an assumed form for the surplus production relationship. We adopt the convention that $F_{MSY} = F_{0.5r} = r/2$, as implied by the Schaeffer surplus production model (Quinn and Deriso 1999).

Within the three categories, F_{MSY} is our primary interest because it takes density-dependent processes into account and hence incorporates information regarding long-term sustainability of a stock. The second category, F_{proxy} , implies an assumed value for recruitment compensation. It is interesting to compare it with F_{MSY} because F_{proxy} is widely used in fishery management. The third category of F_{BRP} based on population growth rate is typically used in conservation but rarely used in fishery management. However, it is often the only method available for long-lived species such as sharks, so it is also informative to include $F_{0.5r}$ as a comparison, noting the potential bias pointed out by Gedamke et al. (2007).

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/f2012-060>.

Parameter estimation using Bayesian hierarchical error-in-variable models (BHEIV)

The LHPs that we investigated were natural mortality rate (M), von Bertalanffy growth coefficient (κ), asymptotic length (L_∞), maximum age (A_{\max}), and habitat type (H). These data were sourced primarily from FishBase, so that model inference would be appropriate when applied to data-poor species where FishBase often represents the only available source of life history information. Species are categorized into five habitat types: bathypelagic (depth about 1000–4000 m), benthopelagic (about 100 m off the bottom of the ocean), demersal (close to the bottom of the ocean), pelagic (near the surface), and reef fish. We group data at class (Teleostei and Chondrichthyes) and order levels to capture major life history variability and to avoid overparameterization at species or stock levels. Along with three F_{BRP} categories (i.e., type), we consider these groups (a matrix composed of taxonomic levels and the type of methods) as multiple populations. The amount of data and their quality vary substantially among these populations (Table 2), but populations share certain similarities in their life history traits and BRPs. Hence, we take the advantage of Bayesian hierarchical modelling to derive robust estimates from such a multilevel structure.

Because natural mortality rate M , growth coefficient κ , asymptotic length L_∞ , and maximum age A_{\max} cannot be accurately measured, ignoring errors in these variables would result in biased estimates of their effects on F_{BRP} . To obtain unbiased estimates, we specifically incorporated measurement errors in these variables by using an error-in-variable (EIV, also called measurement error) model (Fuller 1987; Quinn and Deriso 1999). Let us assume that y_i is the real unobserved values of the observed explanatory variable x_i for species i . The EIV model is then

$$(1) \quad y_i = x_i \exp(\varepsilon_i)$$

where $\varepsilon_i \sim \text{normal}(0, \sigma^2)$. Assuming lognormal distribution for y_i avoids generating negative values and is generally appropriate for LHPs such as natural mortality rate (Hilborn and Mangel 1997). Hence, the general model can be expressed as

$$(2) \quad F_{\text{BRP},t,c,o,i} = \beta_{t,c,o,y} \mathbf{y}_i + e_{t,c,o,i} \\ = \beta_{t,c,o,x} \mathbf{x}_i \exp(\varepsilon_{t,c,o,i}) + e_{t,c,o,i}$$

where \mathbf{x}_i is a matrix of covariates (composed of one or more of M , κ , L_∞ , A_{\max} , and H , depending on the model evaluated), $\beta_{t,c,o,x}$ is the parameter for variable x for method type t , class c , and order o . This model has an additive error structure where $e_{\bullet,i}$ is an independent normal random variable with mean 0 and variance $\sigma_{e,\bullet}^2$. The symbol \bullet indicates that the heterogeneity may vary among types, classes, or orders depending on model specification. We also tested a multiplicative error structure but focused on models of additive error structure because the plot of F_{BRP} with M does not show clear evidence of increasing variability as M increases. The results from the additive error model indicate a more important contribution from each LHP than models of multiplicative error structure. We used the classical stepwise model building as a preliminary step to evaluate relative importance

Table 3. Comparison Bayesian hierarchical error-in-variable models using deviation information criteria (DIC).

Model	Variables	ΔDIC
1	Class, type, M , κ	0
2	Class, type, M	63.4
3	Class, order, type, M , κ , A_{\max} , H	260.3
4	Class, order, type, M , κ , L_∞ , A_{\max} , H	261.8
5	Class, order, type, M , κ , H	278.6
6	Class, order, type, M , κ	316.0
7	Class, order, type, M	322.7

Note: Type is the type of methods (i.e., F_{MSY} , F_{proxy} , and $F_{0.5r}$); M is natural mortality; κ and L_∞ are von Bertalanffy growth parameters; A_{\max} is maximum age; and H is habitat.

Table 4. Posterior mean and standard deviation (SD) of Bayesian hierarchical errors-in-variables model $F_{\text{BRP},i} = \beta_{t,c,M} M_i \exp(\varepsilon_M) + \beta_{\kappa} \kappa_i + e_i$ (t = type of method, c = class), and n is sample size.

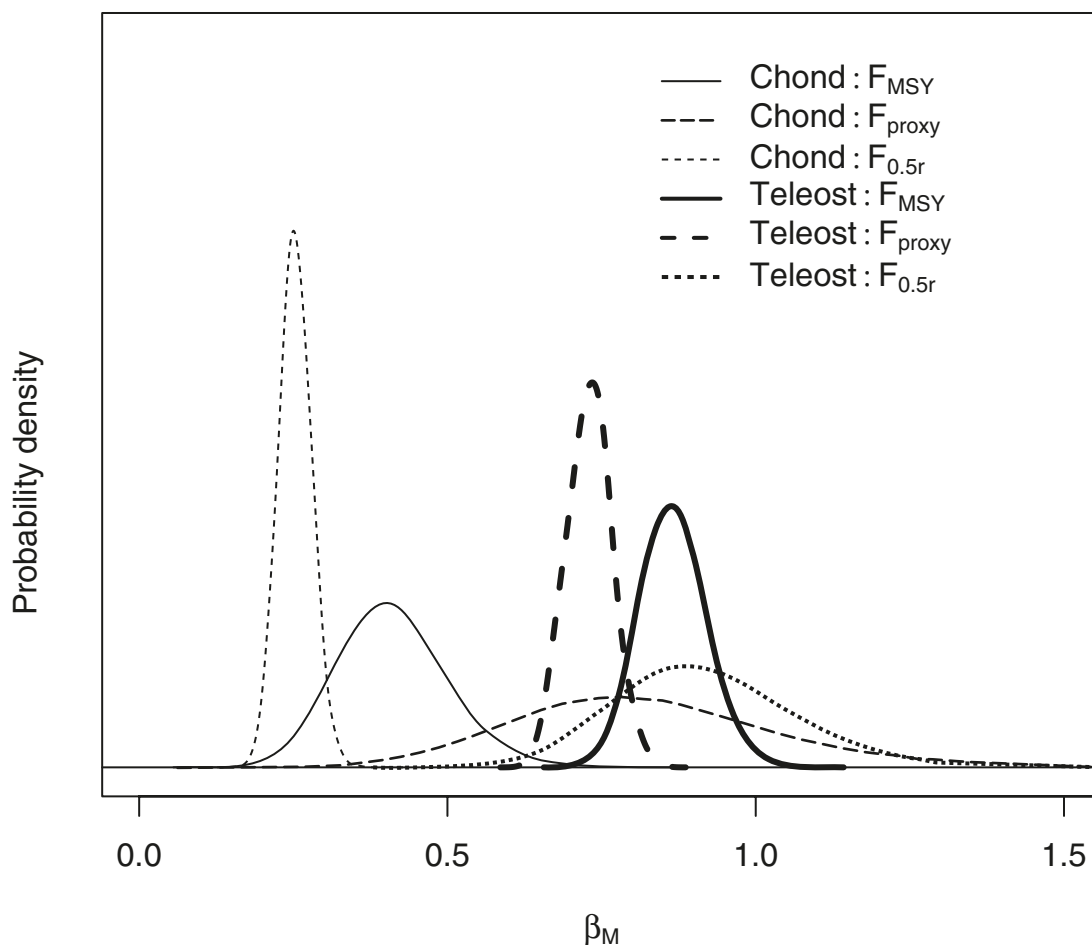
Parameter	Class	Type	Mean	SD	n
$\beta_{1,1,M}$	Chondrichthyes	F_{MSY}	0.411	0.088	12
$\beta_{2,1,M}$	Chondrichthyes	F_{proxy}	0.825	0.215	4
$\beta_{3,1,M}$	Chondrichthyes	$F_{0.5r}$	0.253	0.026	87
$\beta_{1,2,M}$	Teleost	F_{MSY}	0.866	0.053	88
$\beta_{2,2,M}$	Teleost	F_{proxy}	0.730	0.036	131
$\beta_{3,2,M}$	Teleost	$F_{0.5r}$	0.920	0.147	11
β_{κ}	—	—	0.017	0.009	333

of various covariates in eq. 2, but only reported the result of BHEIV models.

We assumed $\beta_{\bullet,x} \sim \text{normal}(\mu_{\beta_x}, \sigma_{\beta_x}^2)$, where μ_{β_x} is the prior mean for parameter β_x , and $\sigma_{\beta_x}^2$ is the variance. As natural mortality is the key predictor, we treated β_M and $\sigma_{\beta_M}^2$ as hyperparameters across populations and assumed $\mu_{\beta_M} \sim \text{normal}(\mu_{\beta_M}, \sigma_{\mu_{\beta_M}}^2)$ and $\sigma_{\beta_M}^2 \sim \text{gamma}(r = 0.01, \mu = 0.01)$ (Gelman 2006; Zhou et al. 2009b). We tested gamma and half-Cauchy distributions for $\sigma_{\mu_{\beta_M}}^2$ but reported $\sigma_{\mu_{\beta_M}}^2 \sim \text{gamma}(r = 0.01, \mu = 0.01)$ as the results were similar. Further, we used a normal distribution with a large variance for the hypermean, $\mu_{\beta_M} \sim \text{normal}(0.5, 1000)$. For the measurement error variance, we specified $\sigma_{\varepsilon,x}^2 \sim \text{gamma}(r = 0.01, \mu = 0.01)$. These specifications provide relatively non-informative priors and hyperpriors, as $\text{gamma}(0.01, 0.01)$ represents a mean of 1 and variance of 100. We tested a range of models (Table 3) with alternative priors and used deviation information criteria (DIC; Spiegelhalter et al. 2003) as primary criteria for model comparison.

We applied the Gibbs sample implemented using the WinBUGS program to sample parameter vectors from the above posterior distribution. Three Markov chains were constructed based on dispersed initial values, and the results of the first 10 000 cycles of each chain were discarded. The results of an additional 30 000 cycles from the three chains were saved for further analysis. We visually examined the chains for each parameter in the model as well as analysed the saved samples by using the CODA package (Best et al. 1996) to ensure that there was no evidence for nonconvergence in the Markov chain Monte Carlo (MCMC) sampling chain.

Fig. 1. Posterior distributions for coefficient of natural mortality $\beta_{\bullet,M}$ by class (chondrichthyans and teleosts) and type (F_{MSY} , F_{proxy} , and $F_{0.5r}$).



Results

We investigated a range of models, ranked by the preliminary stepwise regression and confirmed by BHEIV models. These models included various LHPs with normally distributed and log-normally distributed error structures and heterogeneity among populations for both measurement error $\varepsilon_{\bullet,i}$ and process error $e_{\bullet,i}$ in eq. 2. Most of these models converged quickly, in less than 2000 cycles of the MCMC algorithm. There was no evidence of nonconvergence for any model after sufficient cycles. Comparison of the top seven low DIC models is presented in Table 3. The best model with the lowest DIC has natural mortality M and growth coefficient κ as predictors with a homoscedastic error between populations (Model 1 in Table 3). The posterior mean and standard deviation of parameters are provided (Table 4), and their distributions are illustrated (Fig. 1). Although including growth coefficient κ leads to a reduction in DIC, the parameter β_{κ} itself is very small; the 95% credible interval encompasses zero, meaning it is biologically insignificant (Table 4).

Clearly, the relationship between F_{BRP} and M differs between chondrichthyans and teleosts and among the three types of reference points. For example, the overall $F_{MSY}:M$ ratio (where M is a median as in eq. 1) for chondrichthyans is 0.411, which is about half of the teleost $F_{MSY}:M$ value (0.866). The coefficient of variation (CV) for the posterior mean $F_{MSY}:M$ ratio is 0.21 and 0.06 for chondrichthyans and

teleosts, respectively (Table 4). Their overall predictive CV is 0.55. Most analyses for chondrichthyans are based on the demographic method, which results in a much lower $F_{0.5r}:M$ than $F_{MSY}:M$ (0.253 vs. 0.411). Within teleosts, $F_{proxy}:M$ is smaller than $F_{MSY}:M$ by about 14%.

Models at order level (Models 3–7 in Table 3) have higher DIC than the two models with lowest DIC at class level. However, we present results for Model 6 (which includes M and κ similar to DIC-selected Model 1) to illustrate the effect of taxonomic order on the ratio of $F_{BRP}:M$ (Table 5; Fig. 2). Within chondrichthyans, Carcharhiniforms has a lower $F_{MSY}:M$ ratio than the combined chondrichthyans. However, this is not necessarily true for $F_{proxy}:M$ and $F_{0.5r}:M$ ratios. This indicates that the results of a lower β_M from stock assessment method for carcharhiniforms may be artificial, because the sample size is very small (i.e., only one species in the two non-carcharhiniforms orders). Within teleosts, Scorpaeniformes has the lowest β_M than other orders (Fig. 2). Scorpaeniformes include many groundfish species, and they tend to have a lower productivity (for example, expressed as maximum reproductive rate at low population sizes) than other species (Myers et al. 1999). Again, the parameter β_{κ} is very small at order level, and its 95% credible interval encompasses zero.

The results of the errors-in-variables model (eq. 1) indicated that the values of input covariates from the literature and FishBase contained high uncertainty. For the natural

Table 5. Posterior mean and standard deviation (SD) of Bayesian hierarchical errors-in-variables model $F_{BRP,i} = \beta_{t,c,o,M} M_i \exp(\varepsilon_M) + \beta_{\kappa} \kappa_i + e_i$ (t = type of method, c = class, o = order, and n = sample size).

Parameter	Class	Type	Order	Mean	SD	n
$\beta_{1,1,1,M}$	Chondrichthyes	F_{MSY}	Carcharhiniformes	0.335	0.095	10
$\beta_{1,1,2,M}$	Chondrichthyes	F_{MSY}	Lamniformes	0.463	0.365	1
$\beta_{1,1,3,M}$	Chondrichthyes	F_{MSY}	Other Chondrichthyes	0.967	0.561	1
$\beta_{2,1,1,M}$	Chondrichthyes	F_{proxy}	Carcharhiniformes	0.876	0.323	2
$\beta_{2,1,2,M}$	Chondrichthyes	F_{proxy}	Lamniformes	0.640	0.365	1
$\beta_{2,1,3,M}$	Chondrichthyes	F_{proxy}	Other Chondrichthyes	0.801	0.415	1
$\beta_{3,1,1,M}$	Chondrichthyes	$F_{0.5r}$	Carcharhiniformes	0.266	0.038	55
$\beta_{3,1,2,M}$	Chondrichthyes	$F_{0.5r}$	Lamniformes	0.280	0.101	11
$\beta_{3,1,3,M}$	Chondrichthyes	$F_{0.5r}$	Other Chondrichthyes	0.269	0.086	21
$\beta_{1,2,4,M}$	Teleostei	F_{MSY}	Clupeiformes	0.880	0.200	2
$\beta_{1,2,5,M}$	Teleostei	F_{MSY}	Gadiformes	1.014	0.136	11
$\beta_{1,2,6,M}$	Teleostei	F_{MSY}	Perciformes	0.922	0.092	23
$\beta_{1,2,7,M}$	Teleostei	F_{MSY}	Pleuronectiformes	1.160	0.154	12
$\beta_{1,2,8,M}$	Teleostei	F_{MSY}	Scorpaeniformes	0.694	0.095	35
$\beta_{1,2,9,M}$	Teleostei	F_{MSY}	Other teleost	0.896	0.162	5
$\beta_{2,2,4,M}$	Teleostei	F_{proxy}	Clupeiformes	0.634	0.100	10
$\beta_{2,2,5,M}$	Teleostei	F_{proxy}	Gadiformes	0.718	0.074	21
$\beta_{2,2,6,M}$	Teleostei	F_{proxy}	Perciformes	0.742	0.043	66
$\beta_{2,2,7,M}$	Teleostei	F_{proxy}	Pleuronectiformes	0.715	0.087	19
$\beta_{2,2,8,M}$	Teleostei	F_{proxy}	Scorpaeniformes	0.667	0.132	3
$\beta_{2,2,9,M}$	Teleostei	F_{proxy}	Other teleost	0.683	0.090	12
$\beta_{3,2,4,M}$	Teleostei	$F_{0.5r}$	Clupeiformes	0.843	0.290	1
$\beta_{3,2,5,M}$	Teleostei	$F_{0.5r}$	Gadiformes	1.013	0.200	8
$\beta_{3,2,6,M}$	Teleostei	$F_{0.5r}$	Perciformes	0.752	0.323	1
$\beta_{3,2,7,M}$	Teleostei	$F_{0.5r}$	Pleuronectiformes	0.966	0.324	1
β_{κ}	—	—	—	-3.4×10^{-6}	7.2×10^{-5}	333

mortality M , the log-scale median measurement-error variance $\sigma^2_{\varepsilon,M}$ is 0.23, representing a $CV[M] = \sqrt{\exp(0.23) - 1} = 0.51$. In comparison, the hierarchical Model 2 resulted in $\sigma^2_e = 0.0012$, corresponding to $CV[F_{MSY}] = 0.15$. When measurement error is taken into account, the mean natural mortality for each stock is higher than the reported value, which is assumed to be median-unbiased. Thus, the mean natural mortality will be $\exp(\sigma^2_{\varepsilon,M}/2) = 1.12$ higher than the reported value. This is equivalent to increasing β_M in Tables 3 and 4, which are calculated from the observed median M as in eq. 2. For example, the mean-unbiased $F_{MSY}:M$ ratio becomes 0.970 for teleosts (compared with 0.866) and 0.460 for chondrichthyans (compared with 0.411).

Discussion

This paper appears to be the first research to undertake a comprehensive empirical analysis linking various BRPs to fish life history traits. Through a meta-analysis on more than 200 species, we estimated effects between several fishing mortality-based BRPs and LHPs for different taxonomic groups.

Effect of life history traits on F_{BRP}

Our results show that data collected from stock assessments worldwide generally support previous theoretical research regarding F_{BRP} and LHPs. Specifically, we find that natural mortality is the most important factor affecting F_{BRP} . Other LHPs, such as maximum age, growth coefficient, max-

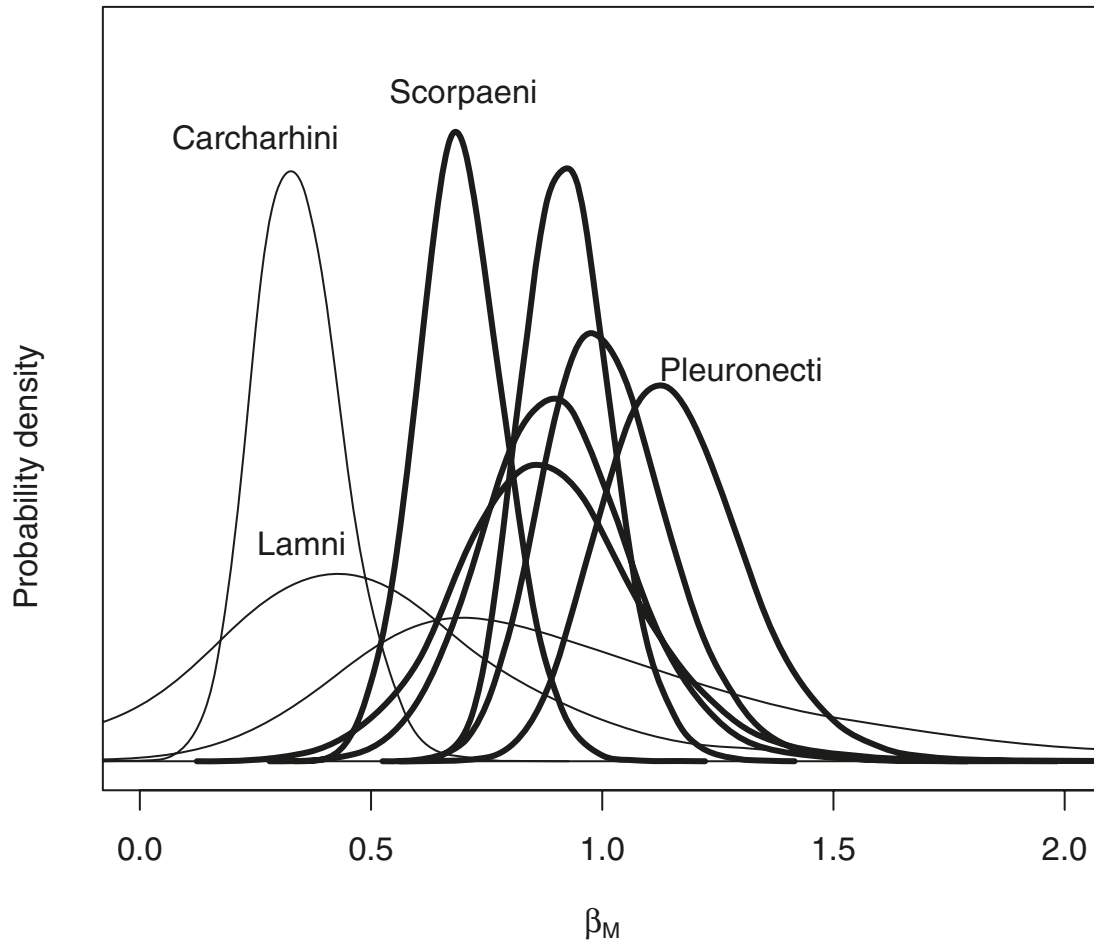
imum length, and habitat type, contribute limited additional improvement to the relationship. Although DIC selects the von Bertalanffy growth coefficient κ in addition to natural mortality M , its 95% credible interval overlaps zero and hence has little interpretable impact on F_{BRP} . One of the possible explanations is that natural mortality M is often incorporated into models that are used to estimate F_{BRP} , thus causing a strong correlation between M and F_{BRP} . Furthermore, natural mortality is rarely estimated in assessment models but often calculated from an assumed relationship between M with κ and L_{∞} . This means that it is in fact κ and (or) L_{∞} that are the reliable predictors (S. Zhou, unpublished data). These von Bertalanffy growth parameters are often available, even for many data-poor species. Because natural mortality correlates with many other LHPs (Charnov 1993; Jennings et al. 1998; Goodwin et al. 2006), including growth rate, and LHPs may involve considerable measurement errors, our result implies that using M alone as the predictor is generally sufficient to determine the F -based BRPs. This result suggests that it may be redundant and overuse of information to include multiple LHPs in qualitative and semi-qualitative assessment of species vulnerability (e.g., Stobutzki et al. 2001; Wesley et al. 2010).

Comparison of $F_{MSY}:M$ ratio between taxonomic groups

Our study reveals significant differences between chondrichthyans and teleosts. Most chondrichthyans are long-lived species with low natural mortality and low fecundity. Their life history traits already make them more vulnerable to fishing (Stevens et al. 2000). On top of this vulnerability, our

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Fig. 2. Posterior distributions for coefficient of natural mortality $\beta_{\bullet,M}$ by class (chondrichthyans and teleosts) and order (Carcharhiniformes, Lamniformes, other Chondrichthyes, Clupeiformes, Gadiformes, Perciformes, Pleuronectiformes, Scorpaeniformes, other Teleostei) for stock assessment method (type F_{MSY}). The thin lines are chondrichthyans and the thick lines are teleosts. Four orders are indicated, while there is only one species in the order of Lamniformes and other chondrichthyes.



analyses demonstrate that the ratio of $F_{MSY}:M$ is much smaller for chondrichthyans than for teleosts (i.e., 0.41 vs. 0.87). Furthermore, the order Carcharhiniformes contains the largest sample size and has a mean $F_{MSY}:M$ ratio of 0.34. Because large species of chondrichthyans have lower growth rates and lower potential population increases (Frisk et al. 2001), the results support the assertion that assuming $F_{MSY} > 0.5M$ for sharks and rays must be carefully justified (Walters and Martell 2002).

We estimate that the $F_{MSY}:M$ ratio is less than 1 for teleosts when observed M is assumed to be a median from a log-normal distribution and when all species are analysed together (mean 0.87, 95% confidence interval (CI) between 0.77 and 0.97). Closer examination reveals some difference among orders. For example, Gadiformes, Perciformes, and Pleuronectiformes have $F_{MSY}:M$ ratio close to 1, while this ratio is less than 0.7 for Scorpaeniformes. This latter order has the largest sample size, which may have lowered the overall estimate to 0.87. The result at order level reinforces that the “rule of the thumb” approximation $F_{MSY} = M$ is by and large acceptable for many teleosts (Alverson and Pereyra 1969; Gulland 1970, 1971). On the other hand, the result at class level (i.e., combining all teleosts) also supports the ar-

gument that F_{MSY} should be lower than M for most species (Thompson 1993; Beddington and Kirkwood 2005).

Few studies have established a link between F_{BRP} and LHP for chondrichthyans. This is understandable, since there have been few quantitative stock assessments using time-series data for this class of fishes. Furthermore, assessments of chondrichthyans often acknowledge uncertainty about basic demographic parameters and instead report results for a wide range of demographic values (Punt 2000; Cortes 2006).

Bayesian hierarchical error-in-variables model

Bayesian hierarchical models have several advantages over classical data analysis methods. Bayesian hierarchical models can explicitly model all variability sources, can be applied to small sample sizes because they borrow information from all studies, and are well-suited for meta-analysis. The hierarchical Bayesian estimates of between-group divergence are less variable than maximum likelihood estimates because they are based on the data from all populations (Lockwood et al. 2001). These improved between-group variance estimates improve the estimation of the optimal degree of shrinkage, which is less affected by sampling variability at each popula-

tion. Bayesian hierarchical modelling has the tendency to shrink population parameters toward the population mean, where parameters with more precise data are pooled less toward the population mean than more variable data. Shrinkage of the model as a whole makes use of the fact that the multi-level estimates of the individual parameters, if treated as point estimates, understate the between-group variance (Gelman and Pardoe 2006).

The challenge of building a credible relationship between BRPs and LHPs hinges on obtaining reliable LHPs. We emphasize the errors-in-variables models because it is clear that the dependent variables such as M cannot be accurately measured, and the estimates are biased when measurement errors are not taken into account (Fuller 1987). The difficulty of estimating LHP is well recognized by fisheries scientists (Quinn and Deriso 1999). The uncertainty in LHP may arise from two major sources: (i) natural variation among stocks of the same species due to variability in stock structure, location, time, and other environmental factors and (ii) true measurement error due to our inability to accurately measure LHP for specific stock at specific time and location. For example, our estimation of large measurement error in natural mortality is consistent with other studies and observations (Quiroza et al. 2010). MacCall (2009) also reported the large standard error (0.56 and 0.50) in estimating M based on the Pauly (1980) and Hoenig (1983) methods, which values are very close to our results. The data in FishBase show that large differences exist in the estimated M for the same species. Different methods may result in very different estimates of M for the same species (Zhou et al. 2011). For these reasons, it is essential to take errors in variables into account when one studies the relationship between BRP and LHP.

The posterior measurement-error variance for natural mortality, $\sigma^2_{\varepsilon,M}$ is substantial. This indicates a skewed distribution of M . If one is interested in the mean value, which is affected by potential outliers, then applying a factor of 1.12 to obtain expected M increases the posterior β_M , pushing $F_{MSY}:M$ ratio closer to 1 for combined teleosts. However, this is not a normal way for specifying M in fishery stock assessments.

Comparison among types of reference points

F_{MSY} is our focus in this study because it is based on analysis of time series data, results from population dynamics across many generations, and takes compensatory processes into account. It is also widely used in stock assessment and harvest control rules. We include F_{proxy} and $F_{0.5r}$ mainly for the purpose of comparison with F_{MSY} . F_{proxy} is based on per-recruit analysis and does not directly take compensatory processes into account. Overall, F_{proxy} (primarily composed of $F_{0.1}$) is a more conservative reference point than F_{MSY} for teleosts (about 15% lower than F_{MSY}). Other studies have also found that more species had F_{MSY} greater than their $F_{0.1}$ (Deriso 1987). In contrast, per-recruit analysis has rarely been applied in chondrichthyans. The small sample size for F_{proxy} (total four species) in chondrichthyans produces a greater F_{proxy} than F_{MSY} with a large variance.

A large number of studies on chondrichthyan population vulnerability are based on demographic analyses of intrinsic growth rate derived from life history tables or Leslie matrices. Our analyses show surprisingly high precision in the posterior $F_{0.5r}$, but the mean value is smaller than F_{MSY} for

chondrichthyans. This method, however, has two major potential problems. Firstly, life history tables and Leslie matrices generally assume no density dependence. They provide an instantaneous rate of population growth for a specified set of life history traits that correspond to a specific population size (Gedamke et al. 2007). Many investigators use these models to compute rates of population growth and claim this is the maximum (intrinsic) population growth rate. However, demographic modelling cannot estimate intrinsic r without additional information. The estimate r in much of the literature is typically population growth rate under special conditions. Secondly, $F_{MSY} = r/2$ is only true when the population dynamics can be expressed by the symmetric Schaeffer surplus production model. On the first of these issues, it is interesting to note that estimates of r for chondrichthyans seem to be biased low by a factor of nearly 0.5. This would be consistent with these estimates being derived from populations that are on average at about half carrying capacity, rather than from highly depleted populations.

Our results, in particular the relationships between F_{MSY} from stock assessment and natural mortality M , will have wide applicability in management of data-poor species. Furthermore, ecosystem-based fishery management is being developed worldwide to conform to increasingly strict environmental and fishery legislation. Combining these issues, fishery scientists and managers are looking for innovative methods that can be utilized for the evaluation of fishing impact on nontarget species that have very limited information. The results of this study will be useful in helping to meet the broad objectives of ecosystem-based fisheries management.

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