

Hierarchical Bayesian estimation of recruitment parameters and reference points for Pacific rockfishes (*Sebastes* spp.) under alternative assumptions about the stock–recruit function

Robyn E. Forrest, Murdoch K. McAllister, Martin W. Dorn, Steven J.D. Martell, and Richard D. Stanley

Abstract: Hierarchical Bayesian meta-analysis can be a useful method for improving estimation of key parameters for harvested fish populations. In hierarchical models, data from multiple populations are used simultaneously to obtain estimates of parameters for individual populations and characterize the variability among populations. Many populations of Pacific rockfishes (*Sebastes* spp.) have declined off the US West Coast since the 1980s, and there is also concern for their conservation in Canada. We develop a hierarchical Bayesian meta-analysis to improve estimates of stock–recruit parameters, characterize management-related parameters (e.g., optimal harvest rate), and address uncertainties in the structural form of the stock–recruit function for Pacific rockfishes. We estimate steepness and optimal harvest rates for 14 populations of Pacific rockfishes under alternative assumptions about the underlying stock–recruit function (Beverton–Holt and Ricker). We provide a posterior predictive distribution of steepness for rockfishes that can be used as a prior in future assessments for similar populations. We also evaluate whether $F_{40\%}$ is an appropriate proxy for F_{MSY} for Pacific rockfishes and show that uncertainty in the natural mortality rate can have a significant effect on management advice derived from meta-analyses of stock–recruit data.

Résumé : Une méta-analyse hiérarchique bayésienne peut être une méthode utile pour améliorer l'estimation des paramètres importants des populations de poissons exploitées. Dans les modèles hiérarchiques, on utilise simultanément des données provenant de plusieurs populations pour obtenir des estimations des paramètres pour les populations individuelles et caractériser la variabilité entre les populations. Plusieurs populations de sébastes (*Sebastes* spp.) du Pacifique connaissent un déclin depuis les années 1980 sur la côte occidentale des É.-U. et il y a aussi des inquiétudes au sujet de leur conservation au Canada. Nous avons mis au point une méta-analyse hiérarchique bayésienne pour améliorer l'estimation des paramètres de stock–recrutement, pour caractériser les paramètres reliés à la gestion (par ex., le taux optimal de récolte) et pour tenir compte de certaines incertitudes concernant la forme structurelle de la fonction stock–recrutement chez les sébastes du Pacifique. Nous estimons l'inclinaison et les taux optimaux de récolte de 14 populations de sébastes du Pacifique sous diverses présuppositions de rechange concernant les fonctions sous-jacentes de stock–recrutement (Beverton–Holt et Ricker). Nous fournissons une distribution prédictive a posteriori de l'inclinaison pour les sébastes qui peut servir de distribution a priori dans des évaluations futures de populations semblables. Nous vérifions aussi si $F_{40\%}$ peut servir de valeur de remplacement de F_{MSY} chez les sébastes du Pacifique et nous démontrons que l'incertitude dans le taux de mortalité naturelle peut avoir un effet significatif sur les recommandations de gestion tirées des méta-analyses des données de stock–recrutement.

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Introduction

More than 70 species of Pacific rockfishes (*Sebastes* spp.) occur along the western coast of North America from the Gulf of California to the Bering Sea (Love et al. 2002). Ap-

proximately 39 of these species occur in waters off British Columbia (BC), Canada. Many populations have declined off the US West Coast since the 1980s (Ralston 1998), and there is also concern for their conservation in Canada. The Committee on the Status of Endangered Wildlife in Canada

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R.E. Forrest,^{1,2} M.K. McAllister, and S.J. Martell. University of British Columbia, Fisheries Centre, AERL, 2202 Main Mall, Vancouver, BC V6T 1Z4, Canada.

M.W. Dorn. National Marine Fisheries Service – NOAA, Alaska Fisheries Science Center, 7600 Sand Point Way N.E., Seattle, WA 98115, USA.

R.D. Stanley. Fisheries and Oceans Canada, Pacific Biological Station, 3190 Hammond Bay Road, Nanaimo, BC V9T 6N7, Canada.

¹Corresponding author (e-mail: Robyn.Forrest@dfo-mpo.gc.ca).

²Present address: Fisheries and Oceans Canada, Pacific Biological Station, 3190 Hammond Bay Road, Nanaimo, BC V9T 6N7, Canada.

(COSEWIC) has assessed the populations of canary rockfish (*Sebastes pinniger*), quillback rockfish (*Sebastes maliger*), and bocaccio (*Sebastes paucispinis*) as “threatened” and rougheye rockfish (*Sebastes aleutianus*), darkblotched rockfish (*Sebastes crameri*), and yelloweye rockfish (*Sebastes ruberrimus*) as populations of “special concern” in British Columbian waters (COSEWIC, <http://www.cosewic.gc.ca>). Fisheries and Oceans Canada have implemented 164 rockfish conservation areas in BC to assist in the management of the shallower rockfish species, some of which are considered to have been overfished (Yamanaka and Logan 2010). With some exceptions, there is a general lack of reliable data for the stock assessment of Pacific rockfishes (Dorn 2002; Hilborn et al. 2002), and in Canada, formal assessments have only been completed for a few species (e.g., Richards and Olsen 1996; Schnute et al. 2001; Stanley et al. 2009).

In the event that a “threatened” status for a rockfish population is approved by the Federal Government of Canada, a recovery strategy would have to be implemented for the population, consistent with requirements of the Canadian Species at Risk Act (SARA). Development of recovery strategies for rockfish species in Canada will involve some use of predictive population models to evaluate performance of alternative management strategies. Performance can be measured in terms of certain metrics relative to agreed reference points, e.g., the ratio of current biomass (B) to biomass at maximum sustainable yield (MSY) (B_{MSY}) or current fishing mortality (F) relative to that which produces maximum sustainable yield (F_{MSY}).

In the US, the Pacific Fishery Management Council has implemented a management plan for Pacific rockfishes that is consistent with the Magnuson–Stevens Fishery Conservation and Management Act (Ralston 2002). The management plan states that fishing mortality should be kept below F_{MSY} and that fishing mortality should be reduced when B is below B_{MSY} . Although Canada has not legislated MSY as a management goal, it does require that fisheries be managed in a precautionary manner (Fisheries and Oceans Canada 2006; Shelton and Sinclair 2008). Therefore, estimates of sustainable fishing thresholds are required for any management plan. F_{MSY} (or its discrete equivalent, annual optimal exploitation rate, U_{MSY}) is widely considered a precautionary limit to fishing mortality that can prevent both growth and recruitment overfishing if successfully implemented (Punt 2000; Mace 2001; Punt and Smith 2001).

Estimation of productivity parameters

F_{MSY} is a function of the productivity of a fish population determined, at least in part, by the magnitude of density-dependent processes affecting the rate of survival of juveniles to recruitment age (Rose et al. 2001; Myers 2002; Walters and Martell 2004). The slope at the origin (α) of the Beverton–Holt (Beverton and Holt 1957) and Ricker (1954) stock–recruit functions describes the maximum recruitment potential in response to reductions in density of spawners due to fishing. This parameter (along with parameters describing the rates of growth and natural mortality and the age at recruitment to the fishery) is one of the principal determinants of F_{MSY} . Although α is an estimable, biologically meaningful parameter, it is not directly comparable among

different populations, as it is sensitive to the units used to measure the spawning biomass. For example, when the independent axis of the stock–recruit function represents absolute numbers of eggs, α represents the maximum rate of survival from egg to recruit and has a maximum value of one. Usually, however, stock–recruit functions are parameterised in terms of spawning stock biomass, which can be measured in many different units. In these cases, α will be unit-dependent, representing the maximum number of surviving recruits per unit of biomass. To permit comparison of recruitment productivity among populations, stock–recruit functions are commonly reparameterised in terms of unitless functions of α . For example, steepness (h) is defined as the proportion of unfished recruits that are produced when spawning stock size is reduced to the arbitrary level of 20% of the unfished stock size (Mace and Doonan 1988). An alternative is the compensation ratio (CR), defined as the ratio of α to the slope of the line drawn between the origin and the point on the stock–recruit curve at which the stock is unfished (Goodyear 1977; Myers et al. 1999; for illustration, see Goodwin et al. 2006 (their fig. 1)).

Reliable estimation of recruitment parameters is dependent on long, contrasting time series of stock–recruit data (Hilborn and Walters 1992; Conn et al. 2010). However, informative data are often not available, leading some stock assessment scientists to simply fix h at an assumed value, despite its key role in determining F_{MSY} and other important reference points. Alternatively, Bayesian methods are often used to quantify the uncertainty surrounding estimates of steepness and other productivity parameters (McAllister et al. 1994; Punt and Hilborn 1997; Chen et al. 2003). If there is too little information in the data, however, posterior estimates of productivity parameters can be strongly influenced by the formulation of the prior probability density function (pdf). Despite recent advances in advice for formulating priors for productivity parameters (Myers et al. 1999, 2002; Mangel et al. 2010), in our experience, the appropriate range of values to admit for steepness (either as a fixed value or as a prior pdf) is one of the most contentious topics in any fisheries stock assessment (see also Punt and Hilborn 1997). Hierarchical Bayesian meta-analysis (Gelman et al. 1995) has been proposed as a method for improving estimation of recruitment productivity parameters when data are uninformative (Liermann and Hilborn 1997; Dorn 2002; Michielsens and McAllister 2004). In hierarchical Bayesian models, data from multiple populations are used simultaneously to obtain estimates of parameters for individual populations. Rather than pooling data, hierarchical models assume that there is a probability distribution for the parameter of interest (e.g., steepness) that is common to all populations. This common distribution is called the prior distribution. Each population is treated as an exchangeable unit for estimating the “hyper-parameters” of this prior distribution (e.g., its mean and standard deviation (SD)). The prior distribution for steepness acts as the prior pdf for each individual population. Multiple stock–recruit data sets are therefore used to jointly estimate the posterior pdfs of steepness for individual populations, while simultaneously estimating posterior pdfs for the hyper-parameters of the prior distribution (Gelman et al. 1995). The assumption of exchangeability of populations helps to reduce the problem of overfitting and enables more precise parameter estimation for populations for which

Table 1. List of parameters.

Parameter	Description (units, if applicable)
F	Instantaneous fishing mortality rate (year^{-1})
U	Annual exploitation rate ($U = 1 - e^{-F}$)
U_{MSY}	Optimal harvest rate
MSY	Maximum sustainable yield (t)
M	Instantaneous natural mortality rate (year^{-1})
h	Steepness
B	Biomass
SSB	Spawning stock biomass
SSB_{Max}	Maximum observed spawning stock biomass
VB	Vulnerable biomass
R	Recruits (numbers)
B	Population total biomass
α	Slope of the stock–recruit function at the origin
β	Scaling parameter of stock–recruit function
CR	Compensation ratio
φ_E	Equilibrium eggs per recruit
φ_B	Equilibrium total biomass per recruit
φ_{VB}	Equilibrium vulnerable biomass per recruit
SPR	Spawning stock biomass per recruit (equivalent to φ_E , see text)
$\%\text{SPR}_0$	Percentage of unfished SPR at a given harvest rate
a_T	Terminal age class (years)
a_{rec}	Age at first recruitment to the fishery (years)
a_{mat}	Approximate age at maturity (years)
m_a	Maturity at age
f_a	Fecundity at age
v_a	Vulnerability at age
w_a	Mean weight at age
Θ	Vector of stock-specific estimated parameters
Φ	Vector of hyper-parameters
σ_k	Variance of errors
τ	Precision of errors (inverse of the variance of errors)
a	Shape parameter of Beta probability density function
b	Shape parameter of Beta probability density function
μ_h	Mean of the prior distribution of h
σ_h	Standard deviation of the prior distribution of h

the data are uninformative (Gelman et al. 1995), although it is important to note that biased results may result if the assumption of exchangeability is violated.

Dorn (2002) used hierarchical Bayesian meta-analysis to estimate steepness for 11 Pacific rockfish populations. One of the intended aims of the analysis was to quantify how steepness varies across populations. The study was the first of its kind for rockfishes and made use of data for rockfish populations from the US West Coast, BC, and Alaska. Compared with estimates obtained from independent individual analyses, the range of mean estimates of steepness for individual populations from the hierarchical analysis was shrunk towards the average steepness among populations (Dorn 2002).

Proxies for productivity: $\%\text{SPR}_0$

In the absence of reliable estimates of F_{MSY} , proxies based on more readily obtainable life history and selectivity data are often used. In US West Coast groundfish fisheries, $F_{35\%}$ was initially adopted as a proxy for F_{MSY} in 1992 (for the history of the decision to use $F_{35\%}$, see Clark 2002). $F_{35\%}$ represents the fishing mortality rate that would reduce spawning stock biomass per recruit (SPR) to 35% of its unfished state (SPR_0) (Gabriel et al. 1989; Clark 1991; Mace and Sissenwine 1993). The 35% adopted for West Coast groundfish was increased to 40% of SPR_0 in 1997 due to concerns about continuing declines of rockfish populations and further work by Clark (1993; see also Mace 1994). Clark (2002) showed that a much more conservative target fishing mortality rate of $F_{60\%}$ was robust to a wide range of uncertainty about productivity of the population, although Hilborn et al. (2002) argued that this may be too cautious for some populations, given uncertainty in natural mortality, and could lead to unnecessary risk of economic loss. Dorn (2002) tested the validity of the $F_{40\%}$ proxy, using the estimates of F_{MSY} derived from his estimates of steepness for 11 rockfish populations. His results suggested that fishing mortality rates in the range of $F_{40\%}$ to $F_{60\%}$ should be considered for data-limited West Coast rockfishes. This result, as well as other research on rockfish productivity, led to the adoption of $F_{50\%}$ as the default F_{MSY} proxy for rockfishes managed by Pacific Fishery Management Council. In contrast, the default F_{MSY} proxy used for rockfish populations in Alaskan water continues to be $F_{35\%}$ (although catch recommendations are based on $F_{40\%}$).

Current study

Despite improvements in the length of time series data for US Pacific rockfishes in recent years, many still lack sufficient contrast to reliably estimate recruitment parameters in individual assessments. Given the current need for estimates of productivity of various rockfishes in BC, it is timely to update the work of Dorn (2002). In this paper, we develop a new hierarchical Bayesian meta-analysis to estimate steepness and U_{MSY} for 14 populations of Pacific rockfishes under alternative assumptions about the underlying stock–recruit function (Beverton–Holt and Ricker). This work builds on the analysis of Dorn (2002), incorporating the original data for eight of his 11 populations, extended data for two of the original populations, and adding data for four “new” Alaskan populations. Data for two of the original Pacific ocean perch populations (Gulf of Alaska and Bering Sea) were combined for consistency with more recent data. Our results provide a posterior predictive distribution of steepness for rockfishes that could be used as a prior in future assessments for similar populations, as well as posterior pdfs of steepness for individual populations. We also update estimates of fisheries reference points for these species and re-evaluate whether $F_{40\%}$ is an appropriate proxy for F_{MSY} for Pacific rockfishes.

Materials and methods

Hierarchical models were developed to estimate parameters for 14 populations of Pacific rockfishes under alternative (Beverton–Holt and Ricker) assumptions about the underlying stock–recruit function. Model parameters referred to frequently in the text are defined in Table 1, the data are described in the next section, and details of the model follow.

Data

The models were fitted to stock–recruit data for 14 populations of Pacific rockfishes using the fixed parameters listed (Table 2) and fixed vulnerability, weight-at-age, and maturity-at-age schedules for each population, provided by the US National Marine Fisheries Service (NMFS; Martin Dorn, NMFS, Alaska Fisheries Science Center, Seattle, Washington).

Stock–recruit data sets were also provided by the Alaska Fisheries Science Center and came from a variety of stock assessments based on fisheries-independent surveys and other data published by the Pacific and North Pacific Management Councils, Fisheries and Oceans Canada, and the stock–recruit database of Myers et al. (1995; for further details, see the references in Table 2 and Dorn (2002)).

The stock–recruit data were all outputs from age- or length-structured stock assessments (Table 2). Care was taken not to use assessments that had predicted recruitment using an informative prior or fixed value for steepness (see Dorn 2002). In the original West Coast Pacific ocean perch assessment (Ianelli and Zimmerman 1998), a prior on steepness had been used, but for the purposes of generating data for this meta-analysis, the prior was turned off.

In the Alaskan assessments, recruitment was modelled as log mean recruitment plus an annual deviance. A likelihood penalty was used to constrain recruitment deviations but no explicit stock–recruit relationship was used. Though it could be argued that this implies a stock–recruit relationship with

Table 2. Life history and selectivity parameters for the 14 rockfish stocks in the analysis.

Common name	<i>Sebastes</i> spp.	Population	Population code	M	a_r	a_{rec}	a_{nat}	Assessment model	N	Reference
Chilipepper rockfish	<i>S. goodie</i>	US West Coast*	Chilipepper	0.24	21	2	~4	SS–length	28	Ralston et al. 1998
Bocaccio	<i>S. paucispinus</i>	US West Coast*	Bocaccio	0.2	21	1	~4.5	SS–length	30	MacCall et al. 1999
Widow rockfish	<i>S. entomelas</i>	US West Coast*	Widow	0.15	20	1	~6.5	SS–age	27	Ralston and Pearson 1997
Canary rockfish	<i>S. pinniger</i>	US West Coast*	Canary	0.08	25	3	~8	SS–age, ADMB–length	28	Crone et al. 1999; Williams et al. 1999
Black rockfish	<i>S. melanops</i>	WA, OR*	Black	0.28	16	6	~11	ADMB–age	7	Wallace et al. 1999
Yellowtail rockfish	<i>S. flavidus</i>	US West Coast*	Yellowtail	0.14	25	4	~10	ADMB–age	27	Taggart et al. 1997
Pacific ocean perch	<i>S. alutus</i>	US West Coast*	POP WC	0.06	25	3	~10	ADMB–age	40	Ianelli and Zimmerman 1998
		Goose Island Gully	POP GIG	0.05	30	7	~7	ADMB–age	26	Richards and Olsen 1996
		Gulf of Alaska†	POP GoA	0.06	25	2	~10	ADMB–age	43	Hanselman et al. 2007
Northern rockfish	<i>S. polypsinis</i>	Bering Sea – Aleutian Islands†	POP BSAI	0.06	25	3	~11	ADMB–age	37	Spencer and Ianelli 2007a
		Bering Sea – Aleutian Islands	Northern BSAI	0.04	23	3	~13	ADMB–age	20	Spencer and Ianelli 2007b
Dusky rockfish	<i>S. variabilis</i>	Gulf of Alaska	Dusky GoA	0.06	23	2	~13	ADMB–age	28	Heifetz et al. 2007
		Gulf of Alaska	Dusky GoA	0.07	21	4	~11	ADMB–age	25	Lunsford et al. 2007
Rougheye rockfish	<i>S. aleutianus</i>	Gulf of Alaska	Rougheye GoA	0.03	25	3	~16	ADMB–age	26	Kalei Shotwell et al. 2007

Note: Source: National Marine Fisheries Service, Alaska Fisheries Science Center, Seattle, Washington (M. Dorn). M , average instantaneous natural mortality rate; a_r , terminal age (note that this may be considerably younger than the population's maximum age); a_{rec} , age at first recruitment, i.e., youngest observed age in fishery; a_{nat} , age at 50% maturity; N , number of years of stock–recruit observations; SS–age, Stock Synthesis (Methot 1989), age-based model; SS–length, Stock Synthesis length-based model; ADMB–age, AD Model Builder (Otter Research 1996), age-structured model; and ADMB–length, AD Model Builder, size-structured model.

*Data same as used by Dorn 2002.

†Data updated since Dorn 2002.

Table 3. Derivation of recruitment parameters for the alternative models.

Beverton–Holt		Ricker	
Eq. no.	Equation	Eq. no.	Equation
T3.1a ^a	$CR = \frac{4h}{1-h}$	T3.1b ^b	$CR = (5h)^{5/4}$
T3.2a	$\alpha_1 = \frac{CR}{\varphi_{E_0}}$	T3.2b	$\alpha_2 = \frac{CR}{\varphi_{E_0}}$
T3.3a	$R_0 = \frac{B_0}{\varphi_{B_0}}$	T3.3b	$R_0 = \frac{B_0}{\varphi_{B_0}}$
T3.4a	$\beta_1 = \frac{\alpha_1 \varphi_{E_0} - 1}{R_0 \varphi_{E_0}}$	T3.4b	$\beta_2 = \frac{\ln(\alpha_2 \varphi_{E_0})}{R_0 \varphi_{E_0}}$
T3.5a ^c	$R_U = \frac{\alpha_1 \varphi_{EU} - 1}{\beta_1 \varphi_{EU}}$	T3.5b	$R_U = \frac{\ln(\alpha_2 \varphi_{EU})}{\beta_2 \varphi_{EU}}$
T3.6 ^d	$MSY = \varphi_{VBUMSY} R_{MSY} U_{MSY}$		
T3.7 ^e	$SSB_{MSY} = R_{MSY} \varphi_{EU_{MSY}}$		
T3.8	$SSB_0 = R_0 \varphi_{E_0}$		

Note: Subscript 0 indicates $U = 0$ and subscript U indicates that the parameter has been calculated with the tested value of U in the survivorship function (eq. T4.2).

^aMyers et al. 1999.

^bMichielsens and McAllister 2004.

^cThis function returns R_{MSY} at U_{MSY} .

^d MSY and U_{MSY} obtained through numerical search (see eq. 5); see Table 4 for definition of φ_{VBUMSY} .

^e $\varphi_{EU_{MSY}}$ obtained using eq. T4.3, with l_a evaluated at U_{MSY} .

a steepness of one, this approach is probably the least likely to influence the results of the present analysis, given the alternatives for setting up stock assessment models. The US West Coast assessments were done using the assessment model Stock Synthesis (Methot 1989; Table 2). Generally, the recruitment time series in these models were estimated as a set of free parameters but could be constrained to follow a stock–recruit relationship depending on the variance assumed. Most of the assessments put very low emphasis on the stock–recruit likelihood component. For example, in the widow rockfish assessment, model runs were structured so that the emphasis placed on the stock–recruit component of the model was quite low, thus preventing the stock–recruit function from having undue influence on the estimation of year-specific recruitment (Ralston and Pearson 1997).

Model description

Two of the most widely used stock–recruit functions are the Beverton–Holt (eq. 1) and Ricker (eq. 2) models, i.e.,

$$(1) \quad R = \frac{\alpha_1 E}{1 + \beta_1 E}$$

$$(2) \quad R = \alpha_2 E e^{-\beta_2 E}$$

where R is the number of recruits and E is the number of eggs. Equations 1 and 2 have parameters α and β , describing productivity and scale, respectively (with subscripts 1 and 2 representing parameters of the Beverton–Holt and Ricker models, respectively). In these formulations, parameter α describes the slope of the function close to the origin (i.e., the maximum rate of survival from egg to recruit if the independent variable is absolute numbers of eggs) and is equivalent for both stock–recruit functions (Myers et al. 1999), although the two functions tend to result in different estimates of α if fitted to the same data (Walters and Martell 2004). Hilborn and Walters (1992) provide a detailed interpretation of β for the two functions. In our analysis, the

number of eggs was assumed to be proportional to spawning stock biomass, where fecundity at age (f_a) was given by

$$(3) \quad f_a = m_a w_a$$

where m_a is the proportion of females mature at age a and w_a is mean weight at age a of females.

Here we define a recruit as a fish of the youngest age observed in the fishery, even if that age class is not fully vulnerable to the fishing gear (ages at recruitment, a_{rec} , were assumed to be constant and are provided in Table 2). Vulnerability at age was assumed fixed over time, according to vulnerability schedules provided by the National Marine Fisheries Service (NMFS). Vulnerability schedules were described by saturating logistic functions for all populations except bocaccio, widow rockfish, yellowtail rockfish, and West Coast Pacific ocean perch, for which vulnerabilities were described by dome-shaped curves.

Models were constructed so that key estimated parameters (leading parameters) were steepness (h) and unfished total biomass (B_0). Steps to transforming h and B_0 to recruitment parameters α and β are provided (Table 3). We first show the relationship between h and the compensation ratio (CR) (eqs. T3.1a and T3.1b) and then the relationship between CR and α (eqs. T3.2a and T3.2b). CR is the ratio of α to the equilibrium unfished slope of the stock–recruit function, i.e., R_0/E_0 , where R_0 is the unfished recruitment and E_0 is the unfished egg production (see Goodwin et al. 2006, their fig. 1). Equilibrium unfished eggs per recruit (φ_{E_0}) and equilibrium unfished total biomass per recruit (φ_{B_0}), used in eqs. T3.2 and T3.3, were obtained using the functions given in Table 4 (eqs. T4.3 and T4.4), with the harvest rate U set to zero in the survivorship function (eq. T4.2). We used a plus group in our calculations of survivorship for the terminal age class (eq. T4.2), as terminal age (a_T) was considerably lower than the maximum age for most populations. We could have combined eqs. T3.1a and T3.2a (and eqs. T3.1b and T3.2b), as in Michielsens and McAllister (2004), but

Table 4. Variables common to all models.

Eq. no.	Variable
Natural survival rate at age^a	
T4.1	$s_a = e^{-M_a}$
Survivorship at age	
T4.2	$l_a = \begin{cases} 1 & \text{if } a = a_{\text{rec}} \\ \ell_{a-1}s_{a-1}(1 - v_{a-1}U) & \text{if } a > a_{\text{rec}} \\ \frac{\ell_{a-1}s_{a-1}(1 - v_{a-1}U)}{(1 - S_{a_T})} & \text{if } a = a_T \end{cases}$
Incidence functions^b	
T4.3	Equilibrium eggs per recruit at U : $\varphi_{EU} = \sum_{a=a_{\text{rec}}}^{\infty} l_a f_a$
T4.4	Equilibrium total biomass per recruit at U : $\varphi_{BU} = \sum_{a=a_{\text{rec}}}^{\infty} l_a w_a$
T4.5	Equilibrium vulnerable biomass per recruit at U : $\varphi_{VBU} = \sum_{a=a_{\text{rec}}}^{\infty} l_a w_a v_a$

Note: M , average instantaneous natural mortality rate (assumed constant for all age classes); a_T , terminal age (maximum age observed in fishery); S_{a_T} , survival rate at terminal age; a_{rec} , youngest observed age in fishery; v_a , vulnerability at age; f_a , fecundity at age; w_a , weight at age; U , annual harvest rate.

^aNote that M_a was fixed in all cases except three populations in scenario S4 (see text and Fig. 1).

^bBotsford 1981.

have chosen to show CR as a separate function to illustrate the analytical linkages between these three important productivity parameters. Note that our eq. T3.2a is the inverse of eq. 10 of Michielsens and McAllister (2004) because of the different formulation of the Beverton–Holt function.

The relationship between α , CR, and φ_{E_0} is the same for both stock–recruit models (eqs. T3.2a and T3.2b). Because $\varphi_{E_0} = \frac{E_0}{R_0}$, the equilibrium unfished slope of the stock–recruit function is simply $(\varphi_{E_0})^{-1}$ and $\text{CR} = \frac{\alpha}{(\varphi_{E_0})^{-1}}$ or $\alpha\varphi_{E_0}$ (Goodyear 1977; Myers et al. 1999).

Under steady-state conditions, eqs. 1 and 2 can be reparameterised in terms of equilibrium eggs per recruit φ_E , which provides a convenient means of initialising dynamic age-structured models (Botsford 1981). This is done by substituting $E = R\varphi_E$ into eqs. 1 and 2 and re-arranging to obtain

$$(4) \quad R = \frac{\varphi_E \alpha_1 - 1}{\beta_1 \varphi_E}$$

and

$$(5) \quad R = \frac{\ln(\alpha_2 \varphi_E)}{\beta_2 \varphi_E}$$

for the Beverton–Holt and Ricker functions, respectively (Walters and Martell 2004). After obtaining α (eqs. T3.2a and T3.2b), eqs. 4 and 5 can be rearranged to obtain β (eqs. T3.4a and T3.4b), completing the steps needed to obtain recruitment parameters from the key estimated parameters.

Following estimation of h and B_0 , U_{MSY} and MSY can be obtained numerically by iteratively searching for the value of U that maximizes long-term yield Y given by

$$(6) \quad Y = UR\varphi_{VBU}$$

where R is equilibrium recruitment under the harvest rate U (eqs. T3.5a and T3.5b) and φ_{VBU} is equilibrium vulnerable

biomass per recruit under U (eq. T4.5, with survivorship evaluated at the tested value of U). Once U_{MSY} has been found by numerical search, eq. 6 can be written more specifically, as in eq. T3.6. It is then possible to calculate the spawning stock biomass at MSY (SSB_{MSY} ; eq. T3.7), unfished spawning stock biomass (SSB_0 ; eq. T3.8), and the fishery reference point B_{MSY}/B_0 (i.e., $\text{SSB}_{\text{MSY}}/\text{SSB}_0$).

Note that under our assumption that fecundity is proportional to female weight at age (eq. 3), φ_E is the equivalent of spawning stock biomass per recruit (i.e., $\text{SPR} = \sum_{a=a_{\text{rec}}}^{\infty} l_a w_a m_a$, where l_a is survivorship at age (eq. T4.2; Gabriel et al. 1989). Equilibrium SPR at harvest rate U (SPR_U) is therefore equivalent to φ_{EU} (eq. T4.3). The reference point $\% \text{SPR}_0$ at U_{MSY} for each population was therefore calculated as the ratio $\varphi_{EU_{\text{MSY}}}/\varphi_{E_0}$, where $\varphi_{EU_{\text{MSY}}}$ was calculated using the mean of the posterior pdf of U_{MSY} for each population.

Hierarchical Bayesian models

In the hierarchical Bayesian model structure, probability distributions link the data, X , to parameters, Θ , and the parameters to hyper-parameters, Φ , with the prior joint distribution of the parameters and hyper-parameters given by

$$(7) \quad p(\Theta, \Phi) = p(\Theta|\Phi)p(\Phi)$$

and the joint posterior distribution given, according to Bayes' rule, by

$$(8) \quad p(\Theta, \Phi|X) \propto p(X|\Theta)p(\Theta|\Phi)p(\Phi)$$

(Gelman et al. 1995; Dorn 2002). In the present analysis, the hierarchical Bayesian models had estimated hyper-parameters (Φ , eq. T5.1; Table 5), estimated population-specific parameters (Θ , eq. T5.2; Table 5), and fixed population-specific life history and selectivity parameters (θ , eq. T5.3; Table 5). For tractability, life history and selectivity parameters for the 14 populations were assumed to be fixed and known

Table 5. Vectors of estimated and fixed parameters for the hierarchical models for $k = 14$ populations (see Table 1 for key to parameter names).

Eq. no.	Vector
Hyper-parameters	
T5.1a	$\Phi = (\mu_h, \sigma_h)$
Individual stock parameters	
T5.2a	$\Theta_k = (h_k, B_{0k}, \tau_k)$
Individual stock parameters (fixed, see Table 2 for values)	
T5.3	$\theta_k = (M_k, a_{T_k}, a_{rec_k})$

perfectly (Table 2). Sensitivity to the assumed values of M was tested (see below).

Likelihood $p(X|\Theta)$

We used a lognormal density function for the likelihood. The negative log likelihood function for K populations is as follows:

$$(9) \quad -\ln L = \sum_{k=1}^K \left(n_k \ln(\sigma_k) + \sum_{i=1}^{n_k} \frac{d_{ki}^2}{2\sigma_k^2} \right) + \text{constant}$$

where d_{ki} is the difference between the log of observed recruits and the log of predicted recruits given (Θ, Φ) for the k th population and i th observation, assuming either Beverton–Holt or Ricker recruitment, and n_k is the number of observations for each population k . σ_k describes the SD of the residuals (i.e., process error) for the k th population and is derived from the estimated precision parameter τ , which is the inverse of the variance of the residuals (i.e., $\sigma_k = \sqrt{1/\tau_k}$). For simplicity, we assumed that there was no autocorrelation in recruitment, a common simplifying assumption.

Nonhierarchical prior $p(\Theta|\Phi)$

For each population, equilibrium unfished total biomass (B_0) was assigned a broad uniform prior with a lower limit of 10% of the maximum observed spawning biomass ($0.1 \text{ SSB}_{\text{Max}}$) and an upper limit of 10 times the maximum observed spawning biomass ($10 \text{ SSB}_{\text{Max}}$). The upper boundary was determined during trial runs by inspecting scatterplots of posterior values of steepness vs. B_0 (Appendix A, Fig. A1) to ensure that most of the posterior probability density was captured in the analysis (i.e., to ensure that there were no significant boundary problems in the MCMC search). As noted by Dorn (2002), who used the data similarly to guide setting of his prior for R_0 , this approach is not strictly within Bayesian principles as it involves using the data twice, but it was necessary to place some boundary on the prior and to curb the tendency of the models to sample extremely large values of B_0 , especially for populations with uninformative data. This upper boundary was sufficient to capture almost all of the posterior probability density for all but a few populations (notably the Bering Sea – Aleutian Islands population of northern rockfish and West Coast Pacific ocean perch), which exhibited extremely long right-hand tails of the posterior probability density for B_0 (Appendix A). Sensitivity to the effects of the upper boundary placed on this prior was tested (see below).

In both models, we followed the approach of Michielsens and McAllister (2004) and defined the prior for the precision of the recruitment deviations (τ , the inverse of the variance) as an uninformative gamma distribution (Gelman et al. 1995), i.e., $\tau \sim \Gamma(0.001, 0.001)$.

Hierarchical parameters and hyper-prior $p(\Phi)$

In a hierarchical model, one or more parameters (h , in this case) are assumed to come from a probability distribution shared by all populations (the prior distribution). The hyper-parameters that describe the prior distribution for h (the hyper-priors; eq. T5.1) are estimated along with parameters for individual populations (eq. T5.2).

The prior distribution for h was assumed to conform to a transformed Beta distribution. The Beta distribution is defined on the interval $(0, 1]$, with its shape determined by two positive parameters, a and b (Gelman et al. 1995). Under Beverton–Holt recruitment, however, h is defined on the interval $[0.2, 1)$. It was therefore necessary to transform the prior, i.e.,

$$(10) \quad h = 0.8 \text{Beta}(a, b) + 0.2$$

Under Ricker recruitment, it is possible for recruitment at 20% unfished stock size to be greater than unfished recruitment and, therefore, for h to take values greater than 1. Although the theoretical limit to h under Ricker recruitment is infinity, there appear to be natural constraints on its value (Winemiller 2005; Mangel et al. 2010). Myers et al. (1999) did not report mean values of CR greater than 123.5 for the 700 populations they analysed, which would correspond to a value of $h = 9.4$ under Ricker recruitment (eq. T3.1b). We consider an upper boundary of 6.0 for the uniform prior distribution of h to adequately contain the range of values that might be possible for rockfishes with Ricker recruitment. This corresponds to a CR of approximately 70.2, which was close to the upper limit of all values reported in Myers et al. (1999) — only two species had a higher mean CR. Similarly, Goodwin et al. (2006) reported CR less than 70 for all except five out of 54 populations they analysed.

To convert the value drawn from the prior Beta probability distribution to the range $[0.2, 6]$, the transformation is therefore

$$(11) \quad h = 5.8 \text{Beta}(a, b) + 0.2$$

The hyper-priors a and b can be derived from the Beta distribution's mean and SD (Gelman et al. 1995). Mean and SD are more easily interpreted than a and b , and it is therefore more straightforward to devise appropriate priors for these parameters. We therefore directly estimated the hyper-priors μ_h and σ_h , representing the mean and SD of the Beta distribution, and then transformed them to a and b (Gelman et al. 1995). Priors for μ_h and σ_h were set to reflect ignorance of the distribution of h . To obtain an uninformative prior distribution for h , we followed the approach of Michielsens and McAllister (2004). First, the prior for μ_h was drawn from an uninformative Beta distribution ($\text{Beta}(2, 2)$). This is not a completely uniform prior, as it places slightly less probability at the unlikely extreme ends of the distribution (Myers et al. 1999; Michielsens and McAllister 2004). Given the constraints on the range of the Beta distribution, it was necessary to constrain the range of σ_h for each sampled μ_h so that

the drawn value stayed between 0 and 1. For any given value of μ_h , assuming a symmetrical distribution of the Beta function, the maximum possible variance, $\max(\sigma^2)$, is given by

$$(12) \quad \max(\sigma^2) = \frac{(h_{\max} - h_{\min})^2}{12}$$

(Evans et al. 2000), where h_{\max} is the upper limit of the range of steepness and h_{\min} is the symmetrical lower limit, corresponding to the value of h that has been drawn (e.g., under Beverton–Holt recruitment, if a value of 0.8 has been drawn, h_{\max} would be 1, h_{\min} would be 0.6, and the corresponding maximum SD from eq. 12 would be ~ 0.12). We assumed that the maximum SD was the most likely value for σ_h , with a linear reduction in probability as σ_h approaches zero (Michielsens and McAllister 2004). The prior for σ_h was therefore obtained from

$$(13) \quad \sigma_h = \sqrt{\max(\sigma^2)} \cdot \text{Beta}(2, 1)$$

(for figures and WinBUGS code, see Michielsens and McAllister 2004). The hyper-priors were then transformed to the a and b parameters of the Beta distribution (Gelman et al. 1995), which were used to derive priors for h for each population (eqs. 10 and 11). The steps above resulted in uninformative steepness priors for each population.

Posterior $p(\Theta, \Phi | X)$

The log joint posterior probability distribution of the hierarchical model is proportional to the sum of the log likelihood, the log prior, and the log hyper-prior (Dorn 2002) (eq. 8). Posteriors were obtained using the Gibbs sampler version of the Markov chain Monte Carlo (MCMC) algorithm implemented using WinBUGS software (Bayesian inference using Gibbs sampling; Lunn et al. 2000; available from www.mrc-bsu.cam.ac.uk/bugs/). For each hierarchical model, we ran the MCMC for 250 000 iterations, discarding the first 200 000 to remove any “burn-in” effects. We initialised the chains from three different starting points and used the Gelman–Rubin diagnostic tool (Brooks and Gelman 1998), within the WinBUGS software, to ensure that the results had not been influenced by initial conditions. We examined trace plots of the Markov chain to make sure that chains had converged and used the autocorrelation tool within WinBUGS to ensure that the values used to produce posterior estimates were not autocorrelated. Posterior values were imported into the R programming environment (R Development Core Team 2006; available from www.r-project.org), using the CODA package for MCMC output. All further analysis was done in the R environment.

Sensitivity analyses

Seven sensitivity analyses were done to test the effects of (i) ranges of some priors, (ii) fixed input parameters (M), and (iii) individual data sets on posterior results. Sensitivity analyses were done using the hierarchical Beverton–Holt model only.

Sensitivity to ranges of nonhierarchical priors

In any Bayesian analysis, it is possible for estimated parameters to be confounded. This is a well-known problem in population dynamics modelling, where scale and produc-

tivity parameters are often highly confounded, especially when there is little contrast in the data (Hilborn and Walters 1992). Therefore, even if priors are completely uninformative (i.e., uniform), the upper and lower limits set on the prior for one parameter may affect the posterior of other parameters. In the present analysis, our prior for h for each population was uniform and bounded by its natural limits of 0.2 and 1 in the Beverton–Holt case and by 0.2 and 6 in the Ricker case (see above for justification of this upper limit). As these priors were uniform and naturally bounded, we did not do further sensitivity tests.

The priors for B_0 , although uniform, were not naturally bounded. As discussed previously, preliminary tests showed that most of the posterior probability density was captured using upper and lower bounds for the B_0 priors of 0.1 SSB_{\max} and 10 SSB_{\max} , respectively, where SSB_{\max} is the maximum observed spawning stock biomass for each population. However, there were some populations for which the posterior distributions of B_0 had very long right-hand tails (Appendix A, Fig. A1). Two sensitivity analyses were done to assess the impact of the range of the B_0 prior on posterior estimates of steepness. In the first (scenario S1), the upper limit of the prior was set to 20 SSB_{\max} for each population (scatterplots of posterior samples of h and B_0 are shown in Appendix A, Fig. A2). For some populations for which 10 SSB_{\max} was already sufficient to capture most of the posterior probability density, setting such a large prior resulted in instability in the posterior pdf for h (e.g., spikes of high density at improbably low values around 0.2). Therefore, in a second sensitivity analysis (scenario S2), the upper limit of the prior was varied for each population. The upper limit ($x \text{ SSB}_{\max}$) was set by visual inspection of scatterplots of posterior samples of h and B_0 (Appendix A, Fig. A2) so that most of the posterior probability density was captured for both parameters, with $x = 5, 10, 15$, or 20 . These cut-off points were arbitrary and somewhat subjective but represented an attempt to reach a compromise between bounding the prior too tightly on one hand and sampling too far at the extremes of the posterior density on the other. We made the assumption that 20 times the maximum observed spawning stock biomass was a sufficiently large upper limit to test and that values greater than this could be considered unlikely.

We also tested sensitivity to the range of the prior used for the precision parameter τ . In this run (scenario S3), the parameters of the gamma distribution were adjusted to give $\tau \sim \Gamma(0.0001, 0.0001)$.

Sensitivity to M

The rate of natural mortality (M) is an important determinant of steepness (Tables 3 and 4). This parameter is difficult to estimate, and for convenience, it is usually assumed to have some fixed value. The present analysis used constant values of M that had been used in previous stock assessments (Table 2; Dorn 2002). For 11 of the populations, M had been assumed fixed across all ages in previous analyses, and these values were used here. For the other three populations (canary rockfish, black rockfish, and yellowtail rockfish), M had been assumed previously to be an increasing function of age (Fig. 1). This is often done in stock assessments to help explain lower than expected observations of

old females. In our baseline analysis, we had assumed an average fixed value of M for canary, black, and yellowtail rockfishes constant across age classes, as reported in Dorn (2002). We tested sensitivity to this assumption by running the model again (scenario S4), incorporating the age schedules of M shown (Fig. 1) for these three populations. We ran two other sensitivity tests to broadly capture the effect of under- or over-estimating M . In the first (scenario S5), M was increased by 20% of its baseline value for all populations. In the second (scenario S6), M was decreased by 20% of its baseline value for all populations.

Effect of excluding individual data sets

To test the assumption of exchangeability among populations and to test whether the posterior predictive distribution of h was sensitive to any one particular data set, the Beverton–Holt hierarchical analysis was run a further 14 times, while systematically excluding one data set in each run.

Results

Posterior estimates were insensitive to initial conditions in all models, and all chains converged. There was little to no autocorrelation in the posterior MCMC chains for any model. It was not our aim to apply formal model-evaluation approaches to evaluate the credibility of alternatives (e.g., computation of Bayes factors; Gelman et al. 1995) and we present the results from the alternative stock–recruit functions as equally likely hypotheses (see Brodziak 2002; Dorn 2002). Fits to the stock–recruit data for both Beverton–Holt and Ricker models are shown (Fig. 2). These were generated using median posterior values of α and β for each population (eqs. T3.2 and T3.4). Many of the data sets had poor contrast, indicated by few or no data points at low population size. Notable exceptions were canary rockfish and West Coast Pacific ocean perch.

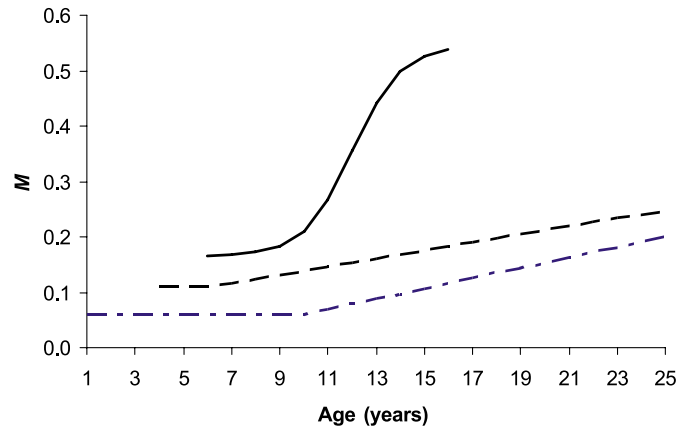
Effects of hierarchical structure on posterior estimates of steepness

Under the assumption of Beverton–Holt recruitment, there was some contraction in the range of median marginal posterior estimates of h from the hierarchical model compared with the independent models, although the change was minor for most populations (Fig. 3a). Populations for which the difference was greatest were chilipepper rockfish, bocaccio, widow rockfish, and Pacific ocean perch (Goose Island Gully), for which the independent models estimated lower h than the hierarchical model. Under Ricker recruitment, the contraction in overall range of median posterior estimates of h was greater, although this was driven mainly by the decrease in the estimate for chilipepper rockfish (Fig. 3b).

Posterior probability distributions for h

Marginal posterior probability distributions of h were obtained from the hierarchical models (Fig. 4; Table 6). The posterior predictive distribution (i.e., the posterior pdf for steepness common to all populations) was obtained by approximating integration across the posterior densities of hyper-parameters μ_h and σ_h . This was done by randomly drawing 10 000 pairs of values of μ_h and σ_h from their joint posterior distribution. Each of these 10 000 joint pairs described one posterior Beta distribution for h (after transforma-

Fig. 1. Age schedules of M used in sensitivity analysis S4 for the canary (dotted–dashed line), black (continuous line), and yellowtail (broken line) rockfish populations. M for all other populations was fixed across age classes.



tion using eq. 10 or eq. 11), from which a random value of h was drawn. The probability density of the resulting 10 000 values of h approximated the posterior predictive distribution of h . Under the assumption of Beverton–Holt recruitment, the posterior mean predictive estimate of h was 0.67, with median 0.69 and SD 0.17 (Fig. 4a). Under the assumption of Ricker recruitment, the posterior mean predictive estimate of h was 0.87, with median 0.80 and SD 0.38 (Fig. 4b).

Management parameters

U_{MSY} and B_{MSY}/B_0

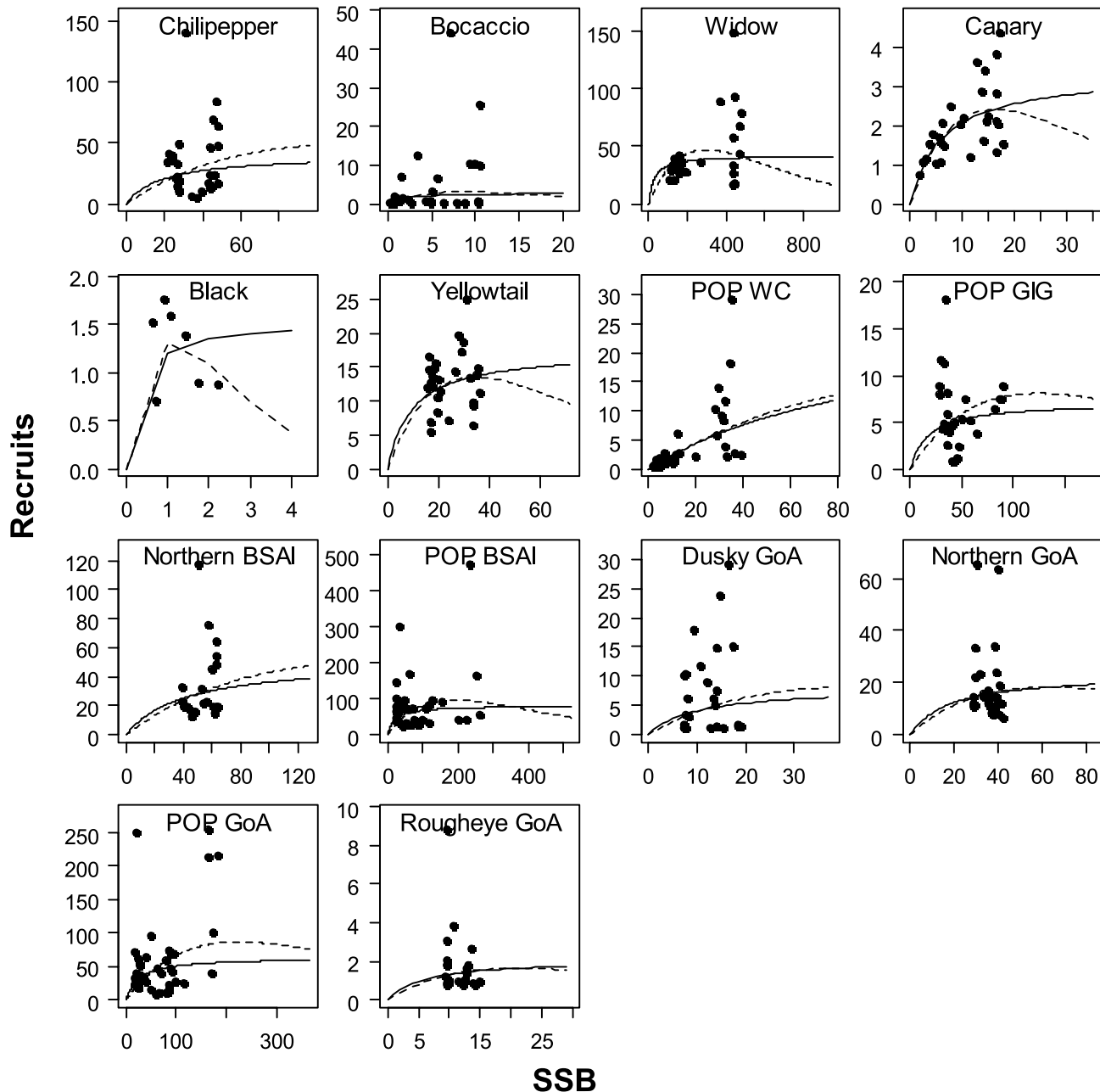
Marginal posterior distributions for optimal harvest rate U_{MSY} (Fig. 5; Table 6) were numerically derived from the posterior estimates of steepness using a Newton–Raphson algorithm. In general, mean values were relatively low (<0.2 in 12 cases and <0.1 in five cases) and posteriors were reasonably precise, although notable exceptions were the chilipepper rockfish and black rockfish populations (Fig. 5; Table 6). Populations with higher mean steepness did not necessarily have higher mean U_{MSY} (Fig. 6). This was the case under both stock–recruit assumptions and reflects that the relationship between these two parameters is unique to individual populations. This relationship is highly nonlinear and is determined by the population’s life history and the selectivity schedule imposed upon it by the fishery (Forrest et al. 2008).

Under the assumption of Beverton–Holt recruitment, mean estimates of B_{MSY}/B_0 ranged from 0.19 to 0.38 (Fig. 7). Mean estimates of B_{MSY}/B_0 were higher under the assumption of Ricker recruitment, ranging from 0.36 to 0.47 (Fig. 7). Under Ricker recruitment, some estimates of B_{MSY}/B_0 were higher than mean estimates of $\%SPR_0$ at U_{MSY} (Table 6), which can happen if fish are first harvested before they mature, as was the case with many of the populations in this study.

$\%SPR_0$ at U_{MSY}

Posterior estimates of $\%SPR_0$ at mean U_{MSY} ranged from 0.21 to 0.58 under Beverton–Holt recruitment and from 0.22 to 0.76 under Ricker recruitment (Table 6). Based on these mean estimates, the proxy used by the North Pacific Fishery

Fig. 2. Fits to stock–recruit data obtained for the 14 stocks under the assumption of Beverton–Holt (continuous lines) and Ricker (broken lines) stock–recruit functions. Units vary among populations. See Table 2 for population codes.

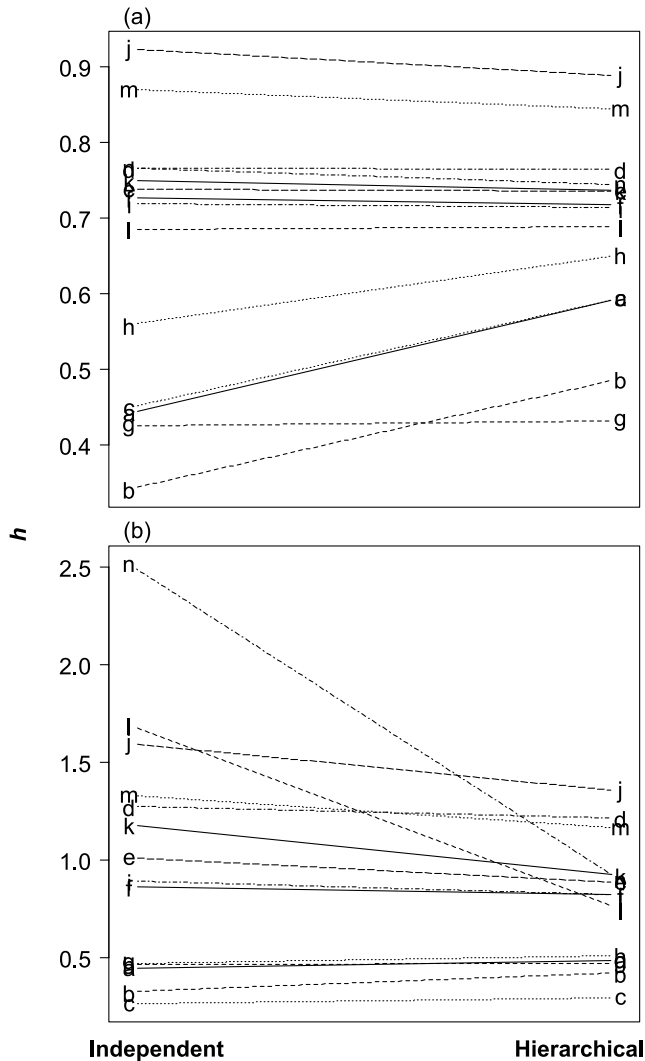


Management Council, $F_{40\%}$, would serve as an adequate precautionary reference point for most of the populations if the stock–recruit relationship could be described by the Beverton–Holt function but would be inadequate for some populations (notably bocaccio and West Coast Pacific ocean perch). It would be an inadequate limit reference point for five populations under a Ricker stock–recruit relationship (Table 6).

Some other observations are worth noting, mainly that the six Alaskan populations all had low $\%SPR_0$ at U_{MSY} (21%–34%), despite having very low M (0.03–0.07 year⁻¹) (Table 6). This is less surprising when it is noted that these populations also tended to have higher estimated steepness (Table 6). For the 14 populations, there was a strong nega-

tive relationship between h and $\%SPR_0$ at U_{MSY} under both Beverton–Holt ($r = -0.96$) and Ricker ($r = -0.94$) recruitment (Figs. 8a, 8b). This might be expected, as populations with stronger recruitment compensation are expected to be able to be sustained at lower levels of spawning biomass. Several populations with high estimated steepness had very low M (Figs. 8c, 8d) and correspondingly low mean estimated U_{MSY} (Pacific ocean perch and Alaskan populations; Table 6). Therefore, although the relationship between $\%SPR_0$ at U_{MSY} and U_{MSY} was negative ($r = -0.32$ and -0.49 for Beverton–Holt and Ricker recruitment, respectively; Figs. 8e, 8f), as might be expected, the relationship was nowhere near as strong as that between $\%SPR_0$ and h . In other words, for many of these populations, M was a

Fig. 3. Median population-specific posterior estimates of h from (a) Beverton–Holt and (b) Ricker models. Independently derived estimates are shown on the left-hand side of each plot. Estimates derived from hierarchical models are shown on the right. Key to populations (see also Table 2): (a) chilipepper; (b) bocaccio; (c) widow; (d) canary; (e) black; (f) yellowtail; (g) POP WC; (h) POP GIG; (i) northern BSAI; (j) POP BSAI; (k) dusky GoA; (l) northern GoA; (m) POP GoA; and (n) rougheye GoA. See Table 2 for population codes.



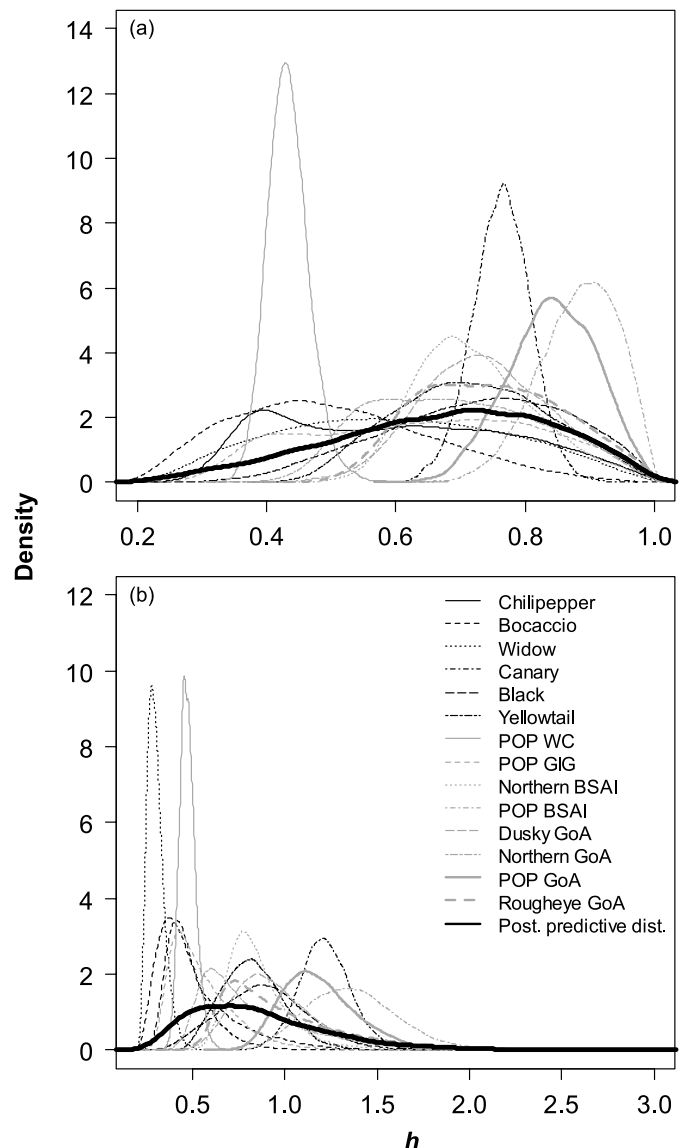
stronger determinant of U_{MSY} , whereas steepness was the strongest determinant of $\%SPR_0$ at U_{MSY} . These two negatively related productivity parameters trade off against each other to produce a much flatter relationship between $\%SPR_0$ at U_{MSY} and U_{MSY} than might be expected. This is an encouraging result in terms of the suitability of $\%SPR_0$ at U_{MSY} as a proxy for U_{MSY} , as it remains relatively stable across a range of estimates of U_{MSY} .

Sensitivity analyses

Sensitivity to ranges of nonhierarchical priors

Increasing the range of values included in the prior distributions for B_0 had a noticeable effect on the mean of the

Fig. 4. Marginal posterior probability distributions of h obtained directly from the hierarchical models for the 14 stocks under (a) Beverton–Holt and (b) Ricker recruitment. The posterior predictive distribution (post. predictive dist.) for h is also shown (thick black line). See Table 2 for population codes.



posterior distribution of steepness for some populations but not others (Table 7). Not surprisingly, steepness posteriors for populations with the most informative data sets (canary rockfish, West Coast Pacific ocean perch, and Bering Sea – Aleutian Island Pacific ocean perch) were almost unaffected by changing the prior for B_0 (scenario S1). For a number of other populations, however, the mean estimate of steepness dropped by 0.04–0.08 when the maximum value of the prior for B_0 was increased to $20SSB_{Max}$. Chilipepper rockfish showed the biggest decrease in mean estimated steepness, with a mean value of 0.52 in scenario S1 compared with the baseline value of 0.6. This was driven by a concentration of posterior density at the bottom end of the range of steepness as the range of the prior for B_0 was increased (see also baseline scenario in Fig. 4). A similar concentration of posterior density was also observed for Goose Island Gully Pa-

Table 6. Posterior mean (standard deviation (SD)) estimates of h and U_{MSY} and mean %SPR₀ at U_{MSY} obtained from the baseline hierarchical models.

	Beverton–Holt			Ricker			M
	h	U_{MSY}	%SPR ₀	h	U_{MSY}	%SPR ₀	
Posterior predictive mean (SD)	0.67 (0.17)	—	—	0.87 (0.38)	—	—	—
Chilipepper	0.60 (0.18)	0.19 (0.10)	0.41	0.56 (0.22)	0.14 (0.07)	0.49	0.24
Bocaccio	0.50 (0.15)	0.11 (0.05)	0.51	0.45 (0.14)	0.09 (0.04)	0.59	0.20
Widow	0.60 (0.17)	0.17 (0.09)	0.40	0.30 (0.05)	0.04 (0.02)	0.76	0.15
Canary	0.76 (0.05)	0.14 (0.02)	0.32	1.22 (0.14)	0.20 (0.03)	0.25	0.08
Black	0.72 (0.14)	0.30 (0.17)	0.24	0.89 (0.24)	0.24 (0.07)	0.30	0.28
Yellowtail	0.72 (0.12)	0.21 (0.09)	0.30	0.83 (0.17)	0.18 (0.04)	0.34	0.14
POP WC	0.43 (0.03)	0.04 (0.01)	0.58	0.47 (0.04)	0.05 (0.01)	0.55	0.06
POP GIG	0.64 (0.17)	0.08 (0.05)	0.36	0.55 (0.18)	0.05 (0.02)	0.48	0.05
Northern BSAI	0.72 (0.09)	0.06 (0.02)	0.32	0.86 (0.18)	0.06 (0.01)	0.33	0.04
POP BSAI	0.88 (0.06)	0.12 (0.03)	0.21	1.37 (0.24)	0.12 (0.02)	0.22	0.06
Dusky GoA	0.74 (0.10)	0.13 (0.05)	0.29	0.96 (0.24)	0.13 (0.04)	0.30	0.07
Northern GoA	0.70 (0.13)	0.08 (0.04)	0.32	0.84 (0.32)	0.08 (0.03)	0.34	0.06
POP GoA	0.84 (0.07)	0.11 (0.03)	0.24	1.19 (0.21)	0.11 (0.02)	0.24	0.06
Rougheye GoA	0.75 (0.11)	0.06 (0.02)	0.29	0.99 (0.34)	0.06 (0.02)	0.29	0.03

Note: Values of M are also shown for comparison. Posteriors, including the mean of the posterior predictive distribution, were obtained using data from all 14 populations. See Table 2 for population codes.

cific ocean perch under S1. Both populations had very uninformative data sets. Similarly, several of the Alaskan populations with very uninformative data (dusky rockfish, rougheye rockfish, and both populations of northern rockfish) also showed strong sensitivity to the range of the prior used for B_0 . These downward shifts in posterior probability estimates for individual populations had the effect of reducing the mean of the posterior predictive distribution from 0.67 to 0.64.

Using the data to select the upper limit of the B_0 prior for individual populations (scenario S2) did curb the tendency of the model to sample from the extreme right-hand tail of the posterior distribution for some populations and resulted in estimates of steepness closer to the baseline estimates, although there was still a slight drop in mean estimated steepness for many populations (Table 7). The mean of the posterior predictive distribution was reduced from 0.67 to 0.66 under this scenario.

Posterior estimates of steepness were almost completely insensitive to the range of values used in the prior for the precision of the recruitment estimates τ (scenario S3; Table 7).

Sensitivity to M

Unsurprisingly, results were very sensitive to the assumptions made about M , although inclusion of age-varying estimates of M for canary, black, and yellowtail rockfishes (scenario S4) had a relatively minor effect on final estimates of steepness. The posterior mean estimate of steepness for canary rockfish was reduced from 0.76 to 0.72 (Table 7). Estimates for black and yellowtail rockfishes changed from 0.72 to 0.74 and 0.71, respectively (Table 7).

Increasing M by 20% (scenario S5) resulted in lower estimates of steepness for all populations (Table 7). Correspondingly, the mean of the posterior predictive distribution was reduced from 0.67 to 0.62. Decreasing M by 20% (scenario S6) had the opposite effect, resulting in higher esti-

mates of steepness for individual populations and an increase in the mean of the posterior predictive distribution from 0.67 to 0.74, with a slight decrease in the SD.

Posterior estimates of U_{MSY} were affected predictably by changes in posterior estimates of steepness, with mean estimates of U_{MSY} increasing with increases in h (Table 7). Similarly, posterior mean estimates of %SPR₀ at U_{MSY} tended to decrease with increases in h and vice versa (Table 8).

Effect of excluding individual data sets

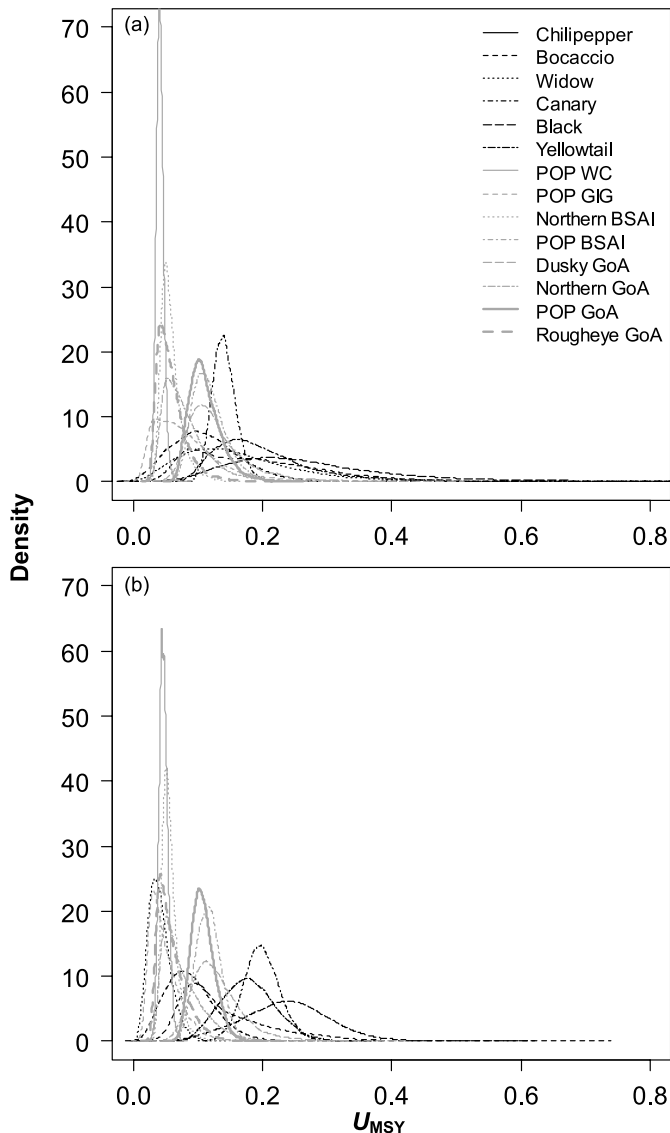
One population (West Coast Pacific ocean perch) had a strong effect on the posterior predictive distribution of steepness (Fig. 9). Box plots indicate that the median of the posterior predictive distribution, when data for West Coast Pacific ocean perch were excluded, was approximately 10% higher than when this population was included. The marginal posterior distribution of h for this population was considerably lower and more precise than for other populations (Fig. 4; Table 6) and had the effect of pulling the posterior predictive distribution towards a lower range of values. The posterior predictive distribution for h was largely insensitive to exclusion of any other population (Fig. 9).

Discussion

Hierarchical Bayesian meta-analysis has been used by a number of authors as a means of overcoming the problem of uninformative data in estimation of productivity parameters (Liermann and Hilborn 1997; Michielsens and McAllister 2004; Su et al. 2004). Hierarchical meta-analysis has the advantage of reducing uncertainty in parameter estimates for data-limited populations by incorporating data from multiple similar populations simultaneously (Gelman et al. 1995).

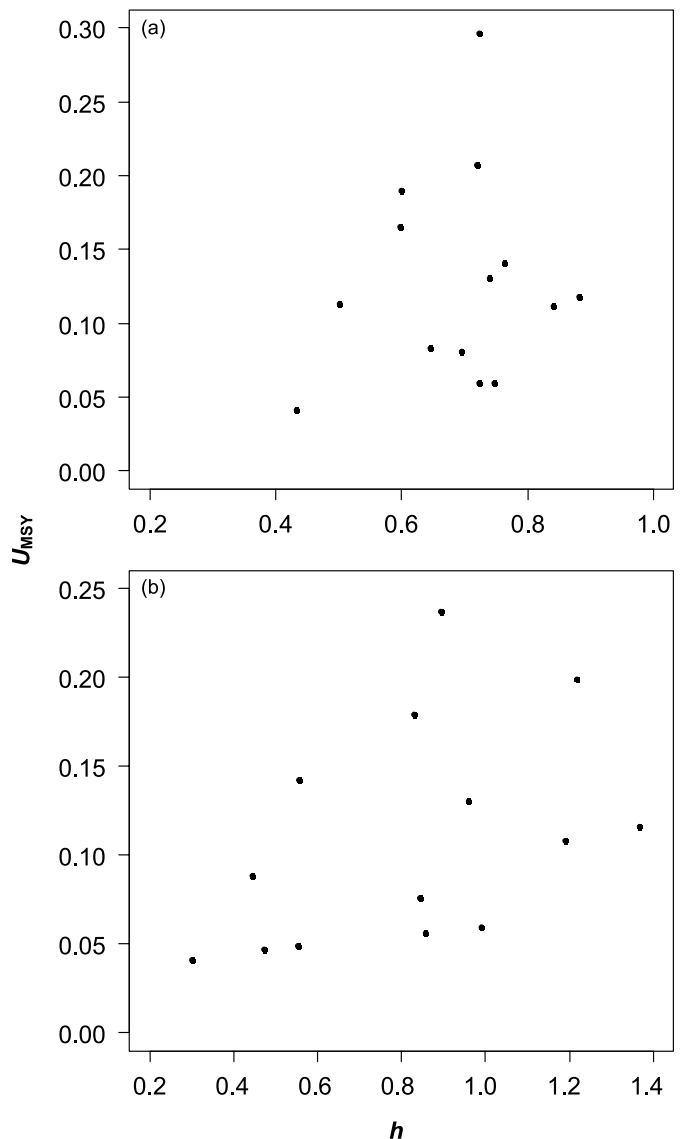
Data sets for most of the populations considered in this study were relatively uninformative, resulting in imprecise marginal posterior distributions for most populations. The posterior predictive distribution for steepness was similarly

Fig. 5. Marginal posterior probability distributions of U_{MSY} , derived numerically from the posteriors for h in (a) Beverton–Holt and (b) Ricker hierarchical models. See Table 2 for population codes.



imprecise with a mean around 0.67 (SD = 0.17) under the assumption of Beverton–Holt recruitment and 0.87 (SD = 0.38) under Ricker recruitment. The mean of the Beverton–Holt posterior predictive distribution for steepness obtained here is consistent with the mode of the posterior predictive distribution reported by Dorn (2002), who reported the highest probability for the bin with midpoint 0.725. To the best of our knowledge, Michielsens and McAllister (2004) were the first to publish a transformation between α and steepness for the Ricker model that accounts for the fact that steepness can take values greater than unity. Dorn (2002) used the transformation given in Myers et al. (2002), which provides the value of steepness for a Beverton–Holt model and thus would never take values greater than unity. We therefore do not directly compare our posterior predictive distributions obtained in the Ricker case with those of Dorn (2002). For individual populations, the marginal Beverton–Holt posterior probability distributions obtained here tended to be higher

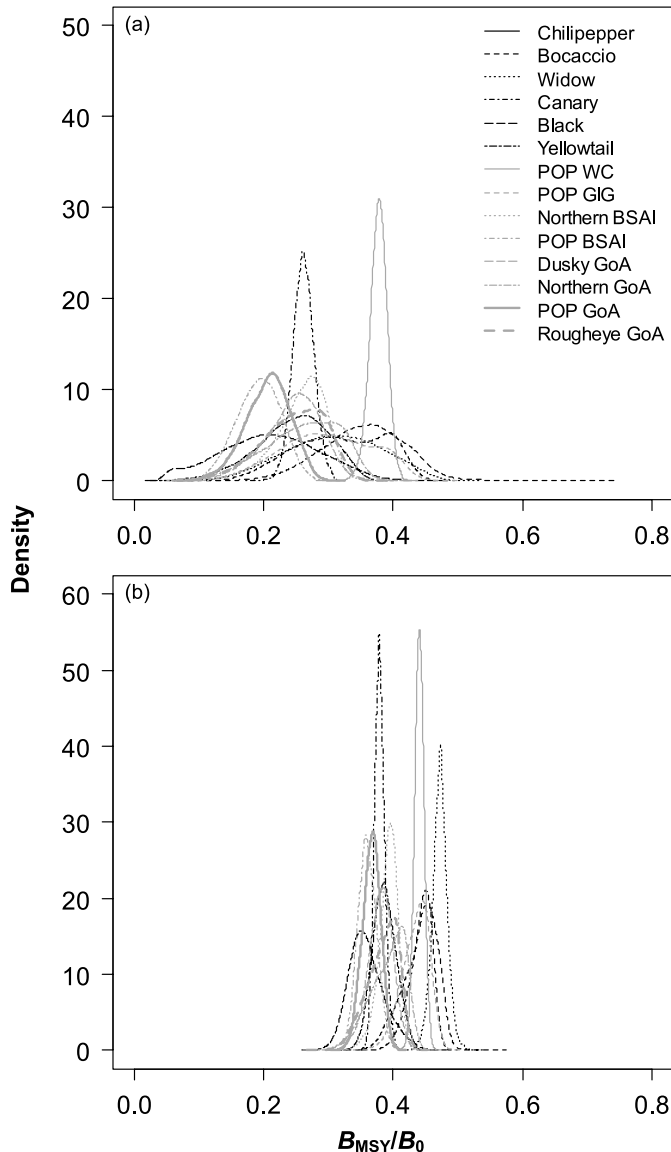
Fig. 6. Relationship between mean of the posterior estimates of h and U_{MSY} from (a) Beverton–Holt and (b) Ricker hierarchical models.



and more precise than those of Dorn (2002), although this is not really surprising given the addition of several new populations with high predicted steepness and the addition of new data for several populations. Sensitivity analysis suggested that differences might have been partially due to differences in the formulation of priors of B_0 . Both Dorn (2002) and Brodziak (2002) reported that data for Pacific rockfishes were not informative enough to distinguish between the Ricker and Beverton–Holt models. We therefore recommend that uncertainty in management advice arising from this structural uncertainty be explicitly acknowledged in future assessments.

Results of our analysis suggest that although there were large differences in posterior estimates of steepness among populations (both within the same hierarchical model and between Beverton–Holt and Ricker models), the range of posterior mean estimates for U_{MSY} among populations was reasonably small.

Fig. 7. Marginal posterior probability distributions of B_{MSY}/B_0 under the two different types of recruitment obtained from (a) Beverton–Holt and (b) Ricker hierarchical models. Biomass refers to spawning stock biomass. See Table 2 for population codes.



We elected to use the discrete form of the survivorship function and present our results in terms of the annual exploitation rate U rather than instantaneous fishing mortality rate F . In a full stock assessment, it would be more appropriate to use the instantaneous formulation, which does not assume separation of natural and fishing mortality and avoids the use of difference equations that can cause problems if biomass is predicted to be less than the catch at any point during simulation runs. In our analysis, we used the discrete form for convenience, as it is computationally more efficient and allowed us to show results in terms of the proportion of the population that can be sustainably harvested, rather than the less intuitive instantaneous rate. Given the low values of U_{MSY} obtained for these species (for values less than 0.2, F and U are similar in value), this is unlikely to have had a major effect on estimated management parameters. For all populations except black and yellowtail rock-

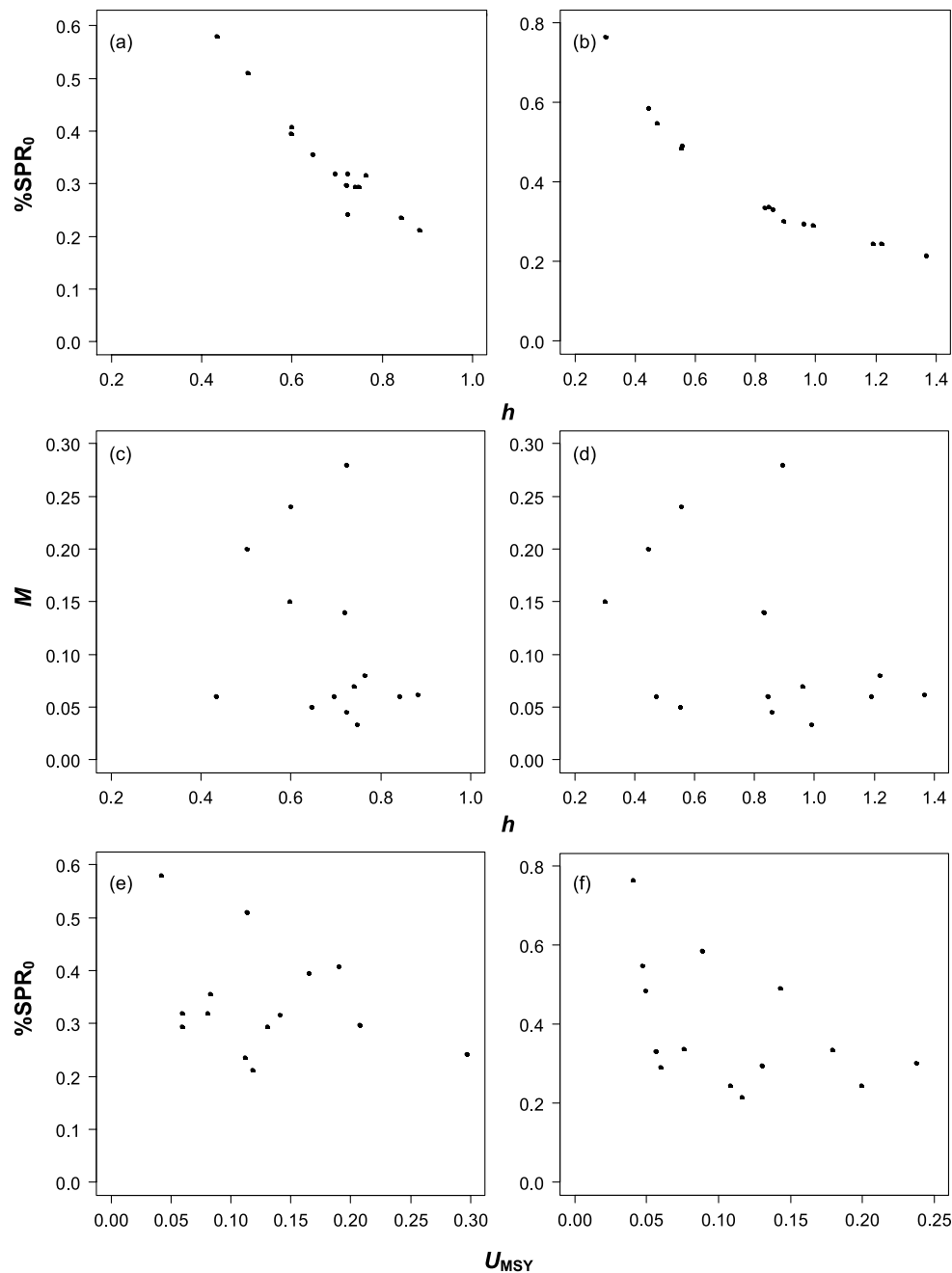
fishes, posterior mean estimates of U_{MSY} were less than 0.2 under both assumptions about the stock–recruit relationship and in all except one of the sensitivity analyses we considered (scenario S6). For several populations, notably the West Coast and Goose Island Gully Pacific ocean perch populations, rougheye rockfish, and both populations of northern rockfish, mean U_{MSY} was less than or equal to 0.1 under both stock–recruit assumptions and in all sensitivity analyses. Under the assumption of Ricker recruitment, bocaccio and widow rockfish also had mean estimates of U_{MSY} in this range.

In general, estimates of U_{MSY} obtained from the Beverton–Holt models were higher than those obtained from the Ricker models, although this was not always the case. This carried through to estimates of B_{MSY}/B_0 and $\%SPR_0$ at U_{MSY} , which tended to be higher (i.e., more conservative) under the assumption of Ricker recruitment in most cases. This is consistent with expectations of lower estimates of α from the Ricker model when extrapolating beyond the range of the data for populations with uninformative data (Walters and Martell 2004). It is interesting to note, however, that for the same given value of α , the Ricker model will tend to predict a higher value of U_{MSY} than the Beverton–Holt model due to the different functions describing the relationship between α and U_{MSY} (Forrest 2008), hence the inconsistency in some cases as to which stock–recruit function predicted higher mean U_{MSY} . Therefore, even though α is equivalent in both Ricker and Beverton–Holt stock–recruit functions (Myers et al. 1999), it is very important to consider which function to use, as the different functions will, in most cases, produce different management advice.

Populations with higher estimated steepness did not necessarily have higher estimated U_{MSY} . Although recruitment compensation is a key determinant of U_{MSY} , other factors are also important, notably growth rate (the rate at which maximum weight is attained), natural mortality rate, age at maturity, and age at which fish are first captured. The relationship between h and U_{MSY} is unique to an individual population and is determined by its life history attributes and the selectivity schedule imposed on it (Forrest et al. 2008; Forrest and Walters 2009). From biological and management perspectives, this means that life history, selectivity, and recruitment compensation all play a role in determining U_{MSY} and the most appropriate harvest strategy. In the present study, around half of the populations (notably the Alaskan populations and the Pacific ocean perch populations) had very low estimates of M (≤ 0.07 year⁻¹) and high estimated h . Corresponding values of U_{MSY} were very low, despite very high steepness. These results serve as a reminder that evidence of high steepness per se is insufficient to make statements about sustainable harvest rates, as other factors, particularly natural mortality and the selectivity schedule, must be considered simultaneously.

One of the primary aims of this analysis was to provide a posterior predictive distribution of steepness that could be used as a prior in assessments of populations similar to the ones included in the meta-analysis. The posterior predictive distribution incorporates data from all of the populations in the meta-analysis, and because of the assumption of exchangeability inherent in hierarchical meta-analysis, it is most

Fig. 8. Relationship between (a, b) mean %SPR₀ at U_{MSY} and mean h ; (c, d) mean h and M ; and (e, f) mean %SPR₀ at U_{MSY} and mean U_{MSY} from the Beverton–Holt (left) and Ricker (right) models for the 14 Pacific rockfish populations. All means are means of the estimated posterior distributions.



appropriate to use the posterior predictive distribution as a prior for steepness in assessment of a new population rather than the marginal posterior distribution for any individual population, even if the new population is the same species as one already in the meta-analysis. On a note of caution, the posterior predictive distribution cannot be used as a prior for any population already included in the meta-analysis, as this is in violation of Bayesian principles (Minte Vera et al. 2005). In such cases, the meta-analysis should be re-run without the population of interest and the resulting posterior predictive distribution used as a prior in the new analysis.

It is possible that inclusion of the West Coast Pacific

ocean perch population in the analysis resulted in violation of the assumption of exchangeability among data sets. Exclusion of the data set for West Coast Pacific ocean perch had a large effect on both the location and precision of the posterior predictive distribution for steepness. None of the other data sets had a noticeable effect when excluded. It is therefore possible that our posterior estimates of steepness are biased downwards. Resulting estimates of U_{MSY} would then also be biased downwards. It might be argued that it would have been more appropriate to remove the data set for this population from the analysis and report results without it. The West Coast Pacific ocean perch population lives

Table 7. Posterior mean (and standard deviation (SD)) estimates of h and mean U_{MSY} obtained from the Beverton–Holt hierarchical model in sensitivity analyses S1–S6.

	S1	x	S2	S3	S4	S5	S6
h							
Posterior predictive mean (SD)	0.64 (0.18)		0.66 (0.17)	0.67 (0.17)	0.68 (0.16)	0.62 (0.18)	0.74 (0.14)
Chilipepper	0.52 (0.18)	5	0.61 (0.17)	0.60 (0.018)	0.62 (0.17)	0.53 (0.20)	0.70 (0.14)
Bocaccio	0.45 (0.15)	10	0.48 (0.15)	0.50 (0.15)	0.53 (0.15)	0.45 (0.15)	0.61 (0.14)
Widow	0.56 (0.17)	10	0.58 (0.17)	0.60 (0.17)	0.62 (0.17)	0.56 (0.18)	0.67 (0.15)
Canary	0.76 (0.05)	10	0.76 (0.05)	0.76 (0.05)	0.72 (0.05)	0.71 (0.05)	0.82 (0.04)
Black	0.69 (0.16)	10	0.71 (0.14)	0.72 (0.14)	0.74 (0.13)	0.66 (0.17)	0.79 (0.11)
Yellowtail	0.70 (0.12)	10	0.71 (0.12)	0.72 (0.12)	0.71 (0.12)	0.66 (0.14)	0.79 (0.09)
POP WC	0.42 (0.03)	20	0.42 (0.03)	0.43 (0.03)	0.51 (0.03)	0.36 (0.03)	0.53 (0.03)
POP GIG	0.58 (0.18)	10	0.64 (0.17)	0.65 (0.17)	0.66 (0.16)	0.59 (0.19)	0.73 (0.14)
Northern BSAI	0.65 (0.09)	20	0.65 (0.09)	0.72 (0.09)	0.72 (0.09)	0.63 (0.11)	0.82 (0.07)
POP BSAI	0.88 (0.06)	10	0.88 (0.06)	0.88 (0.06)	0.88 (0.06)	0.85 (0.08)	0.91 (0.04)
Dusky GoA	0.68 (0.10)	20	0.69 (0.10)	0.74 (0.10)	0.74 (0.10)	0.66 (0.12)	0.82 (0.08)
Northern GoA	0.63 (0.14)	15	0.66 (0.14)	0.69 (0.13)	0.70 (0.13)	0.62 (0.16)	0.78 (0.09)
POP GoA	0.83 (0.07)	10	0.84 (0.07)	0.84 (0.07)	0.84 (0.07)	0.80 (0.08)	0.88 (0.05)
Rougheye GoA	0.69 (0.13)	15	0.72 (0.12)	0.75 (0.11)	0.75 (0.11)	0.68 (0.14)	0.82 (0.08)
U_{MSY}							
Chilipepper	0.15 (0.09)	5	0.19 (0.10)	0.19 (0.10)	0.20 (0.10)	0.15 (0.11)	0.24 (0.09)
Bocaccio	0.09 (0.05)	10	0.11 (0.05)	0.11 (0.05)	0.12 (0.05)	0.09 (0.05)	0.15 (0.05)
Widow	0.15 (0.09)	10	0.16 (0.09)	0.17 (0.10)	0.17 (0.09)	0.15 (0.10)	0.20 (0.09)
Canary	0.14 (0.02)	10	0.14 (0.02)	0.14 (0.02)	0.19 (0.02)	0.12 (0.02)	0.17 (0.02)
Black	0.27 (0.17)	10	0.29 (0.16)	0.29 (0.17)	0.28 (0.10)	0.25 (0.16)	0.35 (0.17)
Yellowtail	0.19 (0.09)	10	0.20 (0.09)	0.21 (0.09)	0.24 (0.09)	0.18 (0.09)	0.25 (0.09)
POP WC	0.04 (0.01)	20	0.04 (0.01)	0.04 (0.01)	0.05 (0.01)	0.03 (0.01)	0.06 (0.01)
POP GIG	0.07 (0.05)	10	0.08 (0.05)	0.08 (0.05)	0.09 (0.05)	0.07 (0.05)	0.10 (0.05)
Northern BSAI	0.05 (0.01)	20	0.05 (0.01)	0.06 (0.02)	0.06 (0.02)	0.05 (0.02)	0.08 (0.02)
POP BSAI	0.12 (0.03)	10	0.12 (0.03)	0.12 (0.03)	0.12 (0.02)	0.11 (0.03)	0.13 (0.02)
Dusky GoA	0.11 (0.04)	20	0.11 (0.04)	0.13 (0.05)	0.13 (0.05)	0.11 (0.05)	0.17 (0.05)
Northern GoA	0.07 (0.04)	15	0.07 (0.03)	0.08 (0.04)	0.08 (0.03)	0.07 (0.04)	0.10 (0.03)
POP GoA	0.11 (0.03)	10	0.11 (0.03)	0.11 (0.03)	0.11 (0.02)	0.10 (0.03)	0.12 (0.02)
Rougheye GoA	0.05 (0.02)	15	0.05 (0.02)	0.06 (0.02)	0.06 (0.02)	0.05 (0.02)	0.07 (0.02)

Note: Key to scenarios: S1, upper limit of B_0 prior = $20 \text{SSB}_{\text{Max}}$; S2, upper limit of B_0 prior = $x \text{SSB}_{\text{Max}}$; S3, $\tau \sim \Gamma(0.0001, 0.0001)$; S4, age schedules for M used for canary, black, and yellowtail rockfishes (see Fig. 1); S5, M increased by 20% for all populations; S6, M decreased by 20% for all populations. See Table 2 for population codes.

at the southernmost extreme of the range of this species and so may be atypical. Like other Pacific ocean perch populations, it was severely exploited during the 1960s and 1970s. Unlike populations in the centre of the range (British Columbia and southern Alaska), however, the West Coast population has been slow to recover and may be more influenced by environmental conditions than its more resilient northern counterparts (Dorn 2002). It may not, therefore, share recruitment characteristics with other populations of the same species. However, an alternative interpretation of the results from West Coast Pacific ocean perch is that it represents a legitimate lower range of values for steepness that should be included in the prior for new populations. Without it, the posterior predictive distribution may be overly precise, as the small sample size of the present analysis (14 populations) may have left out extremes. If it had been possible to sample many more rockfish populations, there could have been a more complete distribution of posteriors obtained for steepness, including both high and low values. In so far as Bayesian analysis aims to represent uncertainty in as true a manner as possible, there would be no

strong reason to reject West Coast Pacific ocean perch from the analysis. Furthermore, with the exception of canary rockfish, the data for West Coast Pacific ocean perch was the most informative of all the data sets, because it contained many observations at low stock size. The high precision of the posterior for this population was one of the reasons for its strong influence on the results. The question is then whether an informative data set can defensively be rejected from the analysis because it exerts a stronger influence on results than any other data set.

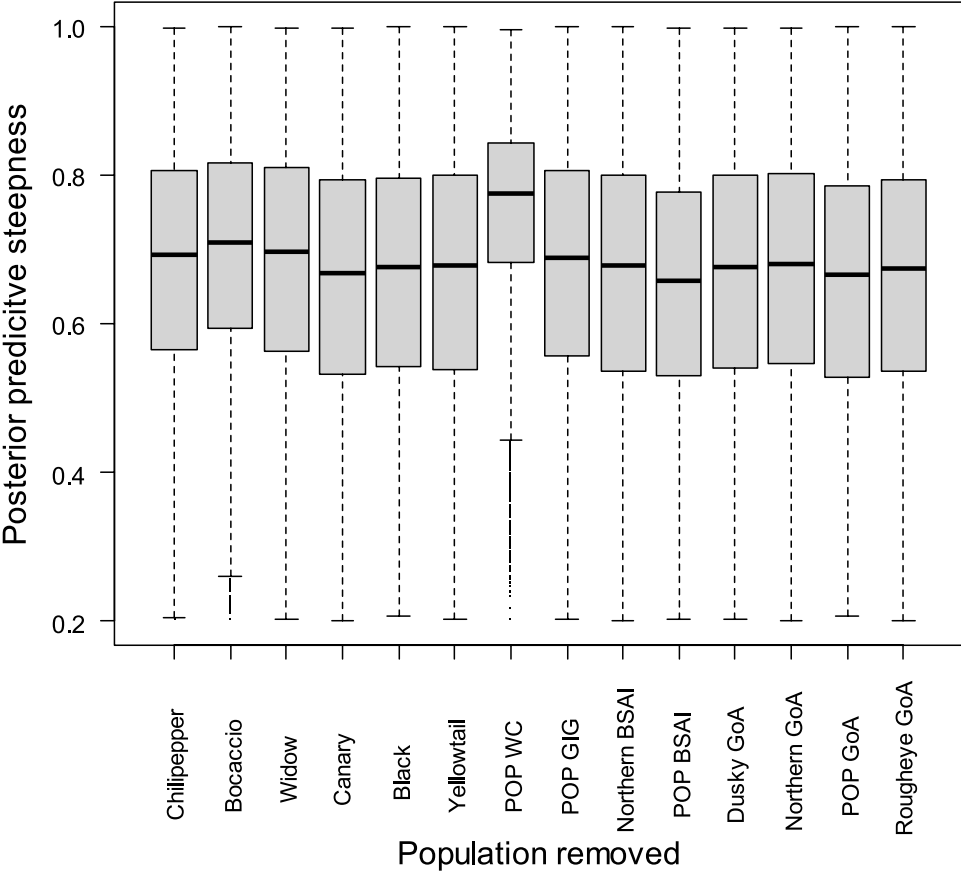
Hierarchical Bayesian meta-analysis rests on the assumption that the different populations in the analysis are exchangeable with respect to the key estimated parameter, i.e., knowing the identity and the associated properties of a given population (e.g., M or vulnerability at age) tells us nothing about the possible value of the parameter for that population (Gelman et al. 1995). Prévost et al. (2003) suggested that the best approach for transferring information from data-rich to data-sparse populations would be to use a meta-analysis that includes one or more covariates (e.g., latitude, natural mortality rate, species) to help predict the parameter of interest

Table 8. Posterior mean estimates of %SPR₀ (calculated using posterior mean estimates of *U*_{MSY}) obtained from the Beverton–Holt hierarchical model in sensitivity analyses S1–S6.

	S1	<i>x</i>	S2	S3	S4	S5	S6
Chilipepper	0.48	5	0.40	0.41	0.40	0.47	0.34
Bocaccio	0.57	10	0.53	0.51	0.48	0.57	0.42
Widow	0.43	10	0.41	0.40	0.38	0.42	0.34
Canary	0.32	10	0.32	0.32	0.38	0.35	0.28
Black	0.27	10	0.25	0.24	0.29	0.29	0.20
Yellowtail	0.31	10	0.30	0.30	0.32	0.34	0.25
POP WC	0.59	20	0.59	0.58	0.51	0.67	0.49
POP GIG	0.40	10	0.36	0.36	0.35	0.40	0.31
Northern BSAI	0.38	20	0.38	0.32	0.32	0.38	0.25
POP BSAI	0.21	10	0.21	0.21	0.22	0.23	0.19
Dusky GoA	0.34	20	0.33	0.29	0.30	0.35	0.24
Northern GoA	0.37	15	0.35	0.32	0.32	0.37	0.26
POP GoA	0.24	10	0.24	0.24	0.24	0.26	0.21
Rougheye GoA	0.33	15	0.31	0.29	0.30	0.34	0.25

Note: Key to scenarios: S1, upper limit of *B*₀ prior = 20 SSB_{Max}; S2, upper limit of *B*₀ prior = *x* SSB_{Max}; S3, $\tau \sim \Gamma(0.0001, 0.0001)$; S4, age schedules for *M* used for canary, black, and yellowtail rockfishes (see Fig. 1); S5, *M* increased by 20% for all populations; S6, *M* decreased by 20% for all populations. See Table 2 for population codes.

Fig. 9. Median and quantiles of posterior predictive distribution for steepness from the hierarchical Beverton–Holt model obtained by systematically removing one population at a time. Median estimates are shown as a black bar inside the box showing the interquartile range (IQR). Whiskers represent 1.5 IQR, with outliers shown as dots. See Table 2 for population codes.



(see also Helser and Lai 2004; Helser et al. 2007). We did not take this approach in the current analysis but recognise that it could be a useful extension of this work, given that there may be species or latitudinal effects influencing re-

cruitment parameters and especially given the relationship between natural mortality and steepness.

In a recent study, a hierarchical model was used to improve accuracy in estimates of selectivity parameters in a

set of 21 Canadian lakes (Askey et al. 2007). The hierarchical model replaced highly unrealistic vulnerability and selectivity parameter estimates from an individual-based approach that may have resulted from sparse and imprecise data with more realistic estimates. In their analysis, there was one lake for which it appeared that a markedly better fit to the data was achieved with the individual model than with the hierarchical model, suggesting that the hierarchical analysis may have produced a biased result for this lake. However, the individual model estimated for this lake what the authors judged to be an unrealistically high probability of removal of large fish, whereas the hierarchical model estimate was far more credible. Given the ubiquity of the problem of poor data for parameter estimation, the advantages of hierarchical meta-analysis may outweigh the disadvantages, as long as reasonable care is taken in the choice of data sets to include and appropriate caution is taken with use of the results.

Mean values of $\%SPR_0$ at U_{MSY} were, in general, lower than those reported by Dorn (2002), although they spanned a similar range of values. The addition of the Alaskan populations in this analysis most likely explains the lower estimates of $\%SPR_0$ obtained here compared with those of Dorn (2002). Most of the new populations had low M and high corresponding posterior estimates of steepness, which in turn pulled all of the estimates of steepness upwards in the hierarchical framework. This in turn resulted in a general trend of lower $\%SPR_0$ at U_{MSY} , although it should be remembered that although we have provided mean point estimates of $\%SPR_0$ at U_{MSY} , our results have the same degree of uncertainty as our posterior estimates of U_{MSY} .

The fishery management plan for rockfishes in Alaska stipulates that when F_{MSY} cannot be calculated, a harvest rate corresponding to $F_{40\%}$ should be adopted, whereas on the US West Coast, an F_{MSY} proxy of $F_{50\%}$ is used. Clark (2002) showed that a much more conservative target fishing mortality rate of $F_{60\%}$ was robust to a wide range of uncertainty about productivity of populations (but see Hilborn et al. 2002). The present results suggest that these reference points should be adequate for most of the populations under consideration here, largely because of the low estimates of $\%SPR_0$ at U_{MSY} obtained for the Alaskan populations. Our results suggests that the trade-off between M and steepness results in a certain degree of stability in $\%SPR_0$ at U_{MSY} across populations with different natural mortality rates and steepness, despite the very strong negative relationship between steepness and $\%SPR_0$ at U_{MSY} . Williams (2002) also showed a negative relationship between steepness and $\%SPR_0$ at U_{MSY} , which was robust to age at first harvest, although his calculations were done with fixed life history parameters and his statement that a population with higher steepness can sustain higher harvest rates is only true if all other parameters are held constant. We encourage further investigation of such relationships among different fish populations.

We caution that $\%SPR_0$ should not be interpreted too simplistically. To illustrate, the populations with the lowest natural mortality rates and lowest estimates of U_{MSY} (Pacific ocean perch populations and Alaskan rockfish populations) were estimated here to have the lowest $\%SPR_0$ at U_{MSY} , whereas the populations with the highest natural mortality

rates and higher estimates of U_{MSY} (chilipepper, widow, and black rockfishes and bocaccio) had the highest estimated $\%SPR_0$. At first, this appears counterintuitive, as populations with lower natural mortality rates would be expected to need to be maintained at higher population biomass to avoid overfishing. However, populations with low natural mortality rate may also be expected to exhibit a greater degree of recruitment compensation (Dorn 2002; Winemiller 2005; Goodwin et al. 2006), resulting in higher recruitment rates at low population size. The trade-off between M and steepness implies that populations with high steepness may have lower U_{MSY} than would be expected from knowledge of steepness alone. In addition, even though $\%SPR_0$ at U_{MSY} may be low for such populations (due to high steepness), lower M and U_{MSY} means that even if productivity is maximized when spawning stock biomass is low, the proportion of the population that can be sustainably harvested will still be low. It is therefore a mistake to assume that low $\%SPR_0$ at U_{MSY} for a population is evidence that the population can be fished harder. For slow-growing populations such as some rockfishes, even low harvest rates can drive the population to very low levels.

SPR harvest rate policies can be implemented either through control of absolute catch (which relies on reliable estimates of catch and population biomass) or through direct control of harvest rate (where the harvest rate is measured, for example, through a tagging program). Hilborn et al. (2002) and Clark (2002) caution against the use of management strategies that rely on estimates of current and unfished biomass. Fixed harvest rate policies may be more robust to uncertainty in population size and are also robust to environmental fluctuation (Walters and Parma 1996; Martell and Walters 2002) but, obviously, cannot be implemented in the absence of estimates of U_{MSY} . Priors for U_{MSY} based on results of analyses such as ours and that of Forrest and Walters (2009) or from simpler proxies (e.g., Gulland 1971; Patterson 1992; Beddington and Kirkwood 2005) may be suitable for use in this management approach. Hilborn et al. (2002) proposed an alternative feedback mechanism based on catch for managing fish stocks in the absence of estimates of U_{MSY} and reliable estimates of population size. Alternatively, efforts to adjust selectivity schedules so that all individuals have had the opportunity to spawn before harvesting can greatly reduce the probability of growth and recruitment overfishing (Myers and Mertz 1998; Froese et al. 2008).

Limitations

Our analysis assumed that life history parameters and selectivity schedules were stationary and perfectly known and that the estimates of stock and recruitment obtained from previous assessment models were representative of the true underlying values. We caution that our estimates of U_{MSY} were strongly determined by the estimates of natural mortality and age-specific selectivity that were used in the models. This is particularly important because the terminal age reported for most populations was much lower than the maximum reported age (i.e., many species of rockfishes live for more than 50 years; Love et al. 2002). Although a plus group was used to account for older age classes, this included the implicit assumption that selectivity on older age

classes was the same as for the reported terminal age. This may not be a serious issue for our analysis, as age classes older than those observed in the fishery tend to become rare after years of fishing. We also assumed stationary growth parameters (i.e., growth not influenced by population size or by environmental conditions). This is a common assumption in fisheries models, and although we recognise that wrong assumptions about growth can affect model results (Sainsbury 1980), it was beyond the scope of this study and the available data to fully account for nonstationary growth effects. Due to the necessary assumptions about constant M and growth and selectivity parameters, the estimated posterior distributions might be considered overly precise.

The natural mortality rate M is often assigned a point value in stock assessment, and in our use of the data, we did not distinguish between stock assessments that estimated M and those that made an assumption about its value. We recognise that our assumptions about M are a limitation of the analysis but suggest that admitting uncertainty in M and attempting to estimate it alongside other parameters would have resulted in overparameterised models due to lack of contrast in the data. We therefore tested sensitivity of the model outputs to the assumed values of M by simulating underestimation and overestimation of M . Results indicated that increasing M led to decreases in the mean estimates of steepness and a corresponding increase in the mean %SPR₀ at U_{MSY} . This implies that if the true value were 20% higher than the assumed value, steepness would be overestimated and %SPR₀ at U_{MSY} would be underestimated. This may appear counterintuitive, as one would expect that underestimating M would lead to a more cautious estimate of %SPR₀ at U_{MSY} . However, lower assumed values of M led to higher estimates of steepness, which we have shown to be very strongly negatively correlated with %SPR₀ at U_{MSY} . Alternatively, low values of M result in higher steepness and correspondingly lower values of %SPR₀ at U_{MSY} , implying that if the assumed value of M is higher than the true value, steepness will be underestimated and %SPR₀ at U_{MSY} will be overestimated. These seemingly counterintuitive results underline the importance of sensitivity analysis for important parameters that are assumed fixed in stock assessments.

Our results were influenced by the assumption that egg production is directly proportional to female body weight. This may be a poor assumption for some rockfish populations, as there is evidence that larger, older females may contribute disproportionately to the production of larvae than females in younger age classes. This is understood to be achieved through production of more viable larvae and more larvae per unit of spawning biomass by older females (Berkeley et al. 2004; Sogard et al. 2008). We did not include such correction factors in our analysis because data were not available for most species (although some data were available for bocaccio, chilipepper, and widow rockfishes). All other things being equal, the effect of ignoring maternal effects on recruitment could be overestimation of U_{MSY} if reproductive success of younger females is overestimated. However, the magnitude of the bias would depend on the natural mortality schedule (proportion of females in older age classes) and, importantly, on the selectivity schedule. Under dome-shaped selectivity, where a proportion of older females is invulnerable to fishing gear, there may be

little effect of incorrect assumptions about maternal effects on estimates of U_{MSY} and other reference points. We suggest that future analyses incorporate information about relative fecundity at age if it is available. Sensitivity analyses can be used to determine the importance of this effect.

It is common for stock–recruit analysis to use results of previous assessments as data. Dorn (2002) discussed this issue with respect to Pacific rockfishes, assessments of which are generally data-poor. He cautioned that spurious trends in population size resulting from imprecise survey indices could bias results. Time-series bias (Hilborn and Walters 1992) caused by nonindependence of population size and recruitment in time series of stock–recruit data is also a possible problem, although Dorn (2002) notes that most of the rockfish populations considered have been fished from a pristine state without reversal in the biomass trend (i.e., a one-way trip), which would reduce the possibility of this type of bias. Although there may be concerns with using model outputs as data, due care was taken in this analysis not to use data generated by models with strong influence of a stock–recruit function (which could lead to overly precise posteriors in the meta-analysis) and no data sets had been generated using a prior for steepness. Direct observations of stock size and recruitment are rare and usually extremely noisy. Use of model outputs in meta-analysis such as this can provide useful insights and can be worthwhile, despite the limitations of the data.

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References

- Askey, P.J., Post, J.R., Parkinson, E.A., Rivot, E., Paul, A.J., and Biro, P.A. 2007. Estimation of gillnet efficiency and selectivity across multiple sampling units: a hierarchical Bayesian analysis using mark-recapture data. *Fish. Res.* **83**(2–3): 162–174. doi:10.1016/j.fishres.2006.09.009.
- Beddington, J.R., and Kirkwood, G.P. 2005. The estimation of potential yield and stock status using life-history parameters. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **360**(1453): 163–170. doi:10.1098/rstb.2004.1582. PMID:15713595.
- Berkeley, S.A., Chapman, C., and Sogard, S.M. 2004. Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. *Ecology*, **85**(5): 1258–1264. doi:10.1890/03-0706.
- Beverton, R.J.H., and Holt, S.J. 1957. On the dynamics of exploited fish populations. Fisheries Investment Series 2, Vol. 19. UK Ministry of Agriculture and Fisheries, London, UK.
- Botsford, L. 1981. Optimal fishing policy for size-specific density-dependent population models. *J. Math. Biol.* **12**(3): 265–293. doi:10.1007/BF00276917.
- Brodziak, J. 2002. In search of optimal harvest rates for West Coast groundfish. *N. Am. J. Fish. Manage.* **22**(1): 258–271. doi:10.1577/1548-8675(2002)022<0258:ISOOHR>2.0.CO;2.

- Brooks, S.P., and Gelman, A. 1998. Alternative methods for monitoring convergence of iterative simulations. *J. Comput. Graph. Statist.* **7**(4): 434–455. doi:10.2307/1390675.
- Chen, Y., Jiao, Y., and Chen, L. 2003. Developing robust frequentist and Bayesian fish stock assessment methods. *Fish. Fish.* **4**: 105–120.
- Clark, W.G. 1991. Groundfish exploitation rates based on life history parameters. *Can. J. Fish. Aquat. Sci.* **48**(5): 734–750. doi:10.1139/f91-088.
- Clark, W.G. 1993. The effect of recruitment variability on the choice of a target level of spawning biomass per recruit. *In* Proceedings of the International Symposium on Management Strategies for Exploited Fish Populations. *Edited by* G. Kruse, D.M. Eggers, R.J. Marasco, C. Pautzke, and T.J. Quinn II. Alaska Sea Grant Report 93-02, University of Alaska, Fairbanks, Alaska. pp. 233–246.
- Clark, W.G. 2002. $F_{35\%}$ revisited ten years later. *N. Am. J. Fish. Manage.* **22**(1): 251–257. doi:10.1577/1548-8675(2002)022<0251:FRTYL>2.0.CO;2.
- Conn, P.B., Williams, E.H., and Shertzer, K.H. 2010. When can we reliably estimate the productivity of fish stocks? *Can. J. Fish. Aquat. Sci.* **67**(3): 511–523. doi:10.1139/F09-194.
- Crone, P.R., Piner, K.P., Methot, R.D., Conser, R.J., and Builder, T.L. 1999. Status of canary rockfish resource off Oregon and Washington in 1999. Appendix to Status of the Pacific coast groundfish fishery through 1999 and recommended acceptable biological catches for 2000. Pacific Fishery Management Council, Portland, Oregon.
- Dorn, M.W. 2002. Advice on West Coast rockfish harvest rates from Bayesian meta-analysis of stock–recruit relationships. *N. Am. J. Fish. Manage.* **22**(1): 280–300. doi:10.1577/1548-8675(2002)022<0280:AOWCRH>2.0.CO;2.
- Evans, M., Hastings, N., and Peacock, B. 2000. Statistical distributions. 3rd ed. John Wiley and Sons, New York.
- Fisheries and Oceans Canada. 2006. A harvest strategy compliant with a precautionary approach. *Can. Sci. Advis. Sec. Sci. Adv. Rep.* 2006/023.
- Forrest, R.E. 2008. Simulation models for estimating productivity and trade-offs in the data-limited fisheries of New South Wales, Australia. Ph.D. thesis, University of British Columbia, School of Resource Management and Environmental Studies, Vancouver, British Columbia, Canada. Available from <http://hdl.handle.net/2429/3417>.
- Forrest, R.E., and Walters, C.J. 2009. Estimating thresholds to optimal harvest rate for long-lived, low-fecundity sharks accounting for selectivity and density dependence in recruitment. *Can. J. Fish. Aquat. Sci.* **66**(12): 2062–2080. doi:10.1139/F09-137.
- Forrest, R.E., Martell, S.J.D., Melnychuk, M., and Walters, C.J. 2008. An age-structured model with leading management parameters, incorporating age-specific selectivity and maturity. *Can. J. Fish. Aquat. Sci.* **65**(2): 286–296. doi:10.1139/F07-156.
- Froese, R., Stern-Pirlot, A., Winker, H., and Gascuel, D. 2008. Size matters: how single-species management can contribute to ecosystem-based fisheries management. *Fish. Res.* **92**(2–3): 231–241. doi:10.1016/j.fishres.2008.01.005.
- Gabriel, W.L., Sissenwine, M.P., and Overholtz, W.J. 1989. Analysis of spawning stock biomass per recruit: an example for Georges Bank haddock. *N. Am. J. Fish. Manage.* **9**(4): 383–391. doi:10.1577/1548-8675(1989)009<0383:AOSBP>2.3.CO;2.
- Gelman, A., Carlin, J.B., Stern, H.S., and Rubin, D.B. 1995. Bayesian data analysis. Chapman and Hall, New York.
- Goodwin, N.B., Grant, A., Perry, A.L., Dulvy, N.K., and Reynolds, J.D. 2006. Life history correlates of density-dependent recruitment in marine fishes. *Can. J. Fish. Aquat. Sci.* **63**(3): 494–509. doi:10.1139/f05-234.
- Goodyear, C.P. 1977. Assessing the impact of power plant mortality on the compensatory reserve of fish populations. *In* Proceedings of the Conference on Assessing the Effects of Power Plant Induced Mortality on Fish Populations, Gatlinburg, Tennessee, 3–6 May 1977. *Edited by* W. van Winkle. Pergamon Press, New York. pp. 186–195.
- Gulland, J.A. 1971. The fish resources of the ocean. Fishing News Books, West Byfleet, UK.
- Hanselman, D., Heifetz, J., Fujioka, J.T., Kalei Shotwell, S., and Ianelli, J.N. 2007. Gulf of Alaska Pacific ocean perch. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska. North Pacific Fishery Management Council, Anchorage, Alaska. pp. 563–622.
- Heifetz, J., Hanselman, D., Courtney, D., and Ianelli, J. 2007. Gulf of Alaska northern rockfish. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska. North Pacific Fishery Management Council, Anchorage, Alaska. pp. 623–674.
- Helser, T.E., and Lai, H.-L. 2004. A Bayesian hierarchical meta-analysis of fish growth: with an example for North American largemouth bass, *Micropterus salmoides*. *Ecol. Model.* **178**(3–4): 399–416. doi:10.1016/j.ecolmodel.2004.02.013.
- Helser, T.E., Stewart, I.J., and Lai, H. 2007. A Bayesian hierarchical meta-analysis of growth for the genus *Sebastes* in the eastern Pacific Ocean. *Can. J. Fish. Aquat. Sci.* **64**(3): 470–485. doi:10.1139/F07-024.
- Hilborn, R., and Walters, C.J. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, New York.
- Hilborn, R.H., Parma, A., and Maunder, M.N. 2002. Exploitation rate reference points for west coast rockfish: are they robust and are there better alternatives? *N. Am. J. Fish. Manage.* **22**(1): 365–375. doi:10.1577/1548-8675(2002)022<0365:ERRPFW>2.0.CO;2.
- Ianelli, J.N., and Zimmerman, M. 1998. Status and future prospects for the Pacific ocean perch resource in waters off Washington and Oregon as assessed in 1998. Pacific Fishery Management Council, Portland, Oregon.
- Kalei Shotwell, S., Hanselman, D.H., and Clausen, D.M. 2007. Gulf of Alaska rougheye rockfish. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska. North Pacific Fishery Management Council, Anchorage, Alaska. pp. 675–734.
- Liermann, M., and Hilborn, R. 1997. Depensation in fish stocks: a hierarchic Bayesian meta-analysis. *Can. J. Fish. Aquat. Sci.* **54**(9): 1976–1984. doi:10.1139/cjfas-54-9-1976.
- Love, M., Yoklavich, M., and Thorsteinson, L. 2002. The rockfishes of the Northeast Pacific. University of California Press, Berkeley, California.
- Lunn, D.J., Thomas, A., Best, N., and Spiegelhalter, D. 2000. WinBUGS — a Bayesian modelling framework: concepts, structure, and extensibility. *Stat. Comput.* **10**(4): 325–337. doi:10.1023/A:1008929526011.
- Lunsford, C.R., Kalei Shotwell, S., Hanselman, D.H., and Clausen, D.M. 2007. Pelagic shelf rockfish. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska. North Pacific Fishery Management Council, Anchorage, Alaska. pp. 781–842.
- MacCall, A., Ralston, S., Pearson, D., and Williams, E. 1999. Status of bocaccio off California in 1999 and outlook for the next millennium. Appendix to Status of the Pacific coast groundfish fishery through 1999 and recommended acceptable biological catches for 2000. Pacific Fishery Management Council, Portland, Oregon.
- Mace, P.M. 1994. Relationships between common biological reference points used as thresholds and targets of fisheries manage-

- ment strategies. *Can. J. Fish. Aquat. Sci.* **51**(1): 110–122. doi:10.1139/f94-013.
- Mace, P.M. 2001. A new role for MSY in single-species and ecosystem approaches to fisheries stock assessment and management. *Fish. Fish.* **2**(1): 2–32.
- Mace, P.M., and Doonan, I.J. 1988. A generalized bioeconomic simulation model for fish population dynamics. *New Zealand Fish. Assess. Res. Doc.* 88/4.
- Mace, P.M., and Sissenwine, M.P. 1993. How much spawning per recruit is enough? *Can. Spec. Publ. Fish. Aquat. Sci.* No. 120. pp. 101–118.
- Mangel, M., Brodziak, J., and DiNardo, G. 2010. Reproductive ecology and scientific inference of steepness: a fundamental metric of population dynamics and strategic fisheries management. *Fish. Fish.* **11**: 89–104.
- Martell, S.J.D., and Walters, C.J. 2002. Implementing harvest rate objectives by directly monitoring exploitation rates and estimating changes in catchability. *Bull. Mar. Sci.* **70**(2): 695–713.
- McAllister, M.K., Pikitch, E.K., Punt, A.E., and Hilborn, R. 1994. A Bayesian approach to stock assessment and harvest decisions using the sampling/importance resampling algorithm. *Can. J. Fish. Aquat. Sci.* **51**(12): 2673–2687. doi:10.1139/f94-267.
- Methot, R.D. 1989. Synthetic estimates of historical abundance and mortality for northern anchovy. In *Mathematical analysis of fish stock dynamics: reviews, evaluations, and current applications*. Edited by E.F. Edwards and B.A. Megrey. AFS Symp. 6, American Fisheries Society, Bethesda, Maryland. pp. 66–82.
- Michielsens, C.G.J., and McAllister, M.K. 2004. A Bayesian hierarchical analysis of stock-recruit data: quantifying structural and parameter uncertainties. *Can. J. Fish. Aquat. Sci.* **61**(6): 1032–1047. doi:10.1139/f04-048.
- Minte-Vera, C.V., Branch, T.A., Stewart, I.J., and Dorn, M.W. 2005. Practical application of meta-analysis results: avoiding the double use of data. *Can. J. Fish. Aquat. Sci.* **62**(4): 925–929. doi:10.1139/f04-245.
- Myers, R.A. 2002. Recruitment: understanding density-dependence in fish populations. In *Handbook of fish biology and fisheries*. Vol. 1. Fish biology. Edited by P.J.B. Hart and J.D. Reynolds. Blackwell Science, Oxford, UK. pp. 123–48.
- Myers, R.A., and Mertz, G. 1998. The limits of exploitation: a precautionary approach. *Ecol. Appl.* **8**(Suppl.): s165–s169.
- Myers, R.A., Bridson, J., and Barrowman, N.J. 1995. Summary of worldwide stock and recruitment data. *Can. Tech. Rep. Fish. Aquat. Sci.* No. 2024.
- Myers, R.A., Bowen, K.G., and Barrowman, N.J. 1999. Maximum reproductive rate of fish at low population sizes. *Can. J. Fish. Aquat. Sci.* **56**(12): 2404–2419. doi:10.1139/cjfas-56-12-2404.
- Myers, R.A., Barrowman, N.J., Hilborn, R., and Kehler, D.G. 2002. Inferring Bayesian priors with limited direct data: applications to risk analysis. *N. Am. J. Fish. Manage.* **22**(1): 351–364. doi:10.1577/1548-8675(2002)022<0351:IBPWLD>2.0.CO;2.
- Otter Research. 1996. An introduction to AD model builder. Otter Research, Sidney, British Columbia.
- Patterson, K. 1992. Fisheries for small pelagic species: an empirical approach to management targets. *Rev. Fish Biol. Fish.* **2**(4): 321–338. doi:10.1007/BF00043521.
- Prévoist, E., Parent, E., Crozier, W., Davidson, I., Dumas, J., Gudbergsson, G., Hindar, K., McGinnity, P., MacLean, J., and Settem, L.M. 2003. Setting biological reference points for Atlantic salmon stocks: transfer of information from data-rich to sparse-data situations by Bayesian hierarchical modelling. *ICES J. Mar. Sci.* **60**(6): 1177–1193. doi:10.1016/j.icesjms.2003.08.001.
- Punt, A.E. 2000. Extinction of marine renewable resources: a demographic analysis. *Popul. Ecol.* **42**(1): 19–27. doi:10.1007/s101440050005.
- Punt, A.E., and Hilborn, R. 1997. Fisheries stock assessment and decision analysis: the Bayesian approach. *Rev. Fish Biol. Fish.* **7**(1): 35–63. doi:10.1023/A:1018419207494.
- Punt, A.E., and Smith, A.D.M. 2001. The gospel of maximum sustainable yield in fisheries management: birth, crucifixion and reincarnation. In *Conservation of exploited species*. Edited by J.D. Reynolds, G.M. Mace, K.H. Redford, and J.G. Robinson. Cambridge University Press, Cambridge, UK. pp. 41–66.
- R Development Core Team. 2006. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from <http://www.R-project.org>.
- Ralston, S. 1998. The status of federally managed rockfish on the U.S. west coast. In *Marine harvest refugia for west coast rockfish: a workshop*. Edited by M.M. Yoklavich. NOAA Technical Memorandum NOAA-TM-NMFS-SWFSC-255 (La Jolla, California). pp. 6–16.
- Ralston, S. 2002. West Coast groundfish harvest policy. *N. Am. J. Fish. Manage.* **22**(1): 249–250. doi:10.1577/1548-8675(2002)022<0249:WCGHP>2.0.CO;2.
- Ralston, S., and Pearson, D.E. 1997. Status of the widow rockfish in 1997. In *Status of the Pacific coast groundfish fishery through 1997 and recommended acceptable biological catches for 1998*. Pacific Fishery Management Council, Portland, Oregon.
- Ralston, S., Pearson, D.E., and Reynolds, J.A. 1998. Status of the chilipepper rockfish in 1998. In *Status of the Pacific coast groundfish fishery through 1998 and recommended acceptable biological catches for 1999*. Pacific Fishery Management Council, Portland, Oregon.
- Richards, L.J., and Olsen, N. 1996. Slope rockfish stock assessment for the west coast of Canada in 1996 and recommended yields for 1997. *Can. Tech. Rep. Fish. Aquat. Sci.* No. 2134.
- Ricker, W.E. 1954. Stock and recruitment. *J. Fish. Res. Board Can.* **11**(5): 559–623.
- Rose, K.A., Cowan, J.H., Jr., Winemiller, K.O., Myers, R.A., and Hilborn, R. 2001. Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. *Fish. Fish.* **2**: 293–327.
- Sainsbury, K.J. 1980. Effect of individual variability on the von Bertalanffy growth equation. *Can. J. Fish. Aquat. Sci.* **37**(2): 241–247. doi:10.1139/f80-031.
- Schnute, J.T., Haigh, R., Krishka, B.A., and Starr, P. 2001. Pacific ocean perch assessment for the west coast of Canada in 2001. Canadian Science Advisory Secretariat Research Document No. 2001/138.
- Shelton, P.A., and Sinclair, A.F. 2008. It's time to sharpen our definition of sustainable fisheries management. *Can. J. Fish. Aquat. Sci.* **65**(10): 2305–2314. doi:10.1139/F08-151.
- Sogard, S.M., Berkeley, S.A., and Fisher, R. 2008. Maternal effects in rockfishes *Sebastes* spp.: a comparison among species. *Mar. Ecol. Prog. Ser.* **360**: 227–236. doi:10.3354/meps07468.
- Spencer, P.D., and Ianelli, J.N. 2007a. Pacific ocean perch. In *Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions*. North Pacific Fishery Management Council, Anchorage, Alaska. pp. 811–814.
- Spencer, P.D., and Ianelli, J.N. 2007b. Northern rockfish. In *Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions*. North Pacific Fishery Management Council, Anchorage, Alaska. pp. 815–816.
- Stanley, R.D., Starr, P.D., and Olsen, N. 2009. Stock assessment for canary rockfish (*Sebastes pinniger*) in British Columbia

- waters. Canadian Science Advisory Secretariat Research Document 2009/013.
- Su, Z., Peterman, R.M., and Haeseker, S.L. 2004. Spatial hierarchical Bayesian models for stock–recruitment analysis of pink salmon (*Onchorhynchus gorbuscha*). *Can. J. Fish. Aquat. Sci.* **61**(2): 2471–2486. doi:10.1139/f04-168.
- Tagart, J.V., Ianelli, J.N., Hoffman, A., and Wallace, F.R. 1997. Status of the yellowtail rockfish resource in 1997. Appendix to Status of the Pacific coast groundfish fishery through 1997 and recommended acceptable biological catches for 1998. Pacific Fishery Management Council, Portland, Oregon.
- Wallace, F.R., Hoffmann, A., and Tagart, J.V. 1999. Status of the black rockfish resource in 1999. Appendix to Status of the Pacific coast groundfish fishery through 1999 and recommended acceptable biological catches for 2000. Pacific Fishery Management Council, Portland, Oregon.
- Walters, C.J., and Martell, S.J.D. 2004. Fisheries ecology and management. Princeton University Press, Princeton, New Jersey.
- Walters, C.J., and Parma, A.M. 1996. Fixed exploitation rate strategies for coping with effects of climate change. *Can. J. Fish. Aquat. Sci.* **53**(1): 148–158. doi:10.1139/cjfas-53-1-148.
- Williams, E.H. 2002. The effects of unaccounted discards and mis-specified natural mortality on harvest policies based on estimates of spawners per recruit. *N. Am. J. Fish. Manage.* **22**(1): 311–325. doi:10.1577/1548-8675(2002)022<0311:TEOUDA>2.0.CO;2.
- Williams, E.H., Ralston, S., MacCall, A.D., Woodbury, D., and Pearson, D.E. 1999. Stock assessment of the canary rockfish resource in the waters off southern Oregon and California in 1999. Appendix to Status of the Pacific coast groundfish fishery through 1999 and recommended acceptable biological catches for 2000. Pacific Fishery Management Council, Portland, Oregon.
- Winemiller, K.O. 2005. Life history strategies, population regulation, and implications for fisheries management. *Can. J. Fish. Aquat. Sci.* **62**(4): 872–885. doi:10.1139/f05-040.
- Yamanaka, K.L., and Logan, G. 2010. Developing British Columbia's inshore rockfish conservation strategy. *Mar. Coast. Fish. Dynamics, Manage., Ecosyst. Sci.* **2**: 28–46.

Appendix A

Figures A1 and A2 follow.

Fig. A1. Scatterplots showing posterior samples of h vs. B_0 for the 14 rockfish populations from the hierarchical Beverton–Holt model, with the upper limit of the priors for B_0 set to $10\text{SSB}_{\text{Max}}$. Units of biomass vary among populations. See Table 2 for population codes.

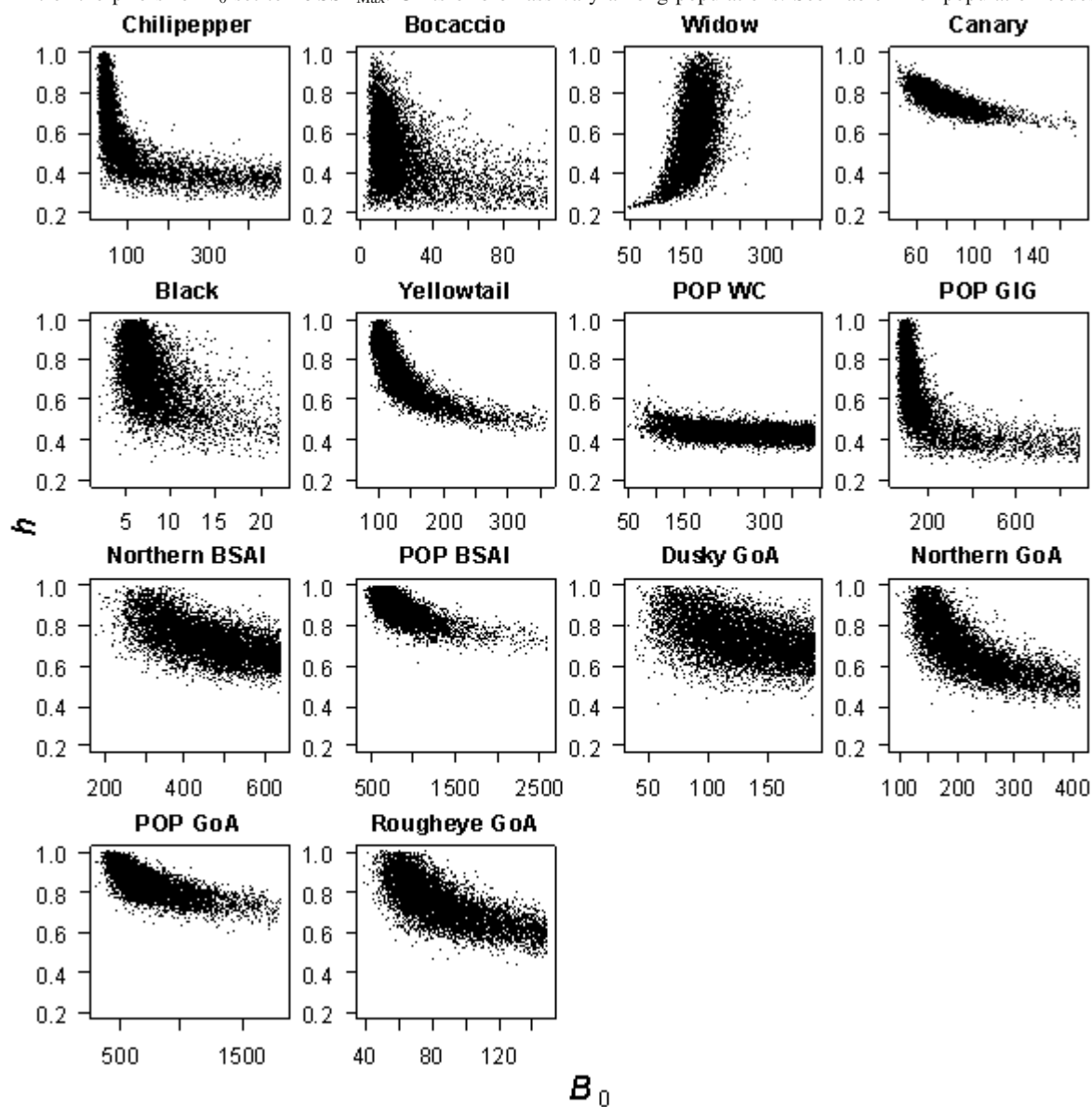


Fig. A2. Scatterplots showing posterior samples of h vs. B_0 for the 14 rockfish populations from the hierarchical Beverton–Holt model, with the upper limit of the priors for B_0 set to $20\text{SSB}_{\text{Max}}$. Units of biomass vary among populations. See Table 2 for population codes.

