

Still more spawner–recruitment curves: the hockey stick and its generalizations

Nicholas J. Barrowman and Ransom A. Myers

Abstract: Estimation of maximum reproductive rate using spawner–recruitment models involves extrapolating survival for very low spawner abundance. Existing spawner–recruitment curves often lead to biologically unreasonable extrapolations or are unable to model nondecreasing spawner–recruitment data adequately. One alternative is a piecewise linear spawner–recruitment model known as the hockey stick. We compare the fit of the Beverton–Holt with the hockey stick for 246 spawner–recruitment data sets. We show that the Beverton–Holt usually estimates a larger carrying capacity of recruits and a larger maximum reproductive rate than the hockey stick. We propose two families of generalizations of the hockey stick, one with a simple interpretation and one that is more complex but smoother. These generalized hockey sticks are more biologically plausible, less subject to numerical difficulties, and of greater utility in metaanalytic models than the hockey stick.

Résumé : Pour estimer le taux maximum de reproduction au moyen de modèles géniteurs–recrutement, on doit extrapoler le taux de survie avec une très faible abondance de géniteurs. Les courbes existantes reliant le nombre de géniteurs et le recrutement donnent souvent lieu à des extrapolations biologiquement incorrectes ou ne permettent pas de modéliser adéquatement les données géniteurs–recrutement non décroissantes. Face à ces difficultés, on peut avoir recours à un modèle géniteurs–recrutement linéaire par morceaux appelé modèle en bâton de hockey. Nous comparons l'ajustement du modèle de Beverton–Holt à celui de ce nouveau modèle pour 246 ensembles de données géniteurs–recrutement. Nous montrons que le modèle de Beverton–Holt donne habituellement une plus grande capacité de charge de recrues et un taux maximum de reproduction plus élevé que le modèle en bâton de hockey. Nous proposons deux familles de généralisations du modèle en bâton de hockey, l'une avec une interprétation simple et l'autre avec une interprétation plus complexe mais plus lisse. Ces modèles en bâton de hockey généralisés sont biologiquement plus plausibles, moins sensibles aux difficultés numériques, et plus utiles dans les modèles méta-analytiques que le modèle en bâton de hockey.

[Traduit par la Rédaction]

Introduction

Even the simplest models may have surprising consequences. Consider models relating spawner abundance, S , to subsequent recruitment, R . Commonly used spawner–recruitment functions suffer from a potentially dangerous flaw: they assume that with decreasing spawner abundance, the number of recruits per spawner is strictly increasing (Getz 1996). Examples of such functions are the Beverton–Holt (Fig. 1a), with parameters $\alpha > 0$ and $K > 0$:

$$(1) \quad R = \frac{\alpha S}{1 + (S/K)}$$

and the Ricker (Fig. 1b), with parameters $\alpha > 0$ and $\beta > 0$:

$$(2) \quad R = \alpha S e^{-\beta S}$$

The parameter α in the above functions has dimensions of recruitment per spawner and gives the slope of the function at the origin. The parameters β and K are the density-dependent terms. In the Ricker model, βS can be interpreted as the density-dependent mortality. In the Beverton–Holt model, the parameter K may be interpreted as the “threshold biomass”: for values of S greater than K , density-dependent effects dominate.

Because egg abundance is often proportional to spawner abundance, we may view the ratio of recruits to spawner abundance, R/S , as an index of survival. The models thus imply that survival increases with declining population until the last spawner disappears, an assumption that may not be realistic. Extrapolation of such models to low population sizes always predicts an increase in the number of recruits produced per spawner. If the assumption of increased survival at low population sizes is not true, the resilience and recovery time for an overexploited population will be overestimated, and the extinction probability will be underestimated, because the slope at the origin is equivalent to the maximum reproductive rate and is critical to the estimation of these parameters (Mace 1994; Myers and Mertz 1998). In this paper, we demonstrate that this can have drastic implications in practice and introduce new models that address some of the difficulties.

Our purpose here is to investigate the consequences of using simple alternative models that do not make the strong

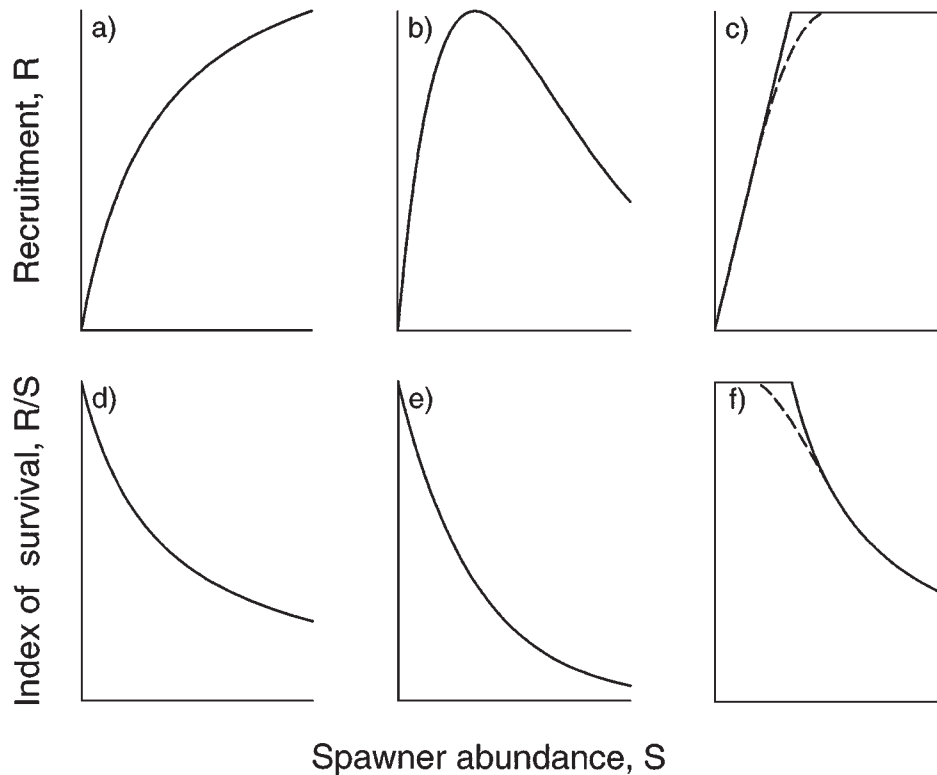
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N.J. Barrowman,¹ Department of Mathematics and Statistics, Dalhousie University, Halifax, NS B3H 3J5, Canada.

R.A. Myers, Killam Memorial Chair in Ocean Studies, Department of Biology, Dalhousie University, Halifax, NS B3H 4J1, Canada.

¹Author to whom all correspondence should be addressed.
e-mail: barrowma@mscs.dal.ca

Fig. 1. Spawner–recruitment curves and corresponding index of survival (= recruitment/spawner abundance) curves for (a and d) the Beverton–Holt model, (b and e) the Ricker model, and (c and f) the two models introduced in this paper, the hockey stick (solid line) and the quadratic hockey stick (dashed line). Subsequent figures show $\log(R/S)$ as an index of survival instead because it enhances the display of the data.



assumption that survival strictly increases with decreasing spawner abundance until zero spawner abundance is reached. Although it may be difficult to choose among models on the basis of goodness of fit, the consequences of different model choice in terms of management action may be dramatically different. For example, Myers et al. (1994) investigated different models to estimate the threshold biomass required to ensure protection of recruitment. They found dramatically different results for the Ricker model versus the Beverton–Holt model, even though the goodness of fit was rarely different.

Example: coho salmon (*Oncorhynchus kisutch*)

A model that extrapolates a higher survival may be biologically unrealistic. For example, in a species in which the juveniles are territorial, e.g., coho salmon (Sandercock 1991), very little density-dependent mortality may occur until territories have filled the habitat, i.e., the stream (Bradford et al. 1997). In this case, we would expect survival to remain relatively constant until the habitat was close to being full, and then, survival would decrease. This would result in recruitment being proportional to spawner abundance at low spawner abundance and then leveling off at higher spawner abundance (Fig. 2). Such models have been considered in the context of individual-based models of contest competition by Lømnicki (1988) and sometimes referred to as “ceiling models” (Akçakaya et al. 1999) and to describe an analytically simple form of density dependence in extinction models by Lande et al. (1997). Note, however, that in

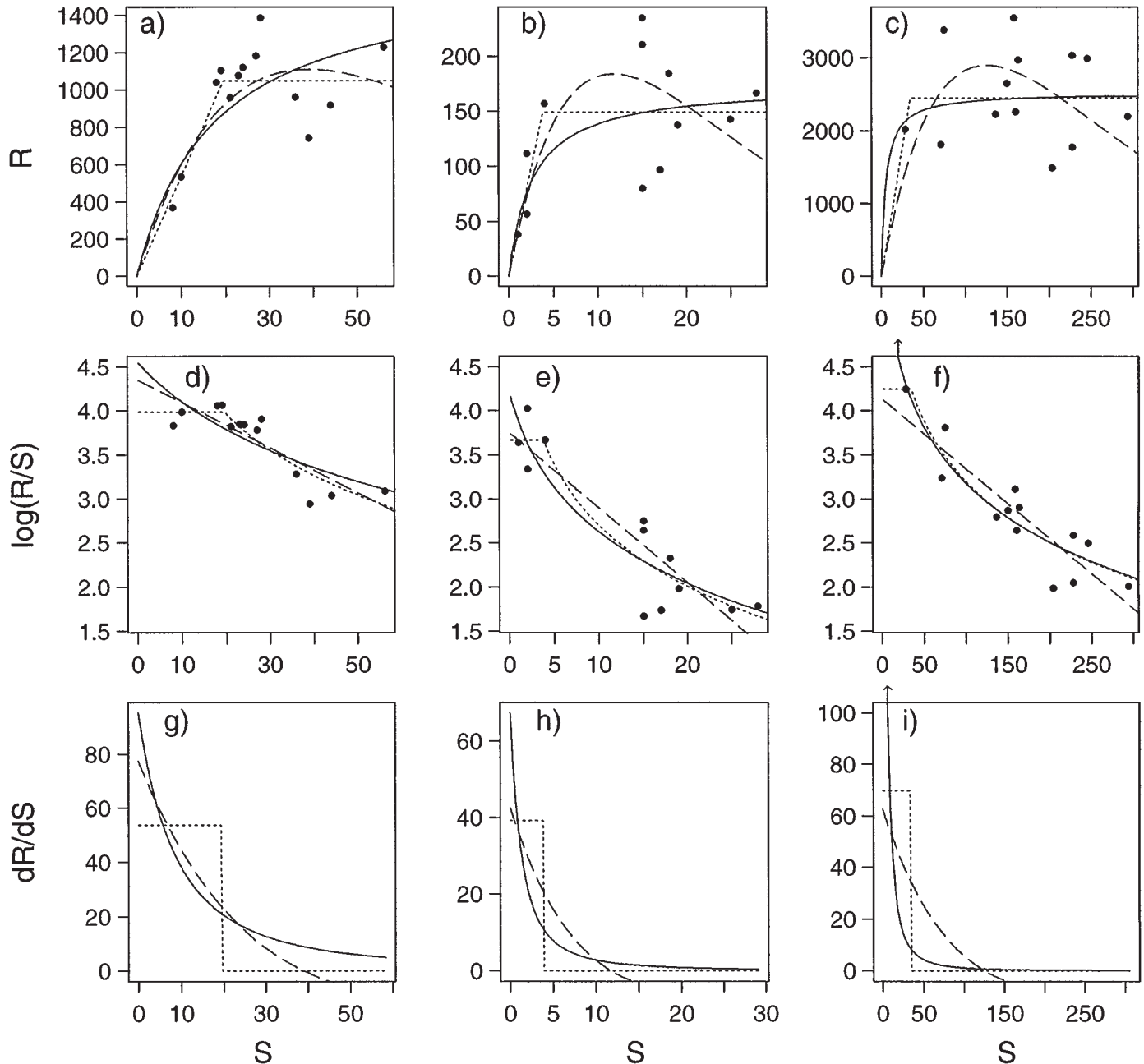
some coho salmon populations, winter habitat may be more limiting than summer habitat, and during the winter, the coho salmon are not territorial (Sandercock 1991).

To illustrate the problem, we use data on coho salmon spawning in Deer Creek and Needle Branch, Oregon, U.S.A. (Knight 1979), and in Hooknose Creek, British Columbia (Hunter 1959) (plus additional information from the Pacific Biological Station, Nanaimo, B.C., salmon archive, BL/2/5), assessed by counting females migrating upstream to spawn, S , and the resulting female seaward migrants, R , called smolts, that migrate downstream approximately 1.5 years later (Fig. 2). An in-depth analysis of these and related data is in Bradford et al. (2000). Note that we assume that the sex ratio of smolts is 1:1 (Dittman et al. 1998). In each case, the populations have been at very low levels: the lowest observed number of female spawners was eight in Deer Creek, one in Needle Branch Creek, and 29 in Hooknose Creek.

In most rivers, female smolts return as mature spawners approximately a year and a half after they migrate to the sea. Ocean survival before fishing occurs has varied greatly over the last 30 years (Bradford et al. 2000); in good years, it can be 15%, while in poor years, it can be 3% or lower.

The difficulty with both the Beverton–Holt and Ricker models is that at low spawner abundance, R/S is often estimated to be above the levels observed (Myers et al. 1994). For example, for the two lowest observations for Deer Creek (Fig. 2d), the Beverton–Holt and Ricker models predict R/S at low abundance to be greater than that observed for any year-class. In Hooknose Creek, a related problem occurs: the

Fig. 2. Coho salmon spawner–recruitment data from (a, d, and g) Deer Creek, Oregon, (b, e, and h) Needle Branch Creek, Oregon, and (c, f, and i) Hooknose Creek, British Columbia, with fitted curves obtained from maximum likelihood fits of the Beverton–Holt model (solid line), the Ricker model (dashed line), and the hockey stick model (dotted line) assuming a lognormal recruitment distribution. The panels in the first row show R versus S and fitted median recruitment curves. The panels in the second row show $\log(R/S)$ versus S and the fitted curves on this scale. Note that these plots have a common vertical scale and that each curve's intercept gives the log of the slope at the origin. The panels in the third row show derivatives of the fitted curves as a function of S . In the case of the Hooknose Creek Beverton–Holt curves (Figs. 2f and 2i), because of a very high log survival and derivative at low values of S , the vertical axes of the plots have been restricted and arrows indicate that the curves continue to rise.



Beverton–Holt estimates an unrealistically high slope at the origin. In fact, for other stocks, an infinite slope at the origin is estimated, i.e., more smolts are predicted to survive than eggs produced! The existing three-parameter spawner–recruitment models are inadequate for solving the problems described above (Appendix A).

The problems discussed above with the Beverton–Holt and Ricker models can be alleviated by fitting a simple seg-

mented regression line that starts with slope $\alpha > 0$ at the origin and then beyond some level of spawner abundance, S^* , becomes constant. We call it the “hockey stick” model and write it as

$$(3) \quad R = \alpha \min(S, S^*) = \begin{cases} \alpha S & \text{if } S < S^* \\ \alpha S^* & \text{if } S \geq S^* \end{cases}$$

For the coho salmon data, the hockey stick model appears to be no less plausible than the Ricker or Beverton–Holt model and often gives more reasonable estimates of the slope at the origin (Fig. 2).

These data are of more than academic interest. Coho salmon are subject to an important commercial and recreational fishery and are a serious conservation concern (Nickelson and Lawson 1998; Walters and Ward 1998). One motivation for this work is that an analysis of the maximum reproductive rate for coho salmon — crucial for extinction models — was not possible using traditional models: they either fit the data poorly or estimated slopes at the origin that were clearly too high.

Importance of the problem

It is often critical to know the reproductive rate of fish populations at low spawner abundance. The most important method for estimating the reproductive rate is using the slope at the origin of the spawner–recruitment data. For example, extinction models critically depend on reasonable estimates of the slope at the origin. In the examples in this paper, we use data from coho salmon because extinction of local populations is an ongoing concern.

Unfortunately, many models presently used, such as the Beverton–Holt, may overestimate the slope at the origin. This may leave managers with a dangerous impression of the resilience of the stock to overfishing (Myers et al. 1994). The alternative models introduced here may be superior to traditional models in this respect. At the very least, these models allow alternative assumptions to be investigated.

The need for investigations of alternative models goes beyond simply obtaining estimates at low population abundance. Recently, international agreements, e.g., the United Nations convention on sustainable fishing, and national fisheries regulations, e.g., the U.S. Sustainable Fisheries Act, have based fishing practices on ideas related to maximum sustainable yield. The estimates of the biomass needed for maximum sustainable yield will require estimates, implicitly or explicitly, of reproductive rates at different levels of spawner abundance. Again, it is unclear that the traditional models are sufficient to describe the population biology of all species. By considering alternative, reasonable assumptions, it may be possible to make more reliable management decisions.

Hockey stick and generalizations

Here, we investigate whether this, and other potential problems with conventional spawner–recruitment models, e.g., bias in the estimation of carrying capacity, can be mitigated by using alternatives such as the hockey stick. We begin by considering difficulties in fitting the hockey stick model, with a focus on profile likelihoods for the model parameters. We then compare Beverton–Holt and hockey stick fits for over 200 spawner–recruitment series. In the model fits, we assume multiplicative lognormal error but later test the robustness of our conclusions using an alternative error distribution, namely the gamma. We use maximum likelihood for model fitting throughout. We do not cover all aspects of estimation of spawner–recruitment functions, in particular, the user should be aware of time series bias (Walters 1985; Hilborn and Walters 1992).

Unfortunately, the hockey stick model has some undesirable properties due to the sharp bend, which represents a (perhaps implausibly abrupt) change from completely density-independent mortality to completely density-dependent mortality. Therefore, we introduce two different generalizations of the hockey stick and show them to be useful. These “generalized hockey sticks” allow for a smooth transition between density-independent mortality and density-dependent mortality. We illustrate the effects of model choice on estimates of α and the minimum harvest rate leading to extinction.

Hockey stick fits

Fitting any model with sharp bends can lead to numerical problems; one should not expect standard numerical methods to work for the hockey stick. The piecewise linear nature of the hockey stick results in a likelihood surface with flat ridges (Fig. 3d) and in some cases multiple local maxima. Depending on the starting values, numerical optimization algorithms may get “stuck” on the flat ridges or may converge to a local maximum rather than the global maximum. For these reasons, a grid search approach is used instead (Lerman 1980).

To help understand the shape of the likelihood surface and what it tells us about the relative plausibility of different parameter values, profile likelihoods can be used (Figs. 3b and 3c). A profile likelihood may be compared to a silhouetted side view of a mountain range. The profile likelihood for S^* , evaluated at a specific value S_0^* , is the maximum over all values of α of the likelihood with S^* fixed at S_0^* . Let S_{\min} and S_{\max} denote, respectively, the smallest and largest observed spawner abundances. For any value of S^* less than S_{\min} , the hockey stick is constant over the entire range of the data, with the constant determined by α ; hence, the profile likelihood for S^* is locally constant for $0 < S^* < S_{\min}$. For any value of S^* greater than S_{\max} , the hockey stick does not bend until beyond the range of the data; hence, the profile likelihood for S^* is locally constant for $S^* > S_{\max}$. Thus, the profile likelihood for S^* has flat regions extending on either side (Fig. 3c).

When recruitment is lognormally distributed, the profile likelihood for S^* can be obtained explicitly. For lognormal recruitment, the spawner–recruitment models considered here can be written in the form

$$(4) \quad R_i = \alpha f_\phi(S_i) e^{\varepsilon_i}, \quad i = 1, \dots, n$$

where we are assuming that there are n year-classes with recruitments R_1, \dots, R_n resulting from spawner abundances S_1, \dots, S_n ; the $\varepsilon_i (i = 1, \dots, n)$ are independent and identically distributed normal errors and $f_\phi(S)$ is a function of S and additional parameters ϕ (e.g., S^* in the case of the hockey stick). The logarithm of eq. 4 is

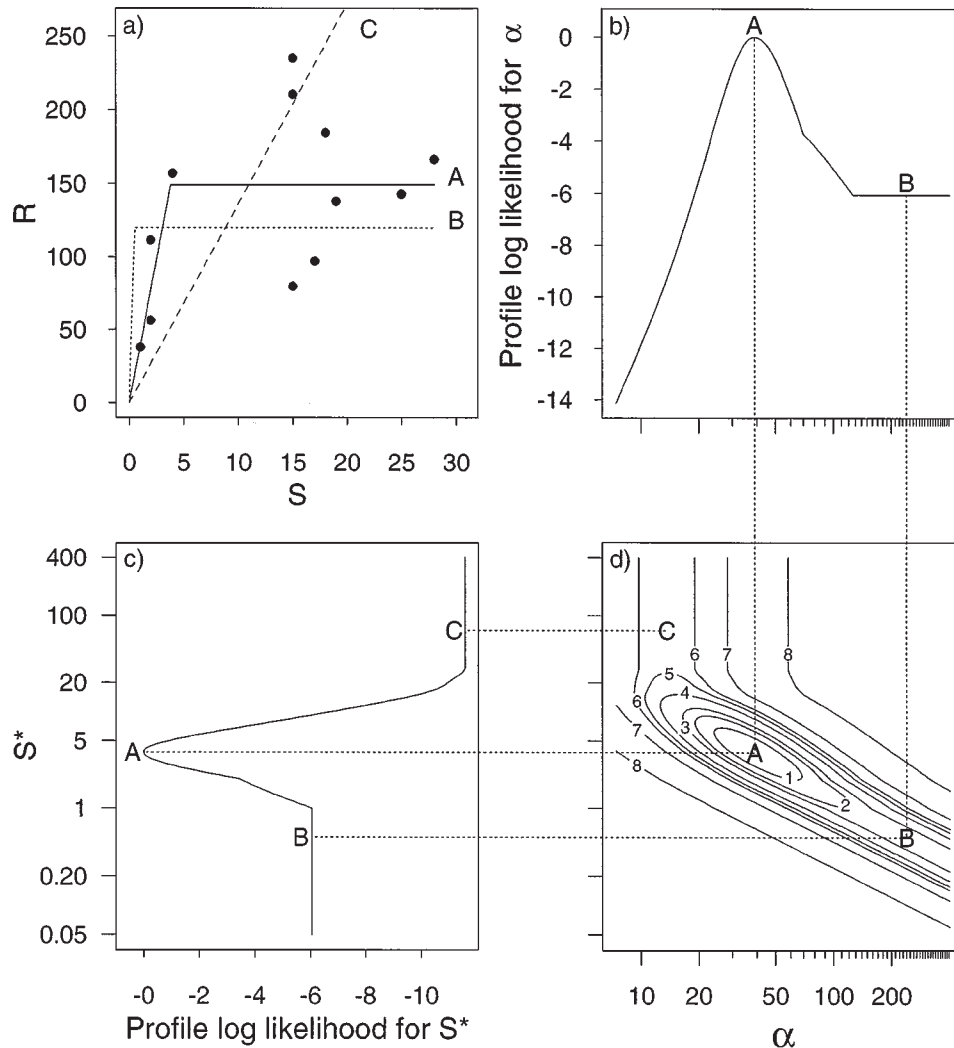
$$\log R_i = \log \alpha + \log f_\phi(S_i) + \varepsilon_i, \quad i = 1, \dots, n$$

and maximum likelihood estimation for this model is identical to least squares, i.e., the objective function is

$$\sum_i \{\log R_i - (\log \alpha + \log f_\phi(S_i))\}^2$$

For a given trial estimate of ϕ , the least squares estimate of $\log \alpha$ is

Fig. 3. Maximum likelihood estimation for the hockey stick model applied to data for coho salmon at Needle Branch Creek, Oregon. Recruitment is assumed to be lognormally distributed. The data are shown (a) with the optimal fit (A) and two nonoptimal fits (B and C). (d) A contour plot of the likelihood as a function of α and S^* is shown with the locations of the parameters of fits A, B, and C indicated. The maximum likelihood is at A. The log likelihood ratios defining the contours are (1) 3.5, (2) 6, (3) 7.5, (4) 10, (5) 11.5, (6) 12.5, (7) 15, and (8) 20. The profile log likelihoods for (b) α and for (c) S^* are also shown, with dotted lines indicating their relationship to the likelihood surface (Fig. 3d). For each of the fits, a nonlinear optimization algorithm reported convergence to the respective fit. The optimal fit A is at the centre of an elliptical peak. The suboptimal fits B and C lie on flat ridges. Both ridges are visible in the profile likelihood for S^* (Fig. 3c), but only one is visible in the profile likelihood for α (Fig. 3b).



$$\widehat{\log \alpha} = \frac{1}{n} \sum_i \log \frac{R_i}{f_\phi(S_i)}$$

(Note that we use the “hat” notation throughout to denote parameter estimates, e.g., to denote an estimate of a parameter θ , we write $\hat{\theta}$.) In the case of the two-parameter spawner–recruitment functions discussed thus far, this reduces the maximum likelihood problem to a one-dimensional one. For the hockey stick model, $f_\phi(S) = \min(S, S^*)$, so that up to an additive constant, the log profile likelihood for S^* is

$$-\frac{n}{2} \log \sum_i \{ \log R_i - (\widehat{\log \alpha} + \log \min(S_i, S^*)) \}^2$$

The profile likelihood for α is also of interest. For a particular value, α_0 , it is defined to be the maximum over all values of S^* of the likelihood with α fixed at α_0 . For any sufficiently large value of α , the likelihood (with α fixed at that value) is maximized by a small enough value of S^* that the hockey stick is constant over the entire range of the data, with the constant determined by S^* . Thus, at high values of α , the profile likelihood for α is locally constant (Fig. 3b).

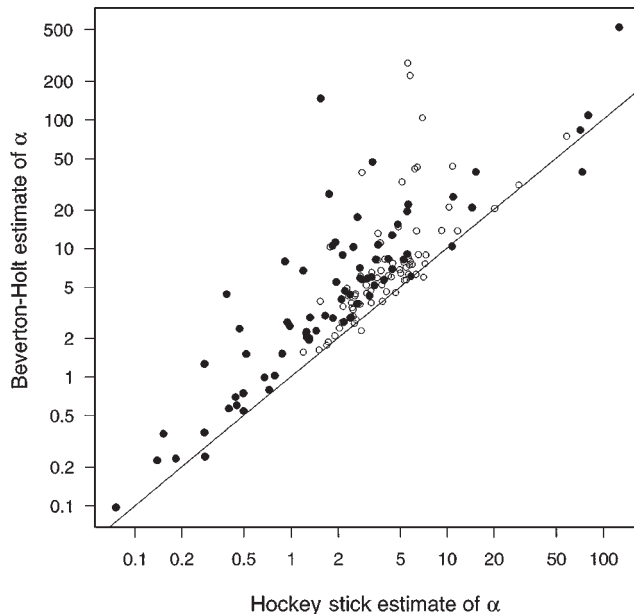
Application to 246 data sets

To obtain a better understanding of the use of the model, we describe its application to the 246 data sets² investigated by Myers et al. (1999). As discussed above, useful estimates cannot always be obtained from either the hockey stick or

²The data are freely available at <http://fish.dal.ca/welcome.html>

Table 1. Results for fitting the hockey stick model and the Beverton–Holt model to 246 spawner–recruitment data sets

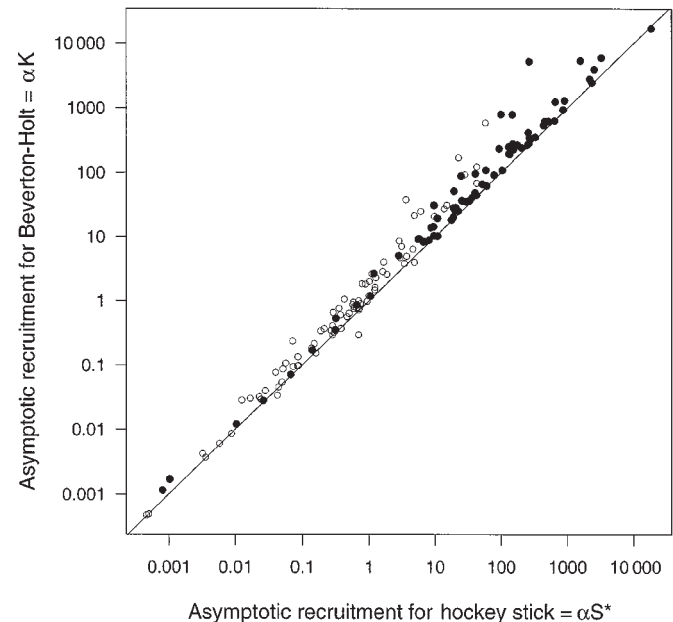
Beverton–Holt	Hockey stick		
	$\hat{S}^* \leq S_{\min}$	$S_{\min} \leq \hat{S}^* \leq S_{\max}$	$\hat{S}^* \geq S_{\max}$
$\hat{K} < S_{\min}/1000$	45	18	0
$S_{\min}/1000 \leq \hat{K} \leq 1000S_{\max}$	10	152	6
$\hat{K} > 1000S_{\max}$	0	4	11

Fig. 4. Estimates of α from hockey stick and Beverton–Holt models assuming lognormally distributed recruitment for well-determined cases. The points shown correspond to the middle cell of Table 1, i.e., data sets for which the hockey stick parameter S^* and the Beverton–Holt parameter K are both well determined. The open circles are Pacific salmon of the genus *Oncorhynchus* and Atlantic salmon (*Salmo salar*), and the solid circles are all other species. In all cases, the units are the maximum number of replacement spawners produced annually by a spawner at low population sizes and no fishing mortality.

the Beverton–Holt model. We consider three cases: (i) the estimate of K or S^* is arbitrarily low, i.e., $\hat{K} \leq S_{\min}$ for the hockey stick (B in Fig. 3) or $\hat{K} < S_{\min}/1000$ for the Beverton–Holt, (ii) the estimate of K or S^* is arbitrarily high, i.e., $\hat{K} \geq S_{\max}$ for the hockey stick (C in Fig. 3) or $\hat{K} > 1000 \times S_{\max}$ for the Beverton–Holt, and (iii) the estimate of K or S^* is intermediate between these extremes.

As expected, the shortcomings of the data resulted in similar problems of indeterminacy in both models (Table 1). For 152 data sets, both the Beverton–Holt and hockey stick models gave estimates falling in the third case above. The Beverton–Holt model gave a larger estimate of α for 95% of these data sets.

We next compare the parameter estimates from the Beverton–Holt and hockey stick models using the slope at the origin parameter, α , and the asymptotic level of recruitment (αK for the Beverton–Holt model and αS^* for the hockey stick). For simplicity, we will concentrate on the 152

Fig. 5. Estimates of the asymptotic level of recruitment from hockey stick and Beverton–Holt models assuming lognormally distributed recruitment for well-determined cases. The points shown correspond to the middle cell of Table 1, i.e., data sets for which the hockey stick parameter S^* and the Beverton–Holt parameter K are both well determined. The units are the asymptotic annual production of replacement spawners, if no fishing occurred, in units of thousands of metric tons for all species (solid circles) except Pacific salmon of the genus *Oncorhynchus* and Atlantic salmon, which are in units of millions (open circles).

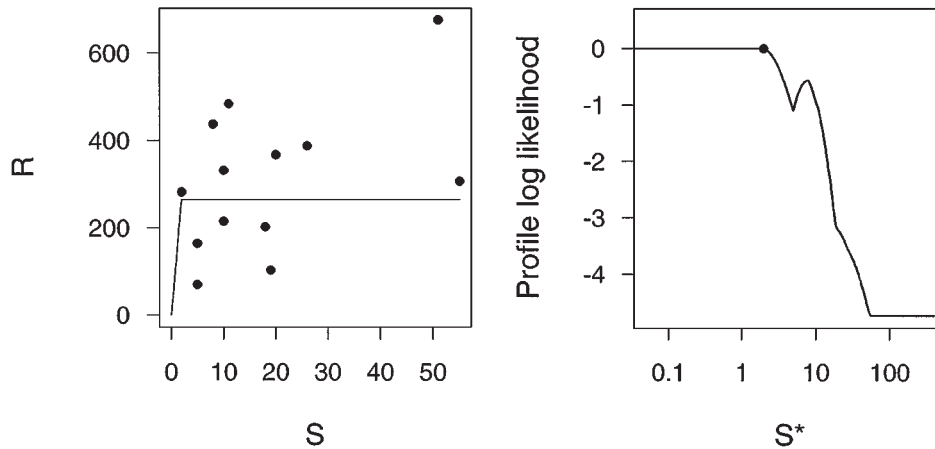
“well-determined” estimates described above. Note that they are well determined only in the sense that there is a unique maximum likelihood estimate for both the Beverton–Holt and hockey stick models.

The hockey stick model almost always gave a lower estimate than the Beverton–Holt model of the slope at the origin (Fig. 4). That is, the use of the hockey stick model would produce lower estimates of maximum sustainable fishing mortality (Myers and Mertz 1998) and population growth rate (Myers et al. 1997) than the use of the Beverton–Holt model. The Beverton–Holt estimates of α tend to be higher than the hockey stick estimates for the following reason. There is usually little data close to the origin and relatively more data at what appears to be the asymptotic level of recruitment. For a Beverton–Holt model to come close to its asymptotic level of recruitment at roughly the same point as a hockey stick model, the Beverton–Holt α must be much larger.

Similarly, the estimate of the asymptotic level of recruitment is usually greater for the Beverton–Holt than for the hockey stick (Fig. 5). This means that the Beverton–Holt tends to overestimate the carrying capacity of a stock compared with the hockey stick.

We also carried out the same type of analysis for the two types of generalized hockey stick models introduced in the next section. In almost all cases, the results were between those estimated for the hockey stick and Beverton–Holt.

Fig. 6. Spawner–recruitment data for coho salmon in Flynn Creek, Oregon, with the hockey stick profile log likelihood for S^* assuming lognormally distributed recruitment. The likelihood is maximized for any value of S^* below 2, the minimum observed number of female spawners. The circle on the profile log likelihood is at $S^* = 2$ and the corresponding hockey stick fit is superimposed on the data.



Despite its attractive properties, the hockey stick model does have shortcomings: the sharp bend is biologically unrealistic, and as noted earlier, the associated likelihood surface has flat ridges and sometimes multiple local maxima. For example, the profile likelihood for S^* for the Flynn Creek, Oregon, data set has a local maximum that is below the flat region for low values of S^* (Fig. 6).

Generalized hockey stick models

We seek a spawner–recruitment function that gives the hockey stick model as one limiting case and behaviour similar to the Beverton–Holt model as another limiting case.

Quadratic hockey stick

A simple approach is to retain the hockey stick model except in a region close to S^* and allow a smooth transition between the two parts of the hockey stick. We define this region of transition to be between $S^* - \zeta$ and $S^* + \zeta$, where $0 \leq \zeta \leq S^*$. It would be reasonable to require a curve with continuous first derivatives at all points. The piecewise polynomial approach (Tishler and Zang 1981) can produce a curve with the desired properties. The resulting equation is

$$R = \begin{cases} \alpha S & \text{if } S \leq S^* - \zeta \\ \alpha \left(S - \frac{(S - S^* + \zeta)^2}{4\zeta} \right) & \text{if } S^* - \zeta < S < S^* + \zeta \\ \alpha S^* & \text{if } S \geq S^* + \zeta \end{cases}$$

We have found it convenient to reparametrize the above equation in terms of a smoothness parameter $\delta = \zeta/S^*$ so that $0 \leq \delta \leq 1$. The term $1 - \delta$ can be interpreted as the proportion of the carrying capacity that must be filled before density-dependent mortality occurs. The above equations become

$$(5) \quad R = \begin{cases} \alpha S & \text{if } S \leq S^* (1 - \delta) \\ \alpha \left(S - \frac{(S - S^* (1 - \delta))^2}{4\delta S^*} \right) & \text{if } S^* (1 - \delta) < S < S^* (1 + \delta) \\ \alpha S^* & \text{if } S \geq S^* (1 + \delta) \end{cases}$$

which we call the “quadratic hockey stick” (Fig. 7). The simplest way to think about the quadratic hockey stick is the two pieces of a hockey stick connected by a parabolic curve, with all the right attributes (continuity and continuity of the first derivative) at the ends of the parabolic curve. The result is a curve that will exhibit some region where density-dependent mortality does not occur ($S \leq S^* (1 - \delta)$), a region where density-dependent mortality steadily becomes more important ($S^* (1 - \delta) < S < S^* (1 + \delta)$), and a region where density-dependent mortality exactly compensates for each new spawner to produce no increase in recruitment ($S \geq S^* (1 + \delta)$). In the transitional region ($S^* (1 - \delta) < S < S^* (1 + \delta)$), the derivative of recruitment with respect to spawner abundance monotonically decreases with spawner abundance. Note, however, that even with $\delta = 1$, the quadratic hockey stick does not reproduce the Beverton–Holt.

If the quadratic hockey stick is directly compared with the Beverton–Holt, it immediately becomes clear what an extreme assumption the Beverton–Holt model is: it assumes that survival will plummet with the addition of one spawner, whereas the quadratic hockey stick allows for more reasonable behaviour. For the same asymptote and slope at the origin, the Beverton–Holt increases much less rapidly as spawner abundance increases (Fig. 7). As we discuss later, this usually causes the Beverton–Holt to estimate a larger slope at the origin.

Despite its advantages, the quadratic hockey stick function has the disadvantage that like the hockey stick (Fig. 3), it results in a profile likelihood for S^* with flat regions at the sides: one up to $S_{\min}/(1 + \delta)$ and the other beyond $S_{\max}/(1 - \delta)$.

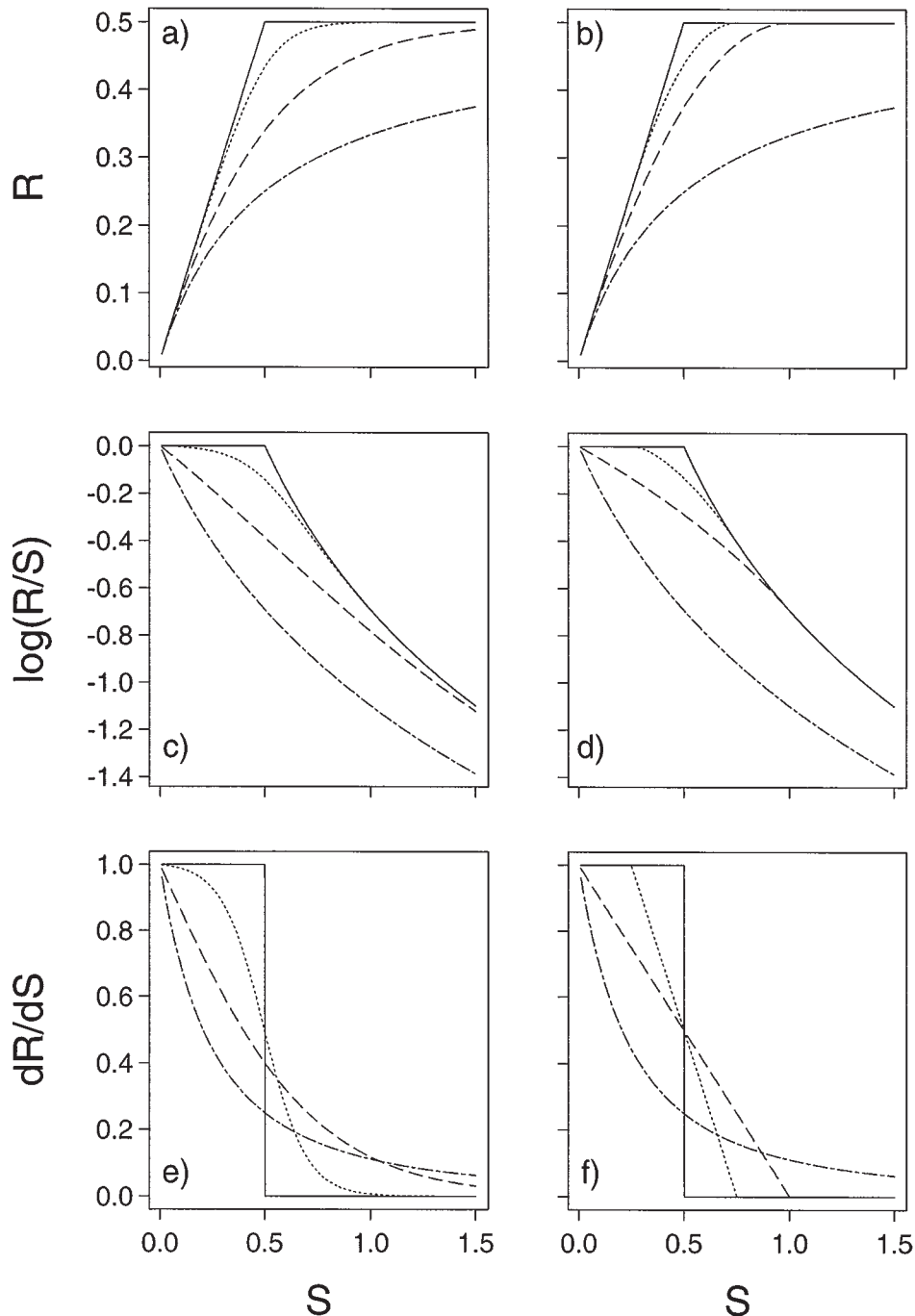
Logistic hockey stick

An alternative approach is to define the spawner–recruitment model in terms of the derivative of recruitment with respect to spawner abundance. For the hockey stick, we have

$$(6) \quad \frac{dR}{dS} = \begin{cases} \alpha & \text{if } S < S^* \\ 0 & \text{if } S \geq S^* \end{cases}$$

We need a generalization of the above model such that the slope at the origin, α , remains comparable in the generalization, and it includes the above model as a special case.

Fig. 7. (a, c, and e) Logistic hockey stick models and (b, d, and f) quadratic hockey stick models compared with a Beverton–Holt model (dashed-dotted line) having the same initial slope ($\alpha = 1$) and asymptotic recruitment (0.5). For the quadratic hockey stick, the density-dependent smoothness parameters are $\delta = 0$ (solid line), 0.5 (dotted line), and 1 (dashed line). For the logistic hockey stick, the density-dependent smoothness parameters are $\theta = 0$ (solid line), 0.2 (dotted line), and 100 (dashed line). Also shown are an index of instantaneous survival ($\log(R/S)$) and the derivative of recruitment with respect to spawner abundance (dR/dS).



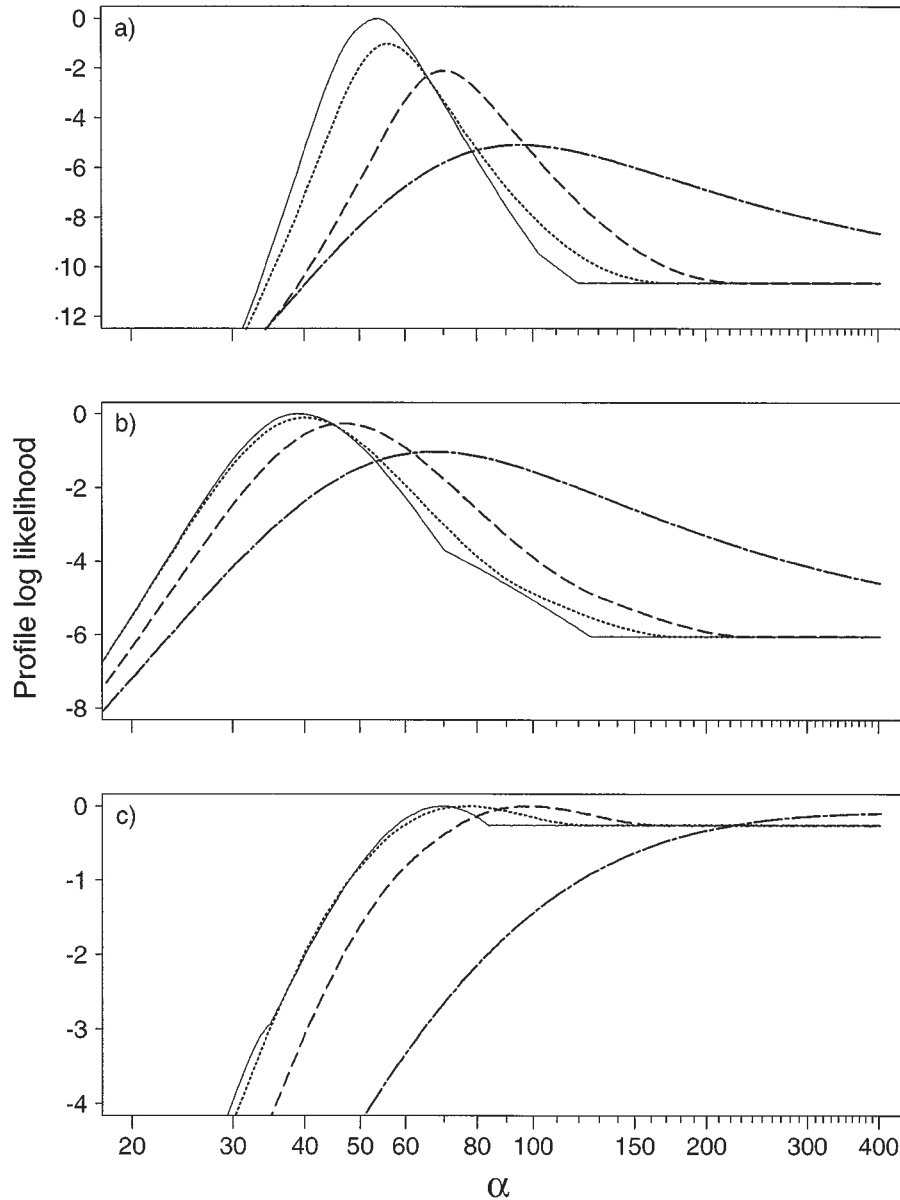
Equation 6 is easily expressed in terms of the limiting case of any of several standard cumulative distribution functions, e.g., the normal or the logistic. We will use the logistic because it has a simple analytic form and will call the model the “logistic hockey stick.” A preliminary version of our generalization is defined by

$$(7) \quad \frac{dR}{dS} = \alpha \frac{1}{1 + \exp\{(S - \mu)/(\theta\mu)\}}$$

where μ is the inflection point of spawner abundance and the product $\theta\mu$ is the scale parameter of the logistic, an analog of the standard deviation parameter in the normal. We parameterize the model in terms of the smoothness parameter θ , an analog of the coefficient of variation of the normal, because it provides a more appropriate tuning parameter. It is easy to see that as $\theta \rightarrow 0$, the hockey stick model is recovered.

This model has the right behaviour, since dR/dS is mono-

Fig. 8. Log profile likelihoods for α at (a) Deer Creek, Oregon, (b) Needle Branch Creek, Oregon, and (c) Hooknose Creek, British Columbia, for the quadratic hockey stick model with $\delta = 0$ (solid line), 0.5 (dotted line), and 1 (dashed line) and for a Beverton–Holt model (dashed-dotted line). In each panel, the maximum log likelihood over all the models has been subtracted from the curves. A difference in log likelihoods of 2 is approximately significant at the 95% level. In comparisons between the generalized hockey stick fits, this is equivalent to using Akaike's information criterion.



tonically decreasing and as $S \rightarrow \infty$, $dR/dS \rightarrow 0$. However, $\lim_{S \rightarrow 0} dR/dS \neq \alpha$ except in the limit as $\mu \downarrow 0$. To ensure that $\lim_{S \rightarrow 0} dR/dS = \alpha$, we multiply by $1 + e^{-1/\theta}$ and eq. 7 becomes

$$\frac{dR}{dS} = \alpha \frac{1 + e^{-1/\theta}}{1 + \exp\{(S - \mu)/(\theta\mu)\}}$$

Integrating this expression with respect to S and setting the integration constant so that $R = 0$ when $S = 0$ gives

$$(8) \quad R = \alpha\theta\mu(1 + e^{-1/\theta}) \left(\frac{S}{\theta\mu} - \log \left(\frac{1 + e^{(S - \mu)/(\theta\mu)}}{1 + e^{-1/\theta}} \right) \right)$$

Note that an application of l'Hôpital's rule gives

$$\lim_{S \rightarrow \infty} R = \alpha\theta\mu(1 + e^{-1/\theta}) \left(\frac{1}{\theta} + \log(1 + e^{-1/\theta}) \right)$$

Note, however, that like the quadratic hockey stick, the logistic hockey stick cannot reproduce the Beverton–Holt (Fig. 7).

Comparison of models

The main difference between the logistic and the quadratic hockey sticks is that in the logistic model, survival will generally decrease at low spawner abundances, but it may do so very slowly at first (Fig. 7). The logistic model also more closely approximates the Beverton–Holt model at higher spawner abundances and is able to describe a broader

Table 2. Comparison of estimates for coho salmon in Deer Creek, Oregon.

	Hockey stick	Beverton–Holt
Maximized log likelihood	7.6	2.5
α (95% confidence interval)	54 (45, 64)	96 (57, 213)
$H_{\text{extinction}}$ (good ocean survival)	88%	93%
$H_{\text{extinction}}$ (poor ocean survival)	38%	65%

Note: $H_{\text{extinction}}$ is the lowest harvest rate that would lead to extinction; $H_{\text{extinction}} = 1 - (\alpha s)^{-1}$, where s is ocean survival. Good ocean survival is taken to be 15% and poor ocean survival is taken to be 3%.

range of spawner abundances over which density-dependent mortality occurs.

That the Beverton–Holt is not the limiting case of two reasonable models that begin with a simple and reasonable model of contest competition should perhaps alert the user to the rather extreme nature of the Beverton–Holt model: it cannot be used to describe many biological processes as they are believed to occur (Beyer 1989).

The profile likelihoods associated with the generalized hockey stick models differ in important ways. With the quadratic hockey stick model, the profile likelihood for S^* has flat regions at the sides, whereas with the logistic hockey stick model, it does not. This inherent smoothness makes models that use the logistic hockey stick more tractable than those using the quadratic hockey stick. The logistic hockey stick may be particularly useful in variance component or metaanalytic models (Myers et al. 1999).

We considered a variety of alternative models to the ones that we proposed (see Appendix B), but none appear to be as suitable.

Generalized hockey stick fits

As demonstrated by the data set for coho salmon in Flynn Creek (Fig. 6), local maxima in the hockey stick profile likelihood can occur. One advantage of the generalized hockey sticks is that they tend to ease such difficulties. For the 246 data sets considered earlier, 56% exhibited multiple maxima in the hockey stick profile likelihood for S^* assuming lognormal recruitment. Using the quadratic hockey stick with $\delta = 0.5$ and the logistic hockey stick with $\theta = 0.2$, such difficulties occurred in only 15% and 6% of the cases, respectively. Examination of Fig. 7 shows that these values of the smoothness parameters are not particularly extreme.

The differences in estimates of the slope at the origin obtained from the Beverton–Holt and generalized hockey stick models are very large (Fig. 8). We repeated the above analyses using the assumption that the variability around the mean spawner–recruitment function is described by a gamma as opposed to a lognormal distribution. For the three stocks considered, there was virtually no difference in any of the conclusions.

Typically, the Beverton–Holt estimate is nearly twice that of the hockey stick. This is true even in the case with the best data, i.e., down to one spawning female with a clear descending limb of the spawner–recruitment curve. In the case of the Deer Creek population, the approximate 95% confi-

dence interval for α does not even include the best estimate for the hockey stick, which provides a far better fit (Table 2).

Discussion

Consequences of model choice

Data for testing scientific hypotheses or assessing management options are filtered through models. Model choice may have drastic effects on the interpretation of the data that may not be apparent to the user. Here, we have investigated the consequences of different assumptions about the behaviour of simple models at low population sizes. In a very simple example (Table 2), the harvest rate estimated to cause extinction under “poor” environmental conditions (Bradford et al. 2000) using the Beverton–Holt model is nearly double that estimated using the reasonable alternative of a hockey stick model. Such drastic changes in prescribed management measures, based on alternative models that describe similar biological processes, are cause for concern.

Biased estimates of the slope at the origin, i.e., the maximum reproductive rate, are not the only way in which the Beverton–Holt model may be misleading. We have also shown that the Beverton–Holt usually estimates a larger carrying capacity of recruits and a larger maximum reproductive rate than the hockey stick (Figs. 4 and 5). That is, the Beverton–Holt tends to overestimate the resilience of the stock to overfishing and the carrying capacity of a stock compared with the hockey stick.

An estimate of the slope at the origin is crucial to many management models. In previous work, we have found that the Beverton–Holt model often produces poor estimates (Myers et al. 1999) and have resorted to using the Ricker or an ad hoc nonparametric approximation (Myers et al. 1997) as an alternative. The generalized hockey sticks appear, in many cases, to provide a reasonable tool for investigating critical issues of the maximum reproductive rate.

Similarly, present management regulations implicitly require estimates of the carrying capacity so that maximum sustainable yield can be estimated.

Models at low population size

Most past attempts to extend classic two-parameter models of spawner–recruitment in fisheries (Deriso 1980; Shepherd 1982; Schnute 1984) and two-parameter density-dependent survival curves in general ecology (Bellows 1981) have been motivated by the desire to have the most general model possible. Although there are cases where this is a desirable property, it is not the motivation here. We seek models that describe known ecological processes but that are not too flexible. We view the parameters δ in the quadratic hockey stick and θ in the logistic hockey stick as parameters to be tuned. In our view, a model should only be as flexible as is consistent with what is ecologically possible.

The generalized hockey stick models provide some clear advantages over the Beverton–Holt and competing models. Each has a smoothness parameter, δ or θ , that allows the researcher to easily test the implications of different ideas of when density-dependent mortality should become important. Each model has considerable, but different, advantages. The

quadratic hockey stick is very easy to understand, and the parameters are easy to interpret. However, many of the difficulties in obtaining model fits remain with the quadratic hockey stick. The logistic hockey stick has the disadvantage of a more complex formulation but has the advantage of being analytically more tractable. It should be used when reasonable behaviour of the second derivative is required.

There are cases where reasonable models of the behaviour of juvenile fish imply Beverton–Holt type models (Walters and Juanes 1993), but such behaviour certainly does not apply in all cases.

While the generalized hockey sticks are more complex than the ordinary hockey stick, they are more useful in practice. The ordinary hockey stick model can be very sensitive to small perturbations of the data, whereas the generalized hockey sticks provide more robust estimates. Also, mixed-effects models for metaanalysis require the additional smoothness provided by these models.

Metaanalytic approaches to estimating population dynamics

As with any spawner–recruitment model, hockey stick estimates based on a single population can be misleading. In our experience, the only feasible way to get around this problem is to model explicitly more than one population at a time (Myers and Mertz 1998; Myers et al. 1999). That is, a hierarchical model, e.g., a mixed or variance-component model, can be used to combine data from several populations in an optimal way. We will investigate these approaches using the logistic hockey stick model in the future.

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Appendix A. Existing three-parameter spawner–recruitment models

Existing three-parameter spawner–recruitment models do not have the properties that we desire. The “Shepherd function” (Shepherd 1982) (termed the “generalized Beverton–Holt model” by Getz 1996) is

$$(A1) \quad R = \frac{\alpha S}{1 + (S/K)^\gamma}$$

This model was first proposed by Maynard Smith and Slatkin (1973) and was discussed by Bellows (1981). The parameter γ may be called the “degree of compensation” of the model, since it controls the degree to which the (density-independent) numerator is compensated for by the (density-dependent) denominator. If $\gamma = 1$, then the Beverton–Holt model is recovered. However, for $\gamma < 1$, survival is infinity as $S \rightarrow 0$; again, in this case, the model cannot be considered as a reliable method for extrapolation to low population sizes. For $\gamma > 1$, the derivative of R/S as $S \rightarrow 0$ will always be zero, a property that we discuss here, but this requires that $R \rightarrow 0$ as $S \rightarrow \infty$, which is not a desirable property for many populations, e.g., the coho salmon in Fig. 2. Getz (1996) referred to γ as the “abruptness” parameter for $\gamma > 1$; however, it also equally describes the degree of overcompensation, which is not desired for the data sets that we wish to model.

The Deriso–Schnute model (Hilborn and Walters 1992), an alternative three-parameter model, has the Ricker and the Beverton–Holt as special cases; it is given by

$$(A2) \quad R = \alpha S(1 - \beta\gamma S)^{\frac{1}{\gamma}}$$

where the Beverton–Holt model is recovered if $\gamma = -1$. However, this is the only value of γ for which the curve has a nonzero asymptote. That is, it also can only mimic the behaviour of the coho salmon data in the special case of the Beverton–Holt model. Also, the second derivative of recruitment with respect to spawner abundance is always negative at zero spawner abundance, which is not the property that we wish in this model. The generalized Ricker model ($R = \alpha S \exp(-\beta S^\gamma)$) suffers from similar difficulties.

The other widely used spawner–recruitment model is the depensatory model proposed by Thompson (1993). This model differs from the previous two in that it only attempts to modify one aspect of the curve, namely its behaviour at low spawner abundances. Although depensatory models are very useful (Myers et al. 1995; Liermann and Hilborn 1997), the coho salmon data that we consider do not show any evidence of depensation, even though the population size is very low, i.e., several populations have less than 10 spawning females.

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Appendix B. Other generalizations of the hockey stick

Here, we briefly discuss alternative formulations and explain why they appear to be inferior to our approach. Seber and Wild (1989) reviewed statistical research in the formulation and estimation of “piecewise regression,” of which the hockey stick model is a special case, and “smoothed transition segmented regression,” of which the generalized hockey stick is a special case. Only the model described in the main text appears to be suitable for the problem at hand. The use of the hyperbolic tangent for a smooth transition results in an unbiological “bulge” at the change point. The use of a hyperbolic smooth transition produces a more realistic smooth transition, but the hyperbolic form causes complications, e.g., the requirement that $R = 0$ if $S = 0$ can only be achieved with a complication of the model that renders the remaining parameters even more difficult to interpret than the logistic hockey stick. The difficulty is that they are all described in terms of the response variable and not the derivative of the response variable.

Another alternative model is a convex combination of a hockey stick and a Beverton–Holt curve, with the two curves having identical slopes at the origin and asymptotic recruitment. This model has the advantage that it gives both curves as special cases but suffers from a number of shortcomings. In particular, except when it reproduces the hockey stick, it lacks differentiability at the join point, and except when it reproduces the hockey stick, the second derivative at the origin cannot be zero.

Appendix B reference

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