Stock-production functions resembling Beverton-Holt

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Abstract

Researchers dissatisfied with the performance of the Beverton-Holt model, in contexts where "Beverton-Holt-like" behavior is expected, have introduced a plethora of alternative model forms. This paper presents a formalization of what constitutes "Beverton-Holt-like behavior" which includes many of these forms, and shows that the class of functions so defined has a coherent and non-trivial mathematical theory. Data from the stock production database assembled by Ransom Myers is used to illustrate why such generalizations have been sought in the first place, and to highlight the difficulties in choosing between model forms on purely empirical grounds. Special attention is given to a parametric family of functions within this class, here called "θ-BH" functions. These functions cover a broad range of shapes, including both the Beverton-Holt and hockey stick functions, and share useful properties with these two widely-used models.

1 Introduction

The stock-production approach to population modeling is to view abundance at some life-stage (e.g., recruitment to the ocean fisheries) as a function of abundance at some antecedent stage (e.g., the number of parent spawners). If X denotes the abundance of the parent stock, and Y the resulting production, the model is that $Y = F(X)$, where the function F is called a "stock-production function" (or "stock-production relation", or "stock-production law"). Although abundances are often expressed as numbers of

individuals (and hence as whole numbers), it is usual to treat X and Y as continuously   8

variable quantities, and F as a continuous (and even piece-wise smooth) function.   9

A stock-production function summarizes, and could in principle could be derived   10

from, a deep analysis of the ecology of an organism. In practice, it is more common to   11

use a stock production function as a *substitute* for such an analysis. That is, one argues   12

on qualitative grounds that the "true" relationship should be at least approximately of   13

a certain algebraic form, and selects parameters for this form by some process that   14

side-steps the need for detailed theories of individual behavior, bioenergetics, and so on.   15

One commonly used form is the "Beverton-Holt" function [1]:   16

$$F(X) = \frac{rX}{1 + rX/K}. \qquad (1)$$

This form is appealing for a number of reasons, not least of which is that it has only two   17

parameters, both of which can be given plausible interpretations as "real" quantities   18

(this will be considered more carefully in Sections 4 and 5). It has become one of the   19

most commonly used of all stock-production models.   20

The Beverton-Holt function has also been frequently criticized, however. Aside from   21

reservations about the usefulness of stock-production theory in general, a recurrent   22

complaint is that theory or empirical data suggest that Beverton-Holt has the wrong   23

qualitative behavior for the situation in hand.   24

For example, while it is trivially true that there must be *some* theoretical upper   25

limit on the population, this might not have any practical meaning for the population   26

under consideration, which might be better described by the Shepherd function   27

$F(X) = rX/(1 + bX^\gamma)$ with $\gamma < 1$ [2]. Or one might expect production to attain a   28

maximum at some finite stock and then decrease, like the Ricker function   29

$F(X) = rX \exp(-\frac{rX}{eK})$ [3]. If Allee effects are a concern, the Thompson function   30

$F(X) = rKX^\delta/(rX^\delta + K)$ might be appropriate [4]. Some of the possibilities are   31

illustrated in Fig 1.

Fig 1. Some frequently used stock-production relationships.

32

This paper is concerned with a different objection: Fitting data to Beverton-Holt   33

functions can produce results which are unsatisfactory even when the data appear   34

"Beverton-Holt-like." To understand this objection, and how it might be addressed, it is 35
necessary to understand which features of the Beverton-Holt function are essential to 36
the conceptual model underlying its adoption, and which are accidental to the 37
particular algebraic form as Eq (1). 38

2   Beverton-Holt-like functions and r-K functions 39

This section formalizes what it means to say that a stock-production function 40
"resembles" or "generalizes" the Beverton-Holt function, and discusses basic properties of 41
the functions so defined. 42

2.1   Definitions 43

In many situations, biological considerations lead to the expectation that production 44
should be nearly proportional to stock when habitat is freely available, and nearly 45
constant when some dimension of habitat is fully utilized. In particular, this is the case 46
when population dynamics is driven principally by contest competition [5,6]. These 47
qualitative expectations can be formalized as constraints on the mathematical form of a 48
stock-production function $Y = F(X)$: 49

(I) For some $0 < r < \infty$, the graph of F approaches the line $Y = rX$ as X goes to 0. 50

(II) For some $0 < K < \infty$, the graph of F approaches the line $Y = K$ as X goes to ∞. 51

Conventionally, r is interpreted as an "intrinsic rate of increase" or a 52
"density-independent survival," and K as the ultimate "carrying capacity" of the habitat 53
(this will be considered more carefully in Section 4). 54

These are typically are the only properties that are justifiable *a priori*, so F should 55
be otherwise unremarkable. A simple formulation of this is: 56

(III) $F(X)$ is non-decreasing and concave. 57

A more stringent notion of "unremarkability" is explored in S1 Appendix. 58

For the rest of this paper, continuous functions satisfying the conditions (I), (II), and 59
(III) will be called *Beverton-Holt-like*. It is mathematically convenient to exclude the 60

case when stock (and hence production) is exactly zero, so Beverton-Holt-like functions will be continuous functions on the positive real numbers.

Continuous functions on the positive real numbers satisfying the conditions (I) and (II) will be called *r-K functions*.

2.2 Standard form and homogeneous families

The limiting values associated with an r-K function F will be denoted $\mathbf{r}(F)$ and $\mathbf{K}(F)$. The (signed) area of the "wedge" between the graph of F and the line $y = \mathbf{K}(F)$ will be called the *defect* of F, and written defect(F); this is one way of measuring how quickly the function approaches its limit. Fig 2 shows a generic Beverton-Holt-like function.

Fig 2. A generic Beverton-Holt-like function (solid line), with its defining asymptotes (dashed lines) and defect (shaded area).

An r-K function f will be said to be in *standard form* if $\mathbf{r}(f) = \mathbf{K}(f) = 1$. If f is in standard form, then the function $F(X) = Kf(rX/K)$ is an r-K function with $\mathbf{r}(F) = r$ and $\mathbf{K}(F) = K$. Conversely, every r-K function F is associated in this way with a unique function in standard form, which will be called the *standard form of F*.

A family $\mathcal{F}$ of r-K functions will be called *homogeneous* if all its members have the same standard form. This common form will be called the *standard form of $\mathcal{F}$*.

A family $\mathcal{F}$ of r-K functions will be called *full* if every possible combination of r and K is represented by at least one member of $\mathcal{F}$.

In practice, Beverton-Holt-like functions encountered in the stock-production literature seem to fall naturally into homogeneous families. This is partially explained by the following observation:

Proposition 1. *Suppose $\mathcal{F}$ is a full family of r-K functions whose members are uniquely characterized by their r and K values. Suppose also that $\mathcal{F}$ is closed with respect to rescaling; that is, for any F in $\mathcal{F}$ and any positive numbers a and b, the function $aF(bX)$ is also in $\mathcal{F}$. Then $\mathcal{F}$ is homogeneous.*

Proof. Let f be the unique member of $\mathcal{F}$ with $\mathbf{r}(f) = 1$, $\mathbf{K}(f) = 1$. If F is any other function in $\mathcal{F}$, say with $\mathbf{r}(F) = r$, $\mathbf{K}(F) = K$, then $F(X)$ and $Kf(rX/K)$ are two members of $\mathcal{F}$ with the same r and K values; by assumption, these must coincide. $\square$

2.3 Examples of Beverton-Holt-like functions

Some examples of Beverton-Holt-like functions are collected in Table 1 in standard form, together with their defects. Fig 3 shows a sampling of these.

Table 1. Examples of Beverton-Holt-like functions in standard form. To express these in the original units for stock and production, apply the substitutions $x = rX/K$, $y = Y/K$, and multiply the defects by K^2/r.

Name	Reference	Standard form*	Defect†‡
hockey stick	[7]	$y = \min(x, 1)$	$\dfrac{1}{2}$
Beverton-Holt	[1]	$y = \dfrac{x}{1 + x}$	∞
Skellam	[8]	$y = 1 - e^{-x}$	1
θ-BH	[9]	$y = \dfrac{x}{(1 + x^\theta)^{1/\theta}}$	$\begin{cases} \infty & \text{if } 0 < \theta \le 1 \\ \frac{1}{\theta} B(\frac{2}{\theta}, 1 - \frac{1}{\theta}) & \text{if } 1 < \theta < \infty \end{cases}$
negative power	[6]	$y = 1 - \left(1 + \frac{x}{\lambda}\right)^{-\lambda}$	$\begin{cases} \infty & \text{if } 0 < \lambda \le 1 \\ \frac{\lambda}{\lambda - 1} & \text{if } 1 < \lambda < \infty \end{cases}$
positive power	(see text)	$y = 1 - \left(1 - \frac{x}{\lambda}\right)^\lambda_+$	$\dfrac{\lambda}{\lambda + 1}$ for $1 \le \lambda < \infty$
logistic hockey stick	[7]	$y = 1 - \log_\lambda\left(1 + (\lambda - 1)\lambda^{-\frac{\lambda}{\lambda - 1}x}\right)$	$-\dfrac{\lambda - 1}{\lambda(\log \lambda)^2} \mathrm{Li}_2(\lambda)$ for $1 < \lambda < \infty$
bent hyperbola	[10]	$y = \dfrac{2x}{x + 1 + \sqrt{x^2 - 2\lambda x + 1}}$	$\begin{cases} \infty & \text{for } -1 \le \lambda < 1 \\ \frac{1}{2} & \text{for } \lambda = 1 \end{cases}$

* $(x)_+$ is $\max(0, x)$.
† $B(\cdot, \cdot)$ is the beta function, $B(u, v) = \int_0^1 t^{u-1}(1 - t)^{v-1}\, dt$ [11, §6.2].
‡ $\mathrm{Li}_2(\cdot)$ is the dilogarithm function, $\mathrm{Li}_2(u) = -\int_1^u \log(t)/(t - 1)\, dt$ [11, §27.7].

Fig 3. Some Beverton-Holt-like functions having the same r and K. See Table 1 for sources and algebraic forms.

Since all Beverton-Holt-like functions look more or less alike to the human eye, it is reasonable to wonder if there is any point to this proliferation of algebraic forms. This will be addressed in Sections 4 and 6; for now, it will just be noted that many of the functions in Table 1 were introduced specifically to address *practical* problems encountered with Beverton-Holt.

The hockey stick, Beverton-Holt, and Skellam functions have all been used by multiple researchers. Moreover, less familiar functions seem invariably to include one or more of these as a special or limiting cases. It is obvious that any Beverton-Holt-like function is bounded above by the hockey stick of the same r and K, and it is shown in S1 Appendix that any Beverton-Holt-like function which is "sufficiently boring" (in a technical sense explained in the Appendix) is bounded above by the Skellam of the same r and K.

The name "θ-BH" was coined for the present paper, in analogy to the θ-logistic differential equation with which it is closely related (Section 3.3). [9] calls it the "δ-power B&H", and derives it from a size-based recruitment model. It makes a fleeting appearance in [12] without acquiring a name there. Despite its simplicity, it has not seen much use as a stock-production model. The θ-BH functions can be obtained from Beverton-Holt by a simple change of variables: Y is a θ-BH function of X if and only if Y^θ is a Beverton-Holt function of X^θ.

The negative power distribution is derived in [6] as a mixture of Skellam functions. Mixtures of Beverton-Holt-like functions will be discussed more generally in Section 2.5. The positive power distribution is a trivial variant of this, but I haven't been able to find a case in which it has been used as a stock-production relation (perhaps because it is not easily fitted by the usual least-squares method).

The logistic hockey stick is presented in [7] as a function in three parameters α, μ, and θ, most naturally expressed as a cumulative integral:

$$Y = \int_0^X \alpha \frac{1 + e^{-1/\theta}}{1 + e^{(x-\mu)/(\theta\mu)}}\, dx \tag{2}$$

The standard form of this turns out to depend only on θ, so this is a natural shape parameter; when working with the standard form, it is convenient to use $\lambda = e^{1/\theta} + 1$, resulting in the (admittedly bizarre) expression in Table 1. The natural domain of λ from this derivation is $1 < \lambda < \infty$, with the limiting cases $\lambda \to 1$ and $\lambda \to \infty$ yielding the Skellam and hockey stick, respectively. The algebraic expression in the table continues to describe a Beverton-Holt-like function for the larger interval $0 < \lambda < \infty$, with a removeable singularity at $\lambda = 1$.

The bent hyperbola is the specialization of the more general bent hyperbola of [13] to the context of Beverton-Holt-like functions. It is presented in [10] as a function in three parameters β, S^*, and γ:

$$Y = \beta \left(X + \sqrt{S^{*2} + \gamma^2/4} - \sqrt{(X - S^*)^2 + \gamma^2/4} \right) \tag{3}$$

The standard forms of these turn out to depend only on the quantity $\lambda = S^*/\sqrt{S^{*2} + \gamma^2/4}$, which is taken as the shape parameter here. The natural domain

of λ from this derivation is the closed unit interval $-1 \leq \lambda \leq 1$, with the limiting cases $\quad$ 129

$\lambda = -1$ and $\lambda = 1$ yielding the Beverton-Holt and hockey stick, respectively. The $\quad$ 130

algebraic expression in the table continues to describe a Beverton-Holt-like function for $\quad$ 131

the larger interval $-\infty < \lambda \leq 1$. $\quad$ 132

The bent hyperbola reveals a limitation of the defect as a measure of distance from $\quad$ 133

the hockey stick: although $\lambda = 1$ is the hockey stick, and the convergence as $\lambda \to 1$ is $\quad$ 134

uniform, the defect is infinite for all $\lambda < 1$. $\quad$ 135

2.4 Cumulative distributions $\qquad$ 136

The definition of Beverton-Holt-like functions given in 2.1 does not include any explicit $\quad$ 137

smoothness requirements. However, it is a standard mathematical result that any $\quad$ 138

concave function must be quite well behaved—for example, locally Lipschitz continuous $\quad$ 139

and differentiable at all but countably many points [14]. $\quad$ 140

In particular, any Beverton-Holt-like F can be written as a cumulative integral: $\quad$ 141

$$F(X) = \int_0^X \varphi(u)\,\mathrm{d}u \qquad (4)$$

where φ is a monotone non-increasing function on $(0,\infty)$ with $\lim_{u\to 0}\varphi(u) = \mathbf{r}(F)$ and $\quad$ 142

$\int_0^\infty \varphi(u)\,\mathrm{d}u = \mathbf{K}(F)$. Conversely, any non-negative, monotone non-increasing function $\quad$ 143

which is bounded above and integrable on $(0,\infty)$ gives rise to a Beverton-Holt-like $\quad$ 144

function via Eq (4). $\quad$ 145

If F is in standard form, φ is a probability density on $(0,\infty)$. This gives an $\quad$ 146

interesting interpretation of the defect: if φ is the density function associated with an f $\quad$ 147

in standard form, then $\quad$ 148

$$\mathrm{defect}(f) = \int_0^\infty u\varphi(u)\,\mathrm{d}u. \qquad (5)$$

That is, $\mathrm{defect}(f)$ is the expected value for the probability distribution associated with $\quad$ 149

f. $\quad$ 150

The Skellam function is associated in this way with the standard exponential $\quad$ 151

distribution [15, Chapter 19], and the hockey stick with the uniform distribution on $\quad$ 152

$(0,1)$ [16, Chapter 26]. $\quad$ 153

Other functions from Table 1 correspond to less familiar distributions: the positive $\quad$ 154

power function is associated with a (non-standardized) beta distribution with   155

$p = 1, q = \lambda$ [16, Chapter 25]; the θ-BH and negative power functions are associated   156

with the special cases $p = \theta, q = 1$ and $p = 1, q = \lambda$, respectively, of the generalized   157

t-distribution of [17].   158

The density corresponding to the logistic hockey stick for $\lambda > 1$ does not seem to   159

have found much use by statisticians to date. For $0 < \lambda < 1$, however, this is the   160

Exponential-Logarithmic distribution of [18] with $p = 1 - \lambda$, $\beta = \frac{\lambda \log \lambda}{\lambda - 1}$.   161

2.5   Mixtures   162

If F and G are Beverton-Holt-like functions and a, b are non-negative constants,   163

$aF + bG$ is also Beverton-Holt-like.   164

More generally, let (Ω, μ) be any measure space, and let $\{F_\omega\}_{\omega \in \Omega}$ be a family of   165

Beverton-Holt-like functions such that the map $(\omega, X) \mapsto F_\omega(X)$ is   166

$\Omega \times (0, \infty)$-measurable. If both $r = \int_\Omega \mathbf{r}(F_\omega) \, d\mu(\omega)$ and $K = \int_\Omega \mathbf{K}(F_\omega) \, d\mu(\omega)$ are finite,   167

the mixture   168

$$F(X) = \int_\Omega F_\omega(X) \, d\mu(\omega) \qquad (6)$$

is Beverton-Holt-like, with $\mathbf{r}(F) = r$ and $\mathbf{K}(F) = K$.   169

Considerations of habitat heterogeneity lead naturally to such mixtures. This will be   170

pursued a bit further in S1 Appendix.   171

The "negative power" function, which includes both Skellam and Beverton-Holt as   172

limiting cases, can be exhibited as a continuous mixture of Skellam functions: 173

$$1 - (1 + \frac{x}{\lambda})^{-\lambda} = \int_0^\infty (1 - e^{-ax}) \, d\nu(a), \qquad (7)$$

where ν is a gamma distribution with expected value 1:   174

$$d\nu(a) = \frac{\lambda^\lambda}{\Gamma(\lambda)} a^{\lambda - 1} e^{-\lambda a} \, da. \qquad (8)$$

If the term $1 + x/\lambda$ is modified to $(1 + x/\lambda)_+$, the negative power function continues   175

to be an r-K function for *negative* values of the parameter λ, and is Beverton-Holt-like   176

when $\lambda \leq -1$. This "positive power" function has some charm: it has the interesting   177

(and biologically natural?) property of actually attaining the production capacity at a   178

finite stock. It is not, however, a mixture of Skellam functions. (This will follow from   179
results in S1 Appendix.)   180

2.6   Composition   181

If Y is a Beverton-Holt-like function of X, and Z is a   182
Beverton-Holt-like function of Y, then Z is also a Beverton-Holt-like function of X.   183
That is, compositions of Beverton-Holt-like functions are again Beverton-Holt-like. In   184
particular, models obtained by iterating Beverton-Holt-like functions cannot produce   185
"interesting" population dynamics, as iteration of Ricker functions famously can [19].   186

Compositions of true Beverton-Holt functions are also true Beverton-Holt functions,   187
whose parameters are simple combinations of the parameters of the constituents.   188
Specifically, if F and G are Beverton-Holt, their composition $G \circ F$ is the Beverton-Holt   189
with parameters   190

$$
\begin{aligned}
\mathbf{r}(G \circ F) &= \mathbf{r}(G)\mathbf{r}(F) \\
\mathbf{K}(G \circ F) &= \left(\mathbf{K}(G)^{-1} + \mathbf{r}(G)^{-1}\mathbf{K}(F)^{-1}\right)^{-1}
\end{aligned}
\tag{9}
$$

This property is sometimes convenient for simulation modeling [20]. It is exploited   191
systematically, for example, in the EDT framework of [21].   192

The Beverton-Holt family is not the only family with a "composition law", however.   193
If F and G are θ-BH for the same value of θ, $G \circ F$ is also θ-BH for this θ, with   194

$$
\begin{aligned}
\mathbf{r}(G \circ F) &= \mathbf{r}(G)\mathbf{r}(F) \\
\mathbf{K}(G \circ F) &= \left(\mathbf{K}(G)^{-\theta} + \mathbf{r}(G)^{-\theta}\mathbf{K}(F)^{-\theta}\right)^{-1/\theta}
\end{aligned}
\tag{10}
$$

Moreover, if F and G are hockey sticks, $G \circ F$ is also a hockey stick, with   195

$$
\begin{aligned}
\mathbf{r}(G \circ F) &= \mathbf{r}(G)\mathbf{r}(F) \\
\mathbf{K}(G \circ F) &= \min(\mathbf{K}(G), \mathbf{r}(G)\mathbf{K}(F))
\end{aligned}
\tag{11}
$$

Since the limit as $\theta \to \infty$ of the θ-BH functions having given r and K parameters is   196
the hockey stick with these parameters, hockey sticks can be thought of as ∞-BH   197
functions; with this convention, Eqs (9) and (11) are both special cases of Eq (10).   198

It turns out that these are the *only* examples of full homogeneous families with composition laws:

Theorem 2. *Suppose that $\mathcal{F}$ is a full homogeneous family of r-K functions, and suppose that $\mathcal{F}$ is closed under composition. Then there is some $0 < \theta \leq \infty$ such that $\mathcal{F}$ is the family of θ-BH functions.*

Since this is a mathematical fact, rather than a biological one, the demonstration is relegated to S2 Appendix.

3 Stock-production and continuous dynamical systems

Stock-production functions can arise as discrete dynamical systems derived from continuous dynamical systems. In particular, the Beverton-Holt function has a natural association with the widely used logistic differential equation for the evolution of populations over time. Furthermore, this association persists even when the parameters of the equation are allowed to vary with time.

This section will describe this connection, and show that the θ-BH functions are associated in the same way with θ-logistic differential equations.

3.1 Differential equations and stock-production

An approach to population modeling with a very long history is to consider abundance as a continuous quantity, varying continuously in time, and satisfying a first-order differential equation derived from consideration of changes in arbitrarily short time increments:

$$\frac{\mathrm{d}P}{\mathrm{d}t} = \varphi(P, t), \quad P(0) = X \tag{12}$$

for the abundance P, where X is the initial population and φ is a continuous function from $(0, \infty) \times [0, \infty)$ into $(-\infty, \infty)$.

It is shown in standard textbooks on differential equations that, under mild assumptions on φ, Eq (12) has a unique solution for any $X > 0$, at least on some non-trivial interval containing $t = 0$ [22] . If there is some interval $[0, T_{\max})$ which works

for *all* $X > 0$, then any T strictly between 0 and $T_{\max}$ gives rise to a stock-production 225

relation F between $X = P(0)$ and $Y = P(T)$. 226

Stock-production functions derived in this way are necessarily monotone, as noted 227

in [23, §3.1.2]. S3 Appendix explores conditions under which they are 228

Beverton-Holt-like. 229

3.2   The exponential and logistic equations 230

Perhaps the oldest population model of all is the differential equation 231

$$\frac{\mathrm{d}P}{\mathrm{d}t} = aP, \tag{13}$$

with a constant. This appears (implicitly) already in the pioneering work of Graunt on 232

human demographics [24]. The solution, $P(t) = P(0)\mathrm{e}^{at}$, gives rise to the 233

stock-production function $Y = rX$, where $r = \mathrm{e}^{aT}$. 234

Malthus observed that exponential growth cannot persist indefinitely, and must 235

therefore be modified by some kind of density dependence [25]. An early mathematical 236

formulation of this is the logistic differential equation of Verhulst [26], 237

$$\frac{\mathrm{d}P}{\mathrm{d}t} = aP - bP^2, \tag{14}$$

with a and b constant, $b > 0$. The solution to this is the classic logistic function 238

$$P(t) = \begin{cases} \frac{aP(0)\mathrm{e}^{at}}{a + bP(0)(\mathrm{e}^{at} - 1)} & \text{if } a \neq 0, \\[2ex] \frac{P(0)}{1 + btP(0)} & \text{if } a = 0; \end{cases} \tag{15}$$

the corresponding stock-production function is therefore the Beverton-Holt function 239

with parameters 240

$$r = \mathrm{e}^{aT}, \ K = \begin{cases} \frac{a}{b}\frac{\mathrm{e}^{aT}}{\mathrm{e}^{aT} - 1} & \text{if } a \neq 0, \\[2ex] \frac{1}{bT} & \text{if } a = 0. \end{cases} \tag{16}$$

3.3   The θ-logistic equation 241

Typical derivations of Eq (14) have an *ad hoc* flavor, starting from the desired 242

qualitative behavior of φ and simply taking the "simplest" form that works [26, 27]. 243

Just what "simplicity" means in this context is not entirely clear, however, and 244

alternatives have been considered from a very early date. In particular, the models 245

$$\frac{\mathrm{d}P}{\mathrm{d}t} = aP - bP^{1+\theta} \tag{17}$$

for $\theta > 0$ already appear in Verhulst's 1838 paper [26, page 116]. 246

Eq (17) is sometimes called the "θ-logistic" equation. In population-modeling 247

contexts, it has been called the "Richards equation" after its appearance in [28]. 248

The substitution $Q = P^\theta$ reduces (17) to the ordinary logistic equation 249

$\mathrm{d}Q/\mathrm{d}t = a\theta Q - b\theta Q^2$, so the associated stock-production model is the θ-BH function 250

with parameters 251

$$r = \mathrm{e}^{aT}, \; K = \begin{cases} \left(\frac{a}{b} \frac{\mathrm{e}^{a\theta T}}{\mathrm{e}^{a\theta T} - 1} \right)^{1/\theta} & \text{if } a \neq 0, \\ \left(\frac{1}{b\theta T} \right)^{1/\theta} & \text{if } a = 0. \end{cases} \tag{18}$$

3.4 Time-varying parameters 252

The models (13), (14), and (17) are "autonomous," that is, the function φ does not 253

depend explicitly on t. Since environmental conditions can be expected to vary over 254

time, it is natural to consider generalizations of these models in which the coefficients 255

are functions of t. From the stock-production point of view, this turns out to add 256

nothing new. 257

Specifically, the general solution to (17), considered as a possibly *non*-autonomous 258

equation, can be written as 259

$$P(t) = \frac{P(0)r(t)p(t)}{\left[p(t)^\theta + P(0)^\theta \left(r(t)^\theta - p(t)^\theta \right) \right]^{1/\theta}}, \tag{19}$$

where $p(t)$ is the particular solution with $p(0) = 1$ and $r(t) = \exp(\int_0^t a(\tau)\,\mathrm{d}\tau)$. If 260

$b(t) \equiv 0$ on the interval $[0, T]$, the corresponding stock-production function is simply 261

$Y = r(T)X$. Otherwise it is θ-BH, with parameters 262

$$r = r(T), \; K = \frac{r(T)p(T)}{(r(T)^\theta - p(T)^\theta)^{1/\theta}}. \tag{20}$$

3.5 Another characterization of θ-BH functions

The stock-production functions associated with a given φ as in Section 3.1 for different choices of T, form a one-parameter family.

More generally, let φ be a continuous function from $(0, \infty) \times [0, \infty)$ into $(-\infty, \infty)$, and suppose that there is some $0 < T_{\max} \leq \infty$ such that, for each $0 \leq s < T_{\max}$ and each $0 < X < \infty$, the initial value problem

$$\frac{\mathrm{d}P}{\mathrm{d}t} = \varphi(P, t), \quad P(s) = X \tag{21}$$

has the unique solution $F^{s,t}(X)$, $s \leq t < T_{\max}$. Then $\mathcal{F} = \{F^{s,t} \mid 0 \leq s < t < T_{\max}\}$ is a two-parameter family of stock-production functions, degenerating to a one-parameter family in the autonomous case (since then $F^{s,t} = F^{0,t-s}$).

In the cases considered in Sections 3.2–3.4, this family was homogeneous. This turns out to be a very special property:

Theorem 3. *Let $\mathcal{F}$ be as above. If the $F^{s,t}$ are all r-K functions having the same standard form, this form is the standard θ-BH for some $0 < \theta < \infty$.*

This result is closely related to Theorem 2. A proof is given in S2 Appendix.

4 Beverton-Holt-like functions as population models

It is hard to avoid the suspicion that all this mathematics is out of proportion to the original problem—that the proliferation of algebraic forms for the stock-production function is more a matter of scholastic hair-splitting than practical biology.

Such doubts are only exacerbated by the fact that such functions are typically used in a crudely empirical way. The usual goal is simply to *describe* a data set, with no pretense that the fitted form is anything other than a conveniently simple approximation to an inconveniently complex reality.

This section and the next will try to explain why so many "alternatives to" or "generalizations of" the basic Beverton-Holt law have nonetheless been proposed over the years.

4.1   Physical interpretation of model parameters   288

In the conceptual model of Section 2, the r and K parameters correspond to "real"   289
quantities: 290

- r is the "intrinsic rate of increase" one would expect to see in the absence of   291
  crowding—a measure of *habitat quality*.   292

- K is the "carrying capacity" or maximum production potential—a measure of   293
  habitat quantity.   294

There are thus *two* sets of "r" and "K" parameters present when a Beverton-Holt-like   295
model is considered: values describing the habitat, and values describing the population   296
dynamics.   297

Some applications of stock-production modeling rely on identifying the two. This   298
can be done in either direction: 299

- One can attempt to obtain information about physical habitat from population   300
  data. For example, parameters obtained by fitting a stock-production model to   301
  population data may be used as estimates of physical values, in the course of   302
  setting harvest levels [29] or estimating extinction risks [30].   303

- One can attempt to obtain information about population dynamics from habitat   304
  data. For example, stock-production models parameterized with physical values   305
  (from survival experiments, habitat mapping, etc.) may be used to game   306
  management or restoration alternatives [20].   307

What makes this identification dangerous is that the r and K parameters *by*   308
definition concern properties of the fitted curve at the fringes of the data (strictly   309
speaking, outside any *possible* range of data). Estimating intrinsic productivity or   310
ultimate carrying capacity parameters from passively-observed stock-production data,   311
by fitting *any* kind of stock-production model, is always extrapolation; such values may 312
be driven as much by the algebraic form of the model as by the data.   313

4.2   Beverton-Holt as a Beverton-Holt-like function   314

A series of papers by Ransom A. Myers, Nicholas J. Barrowman, and others [7, 31, 32]   315
have developed an empirical case that use of the Beverton-Holt model to infer   316

physical-habitat parameters from population dynamics tends to overestimate both r and K, which can lead managers to overestimate the robustness of populations with respect to exploitation or habitat loss.

Of course, it is to be expected that using the wrong model will produce incorrect results—the Beverton-Holt function is not special in this regard. However, if it is *typical* for "true" stock-production curves to sit above the Beverton-Holt curve having the same asymptotes, then fitting Beverton-Holt functions will *typically* over-estimate r and K. And this is precisely what is asserted in in the cited papers.

At the root of these charges is the very slow rate at which the Beverton-Holt function rises toward its asymptote, which corresponds to a seemingly inefficient use of resources. For example, Eq (1) predicts that even when the habitat is 100% over-seeded (in the sense that $X = 2K/r$, the stock which would yield a production of $2K$ in the absence of density-dependence), fully one-third of the productive potential of the habitat will remain unexploited (in the sense that $Y = 2K/3$). Whether this is reasonable or not of course depends on how organisms actually interact with the habitat, and with one another, in the situation at hand. But as a generic assumption, to be used in the absence of population-specific detail, it is at least open to challenge.

One measure of just how slowly the Beverton-Holt function approaches the horizontal asymptote is that the "wedge" between the curve and the asymptote has infinite area. In the notation of Table 1, $\operatorname{defect}(F) = \infty$ when F is a Beverton-Holt function. Since real populations are always finite, it is not clear how to interpret this. However, it is noteworthy that most of the Beverton-Holt-like functions that have been proposed over the years as alternatives to Beverton-Holt have finite defect. If a Beverton-Holt-like function in standard form is interpreted as the cumulative function of a probability density, as in Section 2.4, the defect is finite whenever this density has an expected value; Section 6 of Web Appendix A gives another heuristic under which functions of infinite defect might be considered "unreasonable."

5 Beverton-Holt-like functions in practice

This section will make the discussion of Section 4 more concrete by considering some actual data. Because the papers of Myers et al. are so cogent, and because these

authors have made their data publicly available with the express desire to support   347
"meta-analytic methods to combine results across many populations" [33], they seem   348
particularly well suited to the present purpose. The focus will be on populations of   349
Coho salmon *Oncorhynchus kisutch* discussed in [7].   350

5.1   Coho salmon data   351

Fig 4 shows all the sets of stock-production data from the Myers database [34] for Coho   352
salmon, *Oncorhynchus kisutch,* in which "stock" is female spawners and "production" is   353
outmigrant smolts, arranged very subjectively by shape.

Fig 4. Coho salmon (*Oncorhynchus kisutch*) female-to-smolt data from the Myers
database, with fitted θ-BH curves.

354

The fitted curves will be discussed below. Disregarding these for the moment,   355
several features of these data are worth remarking.   356

First, all the individual datasets are quite small. The largest consists of 26 points.   357
This is typical of stock-production data: monitoring programs that follow a consistent   358
methodology for a quarter of a century are unfortunately (albeit understandably) rare.   359

Next, the data are quite noisy. Again, this is typical of stock-production data: 360
environmental drivers (flow, water temperature, food availability) can vary dramatically   361
from year to year, and the estimates of both stock and production usually come from   362
sampling, with large uncertainties.   363

Because the datasets are small and noisy (or as Ransom Myers put it, "nasty,   364
brutish, and short" [33]), it is unrealistic to expect the data to point unambiguously to   365
a particular algebraic form. One might decide that a dataset seems "Beverton-Holt-ish",   366
or "Ricker-ish", but it seems hopeless to choose between, say, the logistic hockey stick   367
and bent hyperbola, on empirical grounds alone. It will be seen that there are good   368
reasons for considering models with a degree of freedom beyond r and K, but one more   369
"shape" parameter is probably all that can be accommodated.   370

Many of these particular datasets are plausibly Beverton-Holt-like. Considered in   371
isolation, some of these sets (e.g. a–c) plausibly convey information about both r and K,   372
without the need to assume much except a general "Beverton-Holt-like-ness." Others   373
suggest constraints on either r (d–f) or K (g–i), but not necessarily both. Still others   374

(m–o) hint at possible non-Beverton-Holt-like *decreases* in production at high density. 375

5.2 Model fitting 376

The observed stock-production pairs (X_i, Y_i), $1 \leq i \leq n$, are assumed to be related via a 377

stock-production function F from some parametric family $F(\cdot, \mathbf{p})$. Since the purpose 378

here is simply illustrative, a simple multiplicative error structure is assumed: 379

$$\log Y_i = \log F(X_i; \mathbf{p}) + \varepsilon_i \tag{22}$$

where the ε_i are i.i.d. normal deviates with mean 0 and variance σ^2. 380

(Stock-production datasets are typically time-series, with X_i in turn a function of 381

earlier Y_j, $j < i$, and autocorrelation should be taken into account. Furthermore, both 382

X_i and Y_i are usually themselves estimated from sampling data, and hence have error 383

structures of their own. A more general framework here is state-space modeling [35].) 384

Eq 22 gives rise to the log-likelihood 385

$$l(\mathbf{p}, \sigma^2 \mid \{(X_i, Y_i)\}_{i=1}^n) = -\frac{1}{2\sigma^2} \sum_{i=1}^n (\log Y_i - \log F(X_i; \mathbf{p}))^2 - \frac{n}{2} \log(2\pi\sigma^2) \tag{23}$$

The maximum-likelihood estimate for the parameters is $(\hat{\mathbf{p}}, \hat{\sigma}^2)$, where $\hat{\mathbf{p}}$ minimizes the 386

residual sum of squares 387

$$\mathrm{RSS}(\mathbf{p}) = \sum_{i=1}^n (\log Y_i - \log F(X_i; \mathbf{p}))^2 \tag{24}$$

and $\hat{\sigma}^2 = \frac{1}{n} \mathrm{RSS}(\hat{\mathbf{p}})$. 388

The Bayesian Information Criterion is then 389

$$\mathrm{BIC}(F) = n \log \hat{\sigma}^2 + n \log(2\pi) + (k+1) \log(n) \tag{25}$$

where k is the length of $\mathbf{p}$. Given an alternate model form 390

$$\log Y_i = \log G(X_i; \mathbf{q}) + \varepsilon_i, \quad \varepsilon_i \sim N(0, \tau^2) \tag{26}$$

the performances of the maximum-likelihood-fitted models will be compared as $\qquad$ 391

$$\Delta\,\mathrm{BIC}(F,G) = \mathrm{BIC}(F) - \mathrm{BIC}(G)\,. \qquad (27)$$

The quantity $\exp(-\frac{1}{2}\Delta\,\mathrm{BIC}(F,G))$ is interpretable as an evidence ratio. 392

The models considered will all be θ-BH: 393

$$F_\theta(X; r, K) = rKX((rX)^\theta + K^\theta)^{-\theta} \qquad (28)$$

The present concern is how the performance of this model depends on θ. That is, rather 394
than treating θ as a fitting parameter, a range of values for θ are considered, and the 395
log-likelihood maximized with respect to the remaining parameters. The intention is to 396
explore how choice of algebraic form affects the estimation of the "natural" quantities r 397
and K, using the family of θ-BH functions for different values of θ as a convenient 398
surrogate for the full range of possible r-K functions. 399

5.3   Results 400

The methods of Section 5.2 were used to fit θ-BH models to the Myers Coho data for a 401
range of θ. Four of these fitted curves are shown in Fig 4 for each of the data sets. Fig 5 402
shows how the fitted parameters and BIC depend on θ. The $\Delta\,\mathrm{BIC}$ values are all 403
calculated with respect to the model with $\theta = 1$.

Fig 5. Dependence of fitted models on the shape parameter θ. By at least one
widely-used criterion, a broad range of θ values are more-or-less equally compatible with
the data. The fitted r and K parameters however, vary considerably between models
(note the logarithmic scale).

404

In most cases, the fitted curves look very similar to one another. This subjective 405
impression is supported by the evidence-ratio panel of Fig 5: for most of the datasets, 406
the evidence ratio for the θ-BH model is within a factor of three of the Beverton-Holt 407
model over a wide range of values for θ, and thus by a widely-used rule-of-thumb all 408
these models are comparably well supported. The fitted values of r and K, on the other 409
hand, depend quite strongly on θ. 410

To put it more dramatically, it is not possible to estimate r and K very well without 411
committing to a particular model form, and the data themselves are of little help in 412

selecting this form. Recall that this is simply a range of models consistent with the Beverton-Holt-like heuristic: as noted in Section 1, these by no means cover the universe of forms considered seriously in the stock-production literature.

Essentially the same phenomenon is analyzed in [36], where a discretized version of the θ-logistic differential equation discussed in Section 3 is fitted to real and simulated population time-series. These authors show that treating θ as a fitting parameter on par with the (appropriate analogs of) r and K is very unstable, in the sense that small perturbations of the data can result in large changes to the parameter estimates, and in the case of simulated series, that model fitting cannot reliably recover the "true" values used to generate the series in the first place.

5.4   Other taxa

The same patterns are seen for other taxa.

The great majority of stocks in the Myers database are assigned there to one of six orders of bony fishes: Clupeiformes, Gadiformes, Perciformes, Pleuronectiformes, Salmoniformes, and Scorpaeniformes. Of these stocks, 543 have at least five years of stock and production values. Applying the fitting procedure of Section 5.2 to these data yields the evidence-ratio curves shown in Fig 6.

Fig 6. Evidence-ratio curves for θ-BH fits to stock-recruitment time-series for all stocks from selected orders from the Myers database.

All but a handful of these curves are monotone on the entire interval $0.5 \leq \theta \leq 4$. That is, if θ is treated as a parameter on a par with r and K, to be estimated by maximum likelihood, the fitting routine wants to drive the model to one of the two degenerate forms $\theta \to \infty$ or $\theta \to 0$.

The curves which do have a local maximum are very flat: in only eleven cases is the evidence ratio at some intermediate θ more than 20% higher than at both endpoints. For 170 (31%) of the stocks, the curves are "extremely flat," in the sense that they vary no more than 1% across the full range of θ.

5.5 Remarks

It should be emphasized that the analyses of this section are meant to illustrate some general points about stock-production relationships. A serious analysis of the Coho data from the point of view of a regional manager, say, would be much more involved. Such an analysis would require a more careful consideration of error structures, and would probably treat some or all the populations together (as recommended, for example, in [37]).

First and foremost, however, such an analysis would consider environmental covariates. There is a mistaken perception that stock-production ideas are somehow in conflict with environmental explanations for population levels (a legacy, perhaps, of otherwise forgotten ideological/philosophical debates from the early twentieth century [38]). In principle, the relationship between stock and production for any particular cohort is *determined* by the environmental circumstances of that cohort, and should vary, perhaps dramatically, from cohort to cohort. No "explanation" of the data in Fig 4 would be very satisfying which did not succeed in attributing much of the scatter within populations to year-to-year changes in things like stream flow or ocean harvest effort, and differences between populations to things like basin size.

6 Discussion

For the most part, mathematical ecology has outgrown the search for "laws" analogous to those of physics. Forms such as the Beverton-Holt function for discrete population dynamics, or the logistic models for continuous population dynamics, are adopted as conventional starting points for analysis, in the same spirit that linear models or normal distributions are used to explore other kinds of data.

Almost any data analysis these days is likely to include some linear regressions, complete with R^2 statistics, even when there is no particular reason to expect data to come from a truly linear relationship, or for the errors to be independent identically-distributed normal variables. From this point of view, the question of whether to start with Beverton-Holt, or Skellam, or the logistic hockey-stick, is analogous to the question of whether to plot xy-data on plain axes, or to use a log or probit transform on one or both axes.

There are, however, significant differences between the *uses* to which linear model ₄₆₈ fits and stock-production fits are typically put. The mean of a normal fit, or the slope ₄₆₉ of a linear fit, are attempts to capture some property of the "center" or "main body" of ₄₇₀ the data. The r and K parameters of a Beverton-Holt-like function, however, concern ₄₇₁ properties of the fitted curve at the fringes of the data, or in many cases well beyond ₄₇₂ them. ₄₇₃

It is well-known that interpolation is a much safer process than extrapolation, and ₄₇₄ when a fitted model is to be used in an "interpolatory" way, for example, to make ₄₇₅ short-term forecasts, or to explore the implications of modest changes to habitat under ₄₇₆ hypothetical conditions broadly similar to historical conditions, the precise form of the ₄₇₇ fitted model is unlikely to be of great importance. ₄₇₈

However, to estimate a true intrinsic productivity or ultimate carrying capacity from ₄₇₉ passively-observed stock-prodution data, by fitting *any* kind of stock-production model, ₄₈₀ is always an extrapolation. Statistics is not magic, and information which is not present ₄₈₁ in the data to begin with cannot be extracted from it by mathematical manipulations. ₄₈₂ In the case of stock-production: ₄₈₃

- If the data do not include cases of low stock densities, *the data contain no* ₄₈₄ *intrinsic information about productivity at low densities.* Any estimate of intrinsic ₄₈₅ productivity will be driven *primarily* by *a priori* assumptions about the model ₄₈₆ form. ₄₈₇

- If the data do not include cases of production near the carrying capacity, *the data* ₄₈₈ *contain no intrinsic information about carrying capacity.* Any estimate of carrying ₄₈₉ capacity will be driven *primarily* by *a priori* assumptions about the model form. ₄₉₀

- Even if the data do include low or high stock densities, the "best" fit of a model ₄₉₁ form to the overall data need not reflect the actual behavior at these extremes ₄₉₂ very well. ₄₉₃

This is not a problem if there are sound reasons to prefer some model form over ₄₉₄ others, or if policy conclusions are robust with respect to the choice of form. I have ₄₉₅ tried to demonstrate in this paper, however, that the space of "Beverton-Holt-like" ₄₉₆ model forms is much larger than is generally appreciated, and there are important ₄₉₇ application areas in which the choice of form matters a great deal. ₄₉₈

Supporting information

S1 Appendix. Mixtures.

S2 Appendix. Composition Laws.

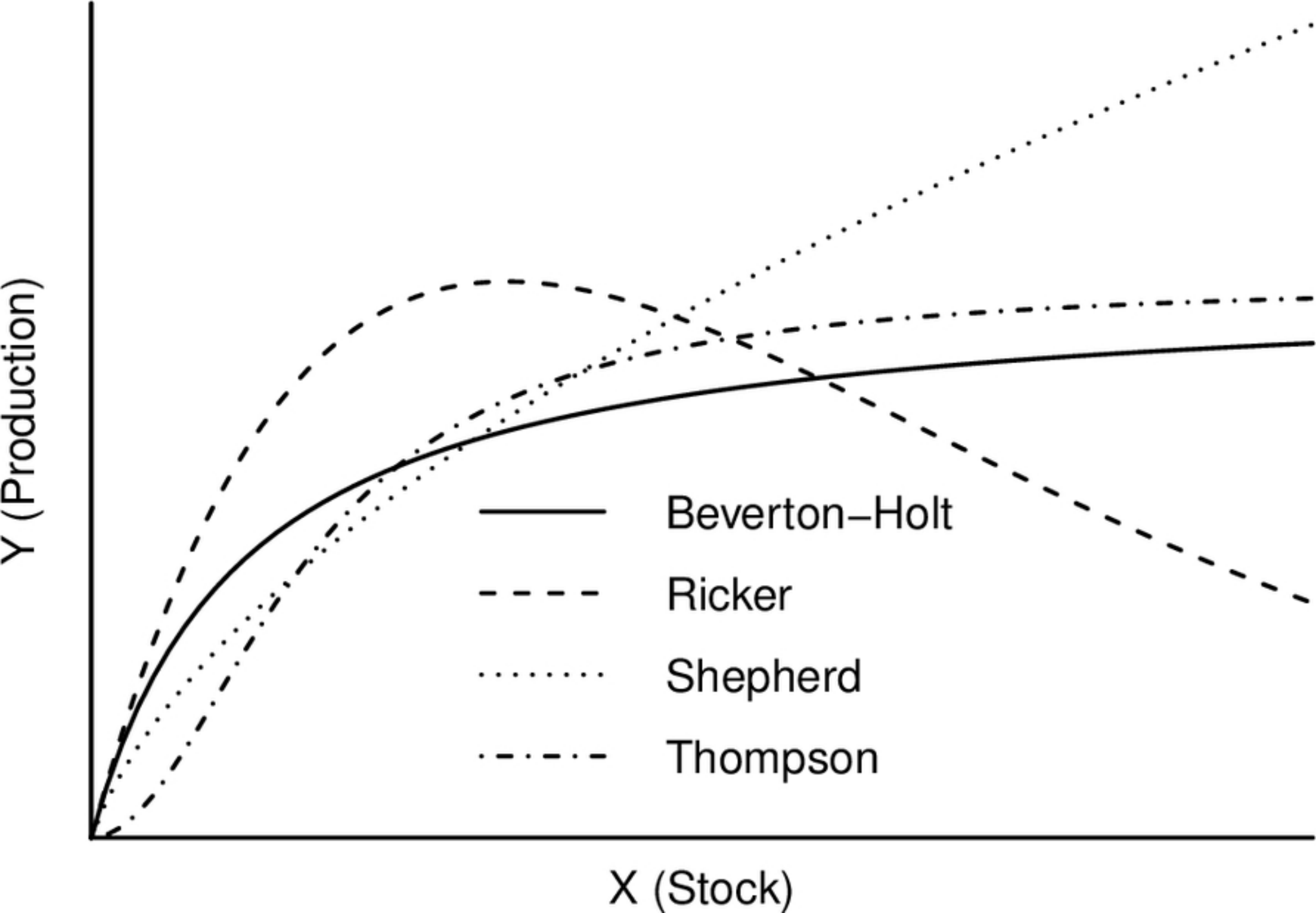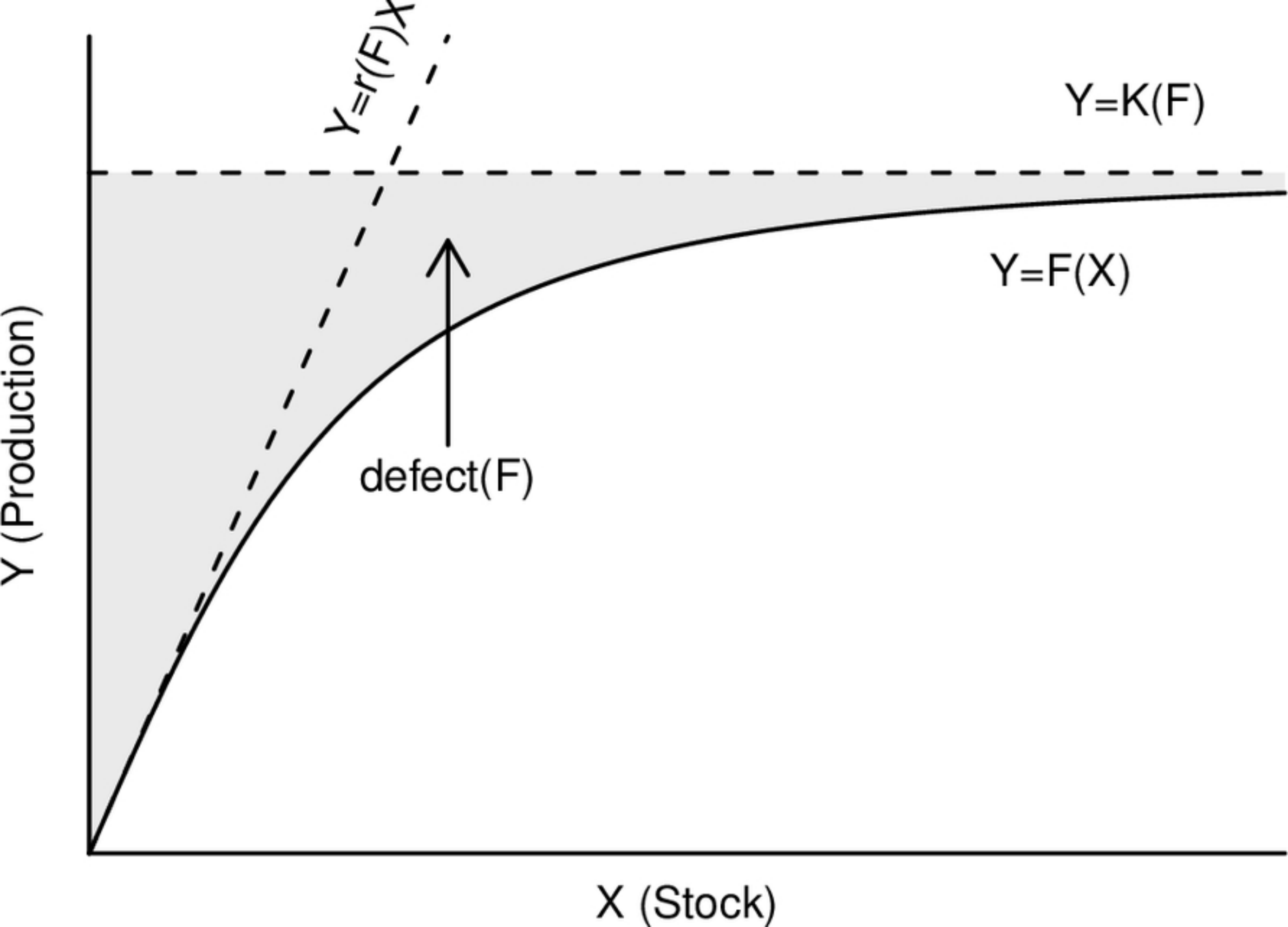**S3 Appendix. Stock-production functions associated with differential equations.**

References

1. Beverton RJH, Holt SJ. On the dynamics of exploited fish populations. Fisheries Investment. 1957;19.

2. Shepherd JG. A versatile new stock-recruitment relationship for fisheries, and the construction of sustainable yield curves. J Cons Int Explor Mer. 1982;40(1):67–76.

3. Ricker WE. Stock and recruitment. J Fisheries Res Board Can. 1954;11:559–623.

4. Thompson GG. A proposal for a threshold stock size and maximum fishing mortality rate. In: Stephen J Smith DR Joseph J Hunt, editor. Risk Evaluation and Biological Reference Points for Fisheries Management Canadian Special Publication of Fisheries and Aquatic Sciences. vol. 120. NRC Research Press; 1993. p. 303–320.

5. Nicholson AJ. An outline of the dynamics of animal populations. Australian Journal of Zoology. 1953;2(1):9–65.

6. Brännström Å, Sumpter DJT. The role of competition and clustering in population dynamics. Proc R Soc B. 2005;272:2065–2072.

7. Barrowman NJ, Myers RA. Still more spawner-recruitment curves: the hockey stick and its generalizations. Canadian Journal of Fisheries and Aquatic Sciences. 2000;57(4):665–676. doi:10.1139/f99-282.

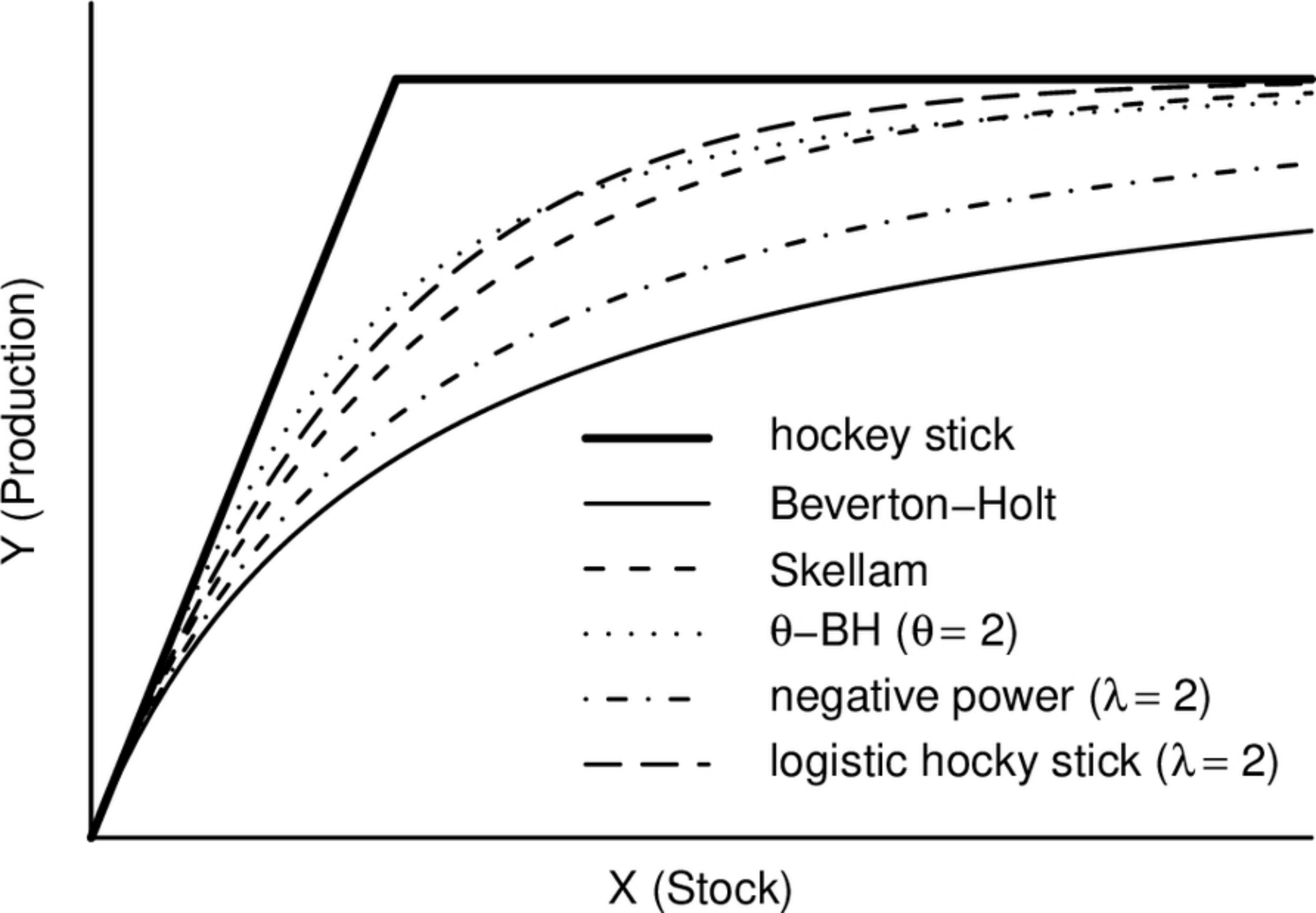8. Skellam JG. Random dispersal in theoretical populations. Biometrika. 1951;38:196–218.

9. Beyer JE. Recruitment stability and survival — simple size-specific theory with examples from the early life dynamics of marine fish. Dana. 1989;7:45–147.

10. Mesnil B, Rochet MJ. A continuous hockey stick stock-recruit model for estimating MSY reference points. ICES Journal of Marine Science. 2010;67(8):1780–1784.

11. Abramowitz M, Stegun IA. Handbook of Mathematical Functions with Formulas, Graphs, and Mathematical Tables. ninth dover printing, tenth gpo printing ed. New York: Dover; 1964.

12. Harris J. The effect of density-dependent mortality on the shape of the stock and recruitment curve. J Cons int Explor Mer. 1975;36(2):144–149.

13. Watts DG, Bacon DW. Using a hyperbola as a transition model to fit two-regime straight line data. Technometrics. 1984;16:369–373.

14. Rudin W. Principles of Mathematical Analysis. 3rd ed. New York: McGraw-Hill; 1976.

15. Johnson NL, Kotz S, Balakrishnan N. Continuous Univariate Distributions, Volume 1. 2nd ed. New York: John Wiley & Sons; 1994.

16. Johnson NL, Kotz S, Balakrishnan N. Continuous Univariate Distributions, Volume 2. 2nd ed. New York: John Wiley & Sons; 1995.

17. MacDonald JB, Newey WK. Partially adaptive estimation of regression models via the generalized t-distribution. Econometric Theory. 1988;4:428–457.

18. Tahmasbi R, Rezaei S. A two-parameter lifetime distribution with decreasing failure rate. Computational Statistics and Data Analysis. 2008;52:3889–3901.

19. May RM. Simple models with very complicated dynamics. Nature. 1976;261:459–467.

20. Moussalli E, Hilborn R. Optimal stock size and harvest rate in multistage life history models. Can J Fish Aquat Sci. 1986;43(1):135–141.
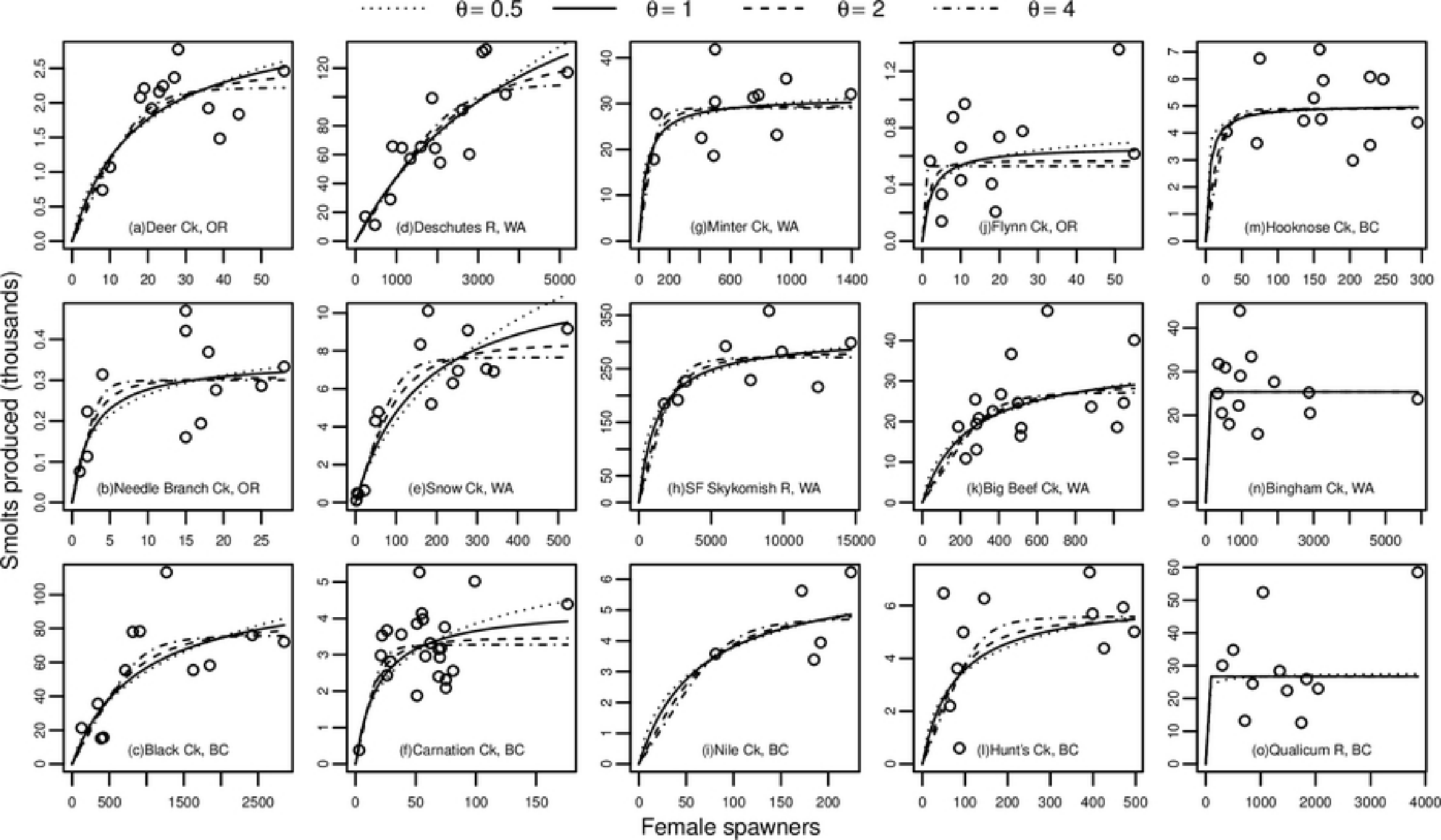
21. Mobrand LE, Lichatowich JA, Lestelle LC, Vogel TS. An approach to describing ecosystem performance "through the eyes of salmon". Can J Fish Aquat Sci. 1997;54(12):2964–2973. doi:10.1139/f97-189.

22. Braun M. Differential Equations and their Applications. 4th ed. New York: Springer-Verlag; 1992.

23. Quinn TJI, Deriso RB. Quantitative Fish Dynamics. New York: Oxford University Press; 1999.

24. Graunt J. Natural and Political Observations. T. Roycroft and T. Dicas, London; 1662.

25. Malthus TR. An Essay on the Principle of Population. 1st ed. J. Johnson, London; 1798.

26. Verhulst PF. Notice sur la loi que la population poursuit dans son accroissement. Correspondance mathématique et physique. 1838;10:113–121.

27. Pearl R, Reed LJ. On the rate of growth of the population of the United States since 1790 and its mathematical representation. Proc Nat Acad Sci. 1920;6(6):275–288.

28. Richards FJ. A flexible growth function for empirical use. Journal of Experimental Botany. 1959;10(2):290–301.

29. Myers RA, Mertz G. The Limits of Exploitation: A Precautionary Approach. Ecological Applications. 1998;8(1):S165–S169.

30. Lande R. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. The American Naturalist. 1993;142(6):911–927.

31. Myers RA, Rosenberg AA, Mace PM, Barrowman NJ, Restrepo VR. In search of thresholds for recruitment overfishing. ICES J Mar Sci. 1994;51:191–205.

32. Myers RA, Barrowman NJ, Hutchings JA, Rosenberg AA. Population dynamics of exploited fish stocks at low population levels. Science. 1995;269:1106–1108.

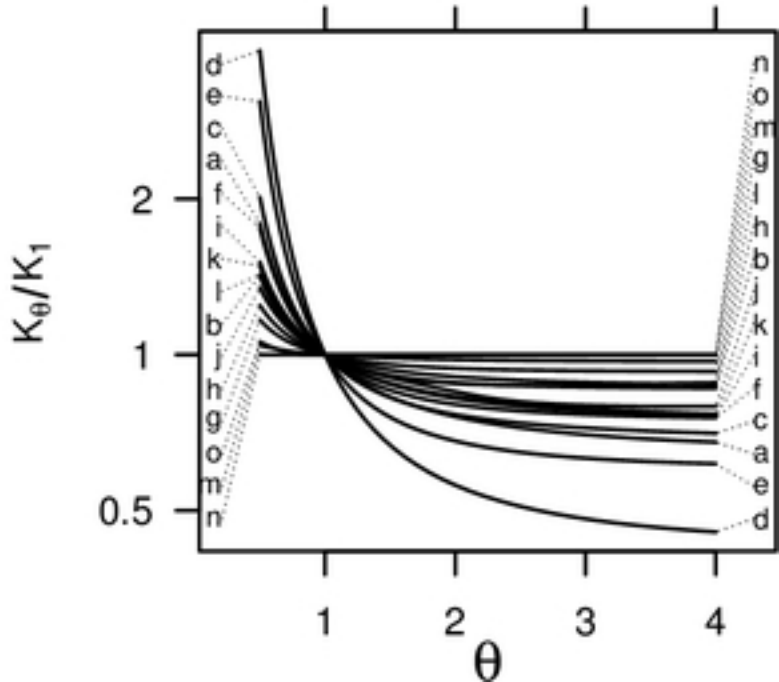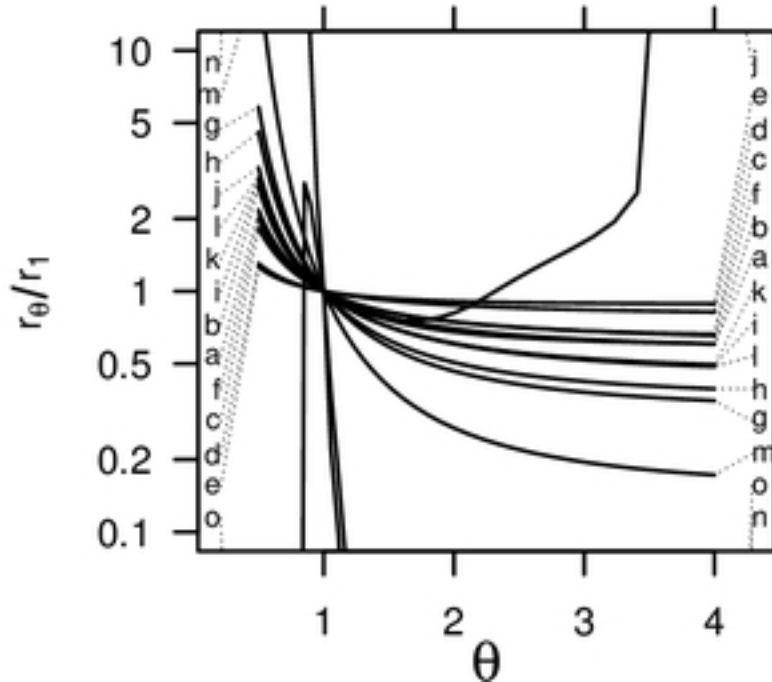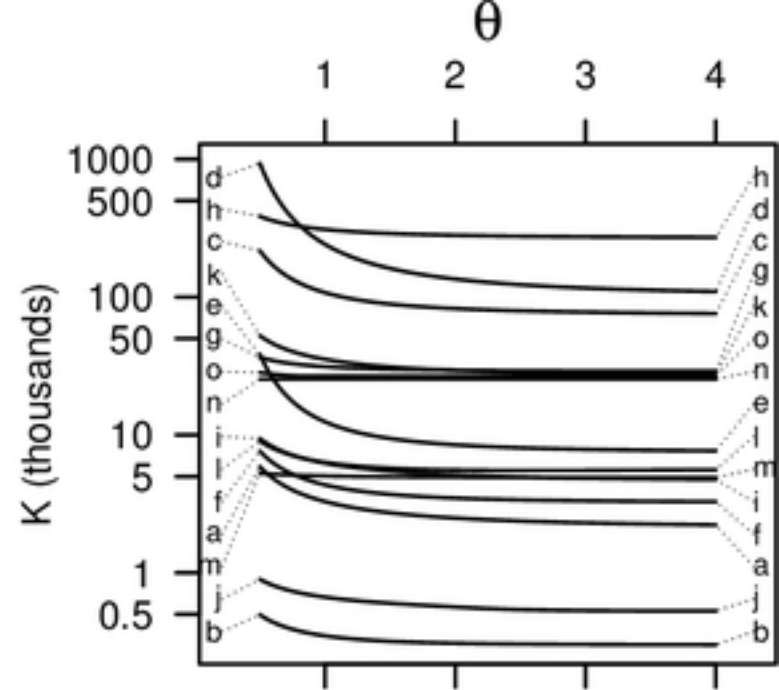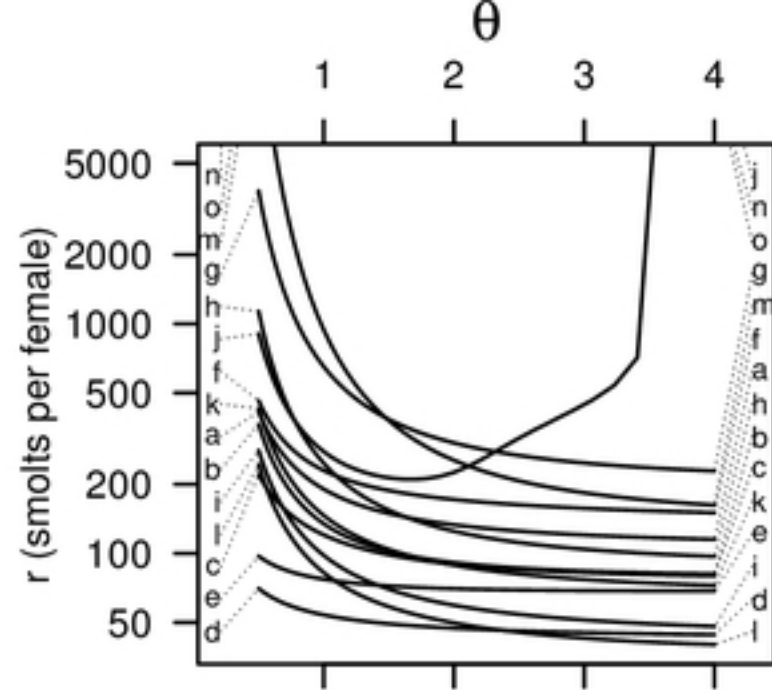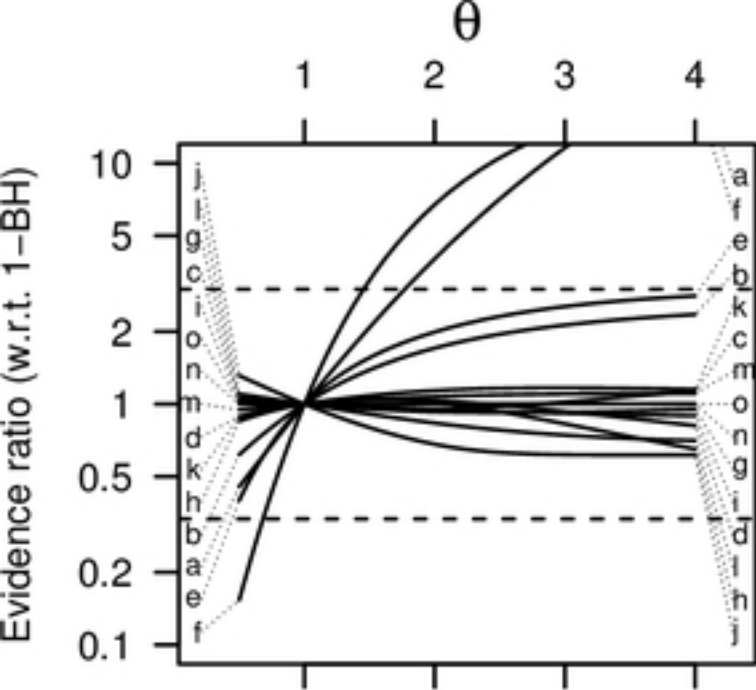33. Myers RA. Stock and recruitment: generalizations about maximum reproductive rate, density dependence, and variability using meta-analytic approaches. ICES Journal of Marine Science. 2001;58:937–951.

34. Myers RA, Bridson JM, Barrowman NJ. Summary of worldwide stock and recruitment data. Can Tech Rep Fish Aquat Sci. 1995;2024.

35. Newman KB, Buckland ST, Morgan BJT, King R, Borchers DL, Cole DJ, et al. Modelling Population Dynamics: Model formulation, fitting and assessment using state-space methods. New York: Springer; 2014.

36. Clark F, Brook BW, Delean S, Akçakaya HR, Bradshaw CJA. The theta-logistic is unreliable for modelling most census data. Methods in Ecology and Evolution. 2010;1(3):253–262.

37. Myers RA, Bowen KG, Barrowman NJ. Maximum reproductive rate of fish at low population sizes. Can J Fish Aquat Sci. 1999;56:2404–2419.

38. Nicholson AJ. Supplement: The Balance of Animal Populations. Journal of Animal Ecology. 1933;2(1):131–178.
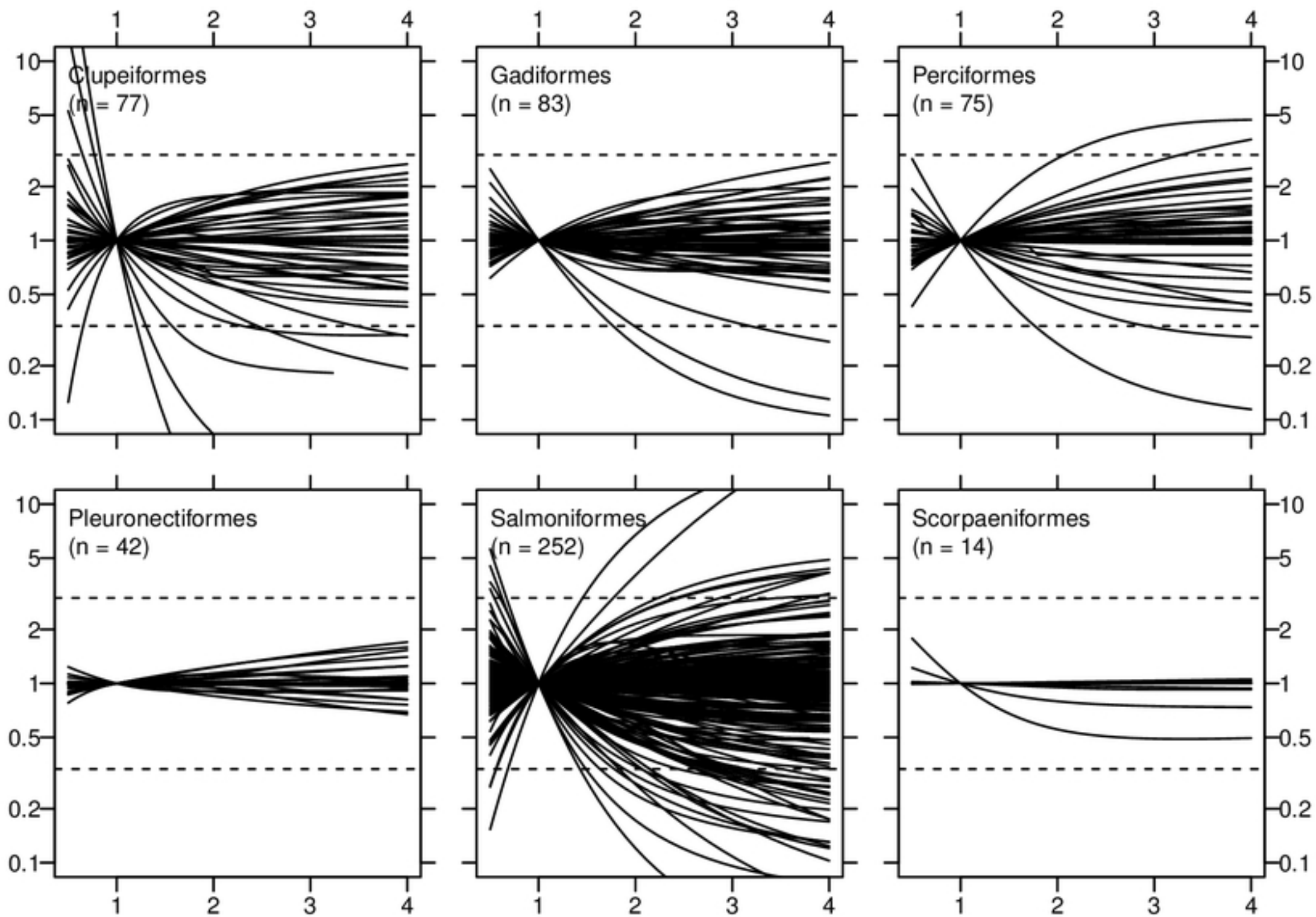
Y (Production)

X (Stock)

Beverton–Holt

Ricker

Shepherd

Thompson

- hockey stick
- Beverton−Holt
- Skellam
- θ−BH (θ = 2)
- negative power (λ = 2)
- logistic hocky stick (λ = 2)

Y (Production)

X (Stock)

Figure legend: θ = 0.5 (dotted), θ = 1 (solid), θ = 2 (dashed), θ = 4 (dash-dot)

(a) Deer Ck, OR
(b) Needle Branch Ck, OR
(c) Black Ck, BC
(d) Deschutes R, WA
(e) Snow Ck, WA
(f) Carnation Ck, BC
(g) Minter Ck, WA
(h) SF Skykomish R, WA
(i) Nile Ck, BC
(j) Flynn Ck, OR
(k) Big Beef Ck, WA
(l) Hunt's Ck, BC
(m) Hooknose Ck, BC
(n) Bingham Ck, WA
(o) Qualicum R, BC

Y-axis: Smolts produced (thousands)

X-axis: Female spawners