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A stochastic Pella Tomlinson model and its maximum sustainable yield



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HIGHLIGHTS

- Pella-Tomlinson and Fox surplus production models with environmental noise are considered.
- The maximum level of noise that a stock can tolerate before extinction is derived.
- New formulas for the maximum sustainable yield (MSY) that account for the random noise are provided.
- Models with a large asymmetry parameter p are most sensitive to environmental noise.

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ABSTRACT

This paper investigates the biological reference points, such as the maximum sustainable yield (MSY), for the Pella Tomlinson and the Fox surplus production models (SPM) in the presence of a multiplicative environmental noise. These models are used in fisheries stock assessment as a firsthand tool for the elaboration of harvesting strategies. We derive conditions on the environmental noise distribution that insure that the biomass process for an SPM has a stationary distribution, so that extinction is avoided. Explicit results about the stationary behavior of the biomass distribution are provided for a particular specification of the noise. The consideration of random noise in the MSY calculations leads to more conservative harvesting target than deterministic models. The derivations account for a possible noise autocorrelation that represents the occurrence of spells of good and bad years. The impact of the noise is found to be more severe on Pella Tomlinson model for which the asymmetry parameter p is large while it is less important for Fox model.

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1. Introduction

Surplus-production models (SPM) are dynamic models especially useful to study the evolution of the biomass of a fishery and to estimate the maximum sustainable yield (MSY), which is the maximum catch that does not jeopardize the long term survival of the population. They are the simplest models available that can assess fish stocks and determine a harvest rate because they regroup recruitment, mortality and growth into a single production function. Furthermore, they require very few data in comparison with more complex models such as age-structured models; only time series of stock abundance indices and the corresponding catches are needed. Accordingly, they can be used when the data is limited (Chaloupka and Balazs, 2007; Hilborn and Walters, 1992). Even if criticized for being less realistic than age-structured models, SPM are still helpful since they can sometimes provide results as useful as those obtained with more complex models at a

To each SPM is associated a production function $f(\cdot)$ which gives the stock production at time t+1 as a function of the stock biomass at time t. The stock biomass difference between time t+1 and t is the difference between the production of the stock biomass and the catches at time t:

$$B_{t+1} - B_t = f(B_t) - C_t, (1)$$

where B_t is the stock biomass at time t, C_t is the catches at time t. Each parameter of the population, except for the catches, is included in the production function. In this paper we focus on the Pella and Tomlinson (1969) model whose production function is given by

$$f(B_t) = \frac{p+1}{p} r B_t \left(1 - \left(\frac{B_t}{K} \right)^p \right), \tag{2}$$

lower cost (Ludwig and Walters, 1985; Laloe, 1995; Chavance et al., 2002). These models are also widely used for fishery management (Panhwar et al., 2012; Prager, 2002). Although this paper focuses on discrete-time models, similar results could be obtained with continuous time as illustrated in Ewald and Wang (2010).

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where $r \in (0, 1)$ characterizes the population growth, K the carrying capacity (the maximum population size for growth to be positive) and parameter p > 0 allows to introduce an asymmetry in the production curve.

Two interesting special cases are p=1, that gives Schaefer's model (Schaefer, 1954) with a symmetric production function $f(B_t) = 2rB_t(1-B_t/K)$, and the limiting case when p tends to 0 corresponds to the Fox model (Fox, 1970) whose production function is $f(B_t) = -rB_t \log(B_t/K)$.

In a deterministic model, the MSY is the maximum over B of f(B); it is the maximum surplus production. The management strategy is to keep the stock biomass equal to the value that maximizes the surplus production and to harvest the latter. For a Pella and Tomlinson model, the biomass which maximizes the production function is $B_{MSY} = K/(p+1)^{1/p}$, the MSY is $rK/(p+1)^{1/p}$ and the optimal fishing rate is $F_{MSY} = MSY/B_{MSY} = r$. Letting p go to 0, the corresponding characteristics for Fox model are $B_{MSY} = K/e$, MSY = rK/e, and $F_{MSY} = r$, where e = 2.718... is Euler's number. Notice that in each case, the deterministic optimal fishing rate is equal to r; this is a consequence of the parametrization of (2).

Deterministic surplus production models have been criticized because of their overly optimistic estimation of MSY (Larkin, 1977; Boerema and Gulland, 1973; Lewis, 1981; Amundsen and Bjorndal, 1999). Doubleday (1976) advised to set harvesting quotas as a fraction (two third) of the deterministic MSY to reduce the risk of stock collapse and suggests that stochasticity should be taken into account. To pursue this objective, we will incorporate a positive multiplicative random noise ε_t (a process error in the terminology of Punt, 2003) with variance σ^2 (Gore and Paranje, 2001) to reflect the natural variability. This leads to the following stochastic model:

$$B_{t+1} = \left[B_t + \frac{p+1}{p} r B_t \left(1 - \left(\frac{B_t}{K} \right)^p \right) - \phi B_t \right] \varepsilon_t, \tag{3}$$

where ϕ is the fishing rate so that, in (1), $C_t = \phi B_t$. The deterministic equilibrium assumption $(B_{t+1} = B_t)$ then becomes a stochastic equilibrium assumption, namely that the distribution of B_{t+1} is the same as the distribution of B_t .

Suppose that a stock experiences an environmental shock that results in an important drop of its biomass. It then grows according its average intrinsic annual growth rate, in the terminology of Reed (1978). For model (3) this growth rate is $\gamma = (p+1)r/p-\phi$. If p is large, it is $r-\phi$ and the stock will take much longer to recover from this unexpected drop than when p is small. This suggests that, in the Pella Tomlinson SPM, the sensitivity to environmental shock increases with p. For the model of Fox, the near zero growth rate is $-r\log(B_t/K)$; it goes to ∞ as B_t goes to 0 and is much larger than for a Pella Tomlinson model. Thus the Fox model might not be as affected by a random environment as it postulates a larger growth when the stock is small. An objective of this work is to investigate this question formally and to characterize the sensitivity to environmental shocks of these models in the stochastic framework given in (3).

Thus our first objective will be to investigate conditions leading to a stochastic equilibrium for the Pella Tomlinson process, insuring the long term survival of a stock. Reed (1978) showed that a constraint on the noise distribution is necessary for the non-extinction of the population in models such as (3). An upper bound to the noise variance, specific to that model, that insures that a stochastic equilibrium exists and that extinction is avoided is proposed. Reed (1978) also compared the long-run average yield of different harvest policies in a stochastic framework. He found that the deterministic approach was overestimating the available resources. His work has been complemented by Bousquet et al. (2008) who focused specifically on the Schaefer model. The second objective of that work is to devise harvesting strategies for the Pella Tomlinson model that take into account the environmental noise.

This paper generalizes the results from Bousquet et al. (2008) to the Pella Tomlinson model (3), thereby a similar framework will be used: first we study the stochastic process defined by (3) and derive conditions on the environmental noise to insure the existence of a stationary distribution. Second, we exhibit a distribution for the innovations ε_t that leads to a closed form expression for the stationary distribution and derive a bound on the innovation variance, which is a sufficient condition to the existence of the process. Then we investigate the impact of the innovation's variance on the optimal reference points by deriving stochastic versions of MSY and F_{MSY} . These calculations are presented in a general context where, besides the innovation variances, the effect of an autocorrelation between innovations is also investigated. This autocorrelation could be associated with spells of good and bad years for the stock. The limiting Fox models is also considered and results, specific for that model, are presented. As an illustration we use the results of the analysis presented in Chaloupka and Balazs (2007) about an Hawaiian stock of green sea turtle to evaluate the impact of an environmental noise on a an harvesting strategy constructed using model (3).

2. A stochastic Pella and Tomlinson model

2.1. Description and stationarity

This section focuses on the study of the stochastic Pella Tomlinson model (3). We exhibit a particular model for the innovations that leads to a closed form for the stationary distribution of (3). We study the tolerance to environmental noise of this process. For given ϕ and r, we derive an upper bound for the innovation variance that insures the stationarity of the model, viz. the long term survival of the stock.

Without loss of generality, we can assume that, in (3), $E(\varepsilon_t) = 1$. Indeed, if $E(\varepsilon_t) = \mu \neq 1$, we can re-parametrize as $\phi_\mu = \phi \mu$, $r_\mu = r\mu + (\mu - 1)p/(p+1)$ and $K_\mu^p = K^p r_\mu/(r\mu)$. This leads to a model with innovations equal to ε_t/μ whose expectation is 1.

Define $Z_t = (B_t/K)(r(p+1)/(p-\phi p+r(p+1)))^{1/p}$. Writing (3) in terms of Z_t gives

$$Z_{t+1} = (1 - \phi + r(p+1)/p)Z_t(1 - Z_t^p)\varepsilon_t.$$
(4)

The multiplicative factor $B_M = K[\{p-\phi p + r(p+1)\}]/\{r(p+1)\}]^{1/p}$ transforms the process Z_t into a biomass process. First we want to derive conditions on the environmental noise distribution that insure the existence of a stationary distribution for the biomass process. Notice that Eq. (4) is well defined as long as $0 < Z_t < 1$. Since the maximal value, in (0,1), of $Z(1-Z^p)$ is $p/(1+p)^{1/p+1}$, Z_t will stay in (0,1) as long as the innovations satisfy $\varepsilon_t \in (0, (1+p)^{1/p+1}/\{p-p\phi+r(p+1)\})$. This condition enters the following theorem, a generalization of Bousquet et al. (2008, Theorem 2.1), that insures the existence and the uniqueness of a stationary distribution for the biomass process, without any assumption on the form of the innovation's density.

Theorem 2.1. Let $\{Z_t\}$ be the Markov chain defined by (4), where ε_t are positive, continuous, independent, identically distributed. If $z_0 \in (0,1)$ and if the support of ε_t is $(0,(p+1)^{1+1/p}/\{p-p\phi+r(p+1)\})$, then the chain is irreducible and aperiodic. Consequently, for almost every initial state z_0 , the chain admits a unique stationary distribution.

The proof is identical to that of Bousquet et al. (2008, Theorem 2.1) who focused on the special case p=1. It suffices to substitute $\lambda(z) = (1-\phi+r(p+1)/p)z(1-z^p)$ in the argument presented in the appendix of their paper. Once this is done the proof for p=1 generalizes to an arbitrary positive value of p. The biomass process is $B_t = B_M Z_t$ and its support is $(0, B_M)$. In a random environment, the

maximum value of B_t is B_M ; it can be much larger than the carrying capacity K.

The next step is to examine the stationary distribution of the process $\{Z_t\}$ in a special case. To this end, the next theorem gives a specific form for the noise distribution that leads to an explicit stationary distribution for $\{Z_t\}$. It involves the beta distribution with parameters $\alpha, \beta > 0$ whose density f(v) is given by

$$f(\nu|\alpha,\beta) = B(\alpha,\beta)^{-1} \nu^{\alpha-1} (1-\nu)^{\beta-1}, \quad \nu \in (0,1),$$

where $B(\alpha, \beta) = \Gamma(\alpha)\Gamma(\beta)/\Gamma(\alpha+\beta)$ is the beta function. All proofs are given in the appendix.

Theorem 2.2. Consider a growth parameter r and a harvesting rate ϕ for which $\gamma = (p+1/p)r - \phi > 0$ and $\sigma_M^2 > 0$ where

$$\sigma_M^2 = \frac{-p\gamma^3 + 3\gamma^2 + 2\gamma}{(1+\gamma)^2(1+p\gamma)}.$$

Let $\sigma^2 \in (0, \sigma_M^2)$ and define α and β by

$$\beta = \frac{1}{2(1+\gamma)\sigma^2} \left[\left(\frac{2}{p} - \gamma - \sigma^2(1+\gamma) \right) + \sqrt{4\sigma^2 \frac{1+p}{p^2} + \left(\frac{2}{p} - \gamma - \sigma^2(1+\gamma) \right)^2} \right]$$

$$\alpha = p\beta\gamma - 1$$
,

If there exists a random variable ε with support in $(0,(p+1)^{1+1/p}/\{p-p\phi+r(p+1)\})$ whose moments are given by

$$E[\varepsilon^{\nu}] = \left(\frac{\beta}{\frac{1}{p} + \frac{\alpha}{p} + \beta}\right)^{\nu} \frac{\Gamma(\beta)\Gamma\left(\frac{\alpha}{p} + \beta + \nu + \frac{\nu}{p}\right)}{\Gamma\left(\frac{\alpha}{p} + \beta + \frac{\nu}{p}\right)\Gamma(\beta + \nu)}$$
(5)

and if the innovations $\{\varepsilon_t\}$ in (4) have moments (5), then the stationary distribution of the chain $\{Z_t^p\}$ is a beta distribution with parameter $(\alpha/p, \beta)$.

When p=1 Theorem 2.2 reduces to Theorem 2.2 of Bousquet et al. (2008). Observe that if the moments of ε_t are given by (5), then $E(\varepsilon_t)=1$ and $E(\varepsilon_t^2)=1+\sigma^2$. Theorem 2.2 is a special case of Theorem 2.1 as it gives an explicit form for the stationary distribution for a particular noise distribution, that fulfills the assumptions of Theorem 2.1. This theorem can be used to calculate a stock's stationary distribution and to evaluate the expected harvest in a random environment.

For illustrative purpose, we use the numerical values obtained by Chaloupka and Balazs (2007) when fitting a Pella and Tomlinson model to a stock of Hawaiian green sea turtle: K=1863~t, p=2.97, r=0.035 and $\sigma^2=0.019$. For this example, the maximum biomass B_M varies between 5200 t and 5300 t, depending on ϕ . At the deterministic fishing rate $\phi=0.035$, the formulas in Theorem 2.2 give the values $\alpha=0.19$ and $\beta=34.09$ for the parameters of the stationary distribution. Thus the stationary biomass is distributed as B_M multiplied by a beta $(\alpha/p, \beta)$ raised to the power 1/p. Its density is given by

$$f_B(b) = \frac{1}{B(\alpha/p, \beta)} (b/B_M)^{\alpha-1} \{1 - (b/B_M)^p\}^{\beta-1} p/B_M, \quad b \in (0, B_M),$$

with expectation $B_M\Gamma(\alpha/p+\beta)\Gamma(\alpha/p+1/p)/\{\Gamma(\alpha/p+1/p+\beta)\Gamma(\alpha/p)\}$. This stationary density is presented in Fig. 1 together with those obtained at ϕ equal to r/4, r/2, and 3r/4 respectively. At the deterministic fishing rate $\phi=r$, the variance $\sigma^2=0.019$ has the same order of magnitude as the variance upper bound in Theorem 2.2 $\sigma_M^2=0.047$. The biomass stationary density has a mode at 0, which means that such a high fishing rate maintains the stock in a precarious position. The stationary biomass has an expectation of 238 t, so that the expected harvest under the deterministic fishing rate is $238 \times 0.035 = 8.3 t$; it is much smaller than the deterministic MSY of $rK/(1+p)^{1/p}=41 t$. Fig. 1 shows that selecting a smaller ϕ -value

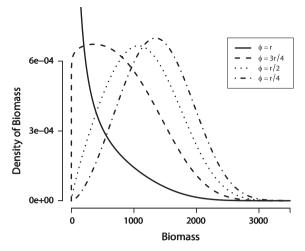


Fig. 1. Stationary biomass density for various values of ϕ .

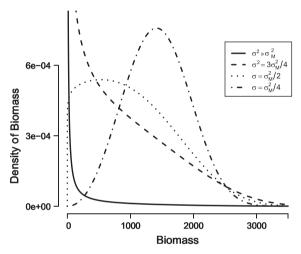


Fig. 2. Biomass density for four values of σ^2 at $\phi = r/4$.

gives a stationary distribution with positive biomasses, bounded away from 0. The expected harvests under the $\phi = r/4, r/2, 3r/4$ scenarios are 12 t, 20 t and 22 t respectively, suggesting to select a fishing rate around $\phi = 3r/4 = 0.026$ to maximize the harvest. The calculation of such optimal fishing rates is discussed in the next section.

In Theorem 2.1, a bounded noise is needed to get a stationary distribution. In Theorem 2.2, the condition $\sigma^2 < \sigma_M^2$, which is a reexpression of the condition that the parameter α/p of the stationary beta distribution must be positive, is necessary for the existence of a stationary distribution, that is for the non-extinction of the stock. Recall that $\gamma = (p+1)r/p - \phi$ is the average intrinsic annual growth rate of Reed (1978). He showed that γ needs to be large enough for non-extinction, with the lower bound depending on the noise distribution. In Theorem 2.2, for reasonable values of r, σ_M^2 is an increasing function of γ . Thus requesting that $\sigma^2 < \sigma_M^2$ amounts to setting a lower bound for γ . When p=1 Bousquet et al. (2008) showed that Reed's lower bound for γ is smaller than that of Theorem 2.2. Therefore the condition for non-extinction in Theorem 2.2 is less restrictive than that of Reed (1978).

Fig. 2 shows the impact of the noise variance on the shape of the stationary distribution of a stock's biomass. It uses the values of K, p and r obtained in Chaloupka and Balazs (2007) and sets $\phi = r/4$. Observe that when σ^2 is close to σ_M^2 , the stationary distribution exists but allows a high probability for very low

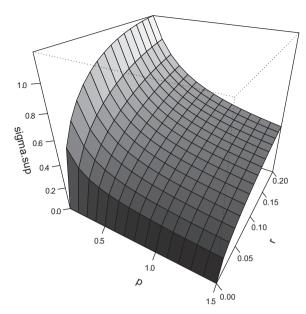


Fig. 3. Plot of the upper bound σ_M^2 as a function of p and r with $\phi = r$.

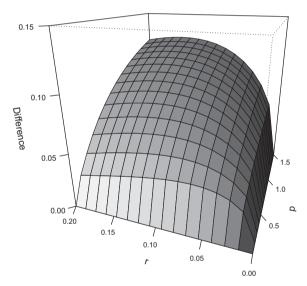


Fig. 4. Plot of the difference between σ_M^2 at $\phi = r/4$ minus σ_M^2 at $\phi = r$.

biomass. Smaller values of σ^2 are needed for the stationary density to be bounded away from 0. Thus even if $\sigma^2 < \sigma_M^2$ is a necessary condition for the non-extinction of the population, we have to be careful. Harvesting a population with a σ^2 close to this upper bound might not give the best yield. Optimizing the harvest in a random environment is considered in Section 3.

Fig. 3 gives a 3D plot of the variance upper bound σ_M^2 as a function of p and r at the deterministic fishing rate $\phi=r$. Notice that a large value of p gives a small upper bound σ_M^2 , suggesting that models with large p-values are more sensitive to environmental variations. In a similar way, σ_M^2 increases with r, up to a maximum value at which it decreases very slowly when p is small. To observe the effect of ϕ on σ_M^2 , Fig. 4 shows the difference of the upper bounds for $\phi=r/4$ and $\phi=r$. Notice first that the difference is positive. Thus the population is able to sustain a larger environmental variability when the harvest rate is decreased or when the growth rate is larger. This effect is

stronger when both p and r are large. As p goes to 0, the difference goes to 0 and the environmental variability does not seem to depend on ϕ when p is small.

At the optimal deterministic fishing rate, $\phi = F_{MSY} = r$, $\gamma = r/p$ and, for any p > 0,

$$\sigma_M^2 = \frac{r(-r^2 + 3r + 2p)}{(1+r)(p+r)^2}.$$

This is a decreasing function of p that is equal to (3-r)/(1+r) for p=0 and that converges to 0 as p goes to infinity. Thus, at the deterministic fishing rate, a fixed noise variance brings stocks following a Pella and Tomlinson with large p's to extinction.

Several authors, such as Punt (2003), use a log-normal distribution for the environmental noise ε_t . When p=1, Bousquet et al. (2008) demonstrated empirically that a distribution with moments given by (5) is close to the lognormal distribution when σ^2 is small. Theorem 2.2 showed that the environmental variance must be smaller than the σ_M^2 upper bound for the non-extinction of the population. One can wonder whether this bound is the smallest possible, i.e. if it provides a sufficient condition for non-extinction. It does so if the assumption of Theorem 2.2 on the existence of a random variable with moments (5) is true. The next proposition guaranties the existence of such a random variable, under additional assumptions.

Proposition 2.1. Let γ , α , and β be as defined in Theorem 2.2. Assume that the shape parameter p is a rational number, e.g. it can be expressed as p = d/q, with d, q two strictly positive integers. If $\beta > \alpha$ and $\alpha/p + \beta > q$. Then there exists a random variable ε_t with support $(0, (p+1)^{1+1/p}/\{p-p\phi+r(p+1)\})$ and whose moments are given by (5).

The case p=1 has been investigated in Bousquet et al. (2008), having $0 < r - \phi \le 1$ is sufficient for the conditions of Proposition 2.1 to be met. For general p, the hypotheses of Proposition 2.1 are actually almost always true and hence non-restrictive. For instance, using the values of r and σ^2 in Chaloupka and Balazs (2007) (r=0.035 and σ^2 =0.019), the assumptions of Proposition 2.1 are met for any rational number p.

2.2. Stationarity for the Fox model

The Fox model corresponds to the special case of (4) where p tends to 0. It is defined by

$$B_{t+1} = B_t \left(1 - \phi - r \log \left(\frac{B_t}{K} \right) \right) \varepsilon_t, \tag{6}$$

for $r \in (0, 1)$. For convenience we re-express the model in terms of $Z_t = B_t \exp((\phi - 1)/r)/K$ as

$$Z_{t+1} = -rZ_t \log(Z_t)\varepsilon_t. \tag{7}$$

Thus the process Z_t does not depend on the harvest rate ϕ . This was already seen in Fig. 4 where the maximum variance did not depend on ϕ when $p\!=\!0$. The harvest rate enters B_t as a scaling factor and acts independently of the environmental noise. Under this model, a stock can tolerate arbitrarily high harvest rates, viz. $\phi \in (0,1)$, without ever collapsing. This resilience is caused by the growth rate γ that goes to ∞ as the biomass B_t goes to 0. In (7), Z_t belongs to (0,1). Assuming $\varepsilon_t \in (0,e/r)$ then insures that $Z_{t+1} \in (0,1)$ and Theorem 2.1 is easily generalized to the Fox model.

There is an explicit stationary distribution for this process, for a particular distribution of the innovations. This involves the gamma

distribution with parameters β , α > 0, whose density f(v) is given by

$$f(x|\alpha,\beta) = \frac{\alpha^{\beta}}{\Gamma(\beta)} x^{\beta-1} e^{-\alpha x}, \quad x > 0.$$

Theorem 2.3. Let $\sigma_{M,0}^2 = (3-r)/(1+r)$ and for $\sigma^2 \in (0, \sigma_{M,0}^2)$ define α_0 and β_0 by

$$\beta_0 = \frac{1}{2r\sigma^2} \! \left(2 - r - \sigma^2 r + \sqrt{4\sigma^2 + (2 - r - \sigma^2 r)^2} \right)$$

$$\alpha_0 = \beta_0 r - 1$$
.

Suppose that there exists a random variable ε with support in (0, e/r) whose moments are given by

$$E[\varepsilon_t^{\nu}] = \left(\frac{\alpha_0 + \nu}{r}\right)^{\nu} \frac{\Gamma(\beta_0)}{\Gamma(\beta_0 + \nu)}.$$
 (8)

If the innovations $\{\varepsilon_t\}$ in (7) have moments (8), then the stationary distribution of the chain $\{-\log(Z_t)\}$ is a Gamma distribution with parameter (β_0, α_0) .

The proof of Theorem 2.3 can be deduced from Theorem 2.2. First one shows that the parameters β_0 , α_0 and $\sigma_{M,0}^2$ are simply the limits, as p goes to 0, of β , α and σ_M^2 defined in Theorem 2.2. In a similar way, the moments (8) are the limits, as p goes to 0, of the moments (5) of Theorem 2.2, which means that the biomass process for the Fox model is the limit of the corresponding process for the Pella and Tomlinson model, as p goes to 0. It also means that for a random variables with moments (8) to exists, it suffices for α_0 , β_0 and p=1/q to fulfill the assumptions of Proposition 2.1 for a large enough integer q. Thus $\beta_0 > \alpha_0 > 1$ is a necessary condition for the existence of a random variable with moments (8). Details are given in Appendix A.

For the Pella and Tomlinson model, Figs. 1 and 2 and Theorem 2.2 show that the harvest rate ϕ and the noise variance σ^2 affect the biomass density. Large values of either one might lead to a stock's extinction. This is not so for the Fox model that can tolerate large fishing rates ϕ as the process (7) does not depend on ϕ . A small noise variance is the only condition needed for non-extinction. Furthermore, in Reed (1978) terminology, the Fox model has an infinite average intrinsic annual growth rate. Accordingly any noise distribution satisfies Reed's (1978) non-extinction condition. This highlights a limitation of Reed's (1978) condition as a bounded noise variable is needed for the non-extinction of a stock for the Fox model.

3. Derivation of biological reference points for stationary SPM processes

When B_t is a stationary process, the optimal harvest rate is the value of ϕ that maximizes $\phi E(B_t)$. This fishing rate is optimal on the long run; it maximizes the average harvest over several years of fishing. Besides its expectation, which is assumed to be equal to 1, the only assumption on the environmental noise ε_t in this section is that its variance σ^2 is small enough for the process B_t to have a non-trivial stationary distribution. The objective is to derive an $o(\sigma^2)$ approximation to the optimal fishing rate in a random environment, e.g. $F_{MSY}(\sigma^2) \approx r + c\sigma^2$, and of the others reference points such as $MSY(\sigma^2)$. For Fox model, the noise and the harvest rate act independently so that $F_{MSY}(\sigma^2)$ is equal to the deterministic fishing rate r and c = 0. This is not so for the Pella and Tomlinson model and the goal of this section is to investigate how the noise's impact varies with the shape parameter p.

The calculations of this section are carried out in a general setting where the innovations ε_t are autocorrelated. Let $\delta_t = \varepsilon_t - 1$ so that $E(\delta_t) = 0$. It is assumed that $\{\delta_t\}$ is a stationary process

satisfying $E(\delta_t \delta_{t+k}) = \rho^k \sigma^2$ for any non-negative integer k. Parameter ρ is the first order error autocorrelation. It introduces a positive correlation between successive environmental shocks experienced by a stock.

For given $p \ge 0$, and $r, \phi \in (0, 1)$, with $\phi < r(p+1)/p$, define

$$\mu = K \left(1 - \frac{p\phi}{(p+1)r} \right)^{1/p},$$

this is the biomass at equilibrium for the deterministic Pella Tomlinson model when harvesting at the rate ϕ . Let $\{B_t\}$ be the corresponding stationary stochastic process obtained with innovations having a variance of σ^2 . All the results of this sections generalize the expansions provided in Bousquet et al. (2008, Section 2.2) for the Schaefer model, that is in the special case p=1 and $\rho=0$. The next proposition derives a first order approximation to $E(B_t)$ when σ^2 goes to 0.

Proposition 3.1. If B_t is distributed according to the stationary distribution of a Pella Tomlinson process, then an $O(\sigma^2)$ approximation to $E(B_t)$ is

$$K \left(1 - \frac{p\phi}{(p+1)r}\right)^{1/p} \left[1 - \frac{(p+1)/2}{1 - (1 - (p+1)r + p\phi)^2} \frac{1 + (1 - (p+1)r + p\phi)\rho}{1 - (1 - (p+1)r + p\phi)\rho} \sigma^2\right]. \tag{9}$$

The expectation of B_t is smaller than μ ; thus in a random environment the deterministic model always overestimates the size of a stock. The MSY is the maximum value of $f(\phi) = \phi E(B_t|\phi)$. The next proposition gives a first order approximation to that quantity derived using the Newton Raphson method.

Theorem 3.1. Let $\{B_t\}$ be a stationary Markov chain defined by (3). Then the maximum sustainable yield satisfies

$$MSY(\sigma^2) = \frac{Kr}{(p+1)^{1/p}} \left(1 - \frac{(p+1)/2}{1 - (1-r)^2} \frac{1 + \rho - r\rho}{1 - \rho + r\rho} \sigma^2 \right) + o(\sigma^2),$$

its associated total biomass is

$$E[B_{MSY}] \approx \frac{K}{(p+1)^{1/p}} \left(1 - \frac{1 + r(p-1)/2}{r(2-r)^2} \frac{1 + \rho - r\rho}{1 - \rho + r\rho} \sigma^2 + \frac{p\rho}{(2-r)(1 - \rho + r\rho)^2} \sigma^2 \right),$$

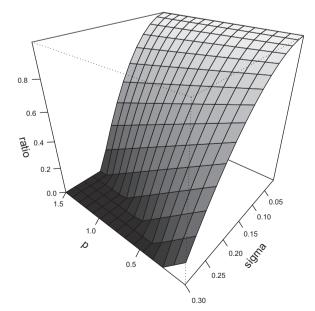


Fig. 5. Plot of the ratio $MSY(\sigma)/MSY(0)$ as a function of σ and p.

and the optimal harvest rate is

$$F_{MSY}(\sigma^2) = r - \frac{p(1-r)(1+\rho-r\rho)}{(2-r)^2(1-\rho+r\rho)}\sigma^2 - \frac{rp\rho}{(2-r)(1-\rho+r\rho)^2}\sigma^2 + o(\sigma^2).$$

To understand the impact of the noise's variance, ratio $MSY(\sigma^2)/MSY(0)$ is displayed in Fig. 5 as a function of the parameters p and σ , with r=0.035 and ρ =0. It starts at 1 when σ =0 and rapidly decreases while σ increases. Notice also that the ratio is smaller when p gets larger. This emphasizes the fact that the population is more sensible to the environmental variability when p is large.

4. Illustration

To get a better understanding of the impact of a random environment on the calculations of biological reference points, consider the Hawaiian green sea turtle stock of Chaloupka and Balazs (2007) studied in Section 2.1, with p = 2.97, r = 0.035 and $\hat{\sigma}^2 = 0.019$. Assume a deterministic Pella Tomlinson model leads to the following reference points:

$$MSY(0) = 41.0 t$$
, $E[B_{MSY}](0) = 1171.1 t$, $F_{MSY}(0) = 0.035$.

Theorem 3.1 gives the following approximations for the optimal reference point that account for a random environment,

$$MSY(\sigma^2) = 18.5 t$$
, $E[B_{MSY}](\sigma^2) = 1000.8 t$, $F_{MSY}(\sigma^2) = 0.021$.

Note that $F_{MSY}(\sigma^2)$ is relatively close to 3r/4 = 0.026, the best fishing rate among the 4 values considered in Fig. 1. Note however that the MSY of 18.5 t is smaller that 22 t, the yield obtained with $\phi = 0.026$ in the discussion for Fig. 1. This highlights that Theorem 3.1 provides first order approximations. Calculating the $O(\sigma^4)$ in the expansions of Theorem 3.1 would produce more accurate results. Such precise expansions are provided in Bousquet et al. (2008) for the Schaefer model.

Chaloupka and Balazs (2007) acknowledge that harvesting at 41.0 tonnes a year is not realistic so they consider setting the yearly harvesting target at 30 tonnes, corresponding to the median of the posterior distribution for MSY. When the impact of the process error is factored in, the maximum value of the $MSY(\sigma^2)$ is less than 30 so, on the long run, harvesting 30 tonne will lead to the extinction of the stock. This can be seen in the biomass boxplot for the 25 year simulations reported in Chaloupka and Balazs (2007, Fig. 7) where very small biomass level can be obtained after 25 years. Considering Fig. 1, at $F_{MSY}(\sigma^2) = 0.021$, the stock's stationary distribution is bounded away from 0 and has a positive mode.

To investigate the sensitivity to the assumption of a null autocorrelation, one can set ρ =0.10 and use the values of Chaloupka and Balazs (2007) for the other parameters. Theorem 3.1 then gives

$$MSY(\sigma^2) = 13.7 t$$
, $E[B_{MSY}](\sigma^2) = 968.5 t$, $F_{MSY}(\sigma^2) = 0.018$.

A small autocorrelation of 0.1 results in a 25% drop in MSY. This highlights the sensitivity of this stock to its random environment.

5. Discussion

This paper has studied the impact of a random environment on surplus production models. Two types of impact have been studied in this work. The maximum innovation variance that a stationary process can tolerate before becoming extinct has been derived. Then the first order contributions of that variance to the biological reference points have been calculated. We have found

that Pella and Tomlinson models with large p, e.g. where the maximum surplus production is more that 50% of the carrying capacity, are more sensitive to environmental noise than those with small p. When fitting a surplus production model, the results presented in this paper can help with the determination of a suitable harvesting strategy that will insure a stock's long term survival.

Appendix A. Proofs of Section 2

A.1. Proof of Theorem 2.2

By construction $\beta>0$. To prove that $\alpha>0$ (and hence $\alpha/p>0$), we show that $\sigma^2<\sigma_M^2=(-p\gamma^3+3\gamma^2+2\gamma)/((1+\gamma)^2(1+p\gamma))$ is equivalent to $\alpha>0$ by substituting β with its expression in terms of p, γ and σ^2 in $\alpha=p\beta\gamma-1$.

Since the conditions of Theorem 2.1 are verified, we have the existence and uniqueness of a stationary distribution. We suppose that $Y_t = Z_t^p$ follows a beta distribution with parameters $(\alpha/p, \beta)$ and then show that the distribution of Y_{t+1} is the same as that of Y_t . The transition equation for Y_t is

$$Y_{t+1} = (1 - \phi + r(p+1)/p)^p Y_t (1 - Y_t)^p \varepsilon_t^p. \tag{A.1}$$

First, notice that if Y_t follows a beta distribution with parameter $(\alpha/p, \beta)$, then for u > 0,

$$E(Y_t^u) = \frac{\Gamma(\alpha/p + \beta)\Gamma(\alpha/p + u)}{\Gamma(\alpha/p)\Gamma(\alpha/p + \beta + u)},$$

and

$$E(Y_t^u(1-Y_t)^{pu}) = \frac{\Gamma(\alpha/p+\beta)\Gamma(\alpha/p+u)\Gamma(\beta+pu)}{\Gamma(\alpha/p)\Gamma(\beta)\Gamma(\alpha/p+\beta+pu+u)}$$

As $1-\phi+r(p+1)/p=1+\gamma$ and $\beta/(1/p+\alpha/p+\beta)=1/(1+\gamma)$, using (5) for $E(\varepsilon_t^{pu})$ leads to $(1-\phi+r(p+1)/p)^{pu}E\{Y_t^u(1-Y_t)^{pu}\}E(\varepsilon_t^{pu})$ for the moments of Y_{t+1} . This is equal to

$$\frac{\Gamma(\alpha/p+\beta)\Gamma(\alpha/p+u)}{\Gamma(\alpha/p)\Gamma(\alpha/p+\beta+u)}$$

which is the uth moment of a beta $(\alpha/p, \beta)$ distribution. Hence Y_{t+1} follows a beta distribution with parameter $(\alpha/p, \beta)$, which is then the stationary distribution of the process.

We need to verify that $E(\varepsilon_t) = 1$ and $Var(\varepsilon_t) = \sigma^2$. Considering the moments of (A.1) and isolating $E(\varepsilon_t^{pu})$, we get $E(\varepsilon_t)$ and $E(\varepsilon_t^2)$ by substituting α and β for their expressions in terms of p, γ and σ^2 .

A.2. Proof of Proposition 2.1

Let $U_0,...,U_{d-1},V_0,...,V_{q-1}$ be d+q independent random variables such that for all i in $\{0,...,d-1\}$, U_i follows a beta distribution with parameter $(\alpha/p+\beta+i)/(d+q),((\beta+i)q-d\alpha/p)/(d(d+q))$ and for all $j\in\{0,...,q-1\}$, V_j follows a beta distribution with parameter $(\alpha/p+\beta+d+j)/(d+q),((\alpha/p+\beta+j-q)d)/(q(d+q))$. The assumptions on α/p and β imply that the parameters of all these beta distributions are positive. Define

$$\varepsilon = \frac{(p+1)^{1+1/p}}{p - p\phi + r(p+1)} \prod_{i=0}^{d-1} U_i^{1/d} \prod_{i=0}^{q-1} V_j^{1/d}.$$

We need to prove that the moments of ε are given by (5), let s=u/d. It is clear that the support of ε is

$$\left(0,\frac{(p+1)^{1+1/p}}{p-p\phi+r(p+1)}\right).$$

Notice first

$$\frac{(p+1)^{1+1/p}}{p-p\phi+r(p+1)} = \frac{\left(\frac{d}{q}+1\right)^{(q/d)+1}}{\frac{d}{q}} \frac{1}{1+\gamma} = \frac{(d+q)^{(q/d)+1}}{dq^{q/d}} \frac{\beta}{\frac{1}{p}+\alpha/p+\beta}.$$

With the calculation of the moments of ε :

$$\begin{split} E(\varepsilon^{ds}) = & \frac{(d+q)^{(d+q)s}}{d^{ds}q^{qs}} \left(\frac{1}{1+\gamma}\right)^{ds} \prod_{i=0}^{d-1} \frac{\Gamma\left(\frac{\alpha/p+\beta+i}{d+q}+s\right) \Gamma\left(\frac{\beta+i}{d}\right)}{\Gamma\left(\frac{\alpha/p+\beta+i}{d+q}\right) \Gamma\left(\frac{\beta+i}{d}+s\right)} \\ & \times \prod_{j=0}^{q-1} \frac{\Gamma\left(\frac{\alpha/p+\beta+d+j}{d+q}+s\right) \Gamma\left(\frac{\alpha/p+\beta+j}{q}\right)}{\Gamma\left(\frac{\alpha/p+\beta+d+j}{d+q}\right) \Gamma\left(\frac{\alpha/p+\beta+j}{q}+s\right)} \end{split}$$

And by using the multiplication formula for the gamma function

$$\Gamma(mz) = \frac{m^{mz-(1/2)}}{(2\pi)^{(m-1)/2}} \Gamma(z) \Gamma\left(z + \frac{1}{m}\right) \Gamma\left(z + \frac{2}{m}\right) \dots \Gamma\left(z + \frac{m-1}{m}\right),$$

for $m \in \mathbb{N}$ we obtain

$$\begin{split} \Gamma\left(\frac{\alpha}{p}+\beta+(d+q)s\right) &= \frac{(d+q)^{(\alpha/p)+\beta+(d+q)s-(1/2)}}{(2\pi)^{(d+q-1)/2}} \Gamma\left(\frac{\alpha/p+\beta}{d+q}+s\right) \\ &\times \Gamma\left(\frac{\alpha/p+\beta+1}{d+q}+s\right) ... \Gamma\left(\frac{\alpha/p+\beta+d+q-1}{d+q}+s\right) \end{split}$$

$$\begin{split} \Gamma\!\left(\!\frac{\alpha}{p}\!+\!\beta\right) = & \frac{(d+q)^{(\alpha/p)+\beta-(1/2)}}{(2\pi)^{(d+q-1)/2}} \Gamma\!\left(\!\frac{\alpha/p\!+\!\beta}{d\!+\!q}\right) \Gamma\!\left(\!\frac{\alpha/p\!+\!\beta\!+\!1}{d\!+\!q}\right) \\ & \times \!\Gamma\!\left(\!\frac{\alpha/p\!+\!\beta\!+\!2}{d\!+\!q}\right) ... \Gamma\!\left(\!\frac{\alpha/p\!+\!\beta\!+\!d\!+\!q\!-\!1}{d\!+\!q}\right) \end{split}$$

$$\begin{split} \varGamma\left(\frac{\alpha}{p} + \beta + qs\right) &= \frac{q^{(\alpha/p) + \beta + qs - (1/2)}}{(2\pi)^{(q-1)/2}} \varGamma\left(\frac{\alpha/p + \beta}{q} + s\right) \varGamma\left(\frac{\alpha/p + \beta + 1}{q} + s\right) \\ &\times \varGamma\left(\frac{\alpha/p + \beta + 2}{q} + s\right) ... \varGamma\left(\frac{\alpha/p + \beta + q}{q} + s\right) \end{split}$$

$$\begin{split} \varGamma\left(\frac{\alpha}{p} + \beta\right) &= \frac{q^{(\alpha/p) + \beta - (1/2)}}{(2\pi)^{(q-1)/2}} \varGamma\left(\frac{\alpha/p + \beta}{q}\right) \varGamma\left(\frac{\alpha/p + \beta + 1}{q}\right) \\ &\times \varGamma\left(\frac{\alpha/p + \beta + 2}{q}\right) ... \varGamma\left(\frac{\alpha/p + \beta + p}{q}\right) \end{split}$$

$$\Gamma(\beta+ds) = \frac{d^{\beta+ds-(1/2)}}{(2\pi)^{(d-1)/2}} \Gamma\left(\frac{\beta}{d}+s\right) \Gamma\left(\frac{\beta+1}{d}+s\right) \Gamma\left(\frac{\beta+2}{d}+s\right) \dots \Gamma\left(\frac{\beta+d-1}{d}+s\right)$$

$$\Gamma(\beta) = \frac{d^{\beta - (1/2)}}{(2\pi)^{(d-1)/2}} \Gamma\left(\frac{\beta}{d}\right) \Gamma\left(\frac{\beta + 1}{d}\right) \Gamma\left(\frac{\beta + 2}{d}\right) \dots \Gamma\left(\frac{\beta + d - 1}{d}\right).$$

Simplifying the resulting expression for $E[\varepsilon^{ds}]$ leads to

$$E[e^{ds}] = \left(\frac{\beta}{\frac{1}{n} + \alpha/p + \beta}\right)^{ds} \frac{\Gamma(\beta)\Gamma(\alpha/p + \beta + ds + qs)}{\Gamma(\alpha/p + \beta + qs)\Gamma(\beta + ds)}$$

By using the property that a bounded distribution is uniquely determined by its moments (Shohat and Tamarkin, 1943), we get the result.

A.3. Elements of the proof of Theorem 2.3

Notice that $\gamma = (p+1)r/p - \phi \sim r/p$ as p goes to 0. The limits as p goes to 0 of the parameter β , α , and σ_M^2 are obtained using the following arguments:

$$\beta = \frac{1}{2(1+\gamma)\sigma^2} \left[\left(\frac{2}{p} - \gamma - \sigma^2(1+\gamma) \right) + \sqrt{4\sigma^2 \frac{1+p}{p^2} + \left(\frac{2}{p} - \gamma - \sigma^2(1+\gamma) \right)^2} \right]$$

$$\begin{split} &\sim \frac{1}{2\frac{r}{p}\sigma^2} \Bigg[\left(\frac{2}{p} - \frac{r}{p} - \sigma^2 \frac{r}{p} \right) + \sqrt{4\sigma^2 \frac{1}{p^2} + \left(\frac{2}{p} - \frac{r}{p} - \sigma^2 \frac{r}{p} \right)^2} \Bigg] \\ &\longrightarrow \frac{1}{2r\sigma^2} [2 - r - \sigma^2 r + \sqrt{4\sigma^2 + (2 - r - \sigma^2 r)^2}] = \beta_0 \end{split}$$

$$\alpha = p\beta\gamma - 1 \sim \beta r - 1 \longrightarrow \beta_0 r - 1 = \alpha_0$$

$$\sigma_{M}^{2} = \frac{-p\gamma^{3} + 3\gamma^{2} + 2\gamma}{(1+\gamma)^{2}(1+p\gamma)} \sim \frac{-\frac{r^{3}}{p^{2}} + 3\frac{r^{2}}{p^{2}} + 2\frac{r}{p}}{\left(1 + \frac{r}{p}\right)^{2}(1+r)}$$
$$\longrightarrow \frac{-r^{3} + 3r^{2}}{r^{2}(1+r)} = \frac{3-r}{1+r} = \sigma_{M,0}^{2}.$$

Now, using Stirling formula $\Gamma(z) \sim \sqrt{2\pi/z}(z/e)^z$ as z goes to ∞ , the limits of the moments (5), as p goes to 0, are given by

$$\begin{split} E(\varepsilon^{\mathrm{v}}) &= \left(\frac{\beta}{\frac{1}{p} + \frac{\alpha}{p} + \beta}\right)^{\mathrm{v}} \frac{\Gamma(\beta)\Gamma\left(\frac{\alpha}{p} + \beta + \nu + \frac{\nu}{p}\right)}{\Gamma\left(\frac{\alpha}{p} + \beta + \nu + \frac{\nu}{p}\right)\Gamma(\beta + \nu)} \\ &\sim \left(\frac{1}{1 + \gamma}\right)^{\mathrm{v}} \frac{\Gamma(\beta)}{\Gamma(\beta + \nu)} \frac{\sqrt{\frac{2\pi}{p} + \beta + \nu + \frac{\nu}{p}}}{\sqrt{\frac{\frac{2\pi}{p} + \beta + \nu + \frac{\nu}{p}}{p}}} \frac{\left(\frac{\alpha}{p} + \beta + \nu + \frac{\nu}{p}\right)^{(\alpha/p) + \beta + \nu + (\nu/p)}}{\left(\frac{\alpha}{p} + \beta + \frac{\nu}{p}\right)} \\ &\sim \left(\frac{1}{1 + r/p}\right)^{\mathrm{v}} \frac{\Gamma(\beta)}{\Gamma(\beta + \nu)} \left(\frac{\frac{\alpha}{p} + \beta + \nu + \frac{\nu}{p}}{\frac{\alpha}{p} + \beta + \frac{\nu}{p}}\right)^{(\alpha/p) + \beta + (\nu/p)} \left(\frac{\alpha}{p} + \beta + \nu + \frac{\nu}{p}\right)^{\mathrm{v}} \\ &\sim \left(\frac{1}{1 + r/p}\right)^{\mathrm{v}} \frac{\Gamma(\beta)}{\Gamma(\beta + \nu)} \left(1 + \frac{\nu}{\frac{\alpha}{p} + \beta + \frac{\nu}{p}}\right)^{(\alpha/p) + \beta + (\nu/p)} \frac{1}{e^{\mathrm{v}}} \left(\frac{\alpha}{p} + \frac{\nu}{p}\right)^{\mathrm{v}} \\ &\sim \left(\frac{\alpha + \nu}{p + r}\right)^{\mathrm{v}} \frac{\Gamma(\beta)}{\Gamma(\beta + \nu)} e^{\nu} \frac{1}{e^{\nu}} \longrightarrow \left(\frac{\alpha_0 + \nu}{r}\right)^{\mathrm{v}} \frac{\Gamma(\beta_0)}{\Gamma(\beta_0 + \nu)} \end{split}$$

which are the moments (8).

Appendix B. Proofs of Section 3

B.1. Proof of Proposition 3.1

Note that $\mu^p = K^p(1 - (p\phi)/((p+1)r))$. In (3), $B_{t+1} = g(B_t)(1 + \delta_t)$ and carrying out a second order Taylor series expansion of $g(B_t)$ around $B_t = \mu$ gives

$$B_{t+1} \sim \mu + \mu \delta_t + (1 + p\phi - (p+1)r)(B_t - \mu) + \frac{p(p+1)\left(\frac{p+1}{p}r - \phi\right)}{2\mu}(B_t - \mu)^2.$$
(B.1)

Since B_t and B_{t+1} follow the same distribution: $E[B_{t+1} - \mu] = E[B_t - \mu]$. We deduce

$$E[B_{t+1} - \mu] \sim -\frac{p+1}{2\mu} E[(B_t - \mu)^2].$$
 (B.2)

Since $E(B_t) = \mu + O(\sigma^2)$, the variance of B_t is approximately $Var(B_t) \sim E[(B_t - \mu)^2]$, and keeping only quadratic terms

$$Var(B_{t+1}) \sim \mu^2 \sigma^2 + (1 + p\phi - (p+1)r)^2 \ Var(B_t) + 2\mu (1 + p\phi - (p+1)r) \ Cov(\delta_t, B_t).$$

We only need to get $Cov(\delta_t, B_t)$. By multiplying (B.1) with δ_{t+1} and by

taking the expectation, we get

$$E[\delta_{t+1}(B_{t+1}-\mu)] \sim \mu E[\delta_{t+1}\delta_t] + (1+p\phi-(p+1)r)E[\delta_{t+1}(B_t-\mu)].$$

And with the law of total expectation:

$$E[(B_t - \mu)\delta_{t+1}] = E[E[(B_t - \mu)\delta_{t+1}|\delta_t]] = \rho E[(B_t - \mu)\delta_t].$$

Then we get, using the equilibrium

$$E[\delta_t(B_t-\mu)] \sim \mu\rho\sigma^2 + (1+p\phi-(p+1)r)\rho E[\delta_t(B_t-\mu)]$$

$$E[\delta_t(B_t - \mu)] \sim \frac{\mu \rho \sigma^2}{1 - (1 + p\phi - (p+1)r)\rho}$$

And we deduce an explicit expression for the variance:

$$Var(B_t) \sim (1 + p\phi - (p+1)r)^2 Var(B_t) + \mu^2 \sigma^2 + 2\frac{\mu^2 (1 + p\phi - (p+1)r)\rho \sigma^2}{1 - (1 + p\phi - (p+1)r)\rho}$$

$$Var(B_t) \sim \frac{1}{1 - (1 + p\phi - (p+1)r)^2} \frac{1 + (1 + p\phi - (p+1)r)\rho}{1 - (1 + p\phi - (p+1)r)\rho} \mu^2 \sigma^2$$

Finally, with (B.2) and by substituting μ , we find

$$E[B_t] = K \left(1 - \frac{p\phi}{(p+1)r}\right)^{1/p} \left[1 - \frac{(p+1)/2}{1 - (1 - (p+1)r + p\phi)^2} \frac{1 + (1 - (p+1)r + p\phi)\rho}{1 - (1 - (p+1)r + p\phi)\rho} \sigma^2\right] + o(\sigma^2).$$

B.2. Proof of Theorem 3.1

We determine the MSY by maximizing $f(\phi) = \phi E[B_t|\phi]$ and by using the Newton–Raphson method. Since $r = F_{MSY}(0)$, the formula to get the first order term is

$$F_{MSY} = r - \frac{f'(r)}{f''(r)}$$

where f'(r) and f''(r) denote the first and second derivatives with respect to ϕ evaluated at $\phi=r$. Since the derivative of $\phi[1-p\phi/\{(p+1)r\}]^{1/p}$ with respect to ϕ and evaluated at $\phi=r$ is 0, the derivatives of f are given by

$$f'(r) = \frac{rK}{(p+1)^{1/p}} \left(-\frac{p(p+1)(1-r)}{(1-(1-r)^2)^2} \frac{1+(1-r)\rho}{1-(1-r)\rho} \sigma^2 - \frac{(p+1)p\rho\sigma^2}{(1-(1-r)^2)(1-(1-r)\rho)^2} \right) + o(\sigma^2)$$

$$f''(r) = -\frac{K(p+1)}{r(p+1)^{1/p}} + O(\sigma^2),$$

which allow us to get

$$\begin{split} F_{MSY} \sim r - & \frac{r^2}{p+1} \Biggl(\frac{p(p+1)(1-r)(1+\rho-r\rho)}{(2r-r^2)^2(1-\rho+r\rho)} + \frac{(p+1)p\rho}{(2r-r^2)(1-\rho+r\rho)^2} \Biggr) \sigma^2 \\ \sim & r - \frac{p(1-r)(1+\rho-r\rho)}{(2-r)^2(1-\rho+r\rho)} \sigma^2 - \frac{rp\rho}{(2-r)(1-\rho+r\rho)^2} \sigma^2. \end{split}$$

Then the MSY is $F_{MSY}E[B_t|F_{MSY}]$.

$$MSY = F_{MSY}K \left(1 - \frac{pF_{MSY}}{(p+1)r}\right)^{1/p} \left[1 - \frac{(p+1)/2}{1 - (1 - (p+1)r + p\phi)^2} \frac{1 + \rho - r\rho}{1 - (1 - \rho + r\rho}\sigma^2\right] + o(\sigma^2).$$

After further simplifications and Taylor expansion, we get

$$MSY = \frac{Kr}{(p+1)^{1/p}} \left(1 - \frac{(p+1)/2}{1 - (1-r)^2} \frac{1 + \rho - r\rho}{1 - \rho + r\rho} \sigma^2 \right) + o(\sigma^2).$$

Finally, its associated biomass is

 $E[B_{MSY}] = MSY/F_{MSY}$

$$\sim \frac{MSY}{r} \left\{ 1 - \frac{p(1-r)(1+\rho-r\rho)}{r(2-r)^2(1-\rho+r\rho)} \sigma^2 - \frac{p\rho}{(2-r)(1-\rho+r\rho)^2} \sigma^2 \right\}^{-1}$$

$$\sim \frac{K}{(p+1)^{1/p}} \left(1 - \frac{(p+1)/2}{1-(1-r)^2} \frac{1+\rho-r\rho}{1-\rho+r\rho} \sigma^2 \right)$$

$$\times \left(1 + \frac{p(1-r)(1+\rho-r\rho)}{r(2-r)^2(1-\rho+r\rho)} \sigma^2 + \frac{p\rho}{(2-r)(1-\rho+r\rho)^2} \sigma^2 \right).$$

This simplifies to

$$E[B_{MSY}] = \frac{K}{(p+1)^{1/p}} \left(1 - \frac{1 + r(p-1)/2}{r(2-r)^2} \frac{1 + \rho - r\rho}{1 - \rho + r\rho} \sigma^2 + \frac{p\rho}{(2-r)(1 - \rho + r\rho)^2} \sigma^2 \right).$$

References

Amundsen, E., Bjorndal, T., 1999. Optimal exploitation of a biomass confronted with the threat of collapse. Land Econ. 75, 185–202.

Boerema, L.K., Gulland, J., 1973. Stock assessment of the peruvian anchovy (*Engraulis ringens*) and management of the fishery. J. Fish. Res. Board Can. 30, 2226–2235.

Bousquet, N., Duchesne, T., Rivest, L.P., 2008. Redefining the maximum sustainable yield for the Schaefer population model including multiplicative environmental noise, J. Theor. Biol. 254, 65–75.

Chaloupka, M., Balazs, G., 2007. Using Bayesian state-space modelling to assess the recovery and harvest potential of the Hawaiian green sea turtle stock. Ecol. Model. 205, 93–109.

Chavance, P., Ba, M., Gascuel, D., 2002. Pecheries maritimes, ecosystemes et societes en Afrique de l'Ouest: un demi-siecle de changement. European Communities, Bruxelles

Doubleday, W. Environmental fluctuations and fisheries management. In: ICNAF Selected Papers, 1976, vol. 1, pp. 141–150.

Ewald, C.O., Wang, W.K., 2010. Sustainable yields in fisheries: uncertainty, risk-aversion, and mean-variance analysis. Nat. Resour. Model. 23, 303–323.

Fox, W.W., 1970. An exponential surplus-yield model for optimizing exploited fish populations. Trans. Am. Fish. Soc. 99, 80–88.

Gore, A., Paranje, S., 2001. A Course in Mathematical and Statistical Ecology. Kluwer Academic Publishers, Dordrecht.

Hilborn, R., Walters, C.J., 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty. Chapman and Hall, New York, NY.

Laloe, F., 1995. Should surplus production models be fishery description tools rather than biological models? Aquat. Living Resour. 8, 1–16.

Larkin, P., 1977. An epitaph for the concept of maximum sustained yield. Trans. Am. Fish. Soc. 106, 1–11.

Lewis, T., 1981. Exploitation of a renewable resource under uncertainty. Can. J. Econ. 14, 422–439.

Ludwig, D., Walters, C.J., 1985. Are age-structured models appropriate for catcheffort data? Cap. J. Fish. Aguat. Sci. 46, 137-144

effort data? Can. J. Fish. Aquat. Sci. 46, 137–144.

Panhwar, S.K., Qun, L., Amir, S.A., Kalhoro, M.A., 2012. Performance comparison between logistic and generalized surplus-production models applied to the Sillago Sihama fishery in Pakistan. J. Ocean Univ. China 11, 401–407.

Pella, J., Tomlinson, P., 1969. A generalized stock production model. Bull. Int.-Am. Trop. Tuna Commun. 13, 416–497.

Prager, M.H., 2002. Comparison of logistic and generalized surplus-production models applied to swordfish, *Xiphias gladius*, in the north atlantic ocean. Fish. Res. 58, 41–57.

Punt, A.E., 2003. Extending production models to include process error in the population dynamics. Can. J. Fish. Aquat. Sci. 60, 1217–1228.

Reed, W., 1978. The steady state of a stochastic harvesting model. Math. Biosci. 41, 273–307

Schaefer, M.B., 1954. Some aspects of the dynamics of populations important to the management of the commercial marine fisheries. Bull. Int.-Am. Trop. Tuna Commun. 1, 247–285.

Shohat, J.A., Tamarkin, J.D., 1943. The Problem of Moments. American Mathematical Society, New York.