Local sensitivity of per-recruit fishing mortality reference points

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ABSTRACT

We study the sensitivity of fishery management per-recruit harvest rates which may be part of a quantitative harvest strategy designed to achieve some objective for catch or population size. We use a local influence sensitivity analysis to derive equations that describe how these reference harvest rates are affected by perturbations to productivity processes. These equations give a basic theoretical understanding of sensitivity that can be used to predict what the likely impacts of future changes in productivity will be. Our results indicate that per-recruit reference harvest rates are more sensitive to perturbations when the equilibrium catch or population size per recruit, as functions of the harvest rate, have less curvature near the reference point. Overall our results suggest that per-recruit reference points will, with some exceptions, usually increase if (1) growth rates increase, (2) natural mortality rates increase, or (3) fishery selectivity increases to an older age.

1. Introduction

Modern fishery management usually involves a quantitative harvest strategy in which annual catch levels are determined using a pre-defined rule that is designed to produce desirable and sustainable outcomes. Harvest decision rules usually involve population (i.e. stock) status zones (healthy, cautious, and critical) and harvest rates that (1) decline from the healthy to the critical zone, and (2) account for uncertainty in stock status. This is commonly referred to as the Precautionary Approach to fisheries management and has been outlined in several UN initiatives [24]. An illustration of such a rule is provided in Figure 1 and is roughly based on the Canadian framework [26]. It is common in fisheries science to express annual harvest rates as instantaneous fishing mortality rates ($F$; see Section 2.1). The zones in Figure 1 are defined by reference points (RPs) such as the $F$ that produces maximum sustainable yield ($F_{msy}$), and the population biomass ($B_{msy}$) that results from fishing at $F_{msy}$ in the long term. Choices for the limit and upper stock status RP’s could be 40% and 80% of $B_{msy}$, and the limit harvest rate could be $F_{msy}$.
Figure 1. Illustration of a precautionary approach fisheries harvest decision rule that involves stock status zones defined by RPs and a harvest rate limit RP. Fisheries may harvest less than the limit.

These MSY RPs are derived from an equilibrium analysis of a population dynamics model. For many major fisheries, age samples are collected regularly and this information can be used to model the annual mortality rates of cohorts. We assume the population is closed, with no immigration or emigration, and the size of a cohort simply declines with age because of mortality processes. MSY RPs depend on growth and mortality rates, and the reproduction rate as a function of parental population size which in many cases is highly variable and difficult to model. Hence, MSY RPs are often difficult to estimate reliably [6]. This has motivated researchers to propose RPs that can be more readily calculated with available information [13, 23]. In this paper we study ‘per-recruit’ $F$ RPs based on the total yield or adult (i.e. spawning) biomass of a cohort, standardized to the initial size of the cohort (see Section 2.2). At equilibrium, the size of each cohort and the age structure of the population each year is constant. Hence, the total population size does not change from year-to-year and the annual population biomass, summed over all ages, is the same as the total weight produced by a cohort over its lifespan. Per-recruit $F$ RPs do not require estimation of the reproduction function and are therefore easier to estimate than $F_{msy}$ and are often considered to be proxies of $F_{msy}$ [13].

Values for RPs can have substantial economic impacts on fishing communities and industry. Fisheries managers and stakeholders often want to know how sensitive RP estimates are to the quality of inputs and underlying assumptions. Reliable and useful RPs should be stable over time and robust to uncertainty [27]. In this paper a sensitivity analysis is presented to describe how per-recruit RPs are affected by perturbations to productivity processes. A sensitivity analysis may generally be interpreted as a study of the impact of changes in model inputs (parameters or data) on model outputs. This can be done using computational methods where some model inputs are varied and the model outputs are re-computed to see if the variations had large impacts. This is typically the approach used in fisheries science and more specifically for per-recruit RPs (e.g. [10, 14, 16]). Perturbation analyses can be local, involving small changes usually to one input at a time, or global, involving larger changes to multiple inputs simultaneously [4, 25].

We pursue an analytical local influence approach similar to [5] who studied sensitivity of a commonly used fish biomass limit RP. Local influence diagnostics, made popular by Cook
are commonly used to assess sensitivity of nonlinear estimators in statistical models. They sometimes produce simple and intuitive influence or sensitivity equations that can be used to deconstruct the sources of influence. In particular, the equations may tell us why some perturbations have a large effect. This understanding is difficult to get from a computational perturbation analysis. Local influence equations can be used to predict the impacts of a perturbation without actually computing the effect. Such a theoretical understanding is useful in the RP context because we could then predict, for different populations or new situations, how RPs will change using only a basic understanding of the productivity processes. However, the predictive capability of the equations depends on how simple they are. The methods we propose are fairly general and can be applied to important outputs from many nonlinear population dynamics model.

The article is organized as follows. In Section 2 we present continuous-time versions of various per-recruit RP methods, including some simple results and illustrations. In Section 3 we derive local influence equations for some specific perturbation schemes and illustrate the utility of the results with simple examples. Finally, in Section 4 we discuss our findings and compare them to other literature results.

2. Per-recruit RPs

Per-recruit models are commonly used in fisheries science. The term recruitment does not have a standard meaning but we define it to be the size of the population at the age when it is first exploited by the fishery. For convenience we denote this reference age as zero. Per-recruit models are usually based on the total yield of a fishery or total production of mature fish (i.e. spawners) per unit of recruitment, commonly referred to as yield-per-recruit (YPR) or spawner per-recruit (SPR) models, respectively. For simplicity (see Section 4), we focus on a continuous time population dynamics model [23]. Results should be qualitatively similar for discrete-time versions. We assume mortality processes are age dependent but otherwise constant over time. This is typical in equilibrium analyses of population dynamics models and when deriving fisheries management RPs.

2.1. Population dynamics

The basic population dynamics for a cohort is assumed to be described by \( \frac{dn(t)}{dt} = -z(t) \) where \( z(t) \) is the age-varying non-negative total mortality rate and

\[
n(t) = n(0) \exp \left\{ - \int_0^t z(x) \, dx \right\}.
\]

Total mortality rates may be split into components due to fishing and natural causes. Let \( z(t) = f(t) + m(t) = f \times s(t) + m(t) \) where:

1. \( s(t) \) is the non-negative fishery selection function of age \( t \) with \( \max_x s(t) = 1 \). Not all ages are caught equally by a fishery; for example, really young fish may be too small to be captured by the fishing gear. Hence, the ratio of \( s(t) \) for two ages is the ratio of fishing mortalities for these ages.

2. \( f \) is the fully selected fishing mortality rate which is \( f(t) \) for the age(s) most vulnerable to the fishing gear.
(3) \(m(t)\) is the non-negative natural mortality rate function which is commonly assumed to be known and usually derived from life-history or other sources of information \([2,15,18]\).

Let \(S(t) = \int_0^t s(x) \, dx\) and \(M(t) = \int_0^t m(x) \, dx\). Note that since \(s(x)\) and \(m(x)\) are both non-negative functions of \(x\) then \(S(t)\) and \(M(t)\) are both positive and monotone increasing in \(t\). Equation (1) can be re-written as

\[
n(t) = n(0) \exp\{-fS(t) - M(t)\}.
\]

We assume that \(\lim_{t \to \infty} m(t) = m > 0\) so that

\[
\lim_{t \to \infty} M(t) = \infty
\]

and \(\lim_{t \to \infty} n(t) = 0\); that is, eventually all individuals in a cohort die. However, the total fishing mortality, \(fS(t)\), may be finite and \(S_\infty \equiv \lim_{t \to \infty} S(t) \leq \infty\). This could happen in a fishery that does not select older and larger fish (i.e. \(\lim_{t \to \infty} s(t) = 0\); for example, many gillnet fisheries may have this property. Let \(\Lambda(t,f)\) denote the survival function of \(t\) and \(f\),

\[
\Lambda(t,f) = \exp\{-fS(t) - M(t)\}.
\]

Property (2) implies that \(\lim_{t \to \infty} \Lambda(t,f) = 0\) for all \(f \geq 0\).

Fishery selectivity will usually be a function of fish size (e.g. length) rather than age. However, size or weight usually increases monotonically with age so that selectivity can still be modelled in terms of age. If \(\tilde{s}(l)\) is the selectivity function of length and \(l(t)\) is the length function of age then \(s(t) = \tilde{s}(l(t))\). A practical difference is when growth rates change over a number of years, which means that \(s(t)\) will change even if \(\tilde{s}(l)\) does not.

### 2.2. YPR RPs

The equilibrium fishery biomass yield is the number caught at age \(t\) times individual weight, and integrated for all \(t\). The catch at age \(t\) is fishing mortality times population size, \(f(t)n(t) = fs(t)n(t)\). Let \(w(t)\) be the non-negative individual fish weight at age \(t\) with asymptotic size \(W_\infty \equiv \lim_{t \to \infty} w(t) < \infty\). Fishery yield is a function of \(f\),

\[
Y(f) = f \int_0^\infty s(t)n(t)w(t) \, dt = n(0)f \int_0^\infty s(t)w(t)\Lambda(t,f) \, dt.
\]

We define the growth rate relative to body weight as

\[
g(t) = \frac{w'(t)}{w(t)},
\]

We assume that \(g(t)\) decreases monotonically with \(t\), as is typical of most body growth models.
The yield-per-recruit, YPR, as a function of $f$ is defined as $YPR(f) = Y(f)/n(0)$. Let $b_e(t,f)$ be the exploitable biomass per-recruit at age $t$ which is also a function of $f$,

$$b_e(t,f) = s(t)w(t)\Lambda(t,f).$$

(4)

YPR is

$$YPR(f) = f \int_0^\infty b_e(t,f) \, dt,$$

(5)

and is usually a quasi-concave function (see examples). It is not difficult to show using integration by parts that

$$\int_0^\infty b_e(t,f) \, dt = \int_0^\infty w(t)\{fs(t) + m(t) - g(t)\}\Lambda(t,f)S(t) \, dt.$$

(6)

This is a useful relationship when interpreting some YPR RPs and sensitivity equations.

YPR F RPs are based on efficiency considerations. An obvious choice is $F_{\text{max}}$, the value of $f$ that maximizes $YPR(f)$. $F_{\text{max}}$ is the solution to $U_Y(F_{\text{max}}) = 0$, where

$$U_Y(f) = \frac{\partial YPR(f)}{\partial f} = \int_0^\infty b_e(t,f)\{1 - fS(t)\} \, dt.$$

(7)

Using Equation (6), if $F_{\text{max}}$ exists then it must satisfy

$$\int_0^\infty (g(t) - m(t))w(t)\Lambda(t,F_{\text{max}})S(t) \, dt = 0.$$

(8)

Note that $w(t)\Lambda(t,F_{\text{max}})S(t)$ is non-negative and greater than zero for some range of $t$ when $F_{\text{max}}$ is finite. Hence, Equation (8) implies that if $g(t) < m(t)$ for all $t$ then $F_{\text{max}}$ will not exist (i.e. be infinite). In this situation, the loss in population biomass due to natural mortality as fish get older exceeds any gain in biomass due to body growth, and the yield from a cohort is therefore maximized by capturing all of the fish when they first recruit to the fishery; that is, $F_{\text{max}} = \infty$. However, this will be disastrous for future fisheries and this illustrates a problem with YPR-based F RPs which we consider further below. Conversely, if $g(t) > m(t)$ for all $t$ then yield is strictly increasing as $f \to 0$ but yield is zero at $f=0$; however, this latter scenario will usually not be plausible because for most body growth functions $\lim_{t \to \infty} g(t) = 0$ but we assume that $\lim_{t \to \infty} m(t) = m > 0$. We restrict our analyses to the situation where a unique interior $F_{\text{max}} \in (0, \infty)$ exists.

The $F_{\text{max}}$ RP does not consider conservation or sustainability considerations. It is based only on maximizing the yield a cohort can produce, and fishing at this level may not produce good long-term yields. Experience with $F_{\text{max}}$ suggests that it leads to harvest rates that are too high [23]. This motivated researchers to propose lower alternatives but still based on the YPR framework with its modest data requirements. In many cases, $YPR(f)$ is fairly flat near $f = F_{\text{max}}$ and a lower value of $f$ can still produce good yields. It was often observed that the increase in yield diminished rapidly as $f$’s increased and approached $F_{\text{max}}$ compared to the increase in yield near the origin. A commonly used but more precautionary RP based on these observations is the value of $f$ such that the slope of $YPR(f)$ is 10%
of the slope at the origin. This is denoted as \( F_{0.1} \) and

\[
\frac{\partial YPR(f)}{\partial f} \bigg|_{f=F_{0.1}} = 0.1 \frac{\partial YPR(f)}{\partial f} \bigg|_{f=0}.
\]

\( F_{0.1} \) is the \( f \) solution to

\[
UY(f) - 0.1 UY(0) = 0. \tag{9}
\]

We illustrate these two YPR RPs using a simple example that is designed to resemble a Northwest Atlantic cod population. We assumed \( m(t) = 0.2 \) for all \( t \) so that the cumulative natural mortality rate was \( M(t) = 0.2t \). We modelled selectivity using the standard normal cumulative probability density function \( \Phi(x) \) centred at age four (Figure 2). In this case, \( S(t) = \int_0^t s(x) \, dx = (t - 4)\Phi(t - 4) + \phi(t - 4) + 4\Phi(-4) - \phi(-4) \), where \( \phi(x) = \Phi'(x) \). \( S(t) \) is approximately \( t-4 \) when \( t > 4 \). We used the Von Bertalanffy (VonB) growth model described in Appendix 2, with \( W_\infty = 25 \) kg, \( k = 0.3 \), and \( \theta \) chosen so that \( w(0)/W_\infty = 0.002 \). There is a large difference between \( F_{\text{max}} \) and \( F_{0.1} \) but a wide range of \( f' \)'s give similar yields (Figure 3) and improvements in yield for \( f > F_{0.1} \) are small.

Figure 2. Selectivity function \( s(t) \) of age \( t \) for the illustrative example.

Figure 3. Illustration of a YPR curve and two fishing mortality RPs, \( F_{\text{max}} \) and \( F_{0.1} \).
2.3. SPR RPs

The YPR RPs do not account for impacts on the adult fish population. The size of the adult population is usually measured in total weight rather than numbers because this may be more related to egg production [23]. In fishery science, this is commonly referred to as the spawning population, or spawning stock biomass (SSB). It is technically possible that fishing at \( f = F_{\text{max}} \) can reduce the SSB and subsequent egg production and recruitment to a very low level in the long term. To avoid this, RPs have been proposed with the objective of preserving some amount of SSB [23].

Denote the population proportion mature at age \( t \) as \( p(t) \), and \( \text{SSB} = \int_0^\infty p(t)n(t)w(t)\,dt \). Let \( b_m(t,f) \) be the mature biomass per-recruit at age \( t \) which is also a function of \( f \),

\[
b_m(t,f) = p(t)w(t)\Lambda(t,f). \tag{10}
\]

The biomass of spawners per-recruit (SPR) is

\[
\text{SPR}(f) = \int_0^\infty b_m(t,f)\,dt.
\]

This is a monotonic decreasing function of \( f \). Commonly used SPR \( F \) RPs have the objective of preserving a fraction of SSB compare to unished SSB when \( f = 0 \); that is,

\[
\frac{\text{SPR}(F_x\%)}{\text{SPR}(0)} = \frac{\text{SSB}(F_x\%)}{\text{SSB}(0)} = x\%.
\]

This fraction is sometimes referred to as the spawner potential ratio. In practise, \( F \)'s are usually chosen so that the spawner potential ratio is in the 20–40 \% range. Clark [8] showed that \( F_{35\%} \) was usually close to \( F_{\text{MSY}} \) for a variety of productivity parameters (i.e. growth, maturation and mortality), but Clark [9] suggested that \( F_{40\%} \) was more appropriate when there is random variation in reproduction and subsequent recruitment to the fishery. \( F_{x\%} \)

![Figure 4. Illustration of a spawner potential ratio curve, SPR(f)/SPR(0), and three fishing mortality RPs, F20%, F35% and F40%.](image-url)
is the solution to

\[ U_S(F_x\%) = \int_0^\infty b_m(t, F_x\%) - x b_m(t, 0) \, dt = 0. \]  \hspace{1cm} (11)

We illustrate these RPs in Figure 4 for \( x = 0.20, 0.35 \) and 0.40. We used the same values for \( m(t) \), \( w(t) \) and \( s(t) \) as in Figure 3 and we used a simple logistic function for \( p(t) \) so that the age at which 50% of the population is mature was 4 and the age at 95% maturity was 5.5 (Appendix 3).

3. Local perturbation analysis

We are interested in the sensitivity of a per-recruit RP, such as \( F_{\text{max}} \) or \( F_{x\%} \), which we denote generally as \( F_{\text{RP}} \). More specifically, we are interested in how a perturbation \( \omega \) of some model input such as \( w(t) \) or \( s(t) \) affects the resulting value of \( F_{\text{RP}} \). Assume that \( \omega = 0 \) is the null perturbation. We could apply many different values of \( \omega \) and re-compute \( F_{\text{RP}}(\omega) \) to examine the relationship between \( F_{\text{RP}}(\omega) \) and \( \omega \). This represents the curve of \( F_{\text{RP}}(\omega) \) versus \( \omega \), which we refer to as the influence curve of \( \omega \) on \( F_{\text{RP}}(\omega) \). Local influence diagnostics are based on \( \frac{\partial F_{\text{RP}}(\omega)}{\partial \omega} \bigg|_{\omega=0} \), which is the slope at the origin of the influence curve. The value of the curve at the origin is the unperturbed RP, \( F_{\text{RP}} = F_{\text{RP}}(\omega)|_{\omega=0} \). This is the root of some characteristic function \( U(f) \), either Equation (7) or similar equations defined using Equation (9) or Equation (11).

If \( U_\omega(f) \) is the perturbed characteristic function then \( F_{\text{RP}}(\omega) \) is the solution to \( U_\omega(F_{\text{RP}}(\omega)) = 0 \). Using the derivative chain rule,

\[
\frac{\partial U_\omega(F_{\text{RP}}(\omega))}{\partial \omega} \bigg|_{\omega=0} = \frac{\partial U_\omega(f)}{\partial \omega} \bigg|_{\omega=0, f=F_{\text{RP}}} + \frac{\partial F_{\text{RP}}(\omega)}{\partial \omega} \bigg|_{\omega=0} \frac{\partial U(f)}{\partial f} \bigg|_{f=F_{\text{RP}}}. 
\]

This can be used to show that

\[
\frac{\partial F_{\text{RP}}(\omega)}{\partial \omega} \bigg|_{\omega=0} = - \left\{ \frac{\partial U(f)}{\partial f} \bigg|_{f=F_{\text{RP}}} \right\}^{-1} \frac{\partial U_\omega(f)}{\partial \omega} \bigg|_{\omega=0, f=F_{\text{RP}}}. 
\]

Equation (12) is the basic diagnostic equation that we use to understand the influence of specific perturbations.

For the YPR RPs, either \( F_{\text{RP}} = F_{\text{max}} \) or \( F_{\text{RP}} = F_{0.1} \), the denominator in Equation (12) is

\[
- \left. \frac{\partial U(f)}{\partial f} \right|_{f=F_{\text{RP}}} = - \left. \frac{\partial^2 \text{YPR}(f)}{\partial f^2} \right|_{f=F_{\text{RP}}} = \int_0^\infty b_c(t, F_{\text{RP}}) S(t) \{ 2 - F_{\text{RP}} S(t) \} \, dt.
\]

We have assumed that \( \text{YPR}(f) \) is concave at \( f = F_{\text{max}} \) and if this is also true at \( f = F_{0.1} \) then the denominator term in Equation (12) is positive for both of these choices of \( F_{\text{RP}} \). If there is not much curvature in \( \text{YPR}(f) \) at \( f = F_{\text{RP}} \) then we expect that \( F_{\text{RP}} \) will be more sensitive. For example, in Figure 3, we expect that \( F_{\text{max}} \) will be more affected by perturbations than \( F_{0.1} \) but the specifics will depend on the perturbation scheme.
The denominator in Equation (12) for the $F_{x\%}$ SPR RPs is

$$- \frac{\partial U(f)}{\partial f} \bigg|_{f=F_{x\%}} = - \frac{\partial \text{SPR}(f)}{\partial f} \bigg|_{f=F_{x\%}} = \int_0^\infty b_m(F_{x\%}, t) S(t) \, dt$$

and is positive. We expect that $F_{x\%}$ will be less sensitive to perturbations when the slope in $\text{SPR}(f)$ at $f = F_{x\%}$ is steep. This usually happens for larger values of $x\%$ (e.g. 40% in Figure 4).

In the following sections, we investigate the sensitivity of F RPs to some specific perturbation schemes to productivity parameters.

### 3.1. Growth model perturbations

The first growth function perturbation we consider is $w_\omega(t) = w_\infty(t)(1 + \omega)$ for which $\frac{\partial w_\omega(t)}{\partial \omega} = w(t)$. The impact of this perturbation is simple. If $U(f)$ is either Equation (7), or defined using Equation (9) or Equation (11), then

$$\frac{\partial U_\omega(f)}{\partial \omega} \bigg|_{\omega=0, f=F_{\text{RP}}} = U(F_{\text{RP}}) = 0 \quad \text{and} \quad \frac{\partial F_{\text{RP}}(\omega)}{\partial \omega} \bigg|_{\omega=0} = 0.$$

That is, YPR and SPR RPs are not affected by a scalar multiplicative change in the growth function. This may be an intuitive result to some, in hindsight.

A more interesting perturbation is to the growth rate parameter, $k_\omega = k(1 + \omega)$ (see Appendix 2). Another way of expressing this is $w_\omega(t) = w(t(1 + \omega))$ and

$$\frac{\partial w_\omega(t)}{\partial \omega} \bigg|_{\omega=0} = tg(t)w(t).$$

To simplify notation let

$$\dot{b}_c(t, F_{\text{RP}}) = \begin{cases} b_c(t, F_{\text{RP}})[1 - F_{\text{RP}}S(t)], & F_{\text{RP}} \equiv F_{\text{max}}, \\ b_c(t, F_{\text{RP}})[1 - F_{\text{RP}}S(t) - 0.1 \exp[F_{\text{RP}}S(t)]], & F_{\text{RP}} \equiv F_{0.1}. \end{cases} \quad (13)$$

Note that $\lim_{t \to \infty} \dot{b}_c(t, F_{\text{RP}}) = 0$ using Equations (2) and (4) when $F_{\text{RP}}$ is finite. The numerator term in Equation (12) is derived using Equation (7). It is

$$\frac{\partial U_\omega(f)}{\partial \omega} \bigg|_{\omega=0, f=F_{\text{RP}}} = \int_0^\infty tg(t) \dot{b}_c(t, F_{\text{RP}}) \, dt \quad \text{for} \quad F_{\text{RP}} \equiv F_{\text{max}} \quad \text{or} \quad F_{0.1}. \quad (14)$$

Using Equation (A1) in the appendix and since $\dot{b}_c(t, F_{\text{max}})$ approaches 0 when $t$ gets larger, if $g(t)$ declines slow enough such that $tg(t)$ is monotonic increasing when $t$ is not large then Equation (14) is negative and $F_{\text{max}}$ will decrease as $k$ increases. A similar argument holds for $F_{0.1}$. However, if the growth rate is high then both these YPR RPs will increase as $k$ increases.
The SPR sensitivity equation is somewhat different. To simplify notation, let
\[ \dot{b}_m(t, F_{x\%}) = b_m(t, F_{x\%})[1 - x \exp(F_{x\%}S(t))], \] (15)
where \( x \) is a proportion. Using Equation (11),
\[ \frac{\partial U_\omega(f)}{\partial \omega} \bigg|_{\omega=0,f=F_{x\%}} = \int_0^\infty t g(t) \dot{b}_m(t, F_{x\%}) \, dt. \] (16)
However, the implications of Equation (16) are the same; that is, for low growth rates SPR \( F_{RP} \)s may decrease but they will increase for higher growth rates.

We illustrate these results using the example in Sections 2.2 and 2.3. We computed \( F_{RP} \)'s for a range of \( \omega \). As \( k \) increased (Figure 5) \( F_{max}, F_{0.1}, F_{20\%} \) and \( F_{40\%} \) all decreased for smaller values of \( k \) but then increased for larger values of \( k \). This behaviour was accurately indicated by the local slopes. Note that in this figure, we showed \( \partial F_{RP}(k)/\partial k \) which is \( k^{-1} \partial F_{RP}(\omega)/\partial \omega \big|_{\omega=0} \). Although the maximum YPR increased as \( k \) increased (Figure 6), the shape of the YPR curve changed such that \( F_{max} \) first decreased and then increased. The change in \( F_{max} \) (Figure 5) was substantial and this \( F \) RP was much higher than the others at very low values of \( k \) for the reason outlined after Equation (8). The results (not shown) were qualitatively similar based on the Gompertz growth model (see Appendix 2) parameterized to be similar to the VonB model. The common expectation in fisheries science is that a population with higher growth rates can sustain higher fishing mortality rates, indicating higher \( F \) RPs. Our results indicate that YPR and SPR \( F \) RPs will not always behave like this.

**Figure 5.** Solid black curves are values of \( F \) RPs for perturbed values of the Von Bertalanffy growth parameter \( k \). Solid grey curves are the local slopes. Reference lines (grey dashed) indicate a local slope of zero and the corresponding value for \( k \).
When fishery selectivity if a function of length rather than age, as outlined in Section 2.1, then the growth rate parameter perturbations affect the selectivity function as well as the weight function. Both of these functions share the same $k$ parameter (see Appendix 2). In this case, the local influence diagnostics are more complicated so we simply illustrated the different impacts of $k$ perturbations on $F_{RP}$’s with an example similar to the ones above. We modelled fish length using the VonB model with asymptotic length $L_{\infty} = 120$ and $l(0) = 0.002 \times L_{\infty}$. The selection function of length was the standard normal cumulative probability density function, centred at the length of an age three fish when $k = 0.2$; hence, $l(3) = 54.27$ cm and $s(3) = \tilde{s}(l(3)) = 0.5$. We scaled the function so that $s(7) = 0.99$; that is, when $k = 0.2$ and $l(7) = 90.47$ cm then $99\%$ of fish were selected. The selectivity function of age $t$ was

$$s(t) = \Phi \left\{ \Phi^{-1}(0.99) \frac{l(t) - 54.27}{90.47 - 54.27} \right\}.$$  

(17)

However, the centering and scaling constants were fixed because we considered these to be attributes of the fishing gear rather than the fish, and we did not apply growth rate perturbations to these. Figure 7 shows how $s(t)$ is more ‘flat-topped’ as $k$ increases, and that for very small values of $k$ only a small fraction of fish younger than age 20 are caught by the fishery. The $s(t)$ function at small $k$ is not realistic and a fishery with such selection would not be practically economical, but we use it for illustration purposes.

We first computed $F_{RP}$’s for a range of $\omega$ perturbations to $k$ when Equation (17) was fixed using $k = 0.2$ to compute $l(t)$, and was not affected by the perturbations. Basically, this meant that we used a slightly different age-based selectivity function than in Figure 2 and the results (solid black lines in Figure 8) were similar to those in Figure 5. However, when selectivity also changed with perturbations to $k$ then the $F_{RP}$’s were substantially different. The RP’s decreased when $k$ increased from small values, but changed little for perturbations to larger values of $k$. The large values of the $F$ RPs at small values of $k$ may
Figure 7. Selectivity function $s(t)$ of age $t$ that is a composite function of a selectivity function $\tilde{s}(l)$ of length $l$ and a length function $l(t)$ of age with growth rate parameter $k$. $s(t) = \tilde{s}(l(t))$.

Figure 8. Solid black curves are values of $F$ RPs for perturbed values of the Von Bertalanffy growth parameter $k$ but a fixed $k = 0.2$ in the length-based selectivity function. Dashed black curves are values of $F$ RPs with perturbed $k$’s in the selectivity function. Grey curves are $F$ RPs scaled by the average selectivity at ages 0–20.

be misleading because of the very low fishery selectivity $s(t)$ for most of the age classes in the population. The average $F$ experienced at ages 0–20 ($F_{RP} \times \tilde{s}$) is shown as grey lines in Figure 8 and is much lower than the RP.

Changes in growth rates may also affect natural mortality rates and maturation rates, and the impacts on $F_{RP}$’s may be even more complicated than in this example. This is considered further in the Discussion section.
3.2. Natural mortality rate perturbations

Values for \( m(t) \) are difficult to estimate in practise [2], and sensitivity to this productivity parameter is often a consideration in per-recruit analyses. Common choices for \( m(t) \) are either a constant value (i.e. \( m(t) = 0.2 \) for all \( t \)) or a decreasing function of \( t \), based on the rationale that there are fewer predators for older and larger fish. We first consider \( m(t) = m \times d(t) \), where \( d(t) \) is some fixed and monotone decreasing function of \( t \). We consider the \( m \)-scale perturbation \( m_\omega(t) = m(1 + \omega)d(t) \) for which \( \partial m_\omega(t)/\partial \omega|_{\omega=0} = m(t) \) and \( \partial M_\omega(t)/\partial \omega|_{\omega=0} = M(t) \). The numerator term in Equation (12) for the YPR RPs is

\[
\left. \frac{\partial U_\omega(f)}{\partial \omega} \right|_{\omega=0,f=F_{RP}} = - \int_0^\infty M(t) \dot{b}_c(t,F_{RP}) \, dt \quad \text{for } F_{RP} \equiv F_{\max} \text{ or } F_{0.1},
\]

and for the SPR RPs it is

\[
\left. \frac{\partial U_\omega(f)}{\partial \omega} \right|_{\omega=0,f=F_{x%}} = - \int_0^\infty M(t) \dot{b}_m(t,F_{x%}) \, dt
\]  (19)

Using Equation (25) and because \( M(t) \) is monotone increasing, Equations (18) and (19) are positive and the F RPs increase if \( m(t) \) increases by a scalar amount. Conversely, they decrease if \( m(t) \) decreases.

The second perturbation scheme we consider is a shift in \( m(t) \), \( m_\omega(t) = m(t + \omega) \), so that \( m_\omega(t) \leq m(t) \) for all \( t \) when \( \omega > 0 \). For this scheme, \( \lim_{t \to \infty} m(t + \omega) = \lim_{t \to \infty} m(t) = m \) whereas for the previous \( m \)-scale perturbation the asymptotic \( m \) increased to \( m(1 + \omega) \). For the \( m \)-shift perturbation, \( \partial m_\omega(t)/\partial \omega|_{\omega=0} = m'(t) \), \( M_\omega(t) = \int_0^t m(x + \omega) \, dx = M(t + \omega) - M(\omega) \) and \( \partial M_\omega(t)/\partial \omega|_{\omega=0} = m(t) - m(0) \). The numerator term for the YPR RPs is

\[
\left. \frac{\partial U_\omega(f)}{\partial \omega} \right|_{\omega=0,f=F_{RP}} = \int_0^\infty \{m(0) - m(t)\} \dot{b}_c(t,F_{RP}) \, dt \quad \text{for } F_{RP} \equiv F_{\max} \text{ or } F_{0.1},
\]

and for the SPR RPs it is

\[
\left. \frac{\partial U_\omega(f)}{\partial \omega} \right|_{\omega=0,f=F_{x%}} = \int_0^\infty \{m(0) - m(t)\} \dot{b}_m(t,F_{x%}) \, dt.
\]  (21)

Since \( m(0) - m(t) \) is a monotone increasing function of \( t \), Equations (20) and (21) are negative and the F RPs decrease if \( m(t) \) is shifted lower. Obviously if \( m(t) \) is constant then this perturbation has no effect and Equations (20) and (21) are both zero because \( m(0) - m(t) = 0 \).

We conclude from both these perturbation schemes that increasing \( m(t) \) results in higher F RPs which is a result usually found in practise [16].

3.3. Selectivity perturbations

The perturbation scheme we consider is \( s_\omega(t) = s(t + \omega) \) which represents a shift in maximum selectivity to a younger age. For this case, \( \partial s_\omega(t)/\partial \omega|_{\omega=0} = \dot{s}(t) \), \( S_\omega(t) = \int_0^t s(x +
\[ \omega \; \text{d}x = S(t + \omega) - S(\omega) \] and \[ \partial S_\omega(t)/\partial \omega|_{\omega=0} = s(t) - s(0). \] For \( F_{\text{RP}} \equiv F_{\text{max}} \) or \( F_{0.1} \),

\[ \frac{\partial U_f(\omega)}{\partial \omega} \bigg|_{\omega=0, f=F_{\text{RP}}} = \int_0^\infty \{m(t) - g(t)\}[1 - s(0)/s(t)]\dot{b}_c(t, F_{\text{RP}}) \; \text{dt}. \] (22)

The numerator term in Equation (12) for the SPR RPs is

\[ \frac{\partial U_f(\omega)}{\partial \omega} \bigg|_{\omega=0, f=F_{x\%}} = -F_{x\%} \int_0^\infty b_m(t, F_{x\%})\{s(t) - s(0)\} \; \text{dt}. \] (23)

Equation (22) is complicated because the behaviour of \( \{1 - s(0)/s(t)\} \) may be complicated. The selectivity functions used in practise may be dome-shaped and a 5-parameter selectivity model is sometimes used for such patterns [20]. Therefore, it is difficult to make general predictions about the impacts of shifting maximum selectivity to a younger age. However, it will often be the case that \( s(0) \approx 0 \) and \( m(t) - g(t) \) is monotone increasing in which case Equation (22) is negative implying that the \( F \) YPR RPs will decrease. This will almost always be true for the SPR RPs because almost always \( s(0) \leq s(t) \) and Equation (23) is negative.

We illustrate this using an example with a selectivity function based on the density function of a gamma random variable minus one, scaled to have a maximum of one (Figure 9). We choose this form so that \( s(0) > 0 \) and to illustrate potential non-monotone behaviour of \( F \) RPs in this situation. The gamma scale parameter was 5 and the shape parameter was chosen so that \( s(10) = 1 \); that is, the shape parameter was \( 1+11/\text{scale} \). Parameters for \( m(t), w(t), \) and \( p(t) \) were the same as the example in Section 3.1. However, the gamma selectivity function produces a more peaked YPR curve and a more steep SPR curve (Figure 10) than the selectivity function in Figure 2. The \( F \) RPs all decreased with \( \omega \) (Figure 11). The dashed line in each panel of Figure 11 indicates the local slope, \( \dot{F}_0 = \partial F(\omega)/\partial \omega|_{\omega=0} \). The approximation \( F(\omega) \approx F + \dot{F}_0 \omega \) is reasonably accurate for \( \omega \in [-1,1] \) which indicates that the local slope provides a fairly good description of the influence curve in this example.

![Figure 9](image-url)  

**Figure 9.** Gamma selectivity functions, \( s(t) \) and \( s_\omega(t) = s(t + 1) \). Vertical lines indicate the age at maximum selection.
Figure 10. Yield and spawner per recruit curves and four fishing mortality RPs, $F_{\text{max}}$, $F_{0.1}$, $F_{20\%}$, and $F_{40\%}$ for $s(t)$ in Figure 9.

Figure 11. Solid black curves are values of $F$ RPs for perturbed values of the selectivity function, $s(\omega(t) = s(t + \omega)$ in Figure 9. Solid grey curves are the local slopes. Reference lines (grey dashed) indicate the local slope at $\omega = 0$.

The intuition of many fisheries scientists is that increasing selectivity towards younger ages will result in decreasing $F$ RPs because a cohort will experience more exploitation. The above example corroborates this. However, we can construct examples where this does not happen. For example, if we move the age at maximum selection down to 2 (Figure 12), then the $F$ RPs decrease (compare Figure 13 to Figure 10) but further decreases (i.e. $\omega > 0$) eventually result in small increases in the $F$ RPs (Figure 14). Hence, in the case that
Figure 12. Gamma selectivity functions, \( s(t) \) and \( s_\omega(t) = s(t + 1) \). Vertical lines indicate the age at maximum selection.

Figure 13. Yield and spawner per recruit curves and four fishing mortality RPs, \( F_{\text{max}}, F_{0.1}, F_{20\%}, \) and \( F_{40\%} \) for \( s(t) \) in Figure 12.

\( t_{\text{max}} = \min \{ t; s(t) = 1 \} \) is close to zero then the impact of changes to selectivity are more difficult to predict.

The YPR curve in Figure 13 is even more peaked than in Figure 10 or Figure 3 and the changes in the \( F_{\text{max}} \) RPs (Figure 14) are much smaller than in Figure 11 or Figure 5. This is what our analytical results indicated; that is, if the curvature of the YPR curve near \( F_{\text{max}} \) and \( F_{0.1} \) is large, or the slope of the SPR curve is steep, then the \( F \) RPs will be less sensitive to perturbations.

3.4. Maturity perturbations

The perturbation scheme we consider is \( p_\omega(t) = p(t + \omega) \) and only affects the SPR RPs because those based on YPR do not use \( p(t) \). Since \( \delta p_\omega(t)/\delta \omega|_{\omega=0} = p'(t) \), the numerator
Figure 14. Solid black curves are values of $F_{RPs}$ for perturbed values of the selectivity function, $s_{\omega}(t) = s(t + \omega)$ in Figure 11. Solid grey curves are the local slopes. Reference lines (grey dashed) indicate the local slope at $\omega = 0$.

The term in Equation (12) is

$$\left. \frac{\partial U_{\omega}(f)}{\partial \omega} \right|_{\omega=0,f=F_{x\%}} = \int_0^\infty \frac{p'(t)}{p(t)} \hat{b}_m(t,F_{x\%}) \, dt.$$  \hspace{1cm} (24)

If $p'(t)/p(t)$ is positive and decreasing in $t$ then Equation (24) is positive indicating that the SPR RPs will increase. This is the case for the logistic maturity function (Appendix 3) that is commonly used. For example, if $\omega = 1$ then $F_{20}$ in Figure 10 increases from 0.40 to 0.48 and $F_{40}$ increases from 0.19 to 0.21.

4. Discussion and conclusions

We showed how the local influence approach to perturbation analysis can be used to derive sensitivity equations that provide a more theoretical understanding of the influence of perturbations on important quantities (i.e. fishing mortality, $F$, RPs) derived from a general model for fish population dynamics. A more realistic continuous-time formulation of the population dynamics model was used to simplify influence diagnostic equations, but we expect quantitative perturbation results to be similar for discrete-time formulations. The latter approach is often used in practice because it is computationally more simple but in preliminary analyses we found that sensitivity equations were more difficult to interpret. Our results indicate that $F$ RPs will tend to be more sensitive to perturbations of productivity inputs when the YPR curve has less curvature near the RP or the SPR curve has less slope. Overall, our results suggest that per-recruit $F$ RPs will, with some exceptions, usually increase if

(1) growth rates increase;
(2) natural mortality rates increase;
(3) fishery selectivity increases to an older age and
(4) for SPR $F$'s, maturity decreases to a younger age.

Of course, changes in maturities have no effect on YPR $F$ Rs. A scalar change to $w(t)$ has no effect on the $F$ Rs we studied whereas a scalar change to $m(t)$ does. In contrast, shifting $w(t)$ has an effect whereas shifting $m(t)$ will have little effect unless $m(t)$ varies substantially with age.

These main conclusions are consistent with the fisheries literature. For example, Brooks [3] found that $F_{30\%}$ nearly doubled when $s(t)$ increased with age compared to when $s(t)$ was constant for all ages, which is what our sensitivity results indicate. Colvin et al. [10] found that $F_{30\%}$ increased when either the constant natural mortality rate increased or the minimum landing size increased. Similarly, Griffiths [16] plotted SPR curves to show that $F_{x\%}$ increased when the natural mortality rate or minimum size at first capture increased, and showed that $F_{\text{max}}$ increased when the natural mortality rate increased. However, we have shown that there can be exceptions to these conclusions. If growth rates are low then a small increase in this rate may result in a decrease in $F$ Rs. If fish are fully selected by the fishery at a young age then a further decrease in the age at maximum selection may lead to a slight increase in $F$ Rs, although the effect may not be large.

As outlined in [23], $F_{\text{msy}}$ depends in part on per-recruit RPs and some of our results will be relevant to $F_{\text{msy}}$ as well.

Values for RPs can have substantial economic impacts on fishing communities and industry. Fisheries managers and stakeholders often want to know how sensitive RP estimates are to the quality of inputs and underlying assumptions. Our results can assist with this. The local slopes for various perturbations of productivity processes can be compared to see which ones are more important (i.e. influential). However, this will depend on the scale of the perturbations. For example, the perturbations $m_\omega(t) = m(t + \omega)$ and $s_\omega(t) = s(t + \omega)$ for $\omega = 1$ may not be equally plausible. A possible solution is to use results of this paper to compute variances of estimates of $F$ Rs based on the variances of the input productivity processes and the delta method, similar to [21] for discrete models. MacCall [19] illustrated how this approach can be used to assess the importance of uncertainty in various productivity inputs. This is a useful area for future research.

Another issue is that the productivity processes will usually not be constant over time because of various ecosystem changes, both biotic and abiotic (e.g. [3,17,22]). The causes of the productivity changes are often poorly understood which impairs our ability to predict what will happen in the future. However, we may have an understanding of the direction of change and our results can be used to predict the basic consequences (i.e. increase or decrease) of such change on RPs.

Our population dynamics models are simple and the standard ones used in fish population analyses. However, more realistic models have been proposed in which natural mortality, body growth and maturation rates are linked [28], as well as fisheries selectivity. We demonstrated how the sensitivity of $F$ Rs to changes in individual growth rates differed when fishery selectivity was length selective rather than age selective. Changes in growth rates could affect other productivity processes. Some allocation of energy switches from growth to reproduction as fish mature. Calduch-Verdiell et al. [7] included this consideration and also maternal effects where egg production and larval survival is an increasing
function of the size of female fish. Parameters may be linked; for example, in the VonB model it is sometimes assumed \[23\] that \(W_\infty\) is inversely related to \(k\) and, in our analyses, perturbations to \(k\) would also affect \(W_\infty\). Such refinements of productivity processes can lead to different \(F\) RPs and possibly better harvest advice for sustainable fisheries. There may be density-dependent effects in growth and natural mortality rates \[17\] that will be important to consider as well. Including stochasticity in the population dynamics equations \[1,12\] is also a useful extension. Fishery yield is usually measured in weight but our results can easily be extended to other measures of yield such as economic value.

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Using Equation (7) and \( U_Y(F_{\text{max}}) = 0 \Rightarrow \int_0^\infty s(t)w(t)\Lambda(t,F_{\text{max}})[1 - F_{\text{max}}S(t)] \, dt = 0 \). Define \( t_1 \) such that \( S(t_1) = F_{\text{max}}^{-1} \). Note that since \( S(t) \) is monotone increasing

\[
\int_0^{t_1} s(t)w(t)\Lambda(t,F_{\text{max}})[1 - F_{\text{max}}S(t)] \, dt = \int_{t_1}^\infty s(t)w(t)\Lambda(t,F_{\text{max}})[F_{\text{max}}S(t) - 1] \, dt.
\]

Similar equations can be developed for other \( F \) RPs.

**Appendix 2**

The Von Bertalanffy (VonB) growth model for weight is

\[
w(t) = W_\infty[1 - \exp(-kt - \theta)]^b.
\]
It is based on the length-weight model \( w(t) = a[l(t)]^b \) and the VonB growth model for length, 
\[
\frac{\partial l(t)}{\partial t} = k[L_\infty - l(t)]
\]
in which change in length declines linearly as length increases. Hence, \( k \) is a growth rate parameter. The asymptotic (as \( t \to \infty \)) weight is \( W_\infty \) and \( \theta \) is the relative size when \( t = 0, \theta = - \log[1 - \{ w(0)/W_\infty \}^{1/b}] \approx \{ w(0)/W_\infty \}^{1/b} \). Usually \( b \) is very close to 3 [23]. The VonB growth rate (Equation (3)),
\[
g(t) = \frac{bk}{\exp(kt + \theta) - 1},
\]
decreases exponentially with age.

Another commonly used growth model for weight is the Gompertz,
\[
w(t) = W_\infty \exp[- \exp(-kt - \theta)]. \tag{A3}
\]
Again \( W_\infty \) is the maximum weight attainable and \( \theta = - \log[\log\{ w(0)/W_\infty \}] \geq 0 \). The growth rate is
\[
g(t) = \frac{k}{\exp(kt + \theta)},
\]
and is also a monotonic decreasing function of \( t \). The \( \theta \) parameters for these two models are related, \( \theta_{gp} = \log[-\log(\theta_{vb})] \).

**Appendix 3**

The logistic maturity function is
\[
p(t) = \frac{\exp(\beta_o + \beta_1 t)}{1 + \exp(\beta_o + \beta_1 t)}.
\]
The inverse is
\[
t = \beta_1^{-1} \left[ \log \left\{ \frac{p(t)}{1 - p(t)} \right\} - \beta_o \right].
\]
If \( t_{50} \) is the age at 50% maturity then \( p(t_{50}) = 0.5, t_{50} = -\beta_o / \beta_1 \) and \( \beta_o = -t_{50} \beta_1 \). \( t_{95} = \{ \log(0.95/0.05) - \beta_o \} / \beta_1 = \log(0.95/0.05) / \beta_1 + t_{50} \). Hence,
\[
\beta_1 = \frac{\log(0.95/0.05)}{t_{95} - t_{50}}, \quad \text{and} \quad \beta_o = \frac{t_{50}}{t_{50} - t_{95}} \log(0.95/0.05).