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Does the concept of spawning per recruit make sense?

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Abstract:

Density dependence means that exploited fish populations exhibit earlier maturity, a faster growth rate, increased fecundity and reduced egg size. Here, the consequences of these effects on population dynamics, the estimation of spawning biomass per recruit and associated biological reference points are examined by a simulation model. The model is a self-regenerating model in which the population parameters (age at maturity, growth, fecundity, egg size) vary according to three classes of population abundance. Early life stages are characterized by a size-dependent growth and mortality model. It is concluded that spawning per recruit is an ambiguous concept because, if density dependence occurs in the adult population, the spawning biomass of a cohort is not proportional to the number recruited. This leads to significant level of uncertainty in the estimates of spawning biomass per recruit and the associated biological reference points such as F_{low}, F_{med}, F_{high} and VSPR.

Keywords: biological reference points, density-dependence, life history, population dynamics, teleost fishes

Introduction

Biological Reference Points are increasingly used for fisheries management. They make a link between management objectives and the characteristics of the fishery (Caddy and Mahon, 1996). Therefore the underlying mathematical models must be as realistic as possible regarding those characteristics of the fishery that are considered important for the management objectives.

Several of the widely used Biological Reference Points (BRP) include recruitment considerations, either by means of a spawner-recruit model, or by considering the spawning biomass per recruit, or both. Such BRP's are designed to avoid recruitment overfishing, which may occur when a population has been exploited to the point where recruitment is substantially reduced (Sissenwine and Shepherd, 1987). For any fishing mortality rate F, a recruited cohort is expected to produce a spawning biomass proportional to the number recruited. The ratio of this biomass to recruitment, spawning per recruit (SPR), can be expressed as a percentage of the virgin SPR, and the associated F, designated $F_{x\%}$, can be used as a BRP (Mace and Sissenwine, 1993). Moreover, for any F there is a single straight line through the origin of the stock-recruitment plot. The slope of this line is the inverse of the spawning biomass per recruit which corresponds to the F level (Shepherd, 1982). The more heavily the stock is exploited, the lower the spawning biomass per recruit, hence the steeper the slope. This line is called a replacement line because it defines the survivorship needed to replace the spawning stock in the future (Sissenwine and Shepherd, 1987). Replacement lines are combined with a spawner-recruit function to define F_{msy}, a well-known BRP, and F_{crash}, the fishing mortality which results in stock collapse (Shepherd, 1982). On the other hand, if a spawner-recruit function is not known, replacement lines can also be combined with the observed series of stock-recruitment points to define widely used BRP's such as F_{rep}, F_{med}, F_{low} and F_{high} (Sissenwine and Shepherd, 1987; Anonymous, 1991), and F_{loss}, used as a lower bound estimate for F_{crash} (Cook, 1998). All these BRP's are widely used (Caddy and Mahon, 1996; Anonymous, 1997; Deriso *et al.*, 1998). Moreover, some of them are involved in the definition of limit reference points used in the precautionary approach (Anonymous, 1997; Anonymous, 1998a). SPR and replacement lines are important concepts in modern fisheries management.

A replacement line is dependent on a number of biological parameters such as growth, maturity and natural mortality, and estimates of these quantities are required to calculate SPR for a stock

(Shepherd, 1982; Cook, 1998). Whereas it was previously thought that density-dependent control of fish populations only occurs during the early years of life (Ricker, 1954; Beverton and Holt, 1957; Shepherd and Cushing, 1980), it is more and more recognised that adult stages may also be regulated by density-dependent mechanisms (e.g. Ware, 1985; Horwood *et al.*, 1986 ; Rijnsdorp, 1994; Trippel, 1995; Rochet, 1998). As population density decreases, growth rate increases, maturity is achieved earlier, fecundity at a given size is higher, and as a result of the younger age of mothers, egg size decreases. Therefore we may ask whether these mechanisms can have an impact on SPR calculations. For a given fishing mortality, can we assume that spawning per recruit will be equal for any recruitment? Or will compensation mechanisms make spawning per recruit decrease as recruitment increases? What is the impact of these compensation mechanisms on our estimates of biological reference points?

This kind of question deserves more than a qualitative answer. It is desirable to quantify this impact to assess the importance of compensation mechanisms among the various uncertainties that affect BRP estimates. For that purpose, the difficulty is to obtain reliable estimates of compensatory effects. Density-dependent effects are difficult to measure precisely because of the concomitant influence of environmental factors (Pitt, 1975; Hempel, 1978; Kotilainen and Aro, 1991; Rijnsdorp *et al.*, 1991; Jakobsen, 1992; Parmanne, 1992; Rijnsdorp and van Leeuwen, 1992). Despite this difficulty, simple compensation functions (such as linear or log-linear models) have been fitted to historic weight-at-age, maturity-at-age and stock biomass or abundance data for Atlantic mackerel (Overholtz *et al.*, 1991), spring-spawning herring (Patterson, 1997) and silver hake (Helser and Brodziak, 1998). These fitted functions were subsequently used in stock projections. All three studies concluded that the classical density-independent models yield over-optimistic and risky assessments compared to alternative density-dependent models. The question is, how general are these results? Moreover, the conclusions may have been affected by environmental changes and autocorrelated time-series data. Can we establish such results, free of this kind of errors?

This paper presents an alternative approach to incorporating density-dependence into SPR calculations by using estimates of fishing effects from a comparative approach (Rochet *et al.*, Submitted). A new method was developed to estimate fishing effect from environments contrasted on the basis of fishing pressure. The comparison of demographic parameters included 84 populations of

49 species subject to various degrees of fishing pressure. It was concluded that increasing fishing pressure significantly decreases age at maturity and average egg size, and increases fecundity at maturity, the slope of the fecundity-length relationship and relative size at maturity. These estimates are considered valid for many exploited species of Teleost, and free of environmental influence such as temperature or biotic interactions thanks to the comparative approach. Here it is assumed that these effects occurred by compensatory mechanisms. The estimates are used as parameters of density-dependent mechanisms and incorporated into a self-regenerating model. This model is used for spawning per recruit analyses and BRP computations for stocks with different life history strategies (cod, sole, sardine), in order to assess the impact of these mechanisms on SPR and BRP's.

Materials and methods

1) A self-regenerating population model

There are two components in the population model: an age-structured model for adults, and a size-based model for the early life stages (Fig. 1). For the adult stock, the population numbers $N_{a,t}$ at age a, in year t, are calculated from:

$$N_{a,t} = N_{a-1,t-1} e^{-M_{a-1}-F_{a-1}} \quad (1)$$

with F_a and M_a instantaneous fishing and mortality rates (assumed invariant with time). The egg-production of the population, $N_{e,t}$, is calculated from i) the proportion mature at age (maturity ogive) according to a normal or exponential distribution with mean A_m and standard deviation σ_{A_m} $V_{a,t} \sim N(A_m, \sigma_{A_m})$ ii) the fecundity-length relationship $E_a = EL_a^{\ b}$ (2) where E and b are constants, and iii) the vector of length-at-age $L_{a,t}$ calculated from the initial length $L_{1,t}$ using a vector of length increments ΔL: $L_{a,t} = L_{a-1,t-1} + \Delta L_{a-1}$. The number of eggs produced in year t is $N_{e,t} = \sum_a N_{a,t} V_{a,t} EL_{a,t}^b$ (3). The weight of these eggs is $W_{e,t}$.

To derive recruitment in year $t+1$ from $N_{e,t}$ and $W_{e,t}$, early life stages are described by a size-dependent model for several reasons. Firstly, egg size is known to influence egg and larval survival and growth abilities (Rijnsdorp and Jaworski, 1990; Miller *et al.*, 1992; Brooks *et al.*, 1997; Trippel, 1998). Secondly, there is growing concern that fishing affects egg size and quality by changing the age and size of mothers (Kjesbu *et al.*, 1996; Reznick *et al.*, 1996; Chambers, 1997; Solemdal, 1997; Trippel *et al.*, 1997; MacKenzie *et al.*, 1998; Marshall *et al.*, 1998; Trippel, 1998). Thirdly, body size is often used for scaling predation processes (Ware, 1978; Silvert and Platt, 1980) and all vital rates (Ware, 1975; Pepin, 1991; Houde, 1997); therefore body size might be of primary importance for understanding recruitment dynamics (Beyer, 1989). Here it is assumed that variations in egg weight will result in variations in recruitment. According to Ware (1975), if growth is allometric ($\frac{dW}{dt} = rW^{1-m}$), and if growth and mortality rates are proportional ($\frac{dN}{dt} = -qW^{-m}N$), then the number $N_{0,t}$ of eggs that survive the incubation period (duration I) and hatch is: $N_{0,t} = N_{e,t}e^{-IqW_{e,t}^{-m}}$ (4). The weight of these newly hatched larvae is $W_{0,t} = pW_{e,t}$, where p is a constant. They recruit to the population at weight $W_{1,t+1}$ and abundance $N_{1,t+1} = \frac{N_{0,t}W_{0,t}}{W_{1,t+1}^{q/r}}$ (5).

Recruitment variability is known to be partly due to environmental perturbations affecting early life history stages (Rothschild, 1986; Cushing, 1996; Chambers and Trippel, 1997). Here it is assumed that environmental fluctuations influence recruit number by determining recruit weight $W_{1,t}$ according to a normal distribution: $W_{1,t} \sim \mathrm{N}\left(\mu_{W_1}, \sigma_{W_1}\right)$ (6). As a consequence, recruitment $N_{1,t+1}$ is determined by the weight and number of larvae, which result from past year events, and by $W_{1,t+1}$ which is constrained by random environmental fluctuations.

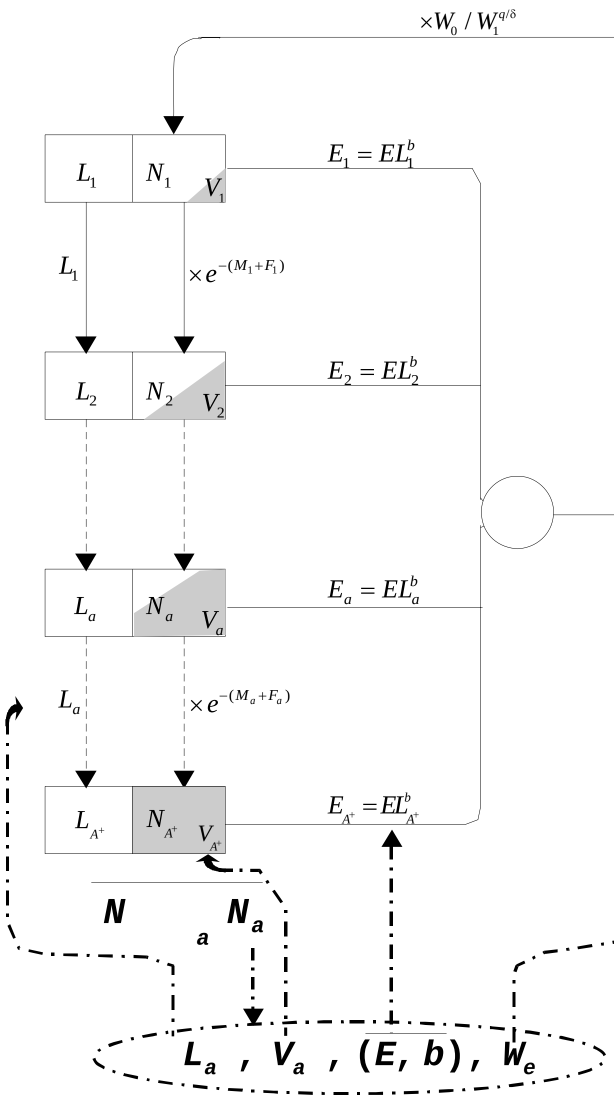

Figure 1. Flow diagram of the population model. Numbers at age N_a survive from N_{a-1} through fishing and natural mortality F_a and M_a. The proportion mature V_a of them reproduce with fecundity $E_a = EL_a^b$, where L_a is length at age a ($L_{a,t} = L_{a-1,t-1} + \Delta L_{a-1}$). The population produces N_e eggs (weight W_e) which hatch into N_0 larvae (weight W_0) which in turn develop into N_1 recruits (weight W_1 determined by environmental variation). Density-dependence is implemented by assuming that the total population size N determines the parameters $V, \Delta L, E, b$ and W_e.

2) Population parameters

All adult stage parameters are estimated from observed values. Three typical Teleost populations with different strategies were chosen to illustrate the effect of density-dependence on BRP's. Their length- and weight-at-age, natural and fishing mortality (eqn 1), mean recruit number and the mean and variance of recruit weight (eqn 6) were taken from reports of ICES Stock Assessment Working Groups. Fecundity-length relationships (eqn 2) and egg size were obtained from the literature. North Sea cod was chosen as a typical Gadoid with large size and fast and indeterminate growth, and a slow increase of fecundity with size (Data from Daan, 1974; Oosthuizen and Daan, 1974; Hislop and Bell, 1987; Anonymous, 1998b; Markovic *et al.*, 1998). Sardine in the Southern Area (VIIIc - IXa fishing areas) is a typical Clupeiforme with small size and more determinate growth (Data from Perez *et al.*, 1985; Perez *et al.*, 1992a; Perez *et al.*, 1992b; Anonymous, 1999b). Sole in the Bay of Biscay has an intermediate strategy, with a less fluctuating recruitment (Data from Arbault and Boutin, 1968; Anonymous, 1992; Anonymous, 1998c). Lengths were converted into weights and the reverse using length-weight relationships $W_{a,t} = \alpha L_{a,t}^{\beta}$ found in Dorel (1986). All parameters definitions and values are summarised in the Appendix.

Reasonable guesses of early life parameters (eqns 4 and 5) are provided by Ware (1975) and Beyer (1989). Field values were gathered by Lorenzen (1996) and measured by Pepin (1991; 1993). Although the latter author does not assume *a priori* that growth and mortality have the same allometric coefficients, his estimates do not differ significantly, and hence can be used for the present simpler model. These parameters were not measured for the stocks considered, but body size may be a more important factor for larval characteristics than species-specific differences (Miller *et al.*, 1992). Therefore various combinations of published early life parameters were used for any stock.

3) Modelling density-dependence

Compensatory effects were estimated by the fishing effects obtained from a previous comparative study (Rochet *et al.*, Submitted, Table 1). In this study, the populations compared were contrasted on the basis of three types of environments with low (1), moderate (2) and high (3) fishing pressure. To incorporate these estimates, density-dependence is described here in a discrete way: the population parameters change with the total abundance of the stock $N_t = \sum_a N_{a,t}$. Thresholds $\tilde{N}_1$ and $\tilde{N}_2$

determine to which abundance level $g_t \in [1,2,3]$ year t belongs : $N_t \le \tilde{N}_1 \Rightarrow g_t = 3$; $\tilde{N}_1 < N_t \le \tilde{N}_2 \Rightarrow g_t = 2$; $N_t \ge \tilde{N}_2 \Rightarrow g_t = 1$. g_t determines the parameters $A_m, \sigma_{A_m}, \Delta L, E, b$ and W_e of eqns 1 to 3.

Density-dependent effects were applied in two ways: g_t determines the population parameters either for the whole population in year *t* (year-effect), or for the cohort born in year *t* (cohort-effect; in this case the model keeps track of the reproduction parameters during the whole life of the cohort). On the one hand, given a limited amount of resources, present abundance may affect the share of these resources available for each individual. There is field and experimental evidence that this in turn may affect their condition, fecundity and egg size (Hay and Brett, 1988; Kjesbu *et al.*, 1991; Reznick, 1993; Marshall *et al.*, 1998). This will result in year-effects of abundance on reproduction. On the other hand, the conditions encountered by a recruit during its early life may influence its characteristics during its subsequent life, *e.g.* its size at age (Rijnsdorp, 1993; Chambers and Leggett, 1996), maturation (Rijnsdorp, 1993; Hutchings, 1997) and mortality (Chambers, 1997). This is known as cohort effect.

Table 1. Relative effect of fishing: coefficients of change in demographic traits under increasing fishing pressure. Relative effect of moderate fishing δ_2: from low (F/M < 1) to moderate (1 ≤ F/M < 2) fishing pressure; δ_3: from low to high (F/M ≥ 2) fishing pressure. For *b*, the relative effect of fishing is additive.

A_m : median age at maturity; L_{rm}: median length at maturity, relative to adult length; E_m: fecundity at the median age at maturity; *Egg*: mean egg volume; *b*: slope of the log-log fecundity-length relationship.

	Relative effect of moderate fishing δ_2	**Relative effect of high fishing** δ_3
A_m	0.94	0.77
L_{rm}	1.05	1.09
E_m	0.25	0.26
Egg	0.73	0.63
b	0.14	0.49

The estimates from the comparative study are used here as follows: the three stocks simulated are presently under high fishing pressure. Their current age at maturity, fecundity-length parameters and length-at-age were used for low abundance levels ($g = 3$). The corresponding traits for higher abundance levels were derived by applying the coefficients in Table 1 as follows: $X_g = \delta_g X_1, \quad g = 2{,}3, \quad X \in \{A_m, E_m, Egg, L_{rm}\}$ and $b_g = b_1 + \delta_g, \quad g = 2{,}3$ where *E_m* is fecundity at median age at maturity, *Egg* is egg volume (converted to egg weight W_e, assuming they have the density of sea water) and *L_{rm}* is length at maturity relative to adult length. The values for the parameter *E* of the fecundity-length relationship (eqn 2) were obtained by $E_g = E_{m,g} \big/ L_{Am,g}^{b_g}, \quad g = 1{,}2{,}3$. Because it is difficult to find growth indices comparable between different species, no direct estimate of density-dependent effects on growth was available from the comparative study. However, growth is known to be highly density-dependent in many fish species (e.g. Beverton and Holt, 1957; Iles, 1971; Burd, 1984; Ross and Almeida, 1986; Overholtz, 1989; Kawasaki and Omori, 1995; Millner and Whiting, 1996; Rijnsdorp and van Leeuwen, 1996; Helser and Almeida, 1997; Tanasichuk, 1997; Shin and Rochet, 1998). Therefore the effects of fishing on the parameters of the von Bertalanffy growth model were tuned to mimic the effects of fishing on relative length at maturity L_{rm}. As these estimates of a compensatory response in growth are indirect, simulations were performed both including them and ignoring them (*i.e.*, keeping growth fixed at its currently observed value across all abundance levels).

Some compensatory responses differ among life history strategies (Rochet *et al.*, Submitted): whereas the effects on age at maturity, egg size and slope of the fecundity-length relationship are consistent among the taxonomic orders analysed, the response in fecundity at maturity differs among orders. Most fish taxa respond to fishing by increasing their fecundity at maturity, but in Clupeiformes fecundity at maturity is decreased by increasing fishing pressure. Therefore I used the mean estimate of fishing effect on E_m for cod and sole, and no fishing effect on E_m for sardine.

To estimate the thresholds $\tilde{N}_1$ and $\tilde{N}_2$ where the population parameters change, an equilibrium analysis was performed by using the classical dynamic pool equations (Thompson and Bell, 1934; Beverton and Holt, 1957) modified to estimate spawning biomass per recruit for each fishing mortality factor under a given exploitation pattern (Sissenwine and Shepherd, 1987; Gabriel *et al.*, 1989). This analysis was performed with the maturity ogive changing with fishing intensity, *i.e.* as the ratio F/M decreases through the threshold values 1 and 2 (which was the criterion used in the comparative analysis to separate the groups of fishing pressure). $\tilde{N}_1$ and $\tilde{N}_2$ are the equilibrium population sizes at these thresholds.

4) Simulating the model and performing sensitivity analysis

Using the above equations, populations were simulated for 100 years. The 20 first simulated years were discarded to devoid results from the influence of initial conditions. Combinations of early-life parameters from within the range of published estimates (appendix B) were tuned to ensure that recruitment and spawning stock biomass during simulations under current fishing mortality remain within the observed window. In addition to these stock-recruitment plots, SSB of cohorts were plotted as a function of numbers recruited, to check the assumption that these two quantities are proportional. Fishing mortality factors were varied from 0 to 2 for cod and sole, and to 3 for sardine, by steps of 0.1, to compute current spawning per recruit CSPR and the following reference points: F_{low}, F_{med}, F_{high}, $F_{30\%}$ (cod and sole) or $F_{35\%}$ (sardine), and virgin spawning per recruit VSPR.

Sensitivity analysis of the population dynamics to early life stages parameters was performed by varying each of these parameters until the first value for which population grows exponentially (mean index of abundance level g_t during a 100-year simulation, $\bar{g} = 1$) or declines to extinction ($\bar{g} = 3$), all other parameters being fixed. Sensitivity of biological reference points to early life stages parameters was analysed by computing BRP's for various sets of these parameters.

Sensitivity of the BRP's to the various hypotheses of the model was also performed with various sets of early life parameters, always keeping simulated recruitment and SSB within the observed window: year effects versus cohort effects, fixed growth versus density-dependent growth, fixed size at recruitment versus size at recruitment varying under environmental influence.

Results

1) Population dynamics

In the absence of environmental variability, changes in population parameters by density-dependent effects generate cycles in population numbers (Fig. 2A). To obtain more realistic stock-recruitment plots and account for the interaction between recruitment variability and density dependence, subsequent simulations included environmental variations. Randomly varying size at recruitment W_1 within its observed range lets simulated recruitment and SSB vary within the observed window (Fig. 3), especially if density-dependent growth is taken into account. However, the spread of simulated recruitments does not span the range of observed recruitments at any SSB, suggesting that the model may underestimate environmental variability (Fig. 3).

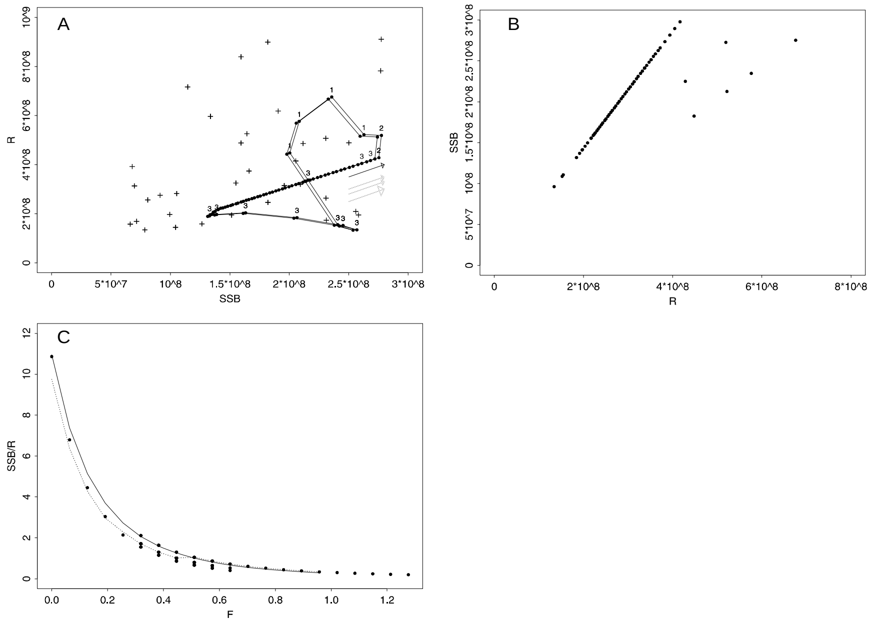

Figure 2. Simulations of the North sea cod population dynamics with a self regenerating model, with density-dependent reproduction, fixed growth, cohort effect and no environmental variability. $I = 20, m = 0.25, r = 0.07, q = 0.055, p = 0.38$.

A) Stock-recruitment plot ($N_{1,t+1}$ versus $SSB_t = \sum_{a=1}^{A^+} N_{a,t} V_{a,t} W_{a,t}$) for a simulation under current fishing pressure (F=0.638). VPA-estimates (+) and simulated points (•). Numbers refer to the abundance level of the corresponding year, arrow shows the direction of the population cycles.

B) Plot of cohort spawning stock biomass ($\sum_{i=1}^{A^+} N_{i,t+i-1} V_{i,t+i-1} W_{i,t+i-1}$) versus number recruited ($N_{1,t}$).

C) Spawning per recruit plots: classical equilibrium analysis (solid line), equilibrium analysis with maturity ogive changing with fishing mortality (dashed line), simulated self-regenerating model (dots).

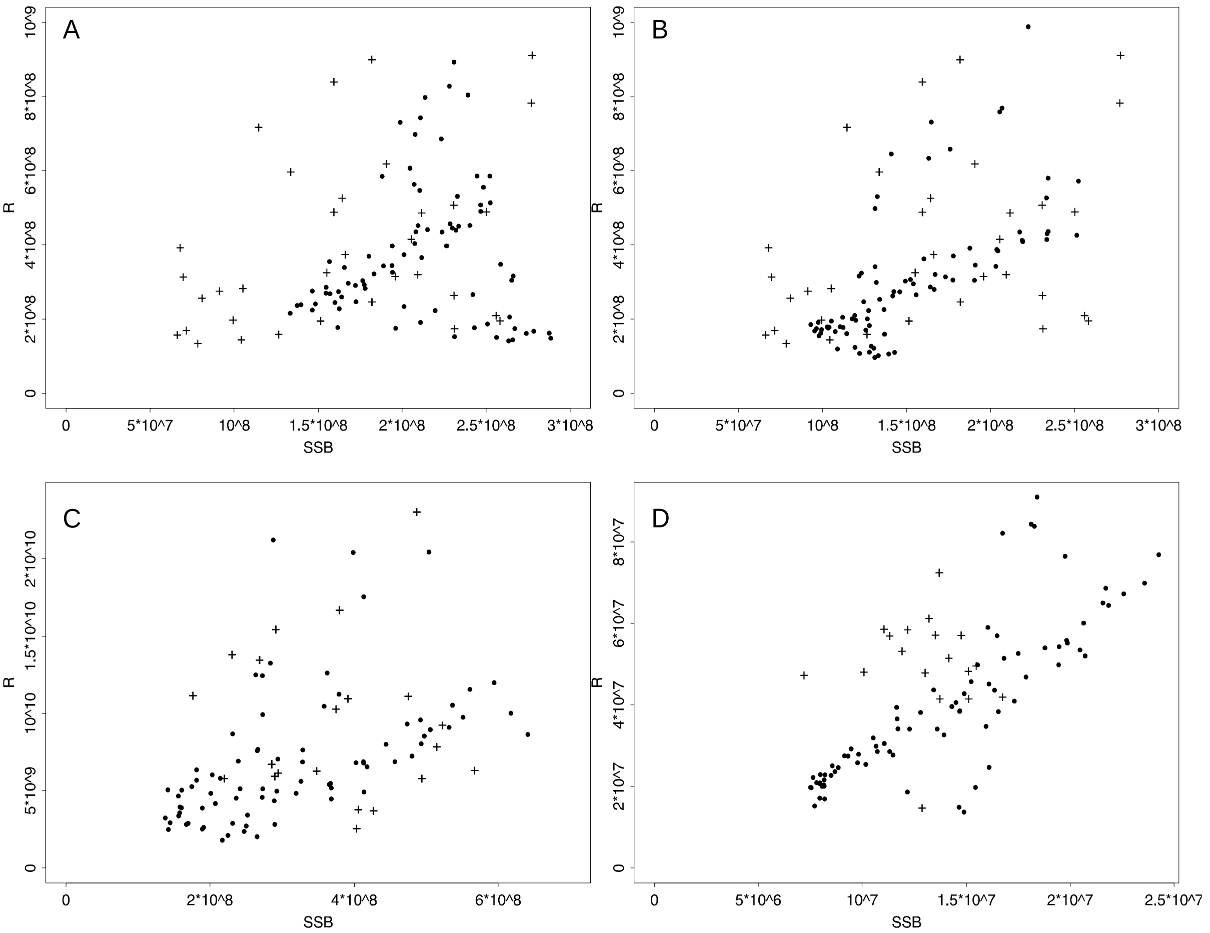

Figure 3. VPA-estimates (+) and simulated (•) stock-recruitment plots under current fishing pressure, including environmental variability.

A) North Sea cod: $I = 20, m = 0.25, r = 0.07, q = 0.055, p = 0.38$, cohort effect, fixed growth.

B) North Sea cod, same parameters, cohort effect, density-dependent growth.

C) Sardine in the Southern Area: $I = 6, m = 0.25, r = 0.23, q = 0.25, p = 0.7$, cohort effect, fixed growth.

D) Bay of Biscay sole: $I = 9, m = 0.2, r = 0.2, q = 0.21, p = 0.38$, cohort effect, density-dependent growth.

Population dynamics is most sensitive to q, the mortality rate of unit weight, and to r, the growth rate of unit weight (table 2). When juvenile mortality becomes too high relative to growth, recruitment is insufficient, and although the population remains in the low abundance level with high reproductive rates, it is driven to extinction. On the other hand, when mortality is low relative to growth, recruited numbers are very large and the population grows exponentially despite the lower reproductive rates associated with high abundances. This can seem unreasonable as regulation mechanisms may be enhanced when conditions get more extreme, but on the other hand there must be some limit to these regulation mechanisms. Unfortunately data collected in extreme conditions are seldom available. Therefore density-dependence effects were deliberately described as discrete and not approximated by a continuous function, to avoid unjustified assumptions outside the observed range of fishing pressures. The duration of the egg incubation period *I*, the ratio of larval to egg weight *p*, and the exponent *m* of weight in growth and mortality rates are less sensitive parameters (table 2). A given change in *m* will result in opposite effects on growth and mortality, explaining why results are the least sensitive to this parameter.

Table 2. Minimum changes in early life parameters necessary to lead to exponential population growth ($\overline{g}=1$) or to population extinction ($\overline{g}=3$) under current exploitation for North Sea cod, simulated with the self-regenerating model with density-dependent reproduction, fixed growth, and randomly varying recruit size.

$\overline{g}$: mean abundance level index during a 100 year simulation. See appendix for definition of the parameters.

Parameter	$\overline{g}$	***I***	***m***	***r***	***q***	***p***
Fixed value	2.2875	20	0.2	0.232	0.15	0.38
Changes to exponential growth	1	–41%	+550%	+15%	–10%	+500%
Changes to population extinction	3	+14%	–2200%	–5%	+4%	–50%

2) Replacement lines

Under classical assumptions, for a given fishing mortality, any recruited cohort will produce a proportional spawning stock biomass. This is why a spawning biomass per recruit and the corresponding replacement line can be computed. But when density-dependent effects in adult population dynamics are taken into account, spawning stock biomass is no longer proportional to recruitment: spawning stock biomass increases less steeply when recruited numbers are high, if density-dependent effects are cohort effects (Fig. 2B and 4A). In the case of year effects, the proportionality is statistically true but perturbed by the variability in weight at age (Fig. 4B). This casts doubts about the concept of spawning biomass *per recruit*, and also of replacement lines of which the slope is the inverse of SPR. This is true for all three populations simulated (Fig. 4C and D). The departure from proportionality is the most important for cod, because i) cod has the oldest age at maturity, therefore a proportional change will have a greater impact on cod than on species with a younger age at maturity; ii) cod has the lowest slope of the fecundity-length relationship *b*, hence an additive change will have a greater impact on cod than on species with higher *b*; iii) in addition, for sardine there is no effect of abundance on fecundity at unit length *E*.

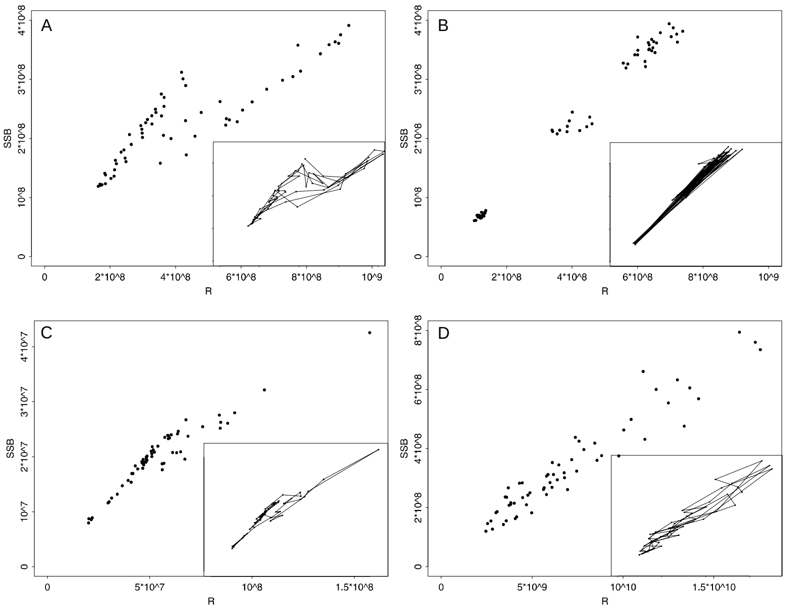

Figure 4. Simulated spawning stock biomass of successive cohorts ($\sum_{i=1}^{A^+} N_{i,t+i-1}V_{i,t+i-1}W_{i,t+i-1}$) versus corresponding number recruited ($N_{1,t}$), applying current fishing pressure (100 year simulations), fixed growth, varying recruit size. Inlays show the population dynamics by linking successive cohorts.

A) North Sea cod: $I = 20, m = 0.2, r = 0.232, q = 0.15, p = 0.38$, cohort effect.

B) North Sea cod, same parameters, year effect.

C) Bay of Biscay sole: $I = 9, m = 0.2, r = 0.2, q = 0.21, p = 0.38$, cohort effect.

D) Sardine in the Southern Area: $I = 6, m = 0.25, r = 0.23, q = 0.25, p = 0.7$, cohort effect.

3) Biological Reference Points

If it is not possible to compute unambiguous spawning biomass per recruit, then it will be difficult to estimate SPR-based biological reference points. One way of avoiding this difficulty is to consider density-dependence as uncertainty or biological variability, and to compute one SPR for each simulated cohort. Then a range of SPR rather than a single value can be associated with any given fishing mortality (Fig. 2C and 5). Changes in the maturity ogive with varying fishing pressure lead to lower expected gains of decreasing fishing mortality for cod, but the difference is small for sole and sardine. Changes in all reproductive parameters with abundance in the self-regenerating model lead to variability in SPR for the range of fishing mortality rates associated with population cycles (Fig. 2C). When environmental variability is introduced into the model, the range of such F's is increased (cohort effects: Fig. 5A) and there is additional variability in SPR due to the subsequent variability in weight at age (cohort effects and year effects: Fig. 5A & B). The range of SPR's is larger for sardine because of the higher variability in recruit weight W_1, reflected in a higher variability of weight at any age.

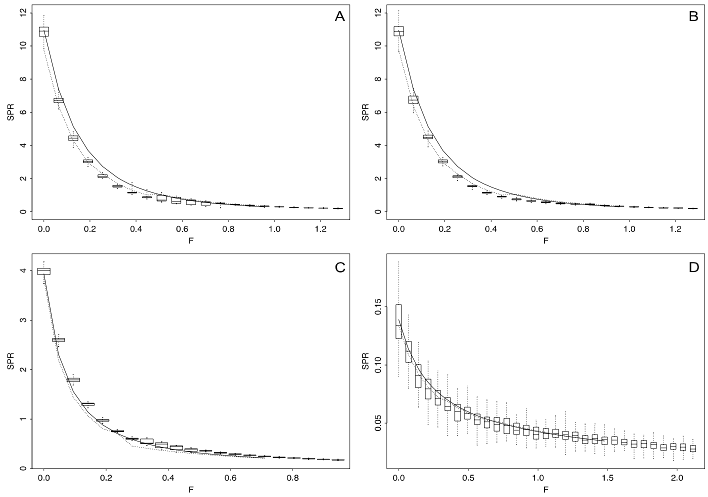

Figure 5. Spawning per recruit plots: classical equilibrium analysis (solid lines), equilibrium analysis with maturity ogives changing with fishing mortality (dashed lines), and the distribution of the simulated self-regenerating model with fixed growth and varying recruit size (boxes: quartiles, whiskers: extremes).

A) North Sea cod: $I = 20, m = 0.2, r = 0.232, q = 0.15, p = 0.38$, cohort effect.

B) North Sea cod, same parameters, year effect.

C) Bay of Biscay sole: $I = 9, m = 0.2, r = 0.2, q = 0.21, p = 0.38$, cohort effect.

D) Sardine in the Southern Area: $I = 6, m = 0.25, r = 0.23, q = 0.25, p = 0.7$, cohort effect.

From the minimum and maximum of all possible SPR's, extreme possible BRP's are computed (Fig. 6, table 3). When environmental variability is not taken into account and for high fishing mortality rates such as F_{med} and F_{high}, the simulated population remains in the low abundance level and there is a single SPR associated to these F's (Fig. 6). On the other hand, as soon as F decreases or environmental variability is introduced in the model, density-dependent effects introduce variability and/or bias compared to the classical density-independent estimates. Introduction of density-dependent growth yields a much lower estimate of VSPR compared to density-independent estimates, and a high uncertainty on all other BRP's. The ranges of these BRP's are wider when i) density effects are cohort effects than year effects ii) growth is density-dependent rather than fixed. Virgin spawning per recruit is largely overestimated by classical methods and is sensitive to density-dependence in any trait. F_{low}, F_{med}, F_{high} and current spawning per recruit have a large range of variation introduced by density-dependence consideration. By contrast, simulated $F_{30\%}$ seem robust to the parameters and hypotheses tested here, except density-dependent growth. This is because density-dependence is simulated in a discrete way in the present model: under low fishing mortality rates such as $F_{30\%}$, population abundance remains in the high level and the population parameters never change. For sardine the dependence of $F_{35\%}$ on biomass makes this BRP sensitive to the high size variability simulated for this stock. The estimated BRP's are not very sensitive to the parameters used for the early life stages.

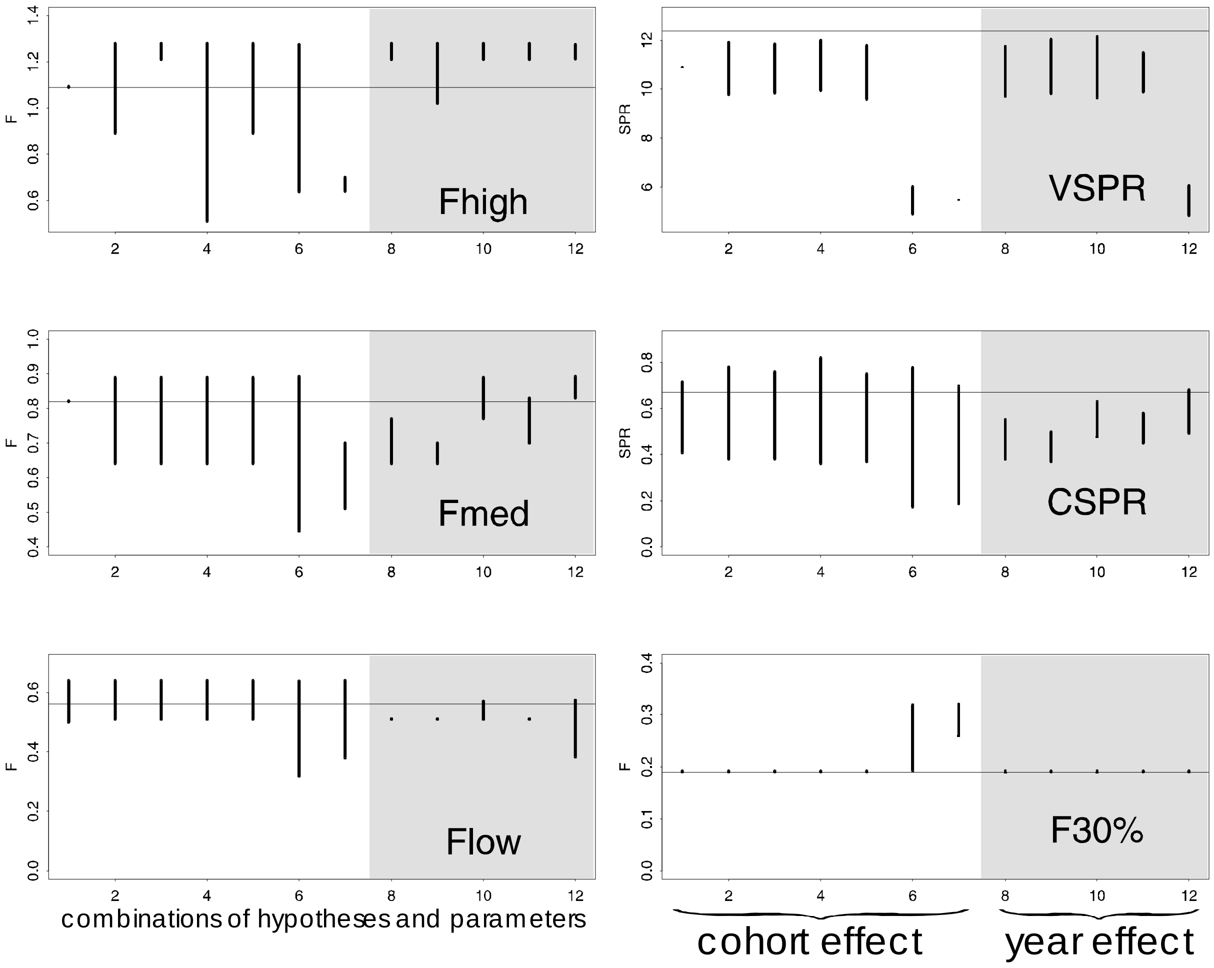

Figure 6. Ranges of Biological Reference Points for North Sea Cod estimated under various sets of hypotheses or early life stages parameters.

Thin horizontal line: classical density-independent equilibrium analysis (current F=0.638).

Index	Env. Var.	Density-dep growth	Year / cohort effect	*I*	*m*	*r*	*q*	*p*
1	No	No	cohort	20	0.25	0.07	0.056	0.38
2	Yes	No	cohort	20	0.25	0.25	0.15	0.38
3	Yes	No	cohort	20	0.25	0.07	0.056	0.38
4	Yes	No	cohort	20	0.2	0.232	0.15	0.38
5	Yes	No	cohort	20	0.11	0.22	0.14	0.38
6	Yes	Yes	cohort	20	0.25	0.07	0.056	0.38
7	No	Yes	cohort	20	0.25	0.07	0.056	0.38
8	Yes	No	year	20	0.25	0.25	0.15	0.38
9	Yes	No	year	20	0.25	0.07	0.056	0.38
10	Yes	No	year	20	0.2	0.232	0.15	0.38
11	Yes	No	year	20	0.11	0.22	0.14	0.38
12	Yes	Yes	year	20	0.25	0.07	0.056	0.38

Table 3. Biological Reference Points for Bay of Biscay sole and sardine in the southern Area, as estimated by classical SPR methods, and range from the self-regenerating model with density-dependent reproduction, fixed growth, and randomly varying recruit size. VSPR, virgin spawning biomass per recruit. CSPR, current SPR.

$\bar{g}$: mean abundance level index during a 100 year simulation, under current exploitation.

(*) For sardine, in all simulations $F_{high} > 2.1$, the largest F-value used in simulations.

Early life stages parameters					$\bar{g}$	**Biological Reference Points**					
I	***m***	***r***	***q***	***p***	$\bar{g}$	**F_{low}**	**F_{med}**	**F_{high}**	**$F_{30\%}$**	**VSPR**	**CSPR**
Bay of Biscay sole, classical equilibrium analysis (F_{ref}=0.4729)											
						0.42	0.56	0.71	0.14	3.94	0.34
Bay of Biscay sole, self-regenerating model, cohort effect											
9	0.2	0.2	0.21	0.38	2.713	0.43-0.47	0.61-0.66	0.76-0.85	0.14	3.74-4.18	0.32-0.42
14	0.25	0.07	0.08	0.38	2.675	0.43-0.47	0.61-0.66	0.80-0.85	0.14	3.68-4.16	0.29-0.42
14	0.25	0.21	0.2	0.38	2.475	0.43-0.47	0.61-0.66	0.76-0.80	0.14	3.80-4.20	0.28-0.42
						F_{low}	**F_{med}**	**$F_{35\%}$**	**F_{high}**	**VSPR**	**CSPR**
Sardine in the southern Area, classical equilibrium analysis (F_{ref}=0.7044)											
						0.07	0.75	0.64	2.54	0.13	0.05
Sardine in the southern Area, self-regenerating model, cohort effect											
6	0.25	0.07	0.082	0.7	1.838	0-0.07	0.35-1.55	0.7-1.06	(*)	0.10-0.17	0.03-0.06
6	0.11	0.2	0.22	0.7	2.188	0-0.07	0.42-1.69	0.85-0.85	(*)	0.09-0.17	0.03-0.07
6	0.25	0.23	0.25	0.7	1.888	0-0.07	0.21-1.41	0.56-0.77	(*)	0.09-0.19	0.03-0.07

Discussion

Spawning per recruit is an ambiguous concept if populations are regulated in a density-dependent way during the adult stage. The spawning biomass developed by an average recruit depends on the number recruited, which varies under the combined influences of the recent history of the population and of environmental fluctuations. Although my figures of spawning stock biomass against recruitment (Fig. 4) look unrealistic because of the discreteness of the estimated effects, they undoubtedly show that these quantities are not proportional, as it would be required to compute spawning per recruit.

The quantitative and practical consequences of this flaw are not negligible. Both density-dependence in growth and reproduction contribute to the non-proportionality of spawning biomass to recruitment, but the quantitative consequences of density-dependence in growth are higher because individual weight is the building stone for SSB. These findings are qualitatively in agreement with previous single-stock studies (Overholtz *et al.*, 1991; Patterson, 1997; Helser and Brodziak, 1998). Predicted stock rebuilding might be overoptimistic when density dependence is neglected. Density dependent effects are expected to affect BRP's computations to a greater extent for large and long-lived fish with a large proportion of growth after maturity (like cod).

These conclusions are orders of magnitude rather than precise estimates, because the model has been deliberately kept as simple as possible, with few parameters, all of which can be estimated, aiming to describe the most important effects of fishing on the life cycle. This choice has the following consequences. i) Only a subset of possible density-dependent processes have been investigated, neglecting for example changes in natural mortality. ii) Stochasticity is introduced in the model process only in the mean weight for recruits. This probably underestimates the influence of environmental variability. For sardine, which has the largest variance in recruit weight, the overlap between the simulated and observed spread in the stock-recruit plot is better than for cod and sole, and the resulting variability in BRP's is high. iii) It was assumed that density-dependent effects can be estimated by fishing effects. Clearly, the novel environment created by fishing may induce both phenotypic responses and evolutionary changes (Stokes *et al.*, 1993), which are confounded in the available estimates. However, plastic responses to food availability may be much larger than evolved responses to high and selective mortality rates (Reznick, 1993). iv) The estimates of density-dependent effects were obtained across many populations. This avoids confusion with effects of environmental influence, but results in estimates of mean effects on all these populations. As all species may not react equally to fishing, the present results improve our insight into the consequences of density-dependence on stock-assessments in general, rather than on any particular stock. v) Two possibilities were tested for the way abundance may affect the reproductive potential of the population: year-effects and cohort-effects. Stock abundance probably acts in both manners on reproduction. It is not possible to decide which of the figures 4-5 A or B is closer to reality; reality is probably somewhere in between, or the sum of both effects. vi) The results are also influenced by the discrete structure of the model. For example, a continuous model would probably conclude that $F_{30\%}$ is not robust to density-independent assumptions, unlike the present model. The discreteness of the model was imposed by the choice of incorporating only observed effects in the model. BRP's such as VSPR or $F_{30\%}$ rely on stock states for which we have few information because they have been seldom observed; hence there is a high uncertainty in their estimates, even if we are not able to quantify this uncertainty.

The uncertainty about density-dependent processes involved in stock dynamics comes in addition to the various sources of errors and uncertainty known to affect stock assessment and BRP's computations. It is of the same magnitude as variations in F_{med} predicted by Jakobsen (1992; 1993) in response to assumed variations in growth and maturity parameters. It is also of the same magnitude as the variability of F_{med} and F_{crash} due to observed recruitment variability, as estimated by bootstrap methods for Georges Bank cod (Murawski *et al.*, 1998) and for North-East Arctic cod and haddock (Jakobsen, 1992). On the other hand, the variability of F_{msy} caused by observed variability in recruitment, weight, selectivity and maturity in Icelandic haddock, estimated by bootstrap methods, may be much larger (Anonymous, 1999a). From this short review it is concluded that density-dependence effects are of practical importance, although they are not the only concern over the precision of BRP's estimates. In addition, SPR computations are projections under a fixed exploitation diagram, whereas the real exploitation diagram is expected to vary. SPR and F_{med} estimates have been shown to be sensitive to such changes (Jakobsen, 1992; Jakobsen, 1993).

More basically, the present study casts doubts about the real meaning of these BRP's, because spawning per recruit is not a well-defined quantity. To avoid reasoning on a 'per recruit' basis would clarify diagnostics. The conceptual weakness of SPR is most preoccupying for BRP's defined directly from replacement lines, such as F_{low}, F_{med}, F_{high} and F_{loss}. Although the idea of dividing the stock-recruitment plot by replacement lines is appealing because it avoids assumptions about the spawner-recruit function, it does not avoid any assumption on stock dynamics. BRP's including a stock recruitment relationship such as F_{msy} or F_{crash} should be less sensitive to this problem because the stock recruitment relationship more or less explicitly includes density-dependent regulations.

In addition, SPR has other disadvantages. There is increasing concern that spawning biomass, considering only weight and proportion mature at age, is not a good index of reproductive potential. It may be improved by additional information such as effects of spawner age or size on fecundity (Leaman, 1986; Lambert, 1990; Katsukawa, 1997; Marshall *et al.*, 1998; Marteinsdottir and Thorarinsson, 1998), and on egg size and egg and larval viability (MacKenzie *et al.*, 1998; Murawski *et al.*, 1998). Another possible improvement would be to monitor more than one or two quantities such as fishing mortality and stock biomass. It has been recommended to use several criteria to manage a fishery because objectives as well as technical criteria are multiple (Caddy and Mahon, 1996). But from a biological point of view, population indices and the associated BRP's are usually fishing mortality rates and/or biomasses, all defined and estimated from the same models and data (e.g. Caddy and Mahon, 1996; Deriso *et al.*, 1998). There is a need to think about other indices of stock potential to be monitored together with these BRP's, such as the growth and condition of spawners (Marshall and Frank, 1999), their hepato-somatic index (Lambert and Dutil, 1997; Marshall *et al.*, 1999), the growth rate of the population (Hutchings and Myers, 1994), life history traits (Rochet, In the press) or other new indices to be found.

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Appendix

Summary of population parameters used in the study

A) Stock-specific parameters

Parameter	Definition	Values		
		North Sea Cod	**Bay of Biscay Sole**	**Southern Sardine**
F_a	Fishing mortality at age	0.065, 0.546, 0.712, 0.637, 0.591, 0.672, 0.67, 0.64, 0.794, 0.548	0.0189, 0.0505, 0.208, 0.3709, 0.7077, 0.6046, 0.4735, 0.5527, 0.5527	0.0673, 0.1414, 0.3775, 0.7635, 0.9131, 0.7635, 0.7635
M_a	Natural mortality at age	0.8, 0.35, 0.25, 0.2, 0.2, 0.2, 0.2, 0.2, 0.2, 0.2	0.1 at all ages	0.33 at all ages
$\tilde{N}_1$, $\tilde{N}_2$	Total abundance thresholds for switching population parameters	703631431, 818522160	241830858, 285634113	12011217184, 13718785797
$A_{m,3}$, $\sigma_{A_m,3}$	Mean and standard error of the proportion mature at age in the lower abundance level	Normal distribution $N(3.67,1.31)$	Normal distribution $N(2.5,0.3)$	Exponential distr. $E(1,0.303)$
E_3, b_3	Parameters of the fecundity-length relationship in the lower abundance level (length in cm)	1.29, 3.29	0.0805, 4.168	5.077, 3.666
$W_{e,3}$	Egg weight (kg) in the lower abundance level	1.03E-06	9.66E-07	1.61E-06
μ_{W_1}, σ_{W_1}	Mean and standard deviation of recruit size (kg)	0.6132, 0.06155 (1963-1996)	0.00672, 0.000669 (1979-1996)	0.0195, 0.003567 (1977-1997)
$\Delta L_{a,3}$	Length increments at age (cm) in the lower abundance level	7.96, 12.58, 14.84, 13.37, 6.33, 4.21, 3.83, 4.37, 1.36, 0.20	7.93, 6.29, 4.99, 3.96, 3.14, 2.49, 1.97, 1.56, 1.24	1.17, 3.81, 0.93, 1.05, 0.58, 2.20, 0.30
α, β	Parameters of the length-weight relationship $W = \alpha L^{\beta}$ (g.cm^{-1})	0.0104, 3.000	0.00482, 3.17533	0.00594, 3.0766
I	Duration of egg incubation period (days)	20	9 to 15	5 to 6
p	Ratio of larval to egg weight	0.38	0.38	0.7

B) Early life stages parameters

Weights are in mg wet weight.

Parameter	**Definition**	**Values from sources**			
		(Ware, 1975)	**(Beyer, 1989)**	**(Pepin, 1993)**	**(Lorenzen, 1996)**
m	Exponent of weight in growth and mortality rates	0.232	0.25	0.11 to 0.18	0.3
r	Growth rate of unit weight (d^{-1})	0.2	0.07	unknown	unknown
q	Mortality rate of unit weight (d^{-1})	0.14	0.04	unknown	0.08