Analysis

Detecting the presence of depensation in collapsed fisheries: The case of the Northern cod stock ☆

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ABSTRACT

Motivated by the evidence that many collapsed stocks have failed to recover despite the fact that fishing mortality has been reduced, or even when a moratorium is in effect, we develop a methodological approach using splines to analyze the stochastic population dynamics of fish stocks at low stock levels. Considering the aggregate Northern cod stock by way of illustration, we find that the species' lack of recovery, despite the moratorium which still remains in force, is consistent with the hypothesis of depensatory population dynamics at low population sizes, as opposed to the compensation estimated by the conventional regression methods used in classic bioeconomic models.

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1. Introduction

The aim of this paper is to provide a simple stochastic mathematical model using a total biomass approach to detect depensation in collapsed fisheries. Specifically, we develop a methodological approach using, at low stock levels, splines (cubic polynomials) which are more flexible than the quadratic or logistic functional forms used in conventional regression methods.

The biomass approach, also termed surplus production model, is widely used in the literature on fisheries economics to describe fish population dynamics and specifies population size and growth in terms of total biomass (Clark, 2006). In this setting, conventional regression methods are used by classic bioeconomic models to find the curve of best fit for the stock data between the families of logistic curves. Since all of these curves are concave this approach accepts the a priori hypothesis of compensatory dynamics at low population sizes in which the intrinsic growth rate increases as the population decreases (e.g. Nøstbakken and Bjørndal, 2003 for the case of North Sea herring).

Conversely, finding the best-fitting spline does not require any a priori assumption and allows us to detect changes in the concavity of the growth function of the species at low population sizes caused by a severe decline in biomass. The focus here is to model the stochastic aggregate stock dynamics of collapsed fisheries.

The implication underlying compensation is that marine fishes are highly resilient to large population reductions thanks to a strong inherent capability to recover from low population sizes. However, there is very little evidence for population recovery from prolonged declines (Hutchings, 2000; Hutchings and Reynolds, 2004; Murawski, 2010). One of the most dramatic cases is the collapse of the Northern cod stock (NCS). 21 years after imposing a moratorium the fishery has not yet recovered. Using the biomass approach for the pre-moratorium period and conventional regression methods the literature on fisheries economics has estimated compensation at low population sizes (Grafton et al., 2000, 2009; Ussif et al., 2004).

The literature on the population dynamics of fish stocks has dealt extensively with the fact that compensation, as estimated by classic bioeconomic models, is unable to cope with the lack of recovery of fish population collapses. Biological mechanisms supporting depensation (per capita growth rate decreases as the population is reduced) and critical depensation (per capita growth rate becomes negative for low enough stock values) have been widely studied (e.g. Frank and Brickman, 2000; Liermann and Hilborn, 2001; Shelton and Healey, 1999). These may include overfishing-induced phenotypic changes to life history parameters (Denney et al., 2002; Hutchings and Reynolds, 2004; Olsen et al., 2004), cultivation–depensation effects (Myers and Worm, 2005; Walters and Kitchell, 2001), unobserved genetic or behavioral diversity due to a complex structure of depleted stocks (Frank and Brickman, 2000; Sterner, 2007), changes in habitat (Hutchings, 2000),

and age-truncated effects due to size-selective harvesting (Anderson et al., 2008). See also Lin et al. (2013), and the reference herein, for a discussion of the dynamical impacts of depensation on predator–prey systems. The analysis of depensation in population dynamics is also mathematically appealing (Clark, 2006) as shown in the enormous body of both bioeconomic and economic growth literature focusing on theoretical implications (see Majumdar and Roy, 2009 for a recent survey).

Despite the extensive literature mentioned above, empirical analysis of depensation is rather scarce due to both the low statistical power of standard methods to detect it, and the lack of knowledge of ecosystem processes where the intrinsic growth rate at low stock levels is affected by demographic uncertainty. Some exceptions can be found in McDonald et al. (2002) and Nash et al. (2009). They show that depensation is difficult to estimate for the case of bluefin tuna and North Sea herring, respectively. The lack of statistical evidence is the cause of the current scarcity of empirical work which in turn hinders the advancement of knowledge in this area.

The spline parameterization method (SPM) developed in this paper allows us to incorporate all possible population dynamics at low population sizes (compensation, depensation, and critical depensation) into stochastic growth functions of marine species. We consider both birth and survival uncertainty of uniform intensity at all stock levels. The SPM shows that in population dynamics with a moderate depensation, demographic uncertainty takes the lead and creates wandering patterns of slow growth consistent with long collapse periods and risk of non-recovery of fish stocks.

Using the NCS by way of illustration, the main contributions of this article include: First, in contrast to the compensation estimated by conventional regression methods, the best fit for the observed population dynamics is depensation (convex–concave growth function at low population sizes). In particular, we show that the combined effects of demographic uncertainty and depensation might be linked to the lack of recovery of the NCS despite the moratorium. This result concurs with the observed collapse and non-recovery of the NCS and seems to confirm that classic bioeconomic models are unable to describe the population dynamics of collapsed fish stocks since they overestimate the growth rate of these species at low population sizes.

Second, the recruitment function associated to the dynamics of best fit for the NCS data is a Ricker type functional form which is concave and decreasing at high enough stock levels (overcompensation) but it exhibits depensation (convex–concave recruitment) at low stock levels.

Third, the SPM allows us to test the safety of limit reference points. In the case of the NCS, we show that both a delay in the implementation of a fishing moratorium and non-compliance with the moratorium in the first two years would have driven the species to extremely low levels where the growth function of the species exhibits depensation and consequently species recovery does not occur. We also show that management actions should have been taken in the 1980's to enforce a high enough biomass precautionary approach reference point.

In Keith and Hutchings (2012), a non-parametric meta-analysis approach is used to estimate trends in per capita recruitment vs. spawning stock biomass (SSB) for 104 species. In their analysis, although many species exhibit strong compensation, others show much weaker compensation than expected. In particular, they show that Atlantic cod, which comprises 19 cod stocks, exhibits weak compensation at moderate SSB levels (as SSB declines the relationship between $\frac{Recruits}{SSB}$ and SSB weakens). In that paper, a pooled analysis of 19 cod stocks is needed in order to avoid the lack of data at low stock levels which is the main barrier to finding weak compensation on a stock-by-stock basis. In their analysis, 61% of the species are represented by a single stock. In the majority of these cases, they found evidence of strong compensation. In Neubauer et al. (2013), a non-parametric global meta-analysis approach is used to find that, on average, fish stocks take twice as long to recover as predicted by simple surplus production (Schaefer) models, and that only substantial reductions in fishing mortality lead to

relatively high certainty that recovery can be achieved within foreseeable time-frames. Vert-pre et al. (2013) show that surplus production functions explain very little of the population dynamics of exploited species, and that temporal regimes of productivity explain far more.

The SPM developed herein is substantially different from the method used in the above literature. In particular, the SPM allows us to estimate a smooth functional relationship between growth and total biomass, and consequently the population dynamics at low stock levels can be numerically simulated in order to determine how a single stock will respond to population declines. In this sense, the SPM can provide a useful tool for testing the safety of biological reference points by analyzing the risk of collapse of endangered species, and by predicting recovery rates when population abundance is low.

2. The Northern Cod Fishery

One of the most dramatic collapses in the history of fisheries has been the collapse of the Northern cod fishery. The NCS, comprising populations of Atlantic cod (*Gadus morhua*) from southern Labrador and eastern Newfoundland (NAFO divisions 2J3KL), was once one of the world's largest commercial fisheries. However, after decades of severe overexploitation, the NCS collapsed in 1992 and a moratorium on fishing had to be imposed. Even after a 21 year moratorium the fishery has not yet recovered (DFO, 2012). Indeed, the NCS has declined 97–99% in the past 3 generations and more than 99% since the 1960s.

2.1. Modeling the Population Dynamics for the NCS

The discrete-time logistic population dynamics for the NCS is given by

$$x_{t+1} = x_t + rx_t\left(1 - \frac{x_t}{K}\right) - h_t = f(x_t) - h_t, \tag{1}$$

where x_t is the biomass at period t, r is the intrinsic growth rate, $K = 5.6$ (million tons) is the environmental carrying capacity, and h_t is the total harvest at period t.

Using conventional nonlinear regression methods, and data for the total biomass (ages 3 and older) for the 1962–1991 pre-moratorium period (Rivard, 1994), an intrinsic growth rate $r \approx 0.3$, as defined in (1), has been estimated by Grafton et al. (2000, 2009) and Ussif et al. (2004) which in turn imply that the population dynamics (1) exhibits compensation due to the high estimated maximum population growth rate r_{max} as measured by the slope of the growth function at the origin $(r_{max} = f'(0) = 1 + r \approx 1.3)$.

The data for the total biomass is now available from 1992 onwards (DFO, 2011a) (see Fig. 2). Using harvest and total biomass data for the period 1962–2010 (DFO, 2011a; Rivard, 1994), the growth function of the species $f(x)$, as defined in (1), can be estimated. Details of the estimated model are provided in Table 1.

We can observe in Table 1 that the estimated intrinsic growth rate $r = 0.296847$ for the entire range of historical data 1962–2010 is similar to that estimated in the literature for the pre-moratorium period (1962–1991) ($r \approx 0.3$).

Thus, the standard growth function of the species estimated by conventional regression methods exhibits compensation ($r_{max} = f'(0) = 1 + r \approx 1.3$) even if the extremely low stock levels from 1992 onwards

Table 1
Estimated parameters of the growth function for the northern cod stock.

Parameter	Estimate	t-Statistic	Standard error	Adjusted R^2
r	0.296847	17.63159	0.016836	0.992703
r*	0.297275	14.17392	0.020973	0.985695

The value r is the estimated intrinsic growth rate for the entire range of historical data (1962–2010). The value r* is the estimated intrinsic growth rate for the pre-moratorium period 1962–1991.

are considered in the estimation process. Based on the a priori assumption of compensation, made by conventional models, the effects of overfishing are reversible and the species should have recovered to a higher population size during the moratorium. Therefore, even though the long moratorium allows us to overcome the scarcity of data, conventional regression methods fail to explain the lack of recovery of fish population collapses.

There are two causes for this failure: first, the logistic functional form used for the regression makes an a priori assumption of compensation; second, the stock values during the collapse (from 1992 onwards) are relatively small compared to the historical records of the NCS during the pre-moratorium period. This means that, even if a more flexible functional form allowing for both compensatory and depensatory dynamics at low stock levels is used for the regression in (1) by considering the entire range of historical data (1962–2010), the relative smallness of the stock values during the collapse would make the regression insensitive to stock fluctuations at low levels.

Fig. 1 represents the growth functions of the species estimated by conventional regression methods for both the entire range of historical data 1962–2010 ($r = 0.3$), and the moratorium period (from 1992 onwards) where the best fit is a linear function given by $x_{t+1} = 1.084x_t$. We can observe in this figure the overestimation of the growth rate at low population sizes (from 1992 onwards) if the entire range of data ($r = 0.3$) is considered for the regression analysis[1].

2.2. Observed Population Dynamics during the Moratorium Period

Fig. 2 represents data for the total biomass from 1992 onwards (DFO, 2011a). We can observe in this figure that the biomass index continued to decline and reached an extremely low level by 1994 (10,000 tons) which in turn implies that the official start of the moratorium (year 1992) does not concur with the observed data for biomass. The drastic decrease in the stock from 1992 to 1994, where the stock declined 94%, can only be explained by the presence of harvesting in the first two years of the moratorium (non-compliance with the moratorium).

The predominant opinion in the fisheries literature maintains that fishing mortality for the NCS has been underestimated, especially during the years preceding the collapse (in the early 1990s), due to high levels of discarding and catch misreporting (e.g. Caddy and Agnew, 2004; Myers et al., 1997; Walters and Maguire, 1996). Shelton and Lilly (2000) show that the catch was underestimated by more than 100% during the years preceding the collapse. Thus, the available evidence suggests that 1994 should be considered the start of the moratorium period due to the non-compliance in 1992 and 1993.

We can observe in Fig. 2 the large confidence intervals on the stock values estimated by the DFO, reflecting the high degree of uncertainty regarding the true stock values during the moratorium period. We can also observe in Fig. 2 that the observed growth pattern of the species during the moratorium period (1994 onwards) can be described as slow growth with backward movements.

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[1] The relative mean square error (RMSE) is given by $RMSE = \frac{1}{n}\sum_{i=1}^{n}\left(\frac{y_i - \hat{y}_i}{y_i}\right)^2$, where y_i and $\hat{y}_i$ are the observed and predicted stock data, respectively, and n is the number of observations. A high RMSE at low stock levels ($x \leq BP$) is obtained if the estimated intrinsic growth rate for the entire range of data ($r = 0.3$) is considered for the regression analysis at low stock levels which in turn implies an overestimation of the growth rate at low population sizes. In particular, RMSE = 0.309 at low stock levels is sixty-one times higher than that obtained for the entire range of data, RMSE = 0.00508. A logistic regression over the whole range of stock data fails to explain the population dynamics at low stock levels due to the biological mechanisms supporting depensation. This indicates that the data structure consists of two intervals, as considered by the SPM.
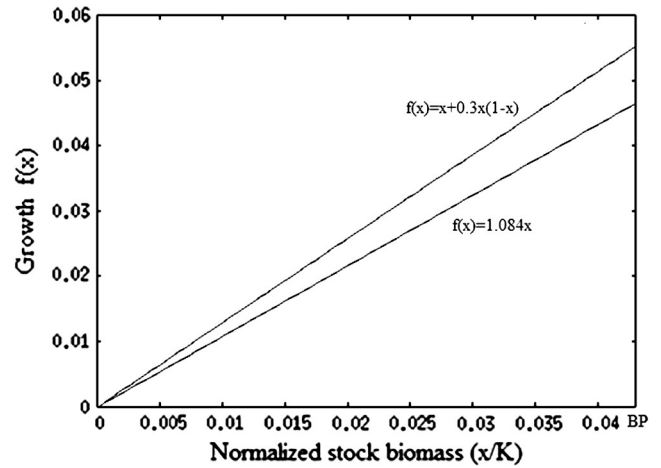

Fig. 1. Growth function of the species estimated by conventional regression methods for the entire range of historical data 1962–2010 (concave function), and for the moratorium period (from 1992 onwards) (linear function).

3. Spline Parameterization Method (SPM)

In this section we describe the SPM using the NCS by way of illustration. The SPM consists of several stages:

i) The stock value *BP* (break-point), below which there has been a drastic decrease in the total biomass, is identified. In the case of the NCS, *BP* = 242,000 tons (Rivard, 1994, see Fig. 2). This is the value of the stock for 1991 which is the beginning of the drastic decline in the NCS.

ii) The growth function of the species is estimated, at high enough stock levels ($x \geq BP$), by conventional regression methods. This means that the population dynamics at high enough stock levels, where $x \geq BP$ and enough empirical evidence (number of observations) is available, follows a standard growth model due to the fact that it fits the data well. In the case of the NCS, we estimate the logistic growth model $f(x)$, as defined in (1), where the estimated intrinsic growth rate is $r = 0.3$ (see Section 2 and Table 1).

iii) A family of splines is constructed to achieve a smooth interpolation of the growth function $f(x)$, as defined in (1), between the origin and *BP*.

A spline is a cubic polynomial that provides smooth interpolation between two points of a curve. Splines are widely used in the statistical
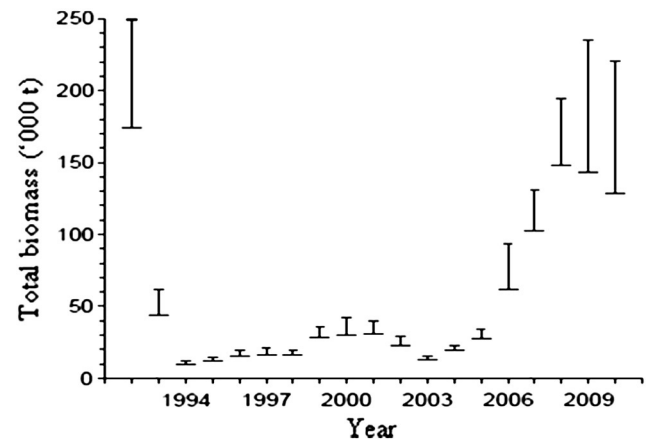

Fig. 2. Total biomass (+2 SE's) estimated by the DFO from 1992 onwards (moratorium period). Error bars indicate the upper limit of the confidence intervals.

literature because of their flexibility and ability to incorporate them into a large range of modeling contexts (e.g. Ruppert et al., 2003).

In our model, the spline is constructed as follows:

$$x_{t+1} = Ax_t^3 + Bx_t^2 + Cx_t + D, \qquad (2)$$

where, x_t is the biomass at period t, $D = 0$ due to the fact that the spline has to pass through the origin, C is the slope of the spline at the origin and is a free parameter, A and B can be obtained as a function of C and BP^2 so that the spline smoothly interpolates the empirical growth function $f(x)$ estimated in ii) at BP.

Thus, the SPM gives rise to a piecewise-defined smooth growth function. In the case of the NCS it is given by

$$f(x_t) = Ax_t^3 + Bx_t^2 + Cx_t \; \forall x_t \leq BP$$
$$f(x_t) = x_t + rx_t \left(1 - \frac{x_t}{K}\right) \forall x_t \geq BP, \qquad (3)$$

where the population dynamics at low enough stock levels ($x \leq BP$) evolves according to the spline, as defined in (2), for a given value of C, and where $r = 0.3$ is the intrinsic growth rate estimated by standard regression methods at high enough stock levels ($x \geq BP$).

Thus, we can construct different splines for different values of C, which in turn implies different population dynamics at low stock levels, $x \in [0, BP]$, but use the same empirical growth function $f(x)$ estimated in ii) when stock levels are above the threshold $x \geq BP$. In this way, the SPM allows us to incorporate all possible population dynamics (compensation, depensation, and critical depensation) for marine species at low stock levels, in contrast to the logistic model, which also depends on a single parameter, r, but always entails compensation. In particular, the growth function of the species $f(x)$ as defined in (3) shows i) critical depensation (convex growth function below the 45 degree line) for $0 \leq C < 1$; ii) depensation (convex–concave growth function above the 45 degree line) for $1 \leq C < C^*$, where $C^* = 1.3$ is the value of the slope of the spline at the origin which coincides with the slope of the estimated growth function at high enough stock levels ($x \geq BP$) if it were fitted to the whole range of data; and iii) compensation (strictly concave growth function) for $C \geq C^*$.

Fig. 3 represents the growth function of the species $f(x)$, as defined in (3), at low enough stock levels $x_t \leq BP$. In particular, it represents different splines as defined in (3) for the case of the NCS (normalized $BP = 0.0432$ (242,000 tons) taking $K = 5.6$ (million tons) as unity) for different values of the slope of the spline C at the origin. This figure shows compensation for $C = 1.3$ (top diagram), depensation for $C = 1.05$ (middle diagram), and critical depensation for $C = 0$ (bottom diagram).

4. Numerical Results: Lack of Recovery of the NCS

The population dynamics of the NCS during the moratorium period can be illustrated with numerical experiments which use the SPM to simulate the population dynamics of the species from the beginning of the moratorium onwards. In order to do this, we develop a simple statistical method for testing the ability of different simulated population dynamics to describe the observed dynamics at low stock levels. This method consists of testing whether the stock level in the last period of simulation, which corresponds to 2010, falls within the confidence interval estimated by the DFO from that year (CIDFO). This is a minimum robustness requirement (MRR) that simulated population dynamics

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[2] Parameters A and B are uniquely determined through the smoothness hypothesis, which imposes two additional constraints: The continuity of the aggregate dynamics, which forces the endpoint of the spline to coincide with the starting point of the logistic curve $f(x)$ estimated in ii) at BP, $y_{BP} = A \cdot BP^3 + B \cdot BP^2 + C \cdot BP = BP + r \cdot BP(1 - BP/K)$, and the coincidence of the derivatives of both functions at that point, $Dy_{BP} = 3 \cdot A \cdot BP^2 + 2 \cdot B \cdot BP + C$. Using this, $A = \frac{1}{BP^3}(Dy_{BP} \cdot BP + C \cdot BP - 2 \cdot y_{BP})$ and $B = \frac{1}{BP^2}(3 \cdot y_{BP} - 2 \cdot C \cdot BP - Dy_{BP} \cdot BP)$.
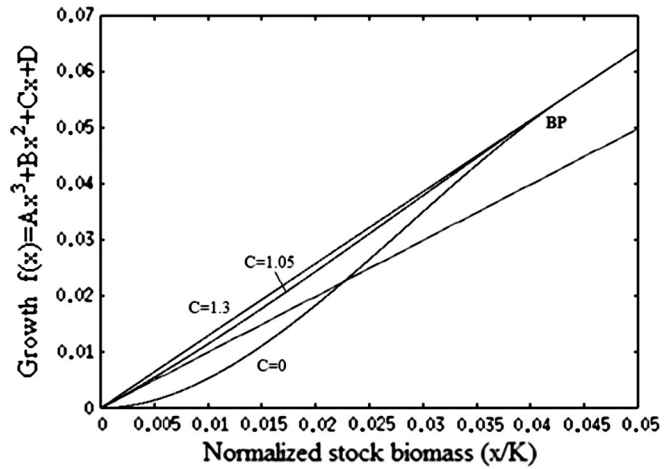

Fig. 3. Different splines for different values of the slope of the spline C at the origin. The concave growth function (compensation) above the 45 degree line (top diagram) corresponds to the case of C = 1.3. The convex–concave growth function (depensation) above the 45 degree line (middle diagram) corresponds to the case of C = 1.05. The convex growth function (critical depensation) below the 45 degree line (bottom diagram) corresponds to the case of C = 0.

must meet in order to describe the observed dynamics. Otherwise, the population dynamics will be rejected[3].

4.1. Deterministic Population Dynamics

In order to gain some intuitive understanding of the population dynamics of the NCS at low stock levels, we first analyze the deterministic case.

In the numerical experiments that follow it is assumed that the population dynamics is as defined in (3), where $BP = 242,000$ tons, and $x_0 = 10,000$ tons, the initial value of the stock in 1994 at the start of the moratorium. Using these parameter values different deterministic population dynamics can be numerically simulated, from the initial condition x_0, by using the SPM (using different splines for different values of the slope of the spline C at the origin). According to the MRR described above, the simulated deterministic population dynamics at low population sizes can be compared with the observed population dynamics (DFO survey estimates) during the moratorium period in order to find the population dynamics of best fit for the observed population. All data in the numerical experiments described below were generated using an Altix3700Bx2 Computer, using code written in standard FORTRAN.

Table 2 summarizes the relevant results from the numerical analysis of the deterministic population dynamics for the NCS for different slope values of the spline C at the origin (column 1). We can see in Table 2, column 2 the stock level in the last period of simulation, X_{2010}, which corresponds to 2010. It should be noted that both the stock value (tons) and the CIDFO (DFO, 2011a) (see Fig. 2) are given by

$$X_{DFO}2010 = 129000$$
$$X_{DFO}2010 \in [37000, 221000], \qquad (4)$$

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[3] If we consider that the numerical simulations cover a 16-year period each (the moratorium period 1994–2010), the fact that the stock level falls within the CIDFO is far from being a normal event, even in the absence of uncertainty. On the contrary, complying with the MRR is about as easy as sinking a long distance basketball shot. Further numerical experiments show that it is enormously difficult for the vast majority of population dynamics to meet the MRR, which indicates that the behavior of population dynamics is highly sensitive to the slope of the spline at origin C and shows that the MRR a rigorous criterion for robustness. It should be mentioned that the SPM can also be developed using Bayesian statistics if the Kullback–Leibler divergence measure is incorporated in our method. For the sake of simplicity, it has not been incorporated due to the fact that we obtain similar results by using the MRR.

Table 2
Numerical results in the deterministic case for
different values of slope of the spline C at the
origin.

C	X_{2010}
1.3	610,400
1.25	453,600
1.2	304,640
1.15	174,160
1.1	83,440
1.05	36,480
1	15,120
0.95	6496
0.9	2352

The value X_{2010} is the stock level in the last
period of simulation which corresponds to 2010.

where the CIDFO is defined as $XDFO2010 \pm 2SE's$, with a standard
error (SE) of 46000.

We can observe in Table 2 that the case of compensation estimated
by conventional regression methods, C = 1.3, does not fit the observed
dynamics since the stock value achieved under compensation, $X_{2010} =$
610400 (see column 2 for the case of C = 1.3), is five times higher
than XDFO2010 = 129000 and consequently, it does not fall within
the CIDFO (4). Compensation does not thus concur with the observed
dynamics for the NCS. In this case, the species should have recovered
to a higher population size during the moratorium.

We can observe in Table 2 that critical depensation (C = 0.95,
C = 0.9), does not fit the observed dynamics either because the stock
is eventually driven close to extinction in these cases.

We can also observe in Table 2 that, in contrast to the compensation
estimated by conventional regression methods (C = 1.3), depensation
at low population sizes (C = 1.05, C = 1.1, and C = 1.15) are the pop-
ulation dynamics of best fit for the moratorium period. In particular,
C = 1.15 is the case of best fit for the observed dynamics due to the
fact that the stock value achieved under depensation, $X_{2010} = 174160$
(column 2 for the case of C = 1.15), falls within the CIDFO (4). Indeed,
it is close to XDFO2010 = 129000.

4.2. Stochastic Population Dynamics: Demographic Uncertainty

Reed's (1979) stochastic growth model has become a standard refer-
ence in discrete-time bioeconomic analysis. In that model, uncertainty is
assumed to be included in the model through a single multiplicative
random growth shock z_t by reflecting environmental variability
(stochastic growth). This implies that regardless of stock size the
whole growth function $f(x)$ is equally affected by environmental fluctu-
ations $z_t f(x)$. While this makes sense at high stock levels, from a biolog-
ical point of view it seems more plausible that biological processes, as
described in Section 1, will be different in low population sizes, especial-
ly for collapsed fisheries. These processes give rise to demographic
uncertainty at low stock levels reflecting random fluctuations in birth
and mortality rates which can have serious consequences for the
recovery of collapsed fisheries. In this section, we analyze the implica-
tions of demographic uncertainty on the lack of recovery of the NCS.

Demographic uncertainty is represented in the model (3) through
two shocks $z_{\beta,t}$ and $z_{b,t}$ reflecting random fluctuations in survival and
birth rates, respectively. The stochastic population dynamics is given by

$$f\left(x_t, z_{\beta,t}, z_{b,t}\right) = z_{b,t} R_S\left(x_t, z_{\beta,t}\right) + z_{\beta,t}\beta x_t = z_{b,t}\left(Ax_t^3 + Bx_t^2 + (C-\beta)x_t\right)$$
$$+ z_{\beta,t}\beta x_t \forall x_t \leq BP$$

$$f\left(x_t, z_{\beta,t}, z_{b,t}\right) = z_{b,t} R_L\left(x_t, z_{\beta,t}\right) + z_{\beta,t}\beta x_t = z_{b,t}\left(x_t + rx_t\left(1-\frac{x_t}{K}\right)-\beta x_t\right)$$
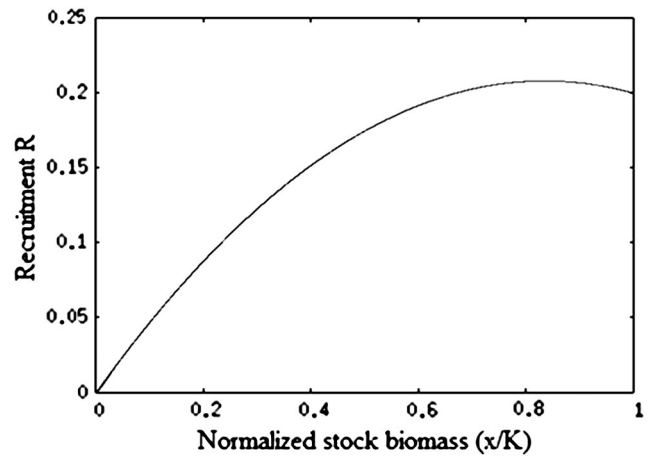$$+ z_{\beta,t}\beta x_t \forall x_t \geq BP, \tag{5}$$

Fig. 4. Recruitment function for different values of the slope of the spline C at the origin
(see Footnote 4).

where R_S is the recruitment function[4] of the species at low stock levels
($x_t \leq BP$), which is a spline as defined in (2); β is the survival rate[5];
and R_L is the logistic recruitment function of the species at high stock
levels ($x_t \geq BP$) (see Footnote 4).

Fig. 4 represents the recruitment function (RF) (see Footnote 4) for
different values of C. We can observe in Fig. 4 that the RF is a Ricker
type functional form which is concave and decreasing at high enough
stock levels (overcompensation). However, Fig. 5 is expanded to show
that the RF exhibits depensation (convex–concave recruitment) at low
stock levels ($x_t \leq BP$) for C < 1.3. We can also observe in Fig. 5 that
the spline R_S, as defined in (5), smoothly interpolates R_L at BP (see
Footnote 4).

Fig. 6 represents the per capita recruitment function (PRF = RF/X)
for different values of C. In the case of compensation (C = 1.3), we
can observe in Fig. 6 that PRF is always a decreasing function, while in
the case of depensation (C = 1.15) PRF increases at low stock levels
but it decreases when stock levels reach a certain level. This indicates
the existence of a stock biomass thresholds x* ≈ BP below which the
per capita growth rate decreases as the population is reduced (increas-
ing per capita recruitment). It should be noted that, at high enough
stock levels, PRF tends to the mortality rate M = 1-β (see Footnote 5)
where the per capita recruitment is equal to the per capita mortality.

Thus, the population dynamics of the NCS also exhibits depensation
(convex–concave recruitment) at low stock levels.

Next, we analyze whether the combined effects of demographic un-
certainty and depensation, might be linked to the lack of recovery of
NCS despite the moratorium.

In the numerical experiments that follow it is assumed that the pop-
ulation dynamics is as defined in (5), where $\beta = 0.2$ (DFO, 2011b). It is
assumed that $z_{\beta,t}$ and $z_{b,t}$ are distributed as N(1,σ_β) and N(1,σ_b), respec-
tively, where $\sigma_\beta = 0.08$ and σ_b are standard deviations.

Table 3 summarizes the relevant results from the numerical analysis
of 500 simulations (16 years each, corresponding with the moratorium
period 1994–2010) of the stochastic population dynamics (5), for differ-
ent values of slope of the spline C at the origin (column 1), and different
levels of demographic uncertainty as measured by σ_b (column 2).

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[4] Using (5), in the deterministic case the smooth recruitment function of the NCS is giv-
en by

$$R(x_t) = R_S(x_t) = Ax_t^3 + Bx_t^2 + (C-\beta)x_t \quad \forall x_t \leq BP$$
$$R(x_t) = R_L(x_t) = x_t + rx_t\left(1-\frac{x_t}{K}\right)-\beta x_t \quad \forall x_t \geq BP.$$

[5] In most ecological stock-assessment models of marine fish populations the natural
mortality M = 1-β is usually assumed to be constant, which in turn implies that random
demographic shocks affecting the population dynamics, as defined in (5), are governed by
changes in recruitment (changes in σ_b).
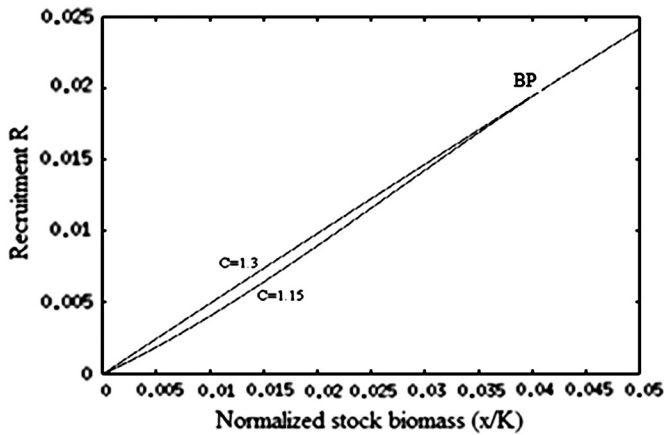
Fig. 5. Recruitment function at low stock levels for different values of C.

Table 3
Numerical results in the stochastic case for $\sigma_\beta = 0.08$, different values of slope of the spline C, different levels of demographic uncertainty, as measured by σ_b, and different values of *BP*.

C	σ_b	$P(X_{2010} \in CIDFO_{2010})$	X_{2010}	BP = 0.0375	BP = 0.059
1.3	0.08	2%	434,929		
1.3	0.15	4%	394,315	3%	5%
1.3	0.2	9%	383,994		
1.25	0.08	12%	314,937		
1.25	0.15	28%	287,696	26%	31%
1.25	0.2	36%	262,920		
1.2	0.08	70%	194,372		
1.2	0.15	80%	169,963	72%	86%
1.2	0.2	76%	170,388		
1.19	0.08	82%	174,360		
1.19	0.15	84%	155,605	81%	92%
1.19	0.2	85%	148,114		
1.17	0.08	95%	131,420		
1.17	0.15	95%	118,803	91%	97%
1.17	0.2	93%	114,014		
1.15	0.08	98%	101,157		
1.15	0.15	97%	915,31	96%	96%
1.15	0.2	93%	88,794		
1.13	0.08	96%	74,173		
1.13	0.15	93%	71,092	92%	85%
1.13	0.2	83%	65,987		
1.1	0.08	63%	45,627		
1.1	0.15	55%	42,114	59%	45%
1.1	0.2	47%	40,086		
1	0.15	0	6485		
0.9	0.15	0	520		

The value X_{2010} is the stock level in the last period of simulation which corresponds to 2010.

We can observe in Table 3 that, regardless of the level of demographic uncertainty, the case of compensation estimated by conventional regression methods (C = 1.3) does not fit the observed dynamics due to the fact that there is a low probability that the stock level in the last period of simulation will fall within CIDFO (4), $P(X_{2010} \in CIDFO_{2010}) \in [2\%, 9\%]$, (column 3 for C = 1.3). Indeed, the expected mean stock value achieved under compensation, X_{2010} (column 4), is at least three times higher than XDFO2010 = 129000. If compensation is at work, the NCS should have recovered to a higher population size during the moratorium.

In the same table we can also see that critical depensation (C = 0.9), does not fit the observed dynamics either because the stock is eventually driven near to extinction in this case. Similar results were obtained for the case of C = 1.

Table 3 shows us that depensation at low population sizes $C \in [1.13, 1.19]$ are the population dynamics of best fit for the observed dynamics during the moratorium period. In particular, C = 1.15 is the case of best fit for the observed dynamics since $P(X_{2010} \in CIDFO_{2010}) = 98\%$, and $X_{2010} = 101157$ is close to the XDFO2010 =129000 (columns 3 and 4 for the case of C = 1.15 and $\sigma_b = 0.08$).

Fig. 7 represents the observed dynamics estimated by the DFO (2011a) from 1994 onwards (moratorium period), the confidence intervals (error bars) on the stock values estimated by the DFO, and three stochastic simulated population dynamics for the cases of C = 1.3, C = 1.17 y C = 1.15. We can observe in this figure that compensation (C = 1.3) does not concur with the observed dynamics. In this case, the simulated dynamics fits the observed dynamics for the period 1995–2000 but the stock drastically increases from 2000 onwards,

Fig. 6. Per capita recruitment function at low stock levels for different values of C.

which indicates that it should have recovered to a higher population size during the moratorium.

We can observe in Fig. 7 that the cases of depensation, C = 1.17 and C = 1.15, are the population dynamics that best describes both the observed growth pattern of the species during the moratorium, slow growth with backward movements, and year-to-year predictions. In particular, they fit the observed dynamics for 13 years of the whole 16-year moratorium. In the case of C = 1.17, we can observe that the simulated population dynamics does not fit the observed dynamics for the period 2003–2005, when there was a drastic decrease in the stock. There is a similar lack of fit in the case of C = 1.15 for both the year 2003, when there was a drastic decrease in the stock, and the period 2007–2008, when there was a drastic increase. It should be noted that, in both cases, the three periods of bad fit for the observed dynamics correspond to high stock level fluctuations. This may be due to cohort effects, which cannot be detected by smooth stochastic dynamics of aggregate fish stocks.

Thus, in contrast to the compensation estimated by classic bioeconomic models, our numerical experiments show that the observed collapse and non-recovery of NCS, even when a moratorium is currently in effect, can be due to the combined effects of demographic uncertainty and depensation at low population sizes.

Additionally, a sensitivity analysis associated with *BP* was performed to test the robustness of our results. The normalized stock levels *BP* analyzed in Table 3, BP = 0.059 (330,000 tons) (column 6) and BP = 0.0375 (210,000 tons) (column 5), are the alternative estimated values of the stock for 1991 and 1992, respectively, which marks the beginning of the drastic decline in the NCS (Bishop et al., 1994; Rivard, 1994). We can observe in Table 3 that, regardless of stock levels *BP*, depensation is the population dynamics of best fit.

5. Testing the Safety on Limit Reference Points

Based on the precautionary approach (PA), the DFO suggested a conservation limit reference point (LRP) for the NCS. The LRP was established to be 300,000 tons of SSB which corresponds to a total
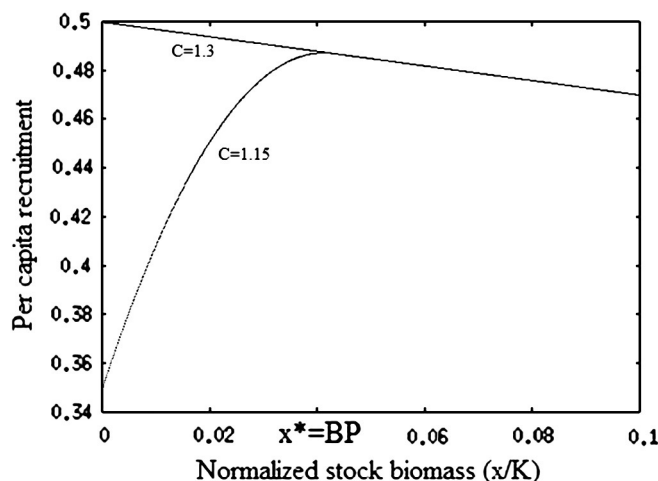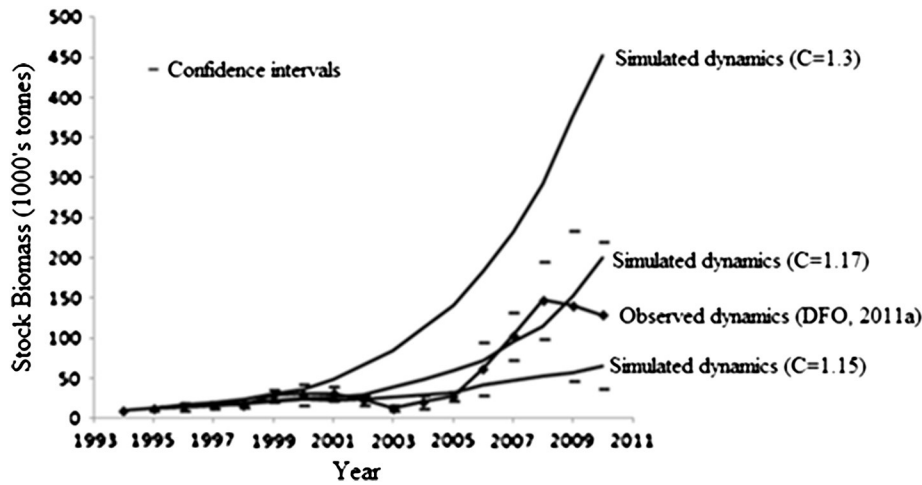
Fig. 7. Observed dynamics estimated by the DFO (2011a) from 1994 onwards (moratorium period), the confidence intervals (error bars) on the stock values estimated by the DFO, and three stochastic simulated population dynamics for the cases of C = 1.3, C = 1.17 y C = 1.15. In all cases, $\sigma_b = 0.15$.

stock biomass of 1.2 million tons (DFO, 2011b). In this section, the safety of the LRP is tested by analyzing the opportunity cost, in terms of longer stock recovery time, of driving fish stocks to collapse. In particular, we use the SPM to establish total stock biomass thresholds below which NCS would take a long time to recover.

According to the arguments provided above, in the numerical experiments that follow it is assumed that the population dynamics, as defined in (5), exhibits depensation (C = 1.15) at low population sizes ($x_t \leq BP$). The expected recovery time (ERT) is defined as the expected time, from the initial condition X_0, required to rebuild the NCS to LRP levels or greater, with probability P(X > LRP). The value X_{ERY} is the stock achieved in the expected year of recovery.

Table 4 summarizes the relevant results from the numerical analysis of the stochastic population dynamics (5) for different initial condition values X_0, which in turn imply different stock biomass thresholds.

Based on the stock value estimated by the DFO for 1992 (the official start of the moratorium), XDFO1992 ∈ [108000,174462] (DFO, 2012; Rivard, 1994), columns 1 and 2 in Table 4 show that the stock should have fully recovered after a 12 to 14-year moratorium, and that there is also a high probability (95%, column 3) of achieving a healthy stock value of $X_{ERY} \approx 1,900,000$ tons (column 4) even in the case of depensation (C = 1.15). However, as described in Section 2, the non-compliance with the moratorium in 1992 and 1993 would have driven the species to extremely low levels in 1994, $X_{1994} = 10,000$ tons, from which the stock will take a long time to recover. In particular, we can see in Table 4 that, from the initial condition $X_0 = 10,000$, a 32-year moratorium, from 1994, is required to rebuild the stock to above LRP levels.

These results concur with recent stock assessments (DFO, 2012), which concluded that at current levels of recruitment and survival the stock will not reach the LRP in the short term. These results also concur with the data reported by Safina et al. (2005). They show that for species with low enough growth rates, as estimated by the SPM for the NCS, stock recovery could take roughly between 30 and 40 years.

Based on the arguments given above and considering that XDFO1991 ∈ [242000,739397] (DFO, 2012; Rivard, 1994), columns 1 and 2 in Table 4 show that if a fishing moratorium had been instituted in 1991 the stock should have fully recovered in 6 to 11 years.

Furthermore, using ICES' terminology (ICES, 2003), to reduce the risk of biomass falling below LRP, the biomass should in practice be kept above LRP. Thus, the DFO should apply a buffer zone by setting a higher biomass reference point Bpa (the biomass precautionary approach reference point). In particular, we can see in Table 4 that, as long as the biomass is at or above Bpa = 145,6000 tons, the probability of it dropping below LRP should be low. Seeing that this Bpa coincides roughly with the average biomass estimated during the 1980's (DFO, 2011a), steps should have been taken at that time to avoid the current collapse of the species. These results concur with recent stock assessments (DFO, 2010) which concluded that the 1980's was the last time any reasonable recruitment was seen. The biomass has been lower than the estimated Bpa after the 1980's and recruitment has been poor, indicating that the stock has dropped to a level where serious harm occurs.

Our numerical analysis, therefore, shows that both a delay in the implementation of a fishing moratorium and non-compliance during the first two years of that moratorium drove the species to levels that were so low that the growth function exhibits depensation and the species, consequently, fail to recover.

6. Discussion and Conclusions

Knowledge of population dynamics of fish stocks at low population sizes is crucial in order to avoid the collapse and non-recovery of marine species. The lack of flexibility at low population sizes of the growth functions estimated using conventional regression methods can lead to an overestimation of the growth rate of the species. The a priori assumption of compensation, made by conventional models, does not concur with the observed lack of recovery of depleted stocks.

In this paper we have developed an SPM which allows us to detect depensation in collapsed fisheries. The concept of depensation remains one of the most controversial issues in population dynamics. For most marine populations the likelihood of depensation is completely

Table 4
Numerical results in the stochastic case for C = 1.15, $\sigma_b = 0.15$, $\sigma_\beta = 0.08$, and different initial condition values X_0.

X_0	ERT	P(X > LRP)	X_{ERY}
10,000	32	96%	2,846,723
20,000	26	96%	2,642,967
40,000	20	95%	2,111,692
80,000	16	97%	2,091,924
108,000	14	95%	1,899,236
174,000	12	96%	1,913,409
242,000	11	98%	2,050,190
739,000	6	95%	1,788,677
1,100,000	5	95%	1,818,941
1,456,000	1	100%	1,223,193

The value ERT is the expected recovery time, from the initial condition X_0, with probability P(X > LRP). The value X_{ERY} is the stock achieved in the expected year of recovery.

unknown (Clark, Chap. 2, 2006). The reasons given in the literature for the lack of statistical evidence are both the lack of data at low population sizes, and the absence of adequate scientific information on how multiple uncertainties affect the population dynamics of fish stocks when they decline significantly. The long-term projections undertaken by the DFO (2011b) to explore the risk of further declines in population suffer from high levels of uncertainty. They should thus not be interpreted as forecasts of future stock status as they are dominated by process error (uncertainty in recruitment rates, mortality rates, etc.). In this sense, their utility is not in providing probabilities of specific outcomes but rather in defining the uncertainty (DFO, 2011b). Thus, it is rare for stock recoveries to coincide with projected rebuilding curves due to inappropriate projection methods, a failure to account for the uncertainty and/or a failure to understand the underlying processes of population dynamics (Nash et al., 2009). In the case of the NCS, this is reflected in the inability to rationally explain the historical trajectory of the species which in turn weakens ongoing attempts to develop credible assessments of this stock (Shelton and Lilly, 2000).

Considering demographic uncertainty, in this paper we have shown that the flexibility of the SPM at low stock levels and the existence of data for collapsed fisheries allow us to partially overcome the above difficulties. Thus, we claim that, at least in the case of NCS, the rigidity of the growth functions estimated by conventional regression methods is really the reason why statistical evidence of depensation is lacking. If we bear in mind that most marine fishes which have suffered dramatic population reductions have experienced little, if any, recovery even when fishing mortality has been reduced following stock collapse, the possible existence of depensation, which cannot be detected by classic bioeconomic models, is something that must be considered, and may even be a concern.

If, as our numerical analysis suggests, depensation does exist, then limit reference points based on compensation, and used in conventional fisheries management, are likely to be inaccurate and possibly non-conservative. In this setting, the collapse and non-recovery of marine species, far from being surprising, should perhaps be considered normal. In the case of the NCS, there is strong evidence that both overexploitation and management actions that were risk-prone were the main causes of the collapse (Shelton, 2007). The weak link between science and decision-makers during the past two decades, as well as the perceived low credibility of scientific knowledge, has resulted in an underutilization of science capacity to evaluate management strategies for robustness to uncertainty and compliance with the precautionary approach (PA) (Shelton, 2007). To evaluate progress towards recovery and sustainability targets, peer reviewed science-based PA reference points are required in order to restore populations to levels that are above the points at which their productivity may become seriously threatened. In this paper, the safety of limit reference points has been tested and a Bpa has been suggested to lower the risk that biomass fall below LRP. In this sense, the SPM can provide a useful tool for testing science-based PA reference points by analyzing the risk of collapse of endangered species, and by predicting recovery rates when population abundance is low.

Taking into account that the NCS collapse has cost the Canadian taxpayers at least $4 billion (Krebs, 2008), there is a fundamental question that needs to be answered: How then should fisheries be managed in view of the likelihood of depensation? The SPM can provide a useful tool for answering this question by incorporating it into a bioeconomic model to obtain optimal management strategies using dynamic optimization techniques.

If age specific data are available, the SPM could also be used in age-structured models (AEM) to detect depensation in the spawner–recruit relationships (SRR) by smoothly interpolating the SRR between the origin and the stock level *BP* below which there has been a drastic decrease in recruitment. However, in the case of the NCS, the biomass approach has no obvious extension to AEM due to the lack of appropriate data. The last Virtual Population Analysis based assessment of the

stock was conducted in 1992 (pre-moratorium period, DFO, 2010). The data for the moratorium period are only available from the DFO autumn research vessel surveys. The changes in age composition in the survey catch rates, due to a switch in survey gears which occurred in 1995, would have an impact in the estimation of an appropriate stock-recruitment function (DFO, 2011b). Thus, both economic and research efforts should be devoted to the production of appropriate data.

Research in these directions is in progress.

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