

## DETERMINISTIC POPULATION DYNAMICS OF FISH STOCKS AT LOW POPULATION SIZES: A PARAMETRIC SPLINE APPROACH

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### ABSTRACT

We develop a methodological approach using splines to analyze the deterministic population dynamics of fish stocks at low stock levels. Considering the aggregate Northern cod stock by way of illustration, we reject the hypothesis of strong compensation estimated by the conventional regression methods used by classic bioeconomic models.

Keywords: Population Dynamics; Compensation; Depensation; Northern Cod Collapse; Splines.

### INTRODUCTION

Conventional regression methods are used by classic bioeconomic models to show that the concave growth function of marine fishes exhibits strong compensatory dynamics at low population sizes (high values of the maximum population growth rate) in which the intrinsic growth rate increases as the population decreases (Clark, 2006, Chap. 2).

The idea underlying strong compensatory dynamics is that marine fishes are highly resilient to large population reductions due to a high intrinsic capability to recover from low population sizes. However, there is very little evidence for population recovery from prolonged declines. 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 (Hutchings, 2000, 2001).

Using the biomass approach (surplus production model), in this paper we develop a spline methodological approach to analyze the deterministic aggregated stock dynamics of fish stocks at low stock levels. Considering the aggregate Northern cod stock by way of illustration, we reject the hypothesis of strong compensation estimated by classic bioeconomic models.

### THE NORTHERN COD FISHERY

One of the most dramatic collapses in the history of fisheries has been the collapse of the Northern cod fishery. Northern cod, comprising populations of Atlantic cod (*Gadus morhua*) of 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 stock collapsed in 1992 and a moratorium on fishing had to be imposed. After a 20 year moratorium, the fishery still has not recovered (Department of Fisheries and Oceans (DFO), 2012).

Using conventional nonlinear regression methods, and data for the total biomass (ages 3 and older) for the period 1962-2010 (Rivard, 1994; DFO, 2011), a logistic natural surplus growth function  $F(x)$  can be estimated for the Northern cod stock

$$F(x) = rx\left(1 - \frac{x}{K}\right), \quad (1)$$

where  $x$  is the biomass,  $F(x)$  is its natural growth,  $r=0.296847$  is the estimated intrinsic growth rate, and  $K=5.6$  (million tonnes) is the environmental carrying capacity.

The discrete population dynamics for the species is given by

$$x_{t+1} = x_t + F(x_t) - h_t, \quad (2)$$

where  $h_t$  is the total harvest at period  $t$ . By defining  $f(x_t) = x_t + F(x_t)$  as the growth function of the species, equation (2) can be rewritten as

$$x_{t+1} + h_t = f(x_t). \quad (3)$$

Taking into account the above estimated intrinsic growth rate, the population dynamics (3) exhibits strong compensatory population dynamics due to the high estimated maximum population growth rate  $r_{max}$  as measured by the slope of the growth function at the origin ( $r_{max}=f'(0)=1+r\approx 1.3$ ) (see also Grafton et al. 2009, and Grafton et al. 2000 for the pre-moratorium period (1962-1991), where the estimated intrinsic growth rates were also  $r=0.3$ ).

Thus, the standard growth function of the species estimated by conventional regression methods exhibits strong compensation ( $r_{max}=f'(0)=1+r\approx 1.3$ ) even if the extremely low stock levels from 1992 onwards are considered in the estimation process. Based on strong compensatory population dynamics the effects of overfishing are reversible and the species should have recovered to a higher population size during the moratorium. Therefore, the strong compensatory population dynamics estimated by classic bioeconomic models does not match with the fact that the Northern cod stock has failed to recover despite the moratorium.

### SPLINE PARAMETERIZATION METHOD

In this section we describe a spline parameterization method (SPM), using the Northern cod stock by way of illustration, in order to analyze the deterministic dynamics of aggregate fish stocks at low population sizes. 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 Northern cod stock,  $BP=242,000$  tonnes (Rivard, 1994). This is the value of the stock for 1991 which is the beginning of the drastic decline in Northern cod stock.
- ii) An empirical growth function of the resource, as defined in (3), is estimated, at high enough stock levels  $x \geq BP$ , by conventional regression methods.
- iii) A family of splines is constructed to achieve a smooth interpolation of the growth function  $f(x)$  between the origin and *BP*.

A spline is a cubic polynomial for smooth interpolation between two points of a curve. In our model, the spline is constructed as follows:

$$x_{t+1} = Ax_t^3 + Bx_t^2 + Cx_t + D, \quad (4)$$

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  $BP$  so that the spline smoothly interpolates the empirical growth function  $f(x)$  estimated in *ii*) at  $BP$ .

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 the same empirical growth function estimated in *ii*) when stock levels are high enough  $x \geq BP$ . In particular, compensatory population dynamics exist for  $C \geq 1$ , and depensatory population dynamics exist for  $0 \leq C < 1$ .

In the case of the Northern cod stock, and using the SPM described above, the deterministic population dynamics at low stock levels is given by:

$$x_{t+1} = f(x_t) - h_t = Ax_t^3 + Bx_t^2 + Cx_t + D, \quad (5)$$

where  $x_t \leq BP$ ,  $h_t = 0$  due to the moratorium, and  $f(x_t)$  is the growth function which is a spline as defined in (4).

## NUMERICAL RESULTS

The deterministic population dynamics of Northern cod at low stock levels (during the moratorium period) can be illustrated through numerical experiments which use the SPM to simulate the population dynamics of the species from the beginning of the moratorium onwards.

In the numerical experiments that follow it is assumed that the population dynamics at low stock levels ( $x_t \leq BP$ ) is as defined in (5), where  $BP = 242,000$  tonnes (see *i*) in previous section), and  $x_0 = 10,000$  tonnes the initial value of the stock in 1994 which corresponds with the start of the moratorium. Using these parameter values, different deterministic population dynamics at low population sizes ( $x_t \leq BP$ ) can be numerically simulated, from the initial condition  $x_0$ , by interpolating smoothly the growth function  $f(x)$  between the origin and the stock value  $BP$  using different splines (different values of the slope of the spline  $C$  at the origin in (5)).

Table I summarizes the relevant results from the numerical analysis of the deterministic population dynamics for Northern cod, for different values of slope of the spline  $C$  at the origin (column I).

**Table I. Numerical results for different values of slope of the spline  $C$  at the origin**

C	$X_{2010}$	RT	RY	$X_{RY}$
1.3	610400	19	2013	1209600
1.25	453600	21	2015	1433600
1.2	304640	22	2016	1260000
1.15	174160	25	2019	1478400
1.1	83440	28	2022	1327200
1.05	36480	35	2029	1467200
1	15120	54	2048	1304800
0.95	6496	-	-	-
0.9	2352	-	-	-

**The value  $X_{2010}$  is the stock level in the last period of simulation which corresponds to 2010. The value RT is the expected recovery time which is defined as the time required for Northern cod stock to reach or surpass the limit reference point (LRP). The value RY corresponds to the year in which the stock has been rebuilt. The value  $X_{RY}$  corresponds to the stock achieved in the year of recovery (RY).**

We can observe in Table I that the case of strong compensation estimated by conventional regression methods,  $C=1.3$ , does not fit the observed dynamics for several reasons:

1. The stock level in the last period of simulation achieved under strong compensation,  $X_{2010} = 610400$  (see column II for the case of  $C=1.3$ ), is five times higher than the most recent DFO stock estimation for 2010,  $X_{2010}^{DFO} = 129000$  (DFO, 2011).

Based on the precautionary approach, the DFO suggested a conservation limit reference point (LRP) for the Northern cod stock. The LRP was established to be 300000 tonnes of spawning stock biomass (SSB) which corresponds to a total stock biomass of 1.2 million tonnes (DFO, 2010). As an illustrative exercise we next explore the recovery time (RT) for the Northern cod stock in the deterministic case. The RT is defined as the time required to rebuild Northern cod stock to above LRP levels.

2. Columns III and IV in Table I show that in the case of strong compensation,  $C=1.3$ , the stock can be rebuilt to healthy levels by 2013. In particular, the stock would surpass the LRP and achieve a stock value of  $X_{RY}=1209600$  tonnes (column V) in 2013 which is nine times higher than the stock level estimated by DFO for 2010,  $X_{2010}^{DFO} = 129000$ .

It should be noted that similar results were obtained for the cases of  $C=1.25$  and  $C=1.2$  (see Table I).

Thus, strong compensatory population dynamics does not concur with the observed dynamics for the northern cod stock. Indeed, the most recent stock assessment concluded that the stock has been well below the LRP since the early 1990s and in 2010 was 90% below the LRP (DFO, 2012). Therefore, the stock is so depleted that it cannot be rebuilt by 2013 as predicted under strong compensation.

We can observe in Table I that dependant population dynamics ( $C=0.95$ ,  $C=0.9$ ), also do not fit the observed dynamics because the stock is eventually driven to extinction in these cases.

We can also observe in Table I that, in contrast to the strong compensation estimated by conventional regression methods ( $C=1.3$ ), weak compensatory population dynamics at low population sizes ( $C=1.05$ ,  $C=1.1$ , and  $C=1.15$ ) 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 for two reasons:

1. The stock value achieved under weak compensation,  $X_{2010} = 174160$  (column II for the case of  $C=1.15$ ), is close to the stock level estimated by the DFO for 2010,  $X_{2010}^{DFO} = 129000$ .

2. The RT (columns III and IV for the case of  $C=1.15$ ) is longer than that obtained when  $C=1.3$ , strong compensation. Specifically, the stock would reach and surpass the LRP in the next seven years. This is a reasonable recovery time taking into account both the absence of uncertainty and the species' lack of recovery.

## CONCLUSIONS

Using the biomass approach, in this paper we have developed a SPM which allows us to numerically analyze the deterministic population dynamics of collapsed fisheries. In the case of the Northern cod, we have shown that the hypotheses of strong compensatory population dynamics at low population sizes can be rejected.

It should be noted that, taking into account the absence of uncertainty, we cannot conclude from the above findings that weak compensatory population dynamics at low population sizes are the population dynamics of best fit for the observed dynamics during the moratorium period. The SPM must be extended to stochastic population dynamics models. Research in this direction is in progress.

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