RAPID COMMUNICATION / COMMUNICATION RAPIDE

Should depensation be dismissed as a possible explanation for the lack of recovery of the northern cod (*Gadus morhua*) stock?

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Abstract: After 7 years of a moratorium on northern cod (*Gadus morhua*), there is no convincing evidence that recovery has commenced. Under the simple assumption of linear density dependence, rapid population growth is predicted. That this has not transpired leads to consideration of less simple assumptions regarding density dependence, such as depensation.

Résumé : Après sept ans de moratoire sur la pêche de la morue du Nord, nous n'avons aucune preuve convaincante d'un début de rétablissement. Sur la base d'une simple hypothèse de dépendance linéaire à l'égard de la densité, on prévoit une croissance rapide de la population. Le fait que cela ne se soit pas vérifié appelle à envisager des hypothèses plus complexes quant à la dépendance à l'égard de la densité, et notamment la dépensation.

[Traduit par la Rédaction]

Simple compensatory models of collapse and recovery

The underlying model that is generally assumed in fisheries assessments is decreasing recruits per unit spawner biomass with increasing spawner biomass. This leads to a spawner stock-recruit function in which recruitment initially increases with increasing spawner biomass and then either reaches an asymptote (Beverton-Holt model) or reaches a peak and then declines (Ricker model). Declining per capita reproductive success with increasing stock size, characteristic of both Beverton-Holt and Ricker models, is termed a "compensatory" response.

The amount of recruitment required to replace the spawner biomass that gave rise to it depends on the postrecruit mortality rate and weights and proportion mature at age. Where these quantities remain constant over time, replacement recruitment can be plotted as a straight line through the origin in the stock-recruit plot, the slope being determined by the postrecruit mortality rate, weight, and maturity values. For constant maturity and weight at age (common assumptions), the slope of the line depends only on postrecruit mortality rate, steeper slopes being associated with higher mortality. When recruitment exceeds the amount

Received May 12, 1999. Accepted July 10, 1999. J15137

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¹Author to whom all correspondence should be addressed. e-mail: shelton@athena.nwafc.nf.ca required to replace the spawner biomass, the population will increase, whereas when it falls below replacement, the population will decline. Equilibrium points occur where the replacement line intersects the recruitment curve. There is a single, nonzero, stable equilibrium point for the Beverton–Holt and Ricker models at moderate exploitation levels.

Based on these simple models, it can be predicted that overharvested stocks will recover to a stable equilibrium at higher spawner population size when fishing mortality is removed, since the slope of the replacement line decreases and intersection with the recruitment curve occurs at a higher spawner biomass. The northern cod (*Gadus morhua*) stock off the east coasts of southern Labrador and Newfoundland has been under a moratorium on commercial fishing since July 1992. However, in the most recent assessment (Lilly et al. 1999), 7 years later, there is no convincing evidence that recovery has commenced.

Depensation and the predator pit

One explanation for lack of recovery of northern cod is that per capita reproductive success (recruits per unit spawner biomass) has declined, perhaps as a result of increased predation on prerecruit fish. When reproductive success declines with decreasing population size, this is termed "depensation." Depensation can cause a second, lower equilibrium point to exist, depending on the slope of the replacement line. This equilibrium point is unstable: any variation in recruitment or spawning stock biomass will cause the population to either grow towards the upper, stable equilibrium point or to collapse to zero. Existence of depensation could therefore slow recovery. If the number of recruits per spawner decreases over some range of low stock sizes, but increases again at even lower stock size, then the potential arises for a second stable equilibrium point to occur where the replacement line intersects the recruitment curve. This "predator pit" phenomenon (Walters 1986, p. 83) could occur in cod if, for example, predator abundance and predation rates on prerecruits do not initially decrease with decreasing cod abundance, but predators switch to alternative prey at some low level of cod abundance. The predator pit provides a mechanism for prolonged low abundance even after fishing mortality has been removed. Recovery would require one or more year-classes that are strong enough to allow the population to escape the predator pit. If mortality is reduced, the slope of the replacement line decreases, increasing the probability of recovery.

Is depensation common in fish stocks?

We are unaware of any attempt to statistically examine stock-recruit data for the predator pit model. However, Myers et al. (1995a) analyzed spawner stock-recruit data for 128 fish stocks (Myers et al. 1995b) for which there were 15 or more years of data to determine whether there was evidence that depensation existed in a significant number of stocks. Only three of 128 stocks showed statistically significant evidence of depensation at the 0.05 level. Through an analysis of statistical power, Myers et al. (1995a) concluded that, if depensation did in fact occur in these stocks, more than three of 128 stocks would be expected to have indicated significant depensation. On the basis of the large sample size, they concluded that depensation does not generally occur in fish stocks and, consequently, the effects of overfishing are reversible. In the absence of depensation, Myers et al. (1997) predicted an annual growth rate of 19% for northern cod following collapse. After 7 years of moratorium on commercial fishing, the stock should have more than tripled in size.

Myers et al.'s (1995a) power analysis

Leaving aside the more difficult (but perhaps more relevant) problem of evaluating the applicability of the predator pit model, we examined the analysis of statistical power performed by Myers et al. (1995*a*) and found that, while having the advantage of being empirically based, it is complicated and leads to an inappropriate estimate of power. We carried out an analysis which, although not empirically based, is more defendable and, from the results, contend that it would be difficult to detect significant depensation at the 0.05 level for most cod populations.

In the analysis by Myers et al. (1995a), the model fitted to the data is the depensatory form of the Beverton–Holt model:

$$R = \frac{\alpha S^{\delta}}{1 + (S^{\delta}/K)}$$

where *R* is recruitment, *S* is spawner biomass, α is the slope of the recruitment curve at *S* = 0, αK is the asymptote, and δ is the depensation parameter. When $\delta = 1$, there is no depensation; depensation occurs for $\delta > 1$. Myers et al. (1995*a*) assumed a lognormal distribution (shape parameter

σ) of residual variability caused by natural variation and measurement error. Myers et al. (1995*a*) obtained maximum likelihood estimates of model parameters with δ = 1 and δ free and performed a likelihood ratio test to determine the significance of improvement in fit for δ free. For nine of the 128 stocks, the model with δ as a free parameter gave a significantly better fit at the 0.05 level, but in only three of these cases was δ significantly greater than 1.

To carry out their power analysis, Myers et al. (1995*a*) first estimated α and *K* with $\delta = 1$ under the constraint that asymptotic recruitment could be no greater than maximum observed recruitment (we call this the constrained non-depensatory Beverton–Holt model) for each of the 128 stocks. They then set $\delta = 2$ and constructed (as opposed to fitted) a depensatory model for each stock that matched the constrained nondepensatory Beverton–Holt model at both 50% asymptotic recruitment and asymptotic recruitment (we call this the constructed depensatory model). We denote the parameters (α and *K*) of the fitted constrained nondepensatory Beverton–Holt model at both 50% the constructed depensatory model. We denote the parameters (α and *K*) of the fitted constrained nondepensatory Beverton–Holt model with subscript "f" and those of the constructed depensatory model with subscript "c." Applying the two constraints required for the constructed depensatory model, one obtains

$$R = \frac{\alpha_{\rm c} S^{\delta}}{1 + (S^{\delta}/K_{\rm c})}$$

where $\alpha_{\rm c} = \frac{\alpha_{\rm f}}{K_{\rm f}^{\delta-1}}$ and $K_{\rm c} = K_{\rm f}^{\delta}$.

Myers et al. (1995a) generated fake recruitment values at each of the observed spawner biomass values for each stock from a lognormal distribution with shape parameter σ estimated from the fitted constrained nondepensatory Beverton-Holt model and mean from the constructed depensatory model. They then fitted nondepensatory and depensatory Beverton-Holt models to the simulated data, as was done initially on the real data, and performed the likelihood ratio test for depensation. The model fits and likelihood ratio test were repeated on 100 sets of simulated recruitment data generated for each stock to estimate the statistical power. They found that at the 0.05 significance level, statistical power for detecting $\delta > 1$ was greater than 0.95 for 26 of 128 stocks for which data were simulated. Based on this result, they argued that if depensation is a general phenomenon in fish populations, they would have expected more than three of the 128 stocks examined to show significant depensation.

We applied the Myers et al. (1995*a*) approach to a hypothetical case. We arbitrarily selected $\alpha = 5$, K = 200, $\sigma = 0.6$, and $\delta = 2$ to give a depensatory Beverton–Holt stock recruit function from which 30 fake recruitment data points were generated for a range of spawner biomass values selected randomly from a uniform distribution between zero and the spawner biomass corresponding to 95% of the asymptotic recruitment (Fig. 1A). We then compared the fit of depensatory and nondepensatory Beverton–Holt models to the data using a likelihood ratio test and found that the depensatory model did not provide a significantly better fit at the 0.05 level. A constrained nondepensatory Beverton–Holt model was then fit to the data generated from this curve. Using the estimated parameters of this function, **Fig. 1.** (A) Depensatory Beverton–Holt stock–recruit function (bold solid line) defined by arbitrarily selected parameters $\alpha = 5$, K = 200, $\sigma = 0.6$, and $\delta = 2$ from which 30 data points were randomly generated. Fits of nondepensatory (light broken line) and depensatory (light solid line) models are compared. (B) Constructed depensatory model (bold solid line) based on the data in Fig. 1A (see text for details) from which a second set of 30 recruit data points were randomly generated. Fits of nondepensatory (light broken line) and depensatory (light solid line) are compared.



we followed the approach of Myers et al. (1995a) and constructed a depensatory model from which a second set of 30 fake recruitment values were generated, corresponding to spawner biomass values as in Fig. 1A, from a lognormal distribution with σ estimated from the fitted constrained nondepensatory model (Fig. 1B). We then compared the fit of the nondepensatory and depensatory Beverton–Holt models to the data generated from the constructed depensatory model and found that the depensatory model provided a

significantly better fit at the 0.05 level. We repeated this exercise 100 times, and in 95% of the cases where the depensatory model did not provide a significant fit to the original data, a significant fit was obtained for a depensatory model applied to the data generated from the constructed depensatory model. This general outcome was robust to a wide range of alternative parameter combinations, number of data points, and range and scatter of spawner biomass values. Thus, we concluded that the arbitrary choice of the form of the constructed depensatory model in the Myers et al. (1995*a*) study exaggerates the power of detecting depensation. Other choices may have led to lower estimates of power.

An alternative analysis

We carried out an alternative, less complicated power analysis that, in general terms, follows an established Monte Carlo approach (Peterman and Routledge 1983; Peterman and Bradford 1987; Peterman 1990). The model used to generate the fake data and the model for which the power is being evaluated are, unlike the Myers et al. (1995a) study, identical. The depensatory Beverton-Holt model was used to generate fake data. The fits of the depensatory Beverton-Holt model and the nondepensatory Beverton-Holt model were then compared. The model that we used to generate fake data was constrained to have the asymptote αK constant. To explore the effect of obtaining data scattered across different ranges of spawner biomass, the upper limit on the recruitment axis from which fake data were generated was set to a predetermined percentage of asymptotic recruitment. This was accomplished by restricting expected recruitment to αK and adjusting γ to explore various ranges of 0,

asymptotic recruitment. Since the range of recruitment values is fixed, adjusting the parameters of the Beverton–Holt model (α and *K* with αK constant) will simply rescale the spawner biomass axis. By scaling the spawner biomass axis

using a factor of $(\gamma K)^{1/\delta}$, power need only be determined for different combinations of δ and σ and for a range of data set sizes variously scattered on the spawner biomass axis.

For each simulation, we generated pseudorandom fake recruitment data (assuming lognormal error about the mean value predicted by the depensatory Beverton-Holt model) at randomly selected (uniformly distributed) spawner biomass values between zero and the predetermined maximum spawner biomass chosen for the trial. Nondepensatory and depensatory Beverton-Holt models were then fit to the data and the likelihood ratio test applied at the 0.05 significance level. This procedure was repeated 100 times for each trial, and 0.95 power isopleths were mapped corresponding to the 0.05 significance level. The isopleths for trials consisting of combinations of 30 and 60 years of data and exploring 90, 95, or 98% of asymptotic recruitment are plotted in σ - δ parameter space as examples (Fig. 2). Because of random variability within each simulation, the 0.95 power isopleths were approximated by applying a quadratic smoother to points in the range 0.93-0.97.

Fig. 2. Simulated approximate 0.95 power isopleths for detecting depensation at the 0.05 significance level in σ - δ parameter space for example trials: A, 60 years of stock-recruit data with spawner biomass range from zero to a spawner biomass corresponding to 90% of asymptotic recruitment; B, 30 years of data, 90% of asymptotic recruitment; C, 30 years of data, 95% of asymptotic recruitment; D, 30 years of data, 98% of asymptotic recruitment.



Depensation is difficult to detect and may be occurring in northern cod

Our results (Fig. 2) show that it will be hard to detect depensation unless δ is large, σ is small, the time series is long, and many data points are concentrated in the range of spawner biomass where depensation occurs (corresponding to a lower percentage of asymptotic recruitment in our analysis). Although our study lacks the empirical basis of the Myers et al. (1995*a*) study, our simulated power isopleths can be placed in an empirical context. For the 23 cod stocks illustrated in Myers et al. (1995*b*), 11 had data for more than 30 years, but for many of these, there is a paucity of data for spawner biomass levels where depensation might be expected to occur. Values of σ were generally high (often greater than 0.5, some greater than 0.8) for the non-depensatory Beverton–Holt model fit in these stocks. True values for δ are of course unknown.

If depensation is difficult to detect, it may not be as rare as previously suggested (also see Liermann and Hilborn 1997). Could it be occurring in northern cod? Recent data (Lilly et al. 1999) do not allow a formal test for depensation because bottom trawl surveys do not appear to be representative of the remaining fish, and accurate model estimates of population numbers at age have not been achieved. However, the remaining fish (upper limit estimated to be 150 000 t) occur in high densities in a few localities in the inshore. The harp seal population was estimated to be about 4.8 million in 1994 and growing at about 5% per year (Shelton et al. 1996). Stenson et al. (1997) estimated that in 1994, harp seals were consuming about 88 000 t of northern cod, mainly prerecruits. The proportion of cod in the nearshore diet of harp seals, although small, has not declined in recent years (G. Stenson, Department of Fisheries and Oceans, St. John's, Nfld., personal communication). These conditions are conducive to depensation. However, other explanations for apparent lack of recovery of northern cod under the moratorium also need to be given consideration, for example, loss of genetic components, continuing fishing activity, and environmental influences.

Acknowledgements

We thankfully acknowledge the comments of two anonymous reviewers that led to substantial improvements to the manuscript.

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