

REPLY COMMENT

Dynamics of the Norwegian Skagerrak cod: intuition vs inference**J.-M. Fromentin^{1,3,*}, O. N. Bjørnstad^{2,3}, N. C. Stenseth^{3,4}, J. Gjøsæter⁴**¹IFREMER, Centre Halieutiques Méditerranéen et Tropicales, BP 171, 34203 Sète cedex, France²Pennsylvania State University, Department of Entomology, 501 ASI Bld, University Park, Pennsylvania 16802, USA³University of Oslo, Division of Zoology, PO Box 1050 Blindern, 0316 Oslo, Norway⁴Department of Coastal Zone Studies, Institute of Marine Research, Flødevigen Marine Research Station, 4817 His, Norway

The comment by Johannessen (2002) criticizes our paper (Fromentin et al. 1997), which was the first in a series of studies on the dynamics of cod *Gadus morhua* along the Norwegian Skagerrak coast. Our 1997 article and subsequent papers published between 1998 and 2001 were the result of a close collaboration between marine ecologists, biologists, statisticians and theoretical population ecologists. Fromentin et al. (1997) aimed at describing the spatial and temporal patterns of recruits of Norwegian Skagerrak cod, pollack and whiting. (However, we only focus on cod in this reply since it has been the focus of the subsequent studies and mechanistic insights.) Our analyses showed important low and high frequencies, leading to bimodal spectra, as also suggested by Fig. 1 of Johannessen (2002, hereafter referred to as the 'TJ Comment'). Low frequencies reflect apparent long-term fluctuations, whereas the high frequencies primarily display a cycle at around 2 to 2.5 yr periodicity (which is the core of the TJ Comment). The spatial analyses indicate that the 0- and I-group cod were sympatric and exhibit strong habitat preferences (see also Fromentin et al. 2000). The spatial structure of the short-term fluctuations is seen to take place at a local scale (<20 km), whereas that of the long-term fluctuation occurs at a large scale. These results and other findings lead us to postulate that: (1) the 2 to 2.5 yr cycle was due to biotic interactions, and (2) the trends were of extrinsic origin. (Note that, contrary to what is implied in the TJ Comment, we never claimed that the 2 to 2.5 yr cycle was the dominant feature, as it may be also seen below.)

The first hypothesis was tested and validated by Stenseth et al. (1999), who used an autoregressive age-structured model, by Bjørnstad et al. (1999b), who developed a non-parametric and non-linear model

based on the GAM, and later by Fromentin et al. (2001), who investigated the local and regional differences in the strengths of the density-dependent and stochastic processes. Fromentin et al. (1998) investigated the second hypothesis and concluded that the trends were not related to large-scale climatic variation nor to variations in zooplankton abundance, but could be partially linked to changes in the bottom flora coverage. Bjørnstad et al. (1999a) gathered the pieces of this puzzle and showed that the high and low frequency signals in the Norwegian Skagerrak cod may in fact be closely linked. The significant asymmetric competition and cannibalism between 0- and I-group cod was found to have the potential of inducing long-term trends by resonating the recruitment variability (which is probably of environmental origin). Details aside, our work provides a mechanistic understanding of how stochasticity, age-structured, and external forcing can interact in fish populations to produce dual scales of variability: generation (or overcompensation) cycles and apparent trends.

Although we welcome critiques and critical scientific challenges of previously published results, the TJ Comment is, unfortunately, misguided for 2 main reasons. Firstly, it fails to properly embrace the dual scales of variability in cod abundance. Secondly, it relies on naïve intuition about a dynamical system that can be shown to be wrong by simple back-of-an-envelope calculations.

The TJ Comment makes the intuitively appealing conjecture that, if inter-cohort interactions occur, then strong (weak) cohorts should be followed by weak (strong) cohorts. Unfortunately, the test designed in the TJ Comment has extremely low power in the face of long-term fluctuations in abundance. While large cohorts will tend to be followed by cohorts that are smaller than the *temporally local* average cohort size, the majority of successive cohorts will tend to be either

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larger or smaller than the *temporally global* average because of the occurrence of long-term fluctuations (making the highest year-classes, including their subsequent years, not randomly distributed in red-shifted time series but found among periods of high abundance). Therefore, it is unlikely that the null hypothesis (successive cohorts are not more dissimilar than a randomized time series) can be rejected on the basis of this test. Johannessen ought to have embraced the dual scales of variability more properly and applied, at least, his intuitive test on detrended time series (he would thus have seen that cod abundance in subsequent years of strong year-classes is indeed well below the temporally local mean of the series). We hasten to add though that we would not advocate such a test, because it remains crude and has limited power. Rather, we advocate testing density-dependent mortality directly, using recent statistical methods described in the ecological literature. In our more recent work, we further found it particularly useful to employ methods that are robust to, or explicitly embrace, observational errors. In doing so, we used 3 unrelated statistical approaches: (1) the Myers (1993) variance components method (Fromentin et al. 2001), (2) the GAM method (Bjørnstad et al. 1999b), and (3) the MCMC applied to the state-space representation of the full age-structured model (Bjørnstad et al. 1999a). These all confirm significant within- and between-cohort interactions (albeit with significant spatial variation as conjectured by Fromentin et al. 1997).

A second central argument of the TJ Comment is that the absence of negative correlation between the 0- and I-group time series would negate any clear inter-cohort interaction. However, this is a case where intuition proves wrong, as such interactions are substantiated by simple calculations. Let us assume the following model for survival of the 0-group into the I-group, as reduced through density-dependent interactions within the 0- and the I-group cohorts:

$$N_{1,t} = N_{0,t-1} e^{-m + \alpha \ln(N_{0,t-1}) + \beta \ln(N_{1,t-1}) + \varepsilon_t}$$

where m represents the average density-independent mortality, α (<0) measures the strength of within-cohort interactions, and β (<0) measures the strength of between-cohort interactions. The last term, ε_t , is a random variable (with zero-mean) that represents stochastic year-to-year variation in survival. Taking the natural logarithms on both sides and collecting terms [denoting $\ln(N_1)$ by y , and $\ln(N_0)$ by x] gives:

$$y_t = -m + (1 + \alpha) x_{t-1} + \beta y_{t-1} + \varepsilon_t$$

From this it is clear that:

$$\begin{aligned} \text{Cov}(y_t; y_{t-1}) &= \beta \sigma_y^2 \\ \text{Cov}(y_t; x_{t-1}) &= (1 + \alpha) \sigma_x^2 \\ \text{Cov}(y_t; x_t) &= 0, \end{aligned}$$

where σ_y^2 is the variance of $\ln(N_1)$ and σ_x^2 the variance of $\ln(N_0)$. That is, inter-cohort interaction should lead to zero cross-correlation between the 0- and I-group and not to a significantly negative one, as intuited in the TJ Comment. (It should be noted that the above calculations are qualitatively identical, yet slightly more elaborate, in the presence of observation errors; see Fromentin et al. 2001).

From a more myopic (and more tedious) statistical and ecological viewpoint, the TJ Comment is littered with a number of other factual errors:

(1) Johannessen (2002) suggests that there are significant 'multiple testing problems' associated with our initial descriptive analysis (Fromentin et al. 1997), because he felt the error rates associated with the randomization tests of each individual spectrum are likely to be inflated, thereby casting doubt on the overall conclusions of our article. The line of reasoning in the TJ Comment is that the spectral analysis of Skagerrak cod relies on estimating the periodogram at $T/2$ frequencies (where T is the length of the time series). As part of general statistical theory, a periodogram-based test for whiteness needs to take into account the number of frequencies in the periodogram. The obvious solution (perhaps implicit in the TJ Comment) would be to use a (sequential) Bonferroni correction. This is, in principle, a good idea. However, it fails to embrace the fact that the randomization tests in Fromentin et al. (1997; and also Bjørnstad et al. 1999a) were not general tests for whiteness, but were dedicated towards testing for generation cycles (fluctuations with 2 to 3 yr periods) and long-term trend (a peak in the periodogram at the $T/2$ frequency as suggested by our exploratory multivariate analysis). Hence, on reflection—and while a slightly moot point—Johannessen is partially right: The randomization test in Fromentin (1997) should have been corrected for *dual* testing (one test at Nyquist frequency and one at the $T/2$ frequency). However, upon reanalysis, it makes no difference to the results nor to the overall conclusions. Johannessen suggests using instead the asymptotic test for whiteness, which has low power in the face of the hypotheses in question, making it harder to reject the null hypothesis. Irrespective of these considerations, these findings have only the weakest scientific bearings on the overall question of intra- and inter-cohort interactions, which have been addressed more directly in our recent studies (see above).

(2) Johannessen took great issue about our use of the first-order difference (FOD)—that is, analyses of time series of population growth rates rather than log-abundance—to correct for spurious results arising from underlying low frequency fluctuations. Perhaps without him realizing so, the TJ Comment nicely illustrates that it is necessary to make some allowance for

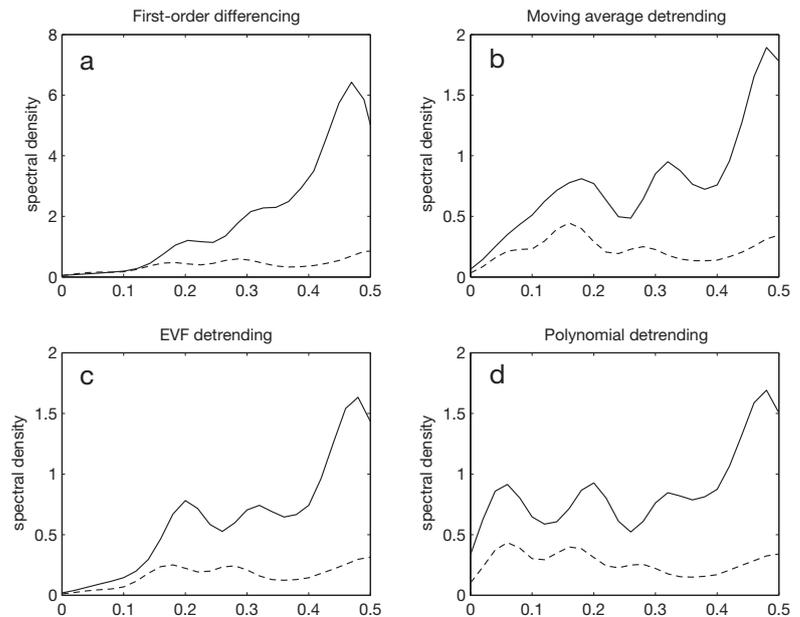


Fig. 1. Results of the spectral densities (using a Parzen window of width 5) computed on cod time series being previously detrended by 4 different methods. (a) First-order differenced data (i.e. same as Fig. 4a of Fromentin et al. 1997); (b) raw data, the moving average fit; (c) raw data, the Eigen-Vector Filtering (EVF); (d) raw data, the third-order polynomial fit. Whatever the detrending method, stations displaying cyclic fluctuations (solid lines) are all dominated by 2 to 2.5 yr cycles (frequencies between 0.4 and 0.5 yr^{-1}), whereas those displaying no special periodicity (dashed lines) remain mainly flat

low frequency fluctuations (see above). We did, however, take care of this in our randomization: Our null distributions were generated on the log-abundance (prior to the differencing) and thus carry the correct cover. We apologize for having communicated this somewhat ambiguously. We did also check that FOD did not generate spurious 2 to 2.5 yr cycles, as suggested in the TJ Comment. FOD is a powerful method to remove medium- to long-term fluctuations, but like all detrending methods (which more commonly consist in calculating the smoothing residuals; see Legendre & Legendre 1998), it can also slightly distort the signal at high-frequency. However, Fig. 1 clearly shows that our results are robust to the choice of the detrending method and that the 2 to 2.5 yr cycle is not an artefact but really part of the data.

(3) A related point of the TJ Comment is the non-standardization of the spectral densities when computing the principal component analysis (PCA) on the patterns of periodicity. Here again, the TJ Comment critique may appear correct as a general rule, but is invalid in our particular case simply because the patterns of periodicity of cod are related to the abundance (see Fig. 6a and the first paragraph of 'The 2 to 2.5 yr oscillation' section of the discussion in Fromentin et al. 1997). As stations of high abundance displayed a clear 2 to 2.5 yr cycle and those of low abundance displayed no clear periodicity (i.e. flat spectrum; see also Fig. 1), computing PCA on a correlation matrix (i.e. standardized spectral densities) or covariance matrix (i.e. non-standardized spectral densities) makes almost no difference (the correlation coefficient between the first components of both PCA is about 0.8).

(4) Another somewhat related point, but a misdirected accusation in the TJ Comment, is that the critique of our functional data analysis of differenced log-spectra of cod (Fromentin et al. 1997) casts doubt on the findings on our studies focusing on rodent dynamics (Bjørnstad et al. 1996, 1998). However, even if the TJ Comment had been valid on this point, it would, strictly speaking, only have applied to conclusions regarding fluctuations at the Nyquist frequency (the generation cycle). Our rodent analyses centered on the multiannual cycles in rodent abundance that would show up as *internal* peaks in periodogram analyses: hence; his argumentation has no bearing whatsoever on rodent dynamics. We will therefore not make any further remarks on this error.

This Reply Comment and the papers published between 1998 and 2001 clearly show that our earlier conclusions on the dynamics of the cod along the Norwegian Skagerrak coast remain valid. However, we are grateful to Johannessen (2002) for allowing us to emphasise this once more and to clarify any confusion that may exist about the age-structured interactions and population dynamics of the Norwegian Skagerrak cod. In a somewhat wider context, the TJ Comment allows us to emphasis 2 important scientific issues. Firstly, the danger that if one roots for the null hypothesis, one can always find the 'least-powerful' test to allow the null to persevere in the face of almost any contrary evidence. Secondly, it is important for biologists to work closely with mathematicians and statisticians, since there is always a danger of believing in naïve intuition in the face of complex ecological interactions.

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Editorial responsibility: Otto Kinne (Editor), Oldendorf/Luhe, Germany

*Submitted: September 10, 2002; Accepted: September 11, 2002
Proofs received from author(s): September 24, 2002*