

A NEW TEST FOR DENSITY-DEPENDENT SURVIVAL: THE CASE OF COASTAL COD POPULATIONS

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Abstract. A new test based on the generalized additive model is proposed to investigate density-dependent mortality in the juvenile cohorts of cod. Density dependence implies that the function linking the count of a cohort in one year to the count in the succeeding year is convex. The method estimates (without functional assumptions) the function linking the two counts and provides a level of significance for any convexity. We investigate the power and bias of the new test on the basis of simulated data. The power compares well with a test of unit slope in a log–log plot (although it is usually somewhat lower). However, in contrast to the latter method, the test for convexity is much more resistant to measurement error. We applied the model to long-term survey data from two areas of the Norwegian Skagerrak coast. In both cases, the variance is intermediate between the Gamma (variance proportional to the squared mean) and the Poisson (variance proportional to the mean) distributions. A negative binomial (with $k \approx 3.5$) describes the variance well. The variance is interpreted as resulting from sampling errors, spatial heterogeneity, and environmental stochasticity. Incorporating this error structure, the optimal models linking the two main juvenile stages are, for each area, nonlinear and significantly convex ($P < 0.05$). The full models are highly significant ($P < 0.001$), and the examination of the residuals does not reveal any remaining structure. We conclude that the survival of juvenile cod along the Norwegian Skagerrak coast is density dependent, probably because of cannibalism, competition for habitat, and food limitation. The functional form of density-dependence in the per capita survival rate is estimated to be approximately log-linear.

Key words: age-structured interactions; cannibalism; competition; *Gadus morhua*; Gamma variance; Generalized Additive Model; negative binomial distribution; Norway; Poisson variance; stochastic population dynamics; time series analysis.

INTRODUCTION

Fish stocks are known to fluctuate extensively over large spatial and temporal scales (e.g., Laevastu 1993, Cushing 1995). The early stages in the life cycle are believed to be critical in determining year class strength (May 1974, Cushing 1995). Survival has been related to abiotic factors, such as changes in temperature, salinity, wind field, and currents (e.g., Cushing 1982, 1995); human exploitation (Hutchings 1996, Myers et al. 1996, Cook et al. 1997); and biological processes, such as predation, competition, and cannibalism (Caley et al. 1996). Sundby et al. (1989) reported evidence suggesting that juvenile mortality in the northeast Atlantic cod is density dependent. Myers and Cadigan (1993) concluded that most of the marine demersal fish populations are regulated through density dependence that takes place during the juveniles stages.

There is, however, no consensus on the functional form of density dependence in fish (see, for example, Ricker 1954, Shepherd and Cushing 1990, Myers and Cadigan 1993). Indeed, uncertainty about functional forms for biotic interactions (such as density dependence and functional responses) is common in many areas of population ecology (see, for example, Abrams 1982, Hanski 1991, Boutin 1995, Pascual et al. 1997). In the following we develop a method that allows the estimation of density-dependent survival without making a priori assumptions about functional forms. From this, we develop a formal test of density dependence. When the test is applied to synthetic data, it is found to have good power and to be relatively resistant to measurement errors. We apply the method to census data of cod (*Gadus morhua*) populations along the Norwegian Skagerrak coast.

THE LIFE CYCLE OF THE NORWEGIAN SKAGERRAK COD

Fromentin et al. (1997) demonstrated significant periodic fluctuations in time series of the Norwegian Skagerrak cod population. The period was $\sim 2\text{-}1/2$ yr,

Manuscript received 26 June 1997; revised 4 May 1998; accepted 4 May 1998; final version received 22 June 1998.

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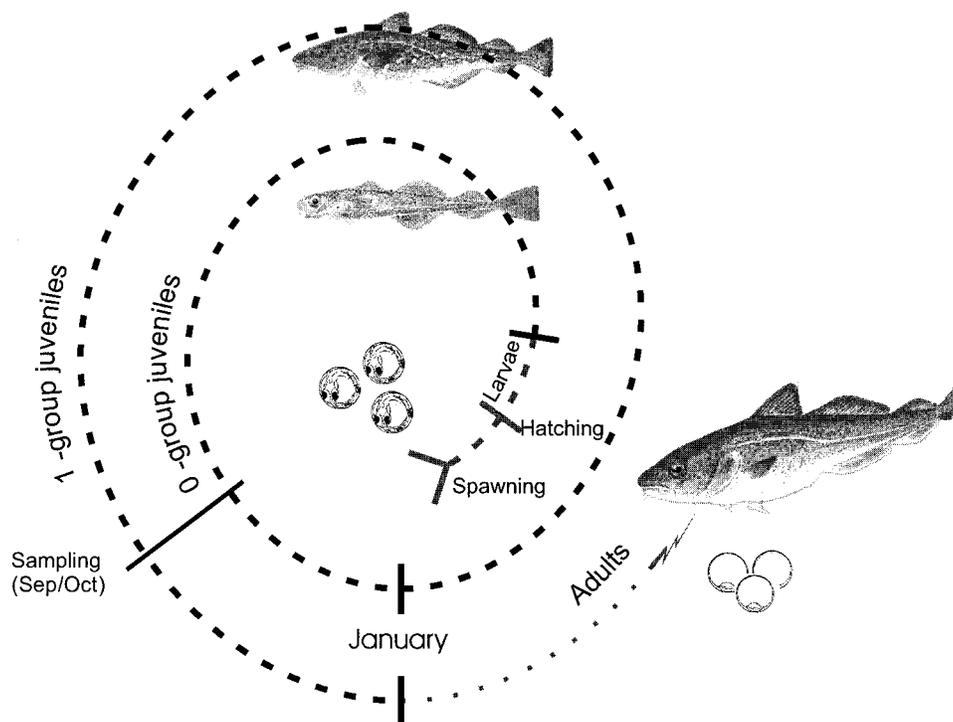


FIG. 1. The life cycle of cod (*Gadus morhua* L.) along the Norwegian Skagerrak coast can be summarized into four main stages: eggs (~2 wk in early March), larvae (~3 mo in the spring), juveniles (the following two years), and adults (maturation occurs at ~2–3 yr).

and the authors hypothesized that the periodicity might be related to interactions between the two main juvenile cohorts, leading to density-dependent mortality. We investigate the long-term data sampled in two different areas along the Norwegian Skagerrak coast in order to test for density-dependent survival. Firstly, we will provide a summary of the population ecology of the cod.

The life cycle of cod (*Gadus morhua* L.) can be divided into four main stages (Fig. 1): eggs (~2 wk), larvae (~3 mo), juveniles (2 yr), and adults (2+ yr). Eggs are buoyant and hatch near the surface 1 or 2 wk after the spawning, which usually occurs in early March along the Norwegian Skagerrak coast. The larvae stay in the water column and feed on zooplankton, mainly copepod nauplii and copepodites. The fish larvae metamorphose into juvenile fishes around May–June in this area. The younger stage of these juveniles constitutes the 0-group, which lives on their nursery ground but settles and feeds on the bottom when they are ~3–5 cm long. The egg and larval stages are variable among years because of starvation and emigration (Skreslet 1989; see also Cushing 1995) and changes in temperature, salinity, wind field, and currents (Koslow and Tompson 1987, Ellersten et al. 1989, Dickson and Brander 1993, Ottersen and Sundby 1995). Juveniles grow at the bottom for ~2 yr after which maturation occurs. The maturation time of 2–3 yr in the Norwegian

Skagerrak cod is short compared to the North Sea and the Arcto-Norwegian cod (Gjøsæter et al. 1996). Tagging experiments have indicated that the Norwegian Skagerrak cod is relatively isolated, with limited migration (individuals appear fjord specific) and limited interchange with individuals of other nearby areas (such as the open sea population from the Skagerrak [Danielssen 1969]). The young juveniles (0-group), the older juveniles (1-group; 1-1/2 year old), and the adults are, thus, considered to be sympatric or parapatric. The adults are, however, generally found in deeper water than the two juvenile cohorts (Gjøsæter 1990, Gjøsæter et al. 1996; see also Dalley and Anderson [1997]).

THE DATA

The time series on cod have been assembled as part of the Flødevigen survey in which fish communities at numerous fixed locations along the Norwegian Skagerrak coast have been censused every September/October since 1919. The sampling has been carried out with beach seines of standardized design since the onset of the study (for more details, see Tveite [1971], Johannessen and Sollie [1994]). The abundances of the two main juvenile cohorts of cod (the 0-group and the 1-group) are well represented in the catch. The 0-group individuals in a given year correspond to the 1-group cohort in the succeeding year (Fig. 1). Because the sampling started a bit later than 1919 in some stations

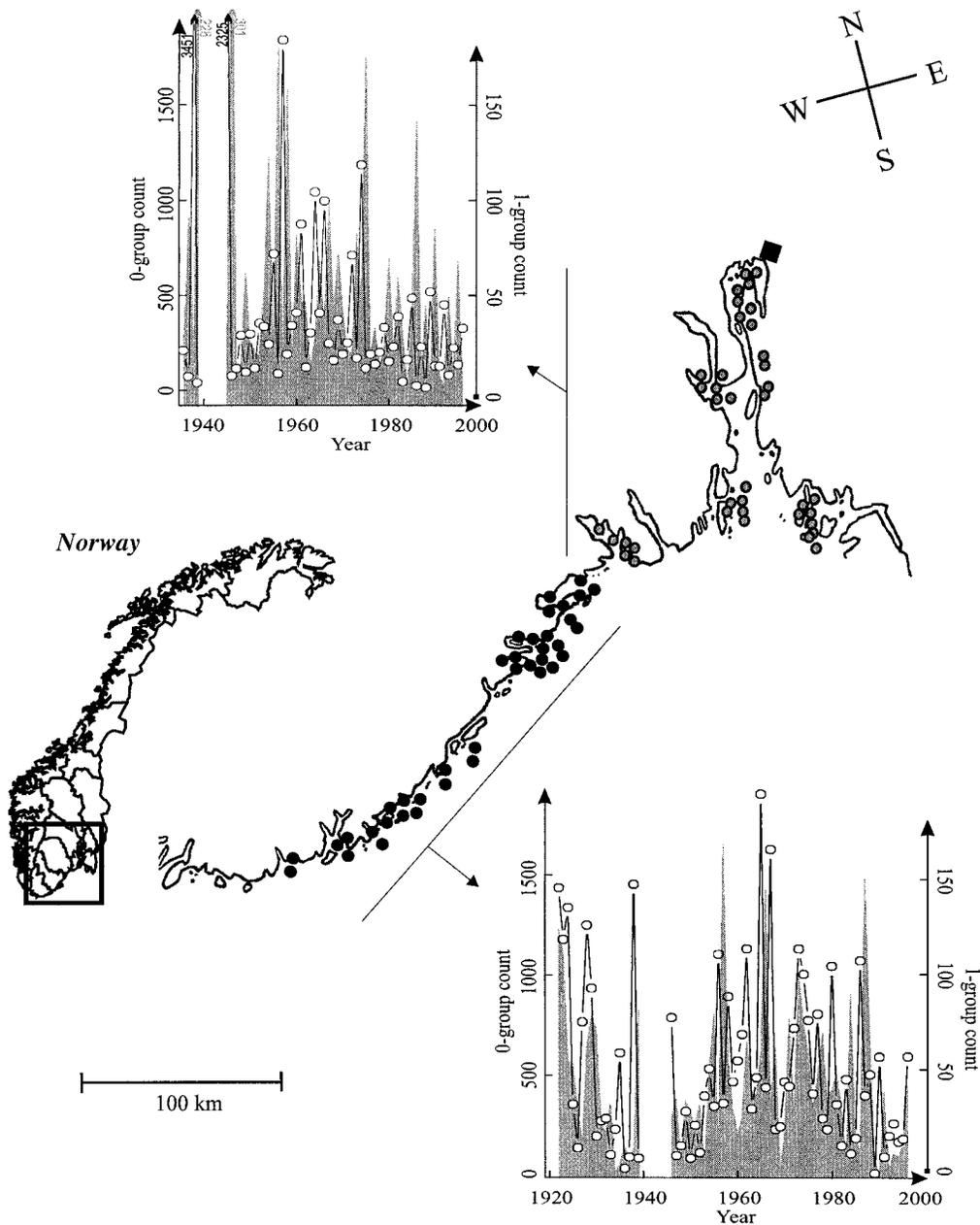


FIG. 2. The Norwegian Skagerrak coast together with a detailed map showing the location of the two broad areas (Southwestern: black dots; Northeastern: grey dots; ■ shows the location of the city of Oslo). The long-term survey data of the 0-group and of the 1-group of the southwest area go from 1921 to 1994, and those of the northeastern area from 1936 to 1994. The time series correspond to the yearly total counts of the two age classes across 38 fixed stations in the former and 37 stations in the latter.

in the southwestern (SW) area (Fig. 2), we study the census data of juvenile cod sampled from 1921 to 1994 (barring the five war years 1940–1944) at 38 fixed stations. A second set of 37 stations in the northeastern (NE) area were sampled from 1936 to 1994 (excluding the war years; Fig. 2).

To obtain a sufficiently large count of 1-group individuals and thus to enhance power, we analyze the

total counts of the two age classes across the 38 SW stations and the 37 NE stations. The data, thus, consist of two series of 69 values from the former and two series of 56 values from the latter (Fig. 2). There is a high level of correlation between the individual series (see Fromentin et al. 1997). This facilitates the aggregation of the counts. Unpublished analyses that break the data up by fjords provide a more detailed geo-

graphic analysis of density dependence (J. M. Fromentin et al., *unpublished manuscript*).

THE MODEL

Density-dependent survival: a test of convexity

Considering that adults are primarily found in deeper waters, density-dependent processes are likely to occur mainly between juveniles of the 0-group during and after settling and juveniles of 1-group, which are already settled on the bottom.

Let y_t denote the number of 1-group and x_t the number of 0-group in year t . According to classical theory for age-structured populations, density-dependent survival of the 0-group cohort into the 1-group of the following year may be written as

$$y_{t+1} = F_s(x_t) \tag{1}$$

where $F_s(\cdot)$ is the survival function (and the per capita survival is given by $F_s(\cdot)/x$). Density-dependent survival implies that this function is nonlinear and convex in the raw abundance. In contrast, the hypothesis of density-independent survival implies the function to be linear with a positive and constant slope (i.e., the proportion surviving is constant across the range of densities). An intercept a ($\neq 0$) may be included in the model to compensate for immigration and emigration in nonclosed populations.

Eq. 1 is a deterministic model that does not incorporate either the stochasticity inherent in natural populations or the variability due to the sampling error. To remedy this, we consider Eq. 1 as the model for the expected (i.e., conditional expectation) survival of the cohort from year t to year $t + 1$:

$$E[y_{t+1}] = F_s(x_t) \tag{2a}$$

where the expectation is taken marginally with respect to the inherent stochasticity and the randomness due to sampling. We define a function, v , for the conditional variance (as in generalized linear models [McCullagh and Nelder 1989]). This variance function defines the law for the variability around the survival function:

$$\text{Var}(y_{t+1} | x_t) = v[E(y_{t+1} | x_t)] = v[F_s(x_t)]. \tag{2b}$$

We consider first measurement error. The variance induced by the counting process will be proportional to the conditional expectation, $\mu_x (=F_s(\cdot))$, if individuals are distributed completely randomly because the numbers will be Poisson distributed (e.g., Pielou 1977). As individuals get very aggregated, however, the variance will be close to proportional to the squared mean (Pielou 1977). At the intermediate scale, the variance may follow the negative binomial variance function, $v = \mu_x + \mu_x^2/k$ (see, for example, Gaston and McArdle 1994, Wilson et al. 1996).

Demographic stochasticity alone will, in constant environment, lead to negative binomial variance (e.g., Kendall 1949, Anderson et al. 1982). Variability due to population growth in a variable environment, in con-

trast, often has a variance that increases with the squared mean (through a Gamma or lognormally distributed steady state [Dennis and Patil 1984, Engen and Lande 1996a, b]). For k small, the negative binomial may be seen as approximating a discrete Gamma distribution. A negative binomial variance function is therefore a natural choice for population counts. For k large, the negative binomial converges on the Poisson distribution.

Census data of marine fish populations are likely to harbor both process variability and measurement error. We determine the appropriate variance function (error structure) from the data by estimating k in the negative binomial as an integral part of the model fitting (using maximum likelihood [see Venables and Ripley 1994]).

Given an appropriate variance function (Eq. 2b), the cohort survival function $F_s(\cdot)$ can be estimated from census data without making assumptions about its functional form (such as a Ricker or Gompertz model [e.g., Lebreton 1989] using tools from nonparametric regression (e.g., Green and Silverman 1994). That is we estimate the entire function itself by building it from a set of basis functions. Different basis functions are possible, but the most commonly used are *splines* (of which we will use B-splines [Green and Silverman 1994]). Splines are piecewise polynomials that are smooth (twice differentiable) in the spline knots (the control points of the splines). Compared to a polynomial basis (i.e., as in polynomial regression), splines are much more flexible and can attain a fit to the underlying function using many fewer degrees of freedom for the model. Splines are, thus, better suited for function estimation both with respect to bias and variance. Ellner and coworkers advocate the use of spline smoothing to ecological time series analysis in the context of estimating *Lyapunov exponents* when the functional form of the underlying interactions are unknown (Ellner and Turchin 1995; see also Ellner et al. [1991], McCaffrey et al. [1992]).

Nonparametric regression with non-Gaussian error may be estimated using the framework of generalized additive models (Hastie and Tibshirani 1990; see Stenseth et al. [1997], Bjørnstad et al. [1998] for applications to population dynamics). We optimize the complexity of the curve (the number of degrees of freedom) using the AIC criterion (Burnham and Andersson 1992). The test for density-dependent survival is equivalent to the test for significant convexity in the estimated function. Since the linear model is nested in the nonlinear model, this can be done by an analysis of deviance (a likelihood-ratio test) of the two models. Denote the sample size by n , the difference in deviance by ΔD , the number of parameters in the linear model by p_1 ($=2$), and the number of parameters of the nonlinear model by p_2 (so that $\Delta p = p_2 - p_1$ is the difference in number of model parameters). Define further the scale parameter on the basis of the nonlinear model as $\phi = \text{deviance}/(n - p_2)$. Under the null hypothesis

of linearity $\Delta D/\phi\Delta p$ will be approximately F distributed with Δp and $n - p_2$ degrees of freedom (McCullagh and Nelder 1989).

An important implication of the variance–mean relationship is that the expected deviation of observations away from the model prediction will vary with the mean. That is, the magnitude of the residuals will depend on the cohort size. This feature of the system may be considered when assessing the goodness-of-fit of the model by using Pearson residuals (residuals that are scaled by their variance McCullagh and Nelder [1989]). Serial dependence in the scaled residuals was further tested for using the 1st order autoregressive model.

The log–log unit slope test

The traditional tests for density dependence in survival use the fact that under the null hypothesis the slope in the regression of $\log(y_i)$ on $\log(x_i)$ will be one (see, for example, Myers and Cadigan 1993). Density dependence leads to a slope significantly smaller than one. This class of tests suffers from inflated type I error in the presence of measurement error (e.g., Kuno 1973, Lebreton 1989), unless the magnitude of the error is known a priori (e.g., through multiple measurements) (see Myers and Cadigan 1993). To investigate the properties of the likelihood-ratio *test of convexity*, we will compare it to the results of a *log–log unit slope test* applied to synthetic data (with various degrees of contamination of measurement error). The likelihood-ratio test for the latter can be constructed by regressing y_i on $\log(x_i)$ using a *log* link (McCullagh and Nelder 1989) and the suitable variance function. The deviance of this model may be compared to the model with a slope fixed at unity (i.e., the regression model that is offset by $\log(x_i)$). Under the null hypothesis, the likelihood-ratio statistic $\Delta D/\phi\Delta p$ will be approximately F -distributed with 1 and $n - 1$ degrees of freedom.

Data sets with varying levels of measurement error were generated by contaminating the predictor with error. An uncontaminated predictor, x , was made by drawing 50 data points from a uniform distribution on [10, 2000], that is, loosely spanning the observations for the 0-group in the SW data set (Fig. 1). The variance of the predictor is thus $(10 - 2000)^2/12$ (see e.g., Ross 1994). The error variance was selected to be 0 (uncontaminated), 1, 5, 10, 25, and 50% of this variance. To simplify calculations, the response, y , was calculated as overdispersed Poisson variates ($v = \phi\mu_x$, where the scale, ϕ , is some constant) with mean λx , rather than strictly following the negative binomial distribution (see McCullagh and Nelder 1989:chapter 6, Wilson et al. 1996). The constant proportion surviving, λ , was set to 0.1, so that the y s loosely span the range of the 1-group. The scale, ϕ , was set to 1, 4, and 9. For this analyses of sensitivity to measurement error on the basis of synthetic data we assume a quasi-Poisson error structure (Lawless 1987, McCullagh and Nelder 1989:chapter 6). The reason why we use this,

rather than using the negative-binomial, is to speed up and facilitate the automation of the calculations across the large number of synthetic data sets. For the 0%-contamination runs, the error rates are estimated on the basis of 60 000 simulations for each of the levels of ϕ . For the remaining levels of measurement error we use 10 000 runs for each parameterization. The smallest parameters are deliberately chosen to represent very weak density dependence.

A preliminary investigation of power was carried out by simulating data under the alternative hypothesis of density-dependent survival. Density dependence was modeled as following a Ricker map (i.e., $y = axe^{-bx}$), or a Gompertz map (i.e., $y = axe^{-b\ln(x)}$) (see, for example, Lebreton 1989). The predictor, x , were assumed to be without measurement error, and both the test of convexity and the log–log test of unit slope were applied. The density-dependent survival rate, a , were tuned to give an average y of 100, to facilitate comparison across models. Rejection rates at a nominal 5% level were assessed on the basis of 10 000 runs.

Most calculations are carried out in S-plus for Windows version 3.3 (Statistical Sciences 1995) with the MASS library attached (Venables and Ripley 1994). The statistical simulations were carried out with S-plus version 3.4 on a SGI Power Challenge L with four R10.000 processors.

RESULTS

Variability of cod counts

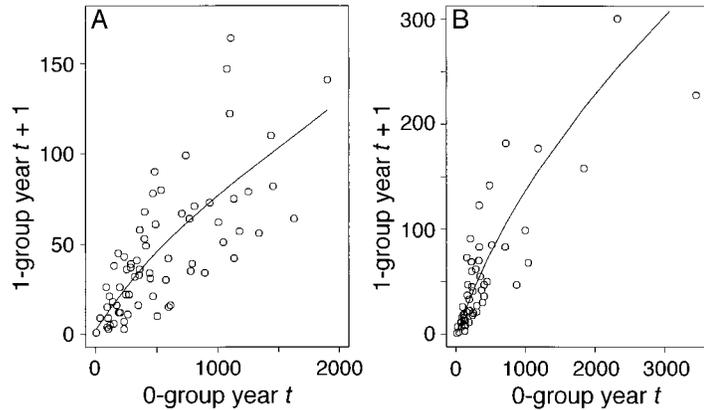
When the additive model with a negative binomial error was applied to the data, the clumping parameter, k , in the negative binomial was estimated to be 3.68 ± 0.70 (mean ± 1 SE) for the SW data and 3.68 ± 0.78 for the NE data. The variance thus increases somewhat faster than in proportion to the mean. The data appear to conform rather well to the negative binomial as the scale parameters were estimated to be 0.98 and 1.16, respectively. There is no evidence of serial correlation in the residuals (SW lag1 autocorrelation = 0.06, $P = 0.64$; NE lag1 autocorrelation = 0.07, $P = 0.59$).

Survival function of juvenile cod

The variability in the data led us to employ a negative binomial error (with $k \approx 3.5$) to estimate $F_s(\cdot)$. The optimal (in the minimum AIC sense) model uses a B-spline with two degrees of freedom to estimate the survival function $F_s(\cdot)$ for both the SW and NE data sets (Fig. 3).

The optimal model (Fig. 3) linking the 1-group to the 0-group in the previous year is highly significant for both the SW ($F_{2,68} = 46.29$, $P < 0.001$) and the NE ($F_{2,51} = 55.46$, $P < 0.001$) areas. The Spearman rank correlation between the predicted and observed values is $\rho_{\text{Spear}} = 0.76$ for the SW and $\rho_{\text{Spear}} = 0.83$ for the NE data. Fig. 3 indicates a wide spread of fish counts

FIG. 3. The relationship between the 0-group in each year to the 1-group in the succeeding year for (A) the southwestern and (B) the northeastern data set. The survival functions are calculated as B-splines with two degrees of freedom, assuming that the variance follows a negative binomial distribution with $k = 3.5$. The estimated curves are convex as predicted for density-dependent mortality, and the nonlinearity is significant at a nominal 5% level in both.



around the fitted cohort survival curve. Residual analysis (assuming negative binomial variance), however, reveal no departure from the assumptions. As noted above the observed variability is consistent with, and no more than expected from (barring a few outlying years), the probabilistic model (in other words, the spread of the counts around the predicted model correspond to what can be expected under the model for the variance).

The estimated curves are both convex as predicted in the case of density-dependent survival. The nonlinearity is significant at a nominal 5% level (SW: $F_{1,68}$

$= 4.34, P = 0.04$; NE: $F_{1,51} = 4.32, P = 0.04$). Hence, the hypothesis of a linear relationship (i.e., density-independent survival) between the 1-group and the 0-group in the preceding year is rejected.

Sensitivity to measurement error

Table 1 summarizes the observed type I error rates (for the nominal 5%) under the null hypothesis of density independence for the convexity test (Table 1A) and also for comparison for the log-log test of unit slope (Table 1B). The simulations reveal that both tests are reasonably well calibrated in the absence of measurement error. The type I error rate is inflated, somewhat, for the convexity test in the presence of measurement error. The bias is modest, however, even as the error of measurement exceeds 10% of the total variance in the predictor. The log-log unit slope test, in contrast, exhibits hugely inflated error in the presence of measurement error. When the error of measurement is 10% of the variance in the predictor, the null hypothesis is rejected nearly half the time at a nominal 5% level. The latter sensitivity to measurement error is a well-known result that has been discussed frequently (see, for example, Kuno 1973, Bulmer 1975, Lebreton 1989).

Power of tests

The simulation to assess the power of the convexity test for density dependence relative to that of the log-log unit slope test is summarized in Table 2. The analysis should be seen as a preliminary analysis. The power of the convexity test is typically somewhat lower than that of the log-log unit slope test. The two tests are comparable in strength, though. The greatest discrepancy is in the presence of weak log-linear density dependence (Gompertz type). This functional form of density dependence is the alternative hypothesis against which the latter test has the greatest power among all forms.

DISCUSSION

In this work, we developed an additive model with negative binomial (or quasi-Poisson) error to test the

TABLE 1. The observed type I error rates (for the nominal 5% level) under the null hypothesis of density independence for (A) the convexity test and (B) the traditional log-log test of unit slope. Each run of a model used $n = 50$ simulated data points.

| Measure- ment error (%) | Variability level, ϕ | | |
|-------------------------------|---------------------------|-------|-------|
| | 1 | 4 | 9 |
| A) Convexity test | | | |
| 0 | 5.32 | 4.63 | 4.10 |
| 1 | 6.41 | 5.48 | 4.48 |
| 5 | 7.03 | 5.52 | 4.92 |
| 10 | 7.95 | 6.56 | 5.78 |
| 25 | 10.97 | 10.64 | 8.86 |
| 50 | 14.5 | 12.33 | 11.99 |
| B) Log-log unit slope test | | | |
| 0 | 5.10 | 6.14 | 8.57 |
| 1 | 12.98 | 11.09 | 13.48 |
| 5 | 32.31 | 27.18 | 25.52 |
| 10 | 50.12 | 42.89 | 39.35 |
| 25 | 79.73 | 73.9 | 69.95 |
| 50 | 94.96 | 93.07 | 91.08 |

Notes: Both tests apply a quasi-Poisson error structure and likelihood ratio tests based on model deviances and estimated scale parameters. The simulations are repeated for three different levels of variability, ϕ , in the response (all assuming the variance proportional to the mean), and six different levels of contamination with measurement error (with variance ranging from 0% to 50% of the variance in the predictor, x). For the 0%-contamination runs the error rates were estimated on the basis of 60 000 simulations for each of the levels of ϕ . For the remaining levels of measurement error we used 10 000 runs.

TABLE 2. Power of the test of convexity and the log–log unit slope test (at the nominal 5%) under various forms of density dependence.

| Model | Log–log | Convexity |
|-----------------------------------|---------|-----------|
| Ricker $b = 0.001$; $a = 0.34$ | 1.00 | 1.00 |
| Ricker $b = 0.0001$; $a = 0.11$ | 0.91 | 0.81 |
| Ricker $b = 0.00005$; $a = 0.11$ | 0.47 | 0.40 |
| Ricker $b = 0.00001$; $a = 0.1$ | 0.09 | 0.11 |
| Gompertz $b = 0.30$; $a = 0.83$ | 1.00 | 0.98 |
| Gompertz $b = 0.20$; $a = 0.41$ | 1.00 | 0.93 |
| Gompertz $b = 0.10$; $a = 0.2$ | 0.92 | 0.61 |
| Gompertz $b = 0.05$; $a = 0.14$ | 0.49 | 0.28 |

Notes: Test equations: $f_s(x) = xe^{a-bG(x)}$, where $G(x) = x$ for Ricker type of density dependence, and $G(x) = \ln(x)$ for Gompertz type of density dependence. The density-independent survival rates, a , were chosen so that the mean number of survivors would be ~ 100 for each model. Each run of a model used $n = 50$ simulated data points. Both tests apply a quasi-Poisson error structure and likelihood ratio tests based on model deviances and estimated scale parameters. The simulations assume pure Poisson variability (the variance is equal to the mean) because type I error rates appear to be inflated in the log–log unit slope test in the presence of overdispersion (Table 1). Four different parameters for density dependence are used for both the Ricker and the Gompertz models. The smallest parameters are deliberately chosen to represent very weak density dependence. Rejection rates at a nominal 5% level were assessed on the basis of 10 000 runs.

hypothesis of density-dependent mortality within the juvenile stages of the Norwegian Skagerrak cod. We argued that considerations of the conditional variance in the data take logical priority over estimation of the survival function. We showed that there is evidence of density-dependent mortality during these early stages. After a discussion of some methodological issues, we will return to biological interpretations of the patterns of variability and density dependence.

A most common methodology (the “log–log unit slope” methods) for testing for density-dependent survival is through regressing log-transformed data assuming a Gompertz or a Ricker model (Ricker 1954, Lebreton 1989). Oftentimes, an assumption of log-normal error, accompanies this class of models (see e.g., Myers and Cadigan 1993, Cushing et al. 1996). Above, we showed that this was not the case for the present data (see Bjørnstad et al. [1998] for a different example). We, therefore, developed likelihood-ratio test for log–log unit slope when the variance is not proportional to the squared mean.

Within the framework of the log–log method, a regression slope smaller than unity is taken as evidence for density dependence (e.g., Lebreton 1989). Thus, with this approach, no relation (a slope of zero) indicates strong density dependence. However, a slope of zero may also result if the population size is measured with error (e.g., Kuno 1973, Bulmer 1975, Lebreton 1989). Thus, measurement error biases this test towards too frequent rejection of the null hypothesis. Our simulation (Table 1B) illustrates this effect. Myers and Cadigan (1993) have developed a log-parametric framework for testing for density dependence in the

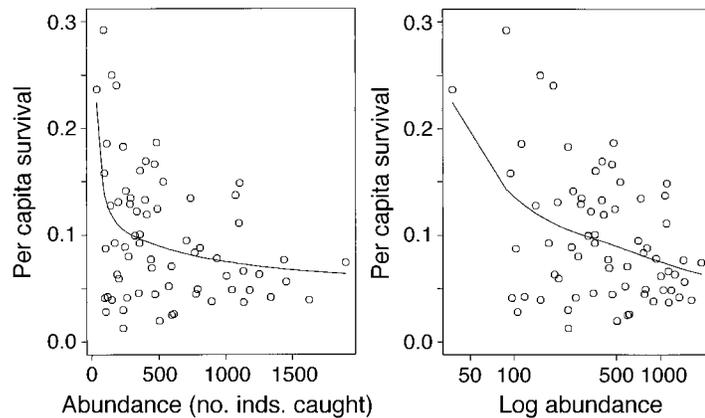
presence of lognormal sampling error. This method requires, however, the magnitude of the measurement error to be known (for instance through repeated sampling).

In the currently proposed methodology, the hypothesis of density dependence refers to the shape of the function for the raw counts. Within this framework, measurement error will also affect the regression slope (by a decrease—as for the log–log approach) and the goodness of fit (by inflating the variance) of the regression. However, measurement error does not strongly affect the curvature of the estimated curve (see Table 1A). In contrast to the log–log test for unit slope, measurement error only mildly affects the type I error rate of the test of curvature (Table 1). We see three main points of interest of the test for curvature (in order of importance). (1) It is nonparametric in the sense that we do not need to make a priori assumptions about the functional form of density dependence. (2) It appears to be relatively robust to measurement error. (3) It appears, therefore, to be permissible even when no information on the magnitude of the measurement variance exists. The power of the test is somewhat lower than alternative test. In our opinion, the relative robustness to measurement error outweighs this drawback, at least to the extent that it should be considered an important (or perhaps even necessary) supplement to the unit slope test.

To illustrate the value of the method being model-free, we can transform the estimated survival functions (Fig. 3) into per capita survival functions (Fig. 4). Plotting the function with various scales along the abscissa allows an investigation of the functional form for the density dependence. Density dependence is believed to be of the Gompertz type in some systems (see, for example, Myers and Cadigan [1993], Saitoh et al. [1997]) but of the Ricker type in other systems (see, for example, Ricker [1954], Turchin [1991], Dennis et al. [1995]). Tests for density dependence may be relatively robust to misspecification of functional forms. The log–log unit slope test, for instance, works best against a Gompertz model. It nevertheless differentiates well against the Ricker type of dependence (Table 2). However, conclusions about the resultant dynamics and the management consequences of misspecification may be dramatic (Pascual et al. 1997). For the cod, the reduction in survival appears close to linear in the log-abundance for the SW area (Fig. 4). The nonparametric curve estimation, thus, reveals that density dependence conforms closer to the Gompertz than to the Ricker model for this system (although there is some evidence of departure from this at low densities in both areas). The proposed methodology may prove useful to elucidate functions for density dependence in data sets of real populations.

There is room to elaborate the statistical machinery to target the hypothesis of convexity more precisely. A reason for that is that when the underlying survival

FIG. 4. The estimated survival function (see Fig. 3) of the southwestern data redrawn as a per capita function. The density dependence is apparent from the nonincreasing per capita functions. Survival (A) as a function of abundance and (B) as a function of log abundance. The nonparametric curve estimation reveals that survival is a nonlinear function of abundance but a linear function in log abundance. One outlying data point for 1988 during which a bloom of toxic algae killed most fish (Underdal et al. 1989, Granéli et al. 1993) (only five 0-group individuals were caught) is excluded.



function is convex and nondecreasing, but observed with error, the optimal B-spline solution may lie outside the subspace of convex and nondecreasing functions (Dole 1999). Dole (1999) develops a smoothing method that generates regression splines subject to convexity (and/or monotonicity) constraints. Reanalyses of the cod data and some preliminary investigations of synthetic data indicate that this constrained smoothing may deserve future attention.

Given multiple measurements to give information about the magnitude of the measurement error (see, for example, Myers and Cadigan [1993]), it may be of interest to extend the test of convexity to take advantage of this information. A method to estimate regression splines in the presence of measurement error has recently been developed by Maca et al. (1998). The methodology is, however, yet in its infancy. Future developments may therefore increase the robustness to measurement error and improve the power further.

The theory of density-dependent population growth in a stochastic environment predicts, under a wide range of population models and in the absence of measurement error, that abundance should be conditionally Gamma (or log-normally) distributed (Dennis and Patil 1984, Engen and Lande 1996a, b). The variance will in this case be proportional to the squared mean. The variability due to the counting process is typically Poisson distributed (although oftentimes with overdispersion [McCullagh and Nelder 1989]), in which case the variance should be proportional to the mean. A Poisson-like or negative binomial variance structure will also result from pure demographic stochasticity (Kendall 1949; see also Anderson et al. 1982). The variance function (conditional variance) for the 1-group of cod appears to conform rather nicely to the negative binomial. Considering the nature of the sampling process for marine populations, this variance function is likely to be dominated by measurement variability. The clumping parameter ($k = 3.5$) is smaller than expected from pure Poisson variance. This is possibly related to the aggregated distribution of the cod, which forms

shoals and concentrate within the protected areas of the fjords (Fromentin et al. 1997). It may also be related to heterogeneity due to year-to-year variability in juvenile migration. These processes generate spatial heterogeneity that will inflate the variance compared to the pure Poisson process (Lawless 1987, Wilson et al. 1996).

The optimal model to summarize the relationship between abundance of the 0-group and 1-group appears to be significantly nonlinear. The full model linking the 0-group with the 1-group in the succeeding year is highly significant. Therefore, we conclude that survival in the 0-group of the Norwegian Skagerrak cod is density dependent. This conclusion is robust because the test we develop is relatively insensitive to measurement error. The conclusion of significant convexity, furthermore, holds if the error is assumed to follow an overdispersed Poisson distribution or a Gamma distribution (unpublished). We have checked for remaining structure in the residuals and none is found. Analyses of long-term census data may be hampered by long-term changes in the environment. Fromentin et al. (1998) and Bjørnstad et al. (1999) provide discussions on the presence and possible sources of long-term trends in the Norwegian Skagerrak cod. From a purely statistical perspective Hart (1996) shows—through the “whitening-by-window” principle—why nonparametric regression, of the kind used to estimate the survival function, is relatively robust to autocorrelated errors that may, for instance, arise from underlying trends. All available information indicates, therefore, that the pattern uncovered in the present study is a true reflection of density-dependent interactions.

The periodic fluctuations identified by Fromentin et al. (1997) in these data, may result from density-dependent survival due to competition and cannibalism within the juvenile stages (see also Bjørnstad et al. 1999). Indeed, theoretical arguments suggest that periodic fluctuations in age-structured populations depend on the manifestation of competition between cohorts (e.g., Caley et al. 1996), with generation-length

or two-generation-length periods (Gurney and Nisbet 1985), although the picture can get more complicated than that (see Nisbet and Onyiah 1994, Mertz and Myers 1996). As a mechanism for the density dependence, competition for space is a candidate. Competition for habitat is likely in the Norwegian Skagerrak cod populations because the different juvenile stages have overlapping habitats and the number of optimal habitats may be limited (Gjøsæter 1987, 1988, Fromentin et al. 1997). Potential mechanisms underlying the competition for space on the bottom might involve food limitation or increased predation risk in the suboptimal habitats. Cannibalism is a second source of density dependence in cod (Bailey and Houde 1989; see also Caley et al. 1996). When the number of young juveniles of the 0-group is high, competition and cannibalism are likely to be more pronounced, especially during the settlement (and the following months) of the 0-group.

In summary, we have introduced a new test for density-dependent survival that tests for significant convexity in the survival function. The test does not require a priori assumptions about functional forms. The type I error rate is shown to be relatively robust to measurement error, and the power appears to be good. We apply the test to census data of cod, and demonstrate significant density dependence. The reduction in survival is shown to be approximately proportional to the log of abundance.

ACKNOWLEDGMENTS

Thanks to the late Rangvald Løversen and to Aadne Sollie who carried out the sampling resulting in the "Flødevigen data set." Financial support from the Norwegian Science Foundation (O. N. Bjørnstad), the University of Oslo (through the "Environmental Program" to N. C. Stenseth) and the MAST-program of the European Union (fellowship contracts to J. M. Fromentin) made the reported analyses possible. This work was completed while O. N. Bjørnstad was at the National Center for Ecological Analysis and Synthesis at University of California Santa Barbara. Philip Dixon and Peter Rothery provided valuable comments on a previous version of the manuscript.

LITERATURE CITED

- Abrams, P. A. 1982. Functional responses of optimal foragers. *American Naturalist* **120**:382–390.
- Anderson, R. M., D. M. Gordon, M. J. Crawley, and M. P. Hassell. 1982. Variability in the abundance of animal and plant species. *Nature* **296**:245–248.
- Bailey, K. M., and E. D. Houde. 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. *Advances in Marine Biology* **26**:1–83.
- Bjørnstad, O. N., M. Begon, N. C. Stenseth, W. Falck, S. M. Sait, and D. Tompson. 1998. Populations dynamics of the Indian meal moth: demographic stochasticity and delayed regulatory mechanisms. *Journal of Animal Ecology* **67**:110–126.
- Bjørnstad, O. N., J.-M. Fromentin, N. C. Stenseth, and J. Gjøsæter. 1999. Cycles and trends in cod population. *Proceedings of the National Academy of Science USA*, *in press*.
- Boutin, S. 1995. Testing predator–prey theory by studying fluctuating populations of small mammals. *Wildlife Research* **22**:89–100.
- Bulmer, M. G. 1975. The statistical analysis of density dependence. *Biometrics* **31**:901–911.
- Burnham, K. P., and D. R. Anderson. 1992. Data-based selection of an appropriate biological model: the key to modern data analysis. Pages 16–30 *in* D. R. McCulloch and R. H. Barrett, editors. *Wildlife 2001: populations*. Elsevier Applied Sciences, London, UK.
- Caley, M. J., M. H. Carr, M. A. Hixon, T. P. Hughes, G. P. Jones, and B. A. Menge. 1996. Recruitment and the local dynamics of open marine populations. *Annual Review of Ecology and Systematics* **27**:477–500.
- Cook, R. M., A. Sinclair, and G. Stefansson. 1997. Potential collapse of the North Sea cod stocks. *Nature* **385**:521–522.
- Cushing, D. H. 1982. *Climate and fisheries*. Academic Press, London, UK.
- . 1995. *Population production and regulation in the sea: a fisheries perspective*. Cambridge University Press, Cambridge, UK.
- Cushing, J. M., B. Dennis, R. A. Desharnais, and R. F. Costantino. 1996. An interdisciplinary approach to understanding nonlinear ecological dynamics. *Ecological Modelling* **92**:111–119.
- Dalley, E. L., and J. T. Anderson. 1997. Age-dependent distribution of demersal juvenile Atlantic cod (*Gadus morhua*) in inshore/offshore northeast Newfoundland. *Canadian Journal of Fisheries and Aquatic Science* **54** (Supplement 1):168–176.
- Danielssen, D. S. 1969. On the migrations of the cod in the Skagerrak shown by tagging experiments in the period 1954–1965. *Fiskeridirektoratets Skriftserie for Havundersøkelser* **15**:331–338.
- Dennis, B., R. A. Desharnais, J. M. Cushing, and R. F. Costantino. 1995. Nonlinear demographic dynamics: mathematical models, statistical methods, and biological experiments. *Ecological Monographs* **65**:261–281.
- Dennis, B., and G. P. Patil. 1984. The gamma distribution and weighted multimodal gamma distribution as models of population abundance. *Mathematical Biosciences* **68**:187–212.
- Dickson, R. R., and K. Brander. 1993. Effects of a changing windfield on cod stocks of the North Atlantic. *Fisheries and Oceanography* **2**:124–153.
- Dole, D. 1999. Flexible estimation of concave, monotonic transformations. *Journal of Business and Economic Statistics*, *in press*.
- Ellersten, B., P. Fossum, P. Solemdal, and S. Sundby. 1989. Relation between temperature and survival of eggs and first feeding larvae of northeast Arctic cod (*Gadus morhua* L.). Rapport et Procès-verbaux des Réunions du Conseil International pour l'Exploration de la Mer **191**:209–219.
- Ellner, S., A. R. Gallant, D. McCaffrey, and D. Nychka. 1991. Convergence rates and data requirements for Jacobian-based estimates of Lyapunov exponents from data. *Physics Letters A* **153**:357–363.
- Ellner, S., and P. Turchin. 1995. Chaos in a noisy world: new methods and evidence from time-series analysis. *American Naturalist* **145**:343–375.
- Engen, S., and R. Lande. 1996a. Population dynamic models generating species abundance distributions of the gamma type. *Journal of Theoretical Biology* **178**:325–331.
- Engen, S., and R. Lande. 1996b. Population dynamic models generating the lognormal species abundance distribution. *Mathematical Biosciences* **132**:169–183.
- Fromentin, J.-M., N. C. Stenseth, J. Gjøsæter, O. N. Bjørnstad, W. Falk, and T. Johannessen. 1997. Spatial patterns of the temporal dynamics of three gadoid species along the Norwegian Skagerrak coast. *Marine Ecology Progress Series* **155**:209–222.

- Fromentin, J.-M., N. C. Stenseth, J. Gjøsæter, T. Johannesen, and B. Planque. 1998. Long-term fluctuations in cod and pollack along the Norwegian Skagerrak coast. *Marine Ecological Progress Series* **162**:265–278.
- Gaston, K. J., and B. H. McArdle. 1994. The temporal variability of animal abundances: measures, methods and patterns. *Philosophical Transactions of the Royal Society London Series B* **345**:335–358.
- Gjøsæter, J. 1987. Habitat selection and inter year class interaction in young cod (*Gadus morhua*) in aquaria. *Flødevigen Report Series* (1987):27–36.
- . 1988. Competition for food and predator–prey relationships among young cod (*Gadus morhua*) and some other fish from shallow waters. *Flødevigen Report Series* (1988):1–15.
- Gjøsæter, J., and D. S. Danielssen. 1990. Recruitment of cod, *Gadus morhua* L., whiting, *Merlangus merlangus*, and pollack, *Pollachius pollachius*, in the Risør area on the Norwegian Skagerrak coast 1946–1985. *Flødevigen Report Series* (1990):11–31.
- Gjøsæter, J., K. Enersen, and S. E. Enersen. 1996. Ressuser av torsk og andre fisk i fjorder på den Norske Skagerrakkysten. *Fisken og havet* **23**:1–28 (in Norwegian).
- Granéli, E., E. Paasche, and S. Y. Maestrini. 1993. Three years after the *Chrysochromullina polylepis* bloom in Scandinavian waters in 1988: some conclusions of recent research monitoring. Pages 25–32 in T. J. Smayda and Y. Shimizu, editors. *Toxic phytoplankton blooms in the sea. Proceedings of the Fifth International Conference on Toxic Marine Phytoplankton* (Newport, Rhode Island, 28 October–1 November, 1991). Elsevier, Amsterdam, The Netherlands.
- Green, P. J., and B. W. Silverman. 1994. *Nonparametric regression and generalized linear models: a roughness penalty approach*. Chapman and Hall, London, UK.
- Gurney, W. S. C., and R. M. Nisbet. 1985. Fluctuation periodicity, generation separation, and the expression of Larval competition. *Theoretical Population Biology* **28**:150–180.
- Hanski, I. 1991. The functional response of predators: worries about scale. *Trends in Ecology and Evolution* **6**:141–2.
- Hart, J. D. 1996. Some automated methods of smoothing time-dependent data. *Nonparametric Statistics* **6**:115–142.
- Hastie, T. J., and R. J. Tibshirani. 1990. *Generalized additive models*. Chapman and Hall, London, UK.
- Hutchings, J. A. 1996. Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stock's collapse. *Canadian Journal of Fisheries and Aquatic Science* **53**:943–962.
- Johannessen, T., and A. Sollie. 1994. Overvåking av gruntvannsfauna på Skagerrakkysten. *Fisken og havet* **10**:1–91 (in Norwegian).
- Kendall, D. G. 1949. Stochastic processes and population growth. *Journal of Royal Statistical Society B* **11**:230–264.
- Koslow, J. A., and K. R. Tompson. 1987. Recruitment to Northwest Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) stocks: influence of stocks size and climate. *Canadian Journal of Fisheries and Aquatic Sciences* **44**:26–39.
- Kuno, E. 1973. Statistical characteristics of the density-independent population fluctuation and the evaluation of density-dependence and regulation in animal populations. *Researches on Population Ecology* **15**:99–120.
- Laevastu, T. 1993. *Marine climate, weather and fisheries*. Blackwell Scientific Publications, Oxford, UK.
- Lawless, J. F. 1987. Negative binomial and mixed Poisson. *Canadian Journal of Statistics* **15**:209–225.
- Lebreton, J.-D. 1989. Statistical methodology for the study of animal populations. *Bulletin of the International Statistical Institute* **53**:267–282.
- Maca, J. D., R. J. Carroll, and D. Ruppert. 1998. Nonparametric kernel and regression spline estimation in the presence of measurement error (preprint). Texas A and M University.
- May, R. C. 1974. Larval mortality in marine fishes and the critical period concept. Pages 3–19 in J. H. S. Blaxter, editor. *The early life history of fish*. Springer-Verlag, New York, New York, USA.
- McCaffrey, D. F., S. Ellner, A. R. Gallant, and D. W. Nychka. 1992. Estimating the lyapunov exponent of a chaotic system with nonparametric regression. *Journal of the American Statistical Association* **87**:682–695.
- McCullagh, P., and J. A. Nelder. 1989. *Generalized linear models*. Second edition. Chapman and Hall, London, UK.
- Mertz, G., and R. A. Myers. 1996. An augmented Clark model for stability of populations. *Mathematical Biosciences* **131**:157–171.
- Myers, R. A., and N. G. Cadigan. 1993. Density-dependent juvenile mortality in marine demersal fish. *Canadian Journal of Fisheries and Aquatic Science* **50**:1576–1590.
- Myers, R. A., J. A. Hutchings, and N. J. Barrowman. 1996. Hypotheses for the decline of cod in the North Atlantic. *Marine Ecology Progress Series* **138**:293–308.
- Nisbet, R. M., and L. C. Onyiah. 1994. Population dynamic consequences of competition within and between age classes. *Journal of Mathematical Biology* **32**:329–344.
- Ottersen, G., and S. Sundby. 1995. Effects of temperature, wind and spawning stock biomass on recruitment of Arcto-Norwegian cod. *Fisheries and Oceanography* **4**:278–292.
- Pascual, M. A., P. Kareiva, and R. Hilborn. 1997. The influence of model structure on conclusions about the viability and harvesting of Serengeti wildebeest. *Conservation Biology* **11**:966–976.
- Pielou, E. C. 1977. *Mathematical ecology*. John Wiley and Sons, New York, New York, USA.
- Ricker, W. E. 1954. Stock and recruitment. *Journal of the Fisheries Research Board of Canada* **11**:559–623.
- Ross, S. 1994. *A first course in probability*. Fourth edition. Prentice Hall, Paramus, New Jersey, USA.
- Saitoh, T., N. C. Stenseth, and O. N. Bjørnstad. 1997. Density dependence in fluctuating grey-sided vole populations. *Journal of Animal Ecology* **66**:14–24.
- Shepherd, J. G., and D. H. Cushing. 1990. Regulation in fish populations: myth or mirage? *Proceedings of the Royal Society of London*, **B 330**:151–164.
- Skreslet, S. 1989. Spatial match and mismatch between larvae of cod (*Gadus morhua* L.) and their principal prey, nauplii of *Calanus finmarchicus* (Gunnerus). *Rapport et Procès-verbaux des Réunions du Conseil International pour l'Exploration de la Mer* **191**:258–263.
- Statistical Sciences. 1995. *S-plus guide to statistical and mathematical analysis*, version 3.3. StatSci, MathSoft, Seattle, Washington, USA.
- Stenseth, N. C., W. Falck, O. N. Bjørnstad, and C. J. Krebs. 1997. Population regulation in snowshoe hare and lynx populations: asymmetric food web configurations between the snowshoe hare and the lynx. *Proceedings of the National Academy of Science USA* **94**:5147–5152.
- Sundby, S., H. Bjorke, A. V. Soldal, and S. Olsen. 1989. Mortality rates during the early life stages and year class strength of the North east Arctic cod (*Gadus morhua* L.). *Rapport et Procès-verbaux des Réunions du Conseil International pour l'Exploration de la Mer* **191**:351–358.
- Turchin, P. 1991. Reconstructing endogenous dynamics of a laboratory *Drosophila* population. *Journal of Animal Ecology* **60**:1091–1098.
- Tveite, S. 1971. Fluctuations in year-class strength of cod and pollack in southeastern Norwegian coastal waters during 1920–1969. *Fiskeridirektoratets Skriftserie for Havundersøkelser* **16**:65–76.

- Underdal, B., O. M. Skulberg, E. Dahl, and T. Aune. 1989. Disastrous bloom of *Chrysochromulina polylepis* (Prymnesiophyceae) in Norwegian coastal waters 1988—mortality in marine biota. *Ambio* **18**:265–270.
- Venables, W. N., B. D. Ripley. 1994. Modern applied statistics with S-plus. Springer-Verlag, New York, New York, USA.
- Wilson, K., B. T. Grenfell, and D. J. Shaw. 1996. Analysis of aggregated parasite distributions: a comparison of methods. *Functional Ecology* **10**:592–601.