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Dynamics of coastal cod populations: intra- and intercohort density dependence and stochastic processes

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Skagerrak populations of Atlantic cod (*Gadus morhua* L.) have been surveyed at several fixed stations since 1919. These coastal populations consist of local stocks with a low age of maturity and a short life span. We investigated 60 time-series of 0-group juveniles (i.e. young of the year) sampled annually from 1945 to 1994. An age-structured model was developed which incorporates asymmetrical interactions between the juvenile cohorts (0-group and 1-group; i.e. one-year-old juveniles) and stochastic reproduction. The model was expressed in delay coordinates in order to estimate model parameters directly from the time-series and thereby test the model predictions. The autocovariance structure of the time-series was consistent with the delay coordinates model superimposed upon a long-term trend. The model illustrates how both regulatory (density-dependent) and disruptive (stochastic) forces are crucial in shaping the dynamics of the coastal cod populations. The age-structured life cycle acts to resonance the stochasticity inherent in the recruitment process.

Keywords: age-structured population dynamics; time-series analysis; autoregressive moving average (ARMA); intracohort competition; intercohort cannibalism; *Gadus morhua*

1. INTRODUCTION

Marine fish populations have long been known for their extensive variation in abundance (e.g. Ljungman 1882). Long- and short-term fluctuations in addition to what appear to be random variation have been described (e.g. Ottestad 1942, 1979, 1986; Cushing & Dickson 1976; Mann & Lazier 1991; Laevastu 1993; Cushing 1995; Kjesbu *et al.* 1996). Temporal fluctuations in the year class strength have been related to abiotic factors (such as changes in temperature, salinity, wind field, currents and food availability; see Hjort 1914, 1926; May 1974; Koslow & Thompson 1987; Cury & Roy 1988; Ellersten *et al.* 1989; Skreslet 1989; Dickson & Brander 1993; Cushing 1996), biotic factors (such as density-dependent survival due to competition and cannibalism; see Sundby *et al.* 1989; Myers & Cadigan 1993) and human exploitation (see Myers *et al.* 1996; Cook *et al.* 1997).

Fromentin *et al.* (1997) analysed the spatio-temporal patterns in the abundance of cod along the Norwegian Skagerrak coast and demonstrated significant cyclicity with a two to three year period, but also noticed a great deal of irregularity. Here we assess the extent to which density dependence and environmental stochasticity can explain the dynamics of coastal cod populations (*Gadus morhua* L.) on the basis of the long-term monitoring data from the Norwegian Skagerrak coast. We developed a mathematical model that includes both deterministic and stochastic processes presumed to be important in the age-structured dynamics of cod populations. The model is expressed in delay coordinates so as to provide a bridge between the model and time-series data on the abundances of the youngest juvenile stages of cod (i.e. the 0-group).

Ever since the publications of Ricker (1954) and Beverton & Holt (1957), the 'stock-recruitment relationship' and density-dependent regulation have been a central issue within the field of fish population dynamics (e.g. Cushing 1971, 1995; Clark 1976; Pitcher & Hart 1982; Rothschild 1986; Shepherd & Cushing 1990). Generally speaking, most stock-recruitment models provide a fairly poor fit to data (e.g. Shepherd & Cushing 1990; Myers *et al.* 1995*a*,*b*). A major difficulty in adopting the approach of fitting a stock-recruitment model to data on both recruitment and spawning stock size is the scarcity of long-term data on the young stages; most available long-term time-series are based on fishery landings which are often contaminated by sociopolitical and technical variations in fishing effort. The yearly abundances of the 0-group (as well as other juvenile stages) are generally estimated by sequential population analysis (including techniques such as virtual population analysis and cohort

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analysis) to reconstruct population recruitment from catches (Ricker 1968; Pope 1972; Ulltang 1977; Gavaris 1988; Megrey 1989; Lapointe *et al.* 1992). The current data represent a direct assessment of the abundance of the 0-group.

2. THE FLØDEVIGEN MONITORING PROGRAMME

The data set analysed in this paper is derived from an extensive monitoring programme along the Norwegian Skagerrak coast (the Flødevigen monitoring programme; see § 2(b)). This monitoring programme was initiated as a result of controversy between Gunder Mathiesen Dannevig (1841–1911), the founder of the Flødevigen Marine Research Station and Johan Hjort (1869–1948), a pioneer in marine research (cf. Solemdal 1997). Dannevig argued for a deterministic relationship between the number of yolk-sac fish larvae and the number of recruits to the population (see Dahl & Dannevig 1906), whereas Hjort (1914) argued that it was the environmental conditions during the critical phases of development which played the essential role (see also May 1974; Cushing 1990). In order to resolve this controversy, they made a series of beach seine hauls in some fjords at the Norwegian Skagerrak coast. Based on the initial results from these hauls, the monitoring programme upon which this paper rests was established (Dahl & Dannevig 1906; Løversen 1946; Dannevig 1949, 1954, 1959, 1963; Tveite 1971, 1984; see also Solemdal *et al.* 1984; Johannessen & Sollie 1994; Solemdal 1997).

Since most earlier work on this system is published in Norwegian, we provide (in § 2(a)) a synoptic presentation of the biology and ecology of the Norwegian Skagerrak cod populations. We emphasize information on the demography, since this is essential for the formulation of a realistic population model.

(a) *The Norwegian Skagerrak cod*

The life cycle of cod can be divided into four main stages (figure 1*a*): eggs, larvae, juveniles and adults. Eggs hatch near the surface one or two weeks after spawning, which for the Norwegian Skagerrak population usually occurs in early March. The larvae stay in the water column and metamorphose into small fishes (juveniles) around May–June. These juvenile fishes constitute the 0-group that live on the nursery grounds and settle and feed on the bottom when they are *ca.* 3–5 cm. The 1-group refers to an older juvenile stage (1.5 years old) and corresponds to the 0-group juveniles of the previous year; the 2- and 3-groups refer to individuals being 2.5 and 3.5 years old, respectively. Age classes beyond the 1-group are collectively referred to as 'older individuals'.

The age and growth of cod from the Norwegian Skagerrak coast were initially studied by both Dannevig (1933, 1954) and Løversen (1946) and, more recently, by Gjøsæter (1990) and Gjøsæter *et al.* (1996). Individuals from these local populations grow faster than those from northern and western populations, but slower than those from the North Sea (cf. Daan 1974; Garrod 1977). The maximum age recorded in the Norwegian Skagerrak populations is 12 years (Gjøsæter *et al.* 1996). However, less than 2% of those reaching an age of one year survive to an age of six years or more.

It appears that maturation occurs at around two years of age in the Norwegian Skagerrak coastal populations (Gjøsæter *et al.* 1996). The 2-group constitutes more than 50% of the spawning stock during the subsequent winter (Gjøsæter *et al.* 1996). Spawning by the 1-group is negligible (*ca.* 5% of stock), whereas the 3-group accounts for *ca.* 25% of the stock. The remaining part of the spawning stock includes older individuals (older than 3.5 years). This group is of minor importance because of the high mortality (and turnover) rate of these coastal cod populations (Gjøsæter *et al.* 1996).

The coastal cod populations exhibit vertical migration related to temperature. They stay in shallow waters during autumn and spring and go into deeper water during summer and winter (Dannevig 1966; Danielssen 1969; Danielssen & Gjøsæter 1994). The 0-group and a fraction of the 1-group are generally found in more shallow waters and closer to the shore than the older individuals (Dahl & Dannevig 1906; see also Dalley & Anderson 1997).

Based upon extensive release and recapture experiments, a sequence of studies have shown that the Norwegian Skagerrak cod consists of non-migratory populations subdivided into semi-isolated local populations (Danielssen & Gjøsæter 1994; see also Ruud 1939; Løversen 1946; Moksness & Øyestad 1984). The recapture rates of the released animals have been up to 15% for fish released as 0-group fish and up to 50% for 1-group and older fish. Very few individuals were recaptured in open waters. Tagging experiments performed on the Danish side of Skagerrak further suggest an absence of migration of individuals from that stock to the Norwegian Skagerrak coastal waters (Danielssen 1969).

Because of the rapid turnover in the life cycle and changes in habitat use (older individuals are partly allopatric to younger individuals), the main density-dependent (regulating) interactions probably occur between individuals of the 0- and 1-groups (Fromentin *et al.* 1997). Stochastic forces are known to be particularly dominant during the early stages of the life cycle, that is in connection with the spawning, hatching and larval stages and settlement (Cushing 1990).

(b) *The data*

Since 1919 a large number of sites between Kristiansand and the Norwegian–Swedish border (figure 2) have been monitored in September–October by beach seines using a standardized protocol. The sampling and recording (including the organization of the data) have been carried out and supervised by two team leaders since 1919. Ninety-eight per cent of the samples were taken between the beginning of September and the middle of October (two-thirds of the stations were censused within the last two weeks of September and one-quarter during the first two weeks of October).

During the initial years of 1919–1920, 85 stations were sampled. Of these, 38 are still monitored (Fromentin *et al.* 1997). During the last 25 years, between 70 and 80 stations have been sampled every year. An important asset of the Flødevigen data is the presence of several fairly long time-series from the same (or similar) biological–ecological processes. However, despite the populations being relatively isolated and migration being

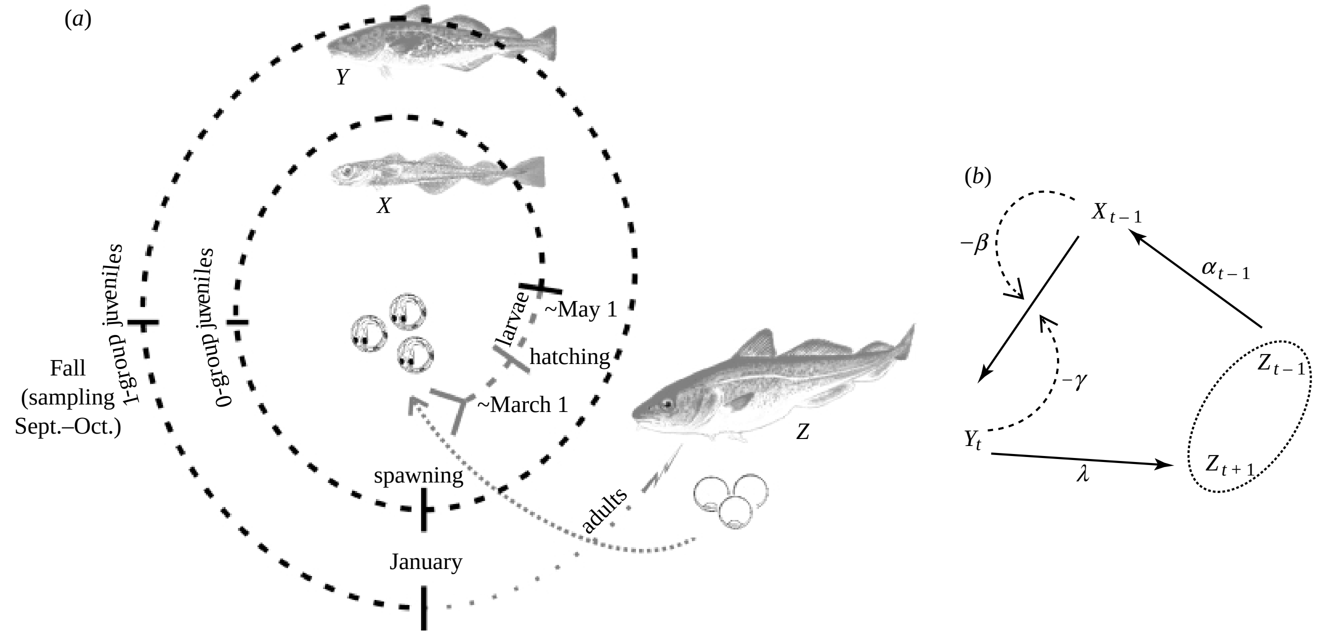

Figure 1. Life cycle of coastal cod (*G. morhua* L.) populations along the Norwegian Skagerrak coast. (*a*) The life cycle of cod together with sampling times. (*b*) The idealized life cycle for a two year semelparous life cycle as modelled in § 3(a).

fairly restricted, neighbouring sites are unlikely to be independent of each other in a statistical sense (Fromentin *et al.* 1997; see below).

The standardized beach seines used are 40 m long and 3.7 m deep, with a 20–30 m long rope and a stretched mesh size of 1.5 cm. An area of up to 700 m^2 is covered by each haul. The greatest depth sampled varies between stations, but ranges from 3 to 15 m. Individuals belonging to the 0- and 1-groups are usually caught in the beach seines, whereas older fish are usually not.

For the present analyses we have selected stations so as to include as long a time-series as possible without missing values. We furthermore trimmed the selected data set to obtain time-series of equal length. Between 1945 and 1994, 60 stations (i.e. the time-series) were complete for the 0-group (and the 1-group). The mean (and standard deviation) abundance of the time-series ranges from 2.32 (3.38) to 66.02 (94.17) for the 0-group cod and from 0.04 (0.20) to 7.30 (18.63) for the 1-group cod. Of these, the six that belong to the polluted Oslofjord area (figure 2) have very low abundances. The average abundance of the 1-group is generally low (51% of all the 1-group data are zeros, as compared to 26% for the 0-group). Numerically speaking, the 0-group data are, therefore, best suited for characterizing the overall population fluctuations. In the analyses reported here we focus on the 0-group. Elsewhere we have investigated the 1-group by using geographically aggregated data sets (Bjørnstad *et al.* 1999*a*,*b*).

Due to the occurrence of zeros (i.e. no catches of cod in particular hauls from given stations), a constant of 1, corresponding to the lowest catchable unit, is added to all series prior to log transformation.

3. THE MODEL

(a) *A mathematical population dynamics model*

The life history of the Norwegian Skagerrak cod is summarized in § 2(a) and figure 1*a*. An idealized and simplified life history is depicted in figure 1*b*. This life-history diagram is developed by assuming that maturation occurs at an age of two years. The abundance of mature individuals in year *t* is denoted Z_t.

As a first approximation we assume functional semelparity. Furthermore, we initially assume that per capita egg production, hatching and survival to 0-group (whose abundance is denoted X_t) is density independent but variable from year to year. The per capita reproductive rate is given as a random variable (cf. Dennis & Patil 1984; Engen & Lande 1996). The production of recruits (X_t) by the spawning stock (Z_t) in year *t* is hence given by

$$X_t = Z_t \exp(\alpha_t), \qquad (1)$$

where α_t is a sequence of normally distributed random variables drawn independently from the same distribution, so that $\exp(\alpha_t)$ is log normal (Engen & Lande 1996).

The survival of the 0-group individuals may be reduced through intracohort and intercohort density dependence. Myers & Cadigan (1993) and Myers *et al.* (1995*c*) argued that density dependence in cod is best approximated by the discrete-time Gompertz (1825) model (i.e. log-linear dependence on density). Bjørnstad *et al.* (1999*b*) demonstrated log-linear density dependence in the survival of the Skagerrak coastal cod populations. Assuming further that the probability of dying due to the different kind of interactions are independent of one another, the proportion of the 0-group fish surviving through to the 1-group (Y_t) in the subsequent year may be approximated by

$$Y_t = X_{t-1} \exp(-\beta \ln X_{t-1}) \exp(-\gamma \ln(Y_{t-1})), \qquad (2)$$

where β and γ are positive constants determining the reduction in survival due to intra- and intercohort density dependence, respectively.

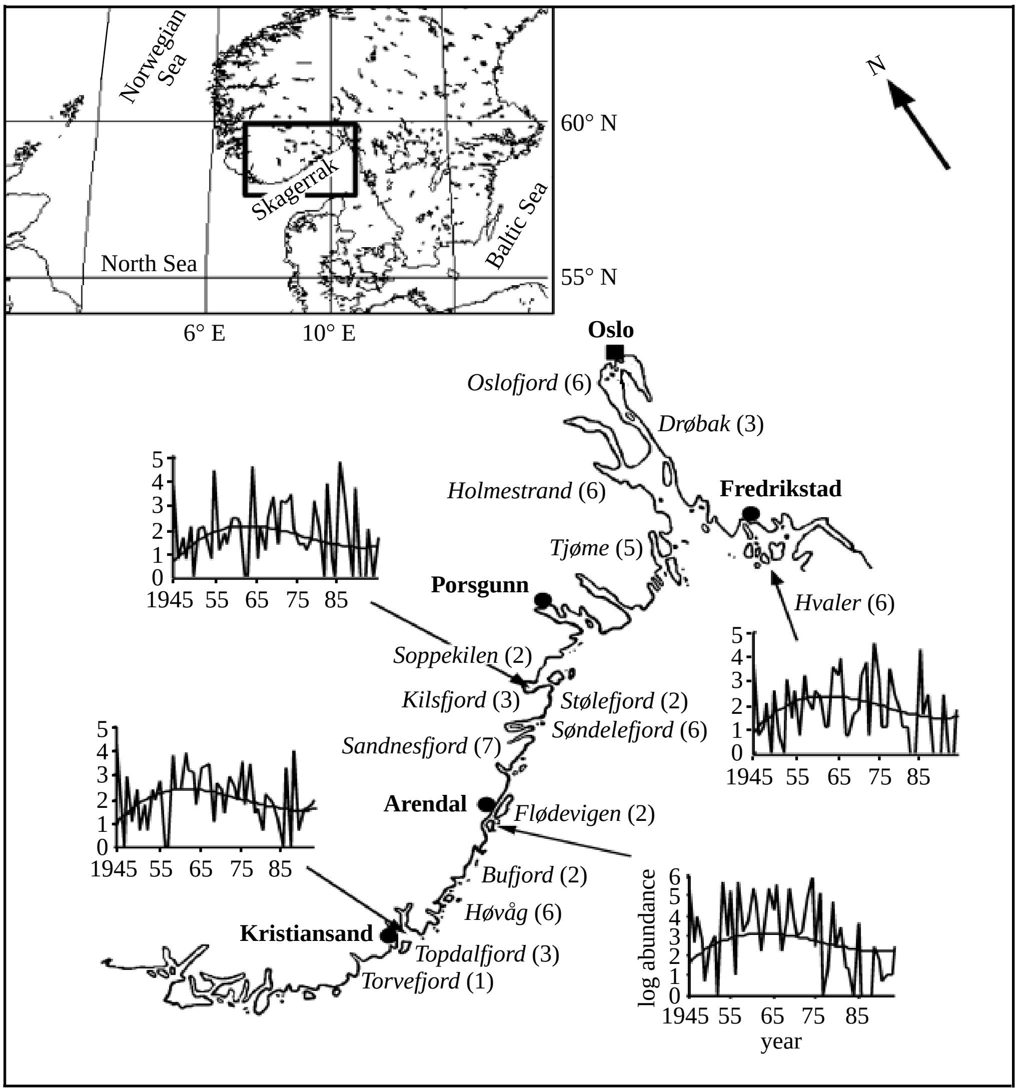

Figure 2. Locations of the stations along the Norwegian Skagerrak coast covered by the Flødevigen monitoring programme; the location of this part of Norway is shown on the Fennoscandian map as the bold rectangle. Numbers in parentheses represent the number of individual sampling stations for the various regions studied in the present analysis. See the text (§ 2(b)) for further details. The four diagrams around the map of the depicted part of the Norwegian Skagerrak coast show representative examples of time-series for the 0-group abundances. The smooth curves on the panels represent the long-term trend estimated from the seemingly unrelated regression (see § 3(c) and equation (8)); the curve is given by $0.21(\pm 0.02) \times t - 9 \times 10^{-3}(\pm 8 \times 10^{-4}) \times t^2 + 9 \times 10^{-5}(\pm 1 \times 10^{-5}) \times t^3$.

To close the life-cycle model (figure 1) we assume density-independent survival of the 1-group individuals into the spawning stock individuals:

$$Z_t = Y_{t-1}\exp(\lambda), \tag{3}$$

where λ is a constant that is assumed to be negative in order to ensure the survival rate is constrained to values between 0 and 1.

The main assumptions in this model can be summarized as follows: (i) the age of first spawning is approximately two years, (ii) the stochasticity during the recruitment processes dominates over the stochasticity in the other life-cycle transitions, and (iii) the main density-dependent processes involve the 0- and 1-groups.

(b) *The statistical model for the dynamics: an ARMA approach*

Log transforming equations (1)–(3) and denoting $\ln(X) = x$, $\ln(Y) = y$ and $\ln(Z) = z$, we obtain the following set of equations as our basic model:

$$x_t = z_t + \alpha_t, \tag{4}$$

$$y_t = (1-\beta)x_{t-1} - \gamma y_{t-1}, \tag{5}$$

and

$$z_t = \lambda + y_{t-1}. \tag{6}$$

Equations (4)–(6) may be back-substituted to give a model for the 0-group in delay-coordinates:

$$x_t = -\gamma x_{t-1} + (1-\beta)x_{t-2} + \alpha_t + \gamma\alpha_{t-1} + c, \tag{7}$$

where $c = \lambda(1 + \gamma)$. Recalling the assumption that $\{\alpha_t\}$ is a sequence of random numbers drawn independently from some distribution, equation (7) represents an ARMA(2,1) model (see e.g. Priestley 1981) with constraints on the parameters. In the following we call the autoregressive coefficients ar_i for ith order autoregressive (AR) process and ma_1 for the first-order moving average (MA) process.

Essentially, our model formulation corresponds to the 'Clark model' (Clark 1976; Horwood 1983; Botsford 1992; Mertz & Myers 1996), where the stock-recruitment relationship is assumed to follow a power law (cf. Haldane 1949, 1953; Cushing 1971). The original Clark model is modified by the inclusion of stochasticity within the per capita egg production, hatching and survival to the 0-group (α_t).

Density-dependent reproduction (i.e. $X_t = Z_t \exp(\alpha_t - \eta_t \ln(Z_{t-1}))$, where η_t measures the strength of the density dependence in reproduction) or density-dependent survival of the 1-group (i.e. $Z_t = Y_{t-1} \times \exp(-\theta \ln(Y_{t-1}))$, where θ measures the strength of density dependence in 1-group survival) give structurally identical predictions—the ARMA(2,1) model. The constraints on the parameters will, however, be different.

In order to derive our basic model, we assume a semelparous life history with maturation at age two years (followed by death). Relaxing this assumption, but maintaining that a major portion of the spawning stock belongs to the 2-group, we anticipate a higher order process, but with a smaller contribution by the higher lags compared to the first and second lags.

Focusing on the log abundance time-series of the 0-group between 1945 and 1994, we make four predictions from our life-cycle model. These predictions can be tested using the ARMA framework (see equation (7)).

(i) The most parsimonious model structure for the time-series is an ARMA model of order two with respect to the autoregressive terms and of order one with respect to the moving average term.
(ii) The second-order autoregressive term should be significantly positive.
(iii) The first-order autoregressive term and the moving average term should be of opposite sign (the former should be negative and the latter positive), but otherwise of the same magnitude.
(iv) Based on the relaxed assumptions discussed above, we furthermore conjecture that any third-order autoregressive terms are small compared to the first- and second-order terms.

A good model should be able to reproduce the spectral properties of the data (Falck *et al.* 1995). Fromentin *et al.* (1997) and Bjørnstad *et al.* (1999*a*) studied the spectral properties of the data in more detail. We provide a preliminary comparison of the spectra of the model versus those of the time-series in § 5.

(c) *Testing the predictions*

A substantial sigmoid-like temporal trend is observed in most of the time-series (figure 2; see Fromentin *et al.* 1997, 1998). We have nevertheless chosen to perform our analysis without doing any form of detrending since moving average terms may contribute significantly to low-frequency fluctuations (Bjørnstad *et al.* 1999*a*; see Priestley (1981) for a general discussion). Detrending may therefore remove an important component of the signal. We will, whenever technically feasible, allow for a trend in time explicitly in the analysis (see below).

The parsimonious structure of the model for the log abundance is classically investigated using the minimum AIC criterion (Akaike 1974) or the small-sample corrected equivalent, $\mathrm{AIC_c}$ (Hurvich & Tsai 1989; see Bjørnstad *et al.* (1995) for an ecological exposition). The most appropriate model for a given time-series according to this information theoretic tool is the one minimizing $\mathrm{AIC_c} = -2\log(\mathrm{likelihood}) + 2p + 2(p+1)(p+2)/(n-p-2)$, where p is the number of model parameters and n is the sample size. A difference of two or less in the AIC (or $\mathrm{AIC_c}$) may be considered 'insignificant', as this corresponds to no improvement in the likelihood with one additional parameter. To test for prediction (i) above, we summarize the $\mathrm{AIC_c}$ over all (univariate) ARMA models including up to five parameters (using *SAS/ETS user guide, v. 6.10*; SAS Institute 1990). In these univariate models, we are unable to separate the trend from low-frequency signals. This lack of accommodation of the external trend may severely impair the results.

Since stochastic forces are so important in fish dynamics, signals embedded in the time-series will probably be rather blurred. In order to maximize the power of the analysis, we should attempt to synthesize information across all the time-series (e.g. Myers & Barrowman 1996). For independent data sets, this can be done *a posteriori* using 'meta-analysis' (i.e. a weighted mixed-effect ANOVA; e.g. Gurevitch & Hedges 1993). However, the different time-series on coastal cod are not statistically independent of one another; rather they are spatially and temporally correlated (Fromentin *et al.* 1997). This autocorrelation makes the use of the meta-analysis unacceptable (e.g. Legendre 1993).

We therefore synthesize the information inherent in the time-series through a multivariate ARMA model in which the residuals in the different series are assumed to be correlated. We exclude the six stations from the Oslofjord area in this analysis, because their abundances are very low. To test predictions (ii)−(iv) of the model, we use the following global model for the stations $j = 1, 2, \ldots, 54$:

$$\begin{aligned} x_{j,t+1} = {} & c_j + ar_1 \times x_{j,t-1} + ar_2 \times x_{j,t-2} + ar_3 \times x_{j,t-3} \\ & + \mathrm{poly}(t,3) + a_{j,t} + ma_1 \times a_{j,t-1}, \end{aligned} \tag{8}$$

where $\alpha_{j,t}$ is distributed according to a multivariate normal distribution ($\mathrm{MVN}(0,\Sigma)$), where the variance–covariance matrix Σ is assumed to have between-station covariance in a given year (i.e. some non-zero, off-diagonal elements). The model is estimated according to a seemingly unrelated regression (see e.g. SAS Institute 1990, Proc Model; Pindyck & Rubinfeld 1991). The mean c_j, is allowed to vary between the series whereas the autoregressive coefficients (ar_i, $i = 1, 2, 3$) and the moving average term (ma_1) are assumed to be the same for all 54 stations; the global trend is incorporated though a third-order polynomial in time ($\mathrm{poly}(t,3)$) (Fromentin *et al.* 1997, 1998).

Disregarding the nuisance parameters for the mean of each series (c_j) and the residual covariance, the model has

Table 1. *Model selection for univariate ARMA models (with up to five parameters) using the minimum AIC$_c$ criterion considering a difference of two as insignificant*

(The number of time-series, out of the total 60 time-series, consistent with the different ARMA models are tabulated. Note that a given time-series can be consistent with more than one model. The parameters ar_1–ar_5 signify the first through to the fifth autoregressive processes whereas ma_1–ma_5 signify the first- to fifth-order moving average processes. The final row (column) signifies the number of series that are consistent with any process of *i*th order with respect to the autoregressive (moving average) term.)

moving average terms	autoregressive terms						
	ar_0	ar_1	ar_2	ar_3	ar_4	ar_5	ma_i
ma_0	—	38	38	14	3	1	56
ma_1	35	25	15	0	0	—	50
ma_2	30	20	1	0	—	—	41
ma_3	14	7	0	—	—	—	17
ma_4	2	1	—	—	—	—	2
ma_5	1	—	—	—	—	—	1
ar_i	52	57	42	14	3	1	—

Table 2. *Parameter estimates for the multivariate ARMA(3,1) model using the 60 time-series*

(Parameters are estimated using seemingly unrelated regression (Proc Model, SAS Institute 1990). The parameter ar_i represents the *i*th order autoregressive parameter whereas ma_1 represents the first-order moving average parameter.)

parameter	estimate	s.e.	*t*-ratio	*p*-value
ar_1	−0.17	0.05	−3.62	<0.001
ar_2	0.13	0.02	6.70	<0.001
ar_3	0.06	0.01	3.96	<0.001
ma_1	0.17	0.05	−3.28	0.002

seven parameters to be estimated from more than 2500 data points. This should ensure reasonable power and a fairly strong test for the hypotheses.

4. RESULTS

According to the minimum AIC$_c$ criterion, 42 (70%) of the 60 time-series are consistent with a model of second order with respect to the autoregressive component (table 1) and 50 (83%) are consistent with a model of first order with respect to the MA component. Hence, there is fair support for an AR(2) structure and an MA(1) structure. This is consistent with our most simplistic model (equation (7)). However, only 15 time-series (25%) are consistent with an ARMA(2,1) model according to the minimum AIC$_c$ criterion. Thus, there is altogether only modest support for the ARMA(2,1) model (however, see § 5).

The parameters of the model defined by equation (8), as estimated from the multivariate, seemingly unrelated regression of the 54 time-series (i.e. excluding the six Oslofjord series), are reported in table 2; as can be seen, they are all significant and may be summarized as follows.

(i) The second-order autoregressive parameter ($ar_2 = (1-\beta)$) is significantly positive (0.13 ± 0.02); hence, the model prediction with respect to this parameter (i.e. intracohort density dependence) is supported.

(ii) The first-order autoregressive parameter ($ar_1 = -\gamma$) is significantly negative at -0.17 ± 0.05 (suggesting intercohort density dependence). The moving average term ($ma_1 = \gamma$) is significantly positive at 0.17 ± 0.05. Hence, the expectation that $ar_1 \approx -ma_1$ is also supported.

(iii) The ar_3 is smaller in magnitude than any of the other parameters (0.06 ± 0.01). Note, however, that this parameter is statistically significant.

The spatial correlation between the processes at the different locations is quantified by the variance–covariance matrix from the seemingly unrelated regression. The average correlation is estimated at 0.20 (range −0.32 to 0.70). Eighty-seven per cent of the pairwise correlations are positive and a visual inspection shows that the correlation decreases with spatial distance. Stations in close proximity have a correlation of approximately 0.5 and the correlation at stations 50–70 km are generally no greater than the average (0.20); even the most distant populations (*ca.* 200 km apart) are on average positively correlated (at around 0.15).

The lag-one autocorrelation in the residuals ranges from −0.26 to 0.40. A formal test for the whiteness of the residuals (the Ljung Box version of the Portmanteau test; e.g. Tong 1990) only rejects the null hypothesis for three of the 54 time-series at a nominal 5% level. This is no more than expected by chance alone due to multiple testing. Thus, there is no statistical evidence of any remaining signals in the residuals. Note, however, that our ecological conclusion, that these populations arise from a highly stochastic process, implies that the statistical power of any residual test will probably be low.

5. DISCUSSION: DENSITY DEPENDENCE AND STOCHASTICITY

The biological processes underlying the population dynamics of the Norwegian Skagerrak cod appear to be density dependent both within and between juvenile cohorts. The density dependencies appear to interact with the stochastic processes. The stochasticity may in part explain the vagueness commonly observed in stock

Table 3. *Spearman rank correlation between the mean periodogram of the cod time-series and 100 stochasitc realizations of equation (8) but with varying ARMA skeletons*

(All models were estimated using the seemingly unrelated regression (Proc Model, SAS Institute 1990). The best correlation is indicated in bold.)

	autoregressive terms			
moving average terms	ar_0	ar_1	ar_2	ar_3
ma_0	0.52	0.51	0.51	0.48
ma_1	0.55	0.54	**0.61**	0.54

recruitment relationships (see e.g. Cushing 1996). The density dependence in survival is most probably due to asymmetrical competition and probably cannibalism of the 1-group on the 0-group. Cannibalism has been suggested to be an important mechanism in cod populations (Ricker 1962, 1979; Nellen 1986; Hop *et al.* 1992; Folkvord 1993; Folkvord *et al.* 1994; Nilssen *et al.* 1994; see also Kanapathippillai *et al.* 1994). The asymmetry in the interaction may be a major reason why two strong year-classes of cod seldom succeed each other in these populations (e.g. Ricker 1962; Phil & Umstrand 1988; Gjøsæter & Danielssen 1990). We have explored the density dependence in survival in more detail in Bjørnstad *et al.* (1999*b*).

The process observed in the cod population shows a resonance of the reproductive stochasticity through the life cycle. This interaction is mathematically defined by the $\gamma\alpha_{t-1}$ term in equation (7), an interaction that does not necessarily lead to a density-dependent reduction in the recruitment variability. This may be an important component of stochastic age-structured dynamics. Bjørnstad *et al.* (1999*a*) explored this interaction in more detail. The echoing of stochastic forces in the age structure provides an ecological and mechanistic basis for a specified group of log ARMA models. The data from the Flødevigen monitoring programme analysed in this paper give support to the prediction that an ARMA process captures some of the underlying processes in these populations. However, while the estimated coefficients were in tight agreement with the models given by equations (7) and (8), the model selection gave weak support for an ARMA(2,1) structure. Considering the precision of the multivariate model, we are inclined to trust that model the most.

In order to test the model structure from an alternative angle, we estimated the multivariate model for different ARMA models and simulated stochastic realizations of equation (8) (with the alternative ARMA structures). The average periodogram from 100 realizations is compared with the average periodogram of the 60 time-series in table 3. From this table it is seen that the model with an ARMA(2,1) structure is the one which best predicts the spectral properties of the series. We are therefore led to think that the univariate minimum AIC_c criterion is not a strong test for the current system and that the simplistic model presented above is an important tool for understanding coastal cod dynamics. The divergent conclusions from the analyses highlight how the most parsimonious model for short-term prediction (the minimum AIC model) is not necessarily the model that best captures the dynamic behaviour (for example, as reflected in the spectral densities).

ARMA-type models have often been considered difficult to 'reconcile with what seems to be underlying recruitment-related phenomena' (cf. Rothschild 1986, p. 124; see also Boudreault *et al.* 1977; Madenjian *et al.* 1986; Noakes 1986; Mendelssohn & Cury 1987, 1989; Fogarty 1988; Kope & Botsford 1988; Goldman *et al.* 1989). Hilborn & Walters (1992) noted further that time-series analysis 'has not proven terribly useful in analysis of fisheries stock dynamics' (p. 309) (but see for example Myers *et al.* 1995*a*, 1996). Our emergent hypothesis refines this notion by demonstrating how the life cycle of cod may (mechanistically) motivate a particular class of log ARMA models. These models may be seen to provide a framework for combining the stochastic theories of fish dynamics (e.g. the match–mismatch hypothesis; cf. Cushing 1990) with the density-dependent theories (Shepherd & Cushing 1990; Myers & Cadigan 1993; Wyatt *et al.* 1994, 1995).

The parameters $(1-\beta)$ and γ are indices of density dependence (Cushing 1971; see also Royama 1992). We have divided the density-dependent component into intra- $(1-\beta)$ and intercohort (γ) components. These were estimated to be 0.10–0.20 for our data (table 2), corresponding to estimates reported by Cushing (1971; see also Cushing & Harris 1973; Myers *et al.* 1995*a*,*b*). However, it should be noted that we have assumed no measurement errors; the presence of such errors will generally overestimate the degree of density dependence (see e.g. Lebreton 1989; Myers & Cadigan 1993). Consequently, the absolute value of the estimates should be treated with caution.

The parameterized ARMA(2,1) model (table 2) has dynamic behaviour corresponding to a 2–2.5 year cycle. Fromentin *et al.* (1997) documented such a cycle for the Norwegian Skagerrak cod, pollack (*Pollachius pollachius* L.) and whiting (*Merlangius merlangus* L.). The deterministic skeleton gives dampened oscillation, but the stochastic forcing may sustain the periodic behaviour (cf. Stenseth *et al.* 1996). The resonance further led to long-term fluctuations (Bjørnstad *et al.* 1999*a*). The nature of the long-term fluctuations of the present data have been discussed by Fromentin *et al.* (1998) and Bjørnstad *et al.* (1999*a*).

Steele (1976, 1985; Steele & Henderson 1994) argued that environmental stochasticity plays an important role in the generation of temporal variation in marine systems, possibly more so than in terrestrial systems. Steele (1976, 1985) concluded that the dynamics of terrestrial systems will probably be determined by system-internal, dynamic interactions. In the marine environment, external and non-responsive processes may be more important. Our analysis highlights how stochastic recruitment may interact with population-intrinsic, density-dependent processes, so as to generate a resonance structure in the time-series. We have also found the signatures of deterministic processes in the recruitment to the adult part of the population emphasized by Dahl & Dannevig (1906). Thus, the Flødevigen monitoring programme, which was developed from the controversy between Hjort and Dannevig, has helped to refine the current view that both disruptive and regulative processes are paramount in cod dynamics. On the basis of our analysis we conclude that the erratic fluctuations in cod abundance are not a function of external, stochastic forces alone. Nor are they functions of internal, 'chaotic' forces. Rather, the fluctuations may be due to resonance of the stochastic forces by the age-structured deterministic processes.

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