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Density-dependent juvenile mortality in marine demersal fish

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Density-Dependent Juvenile Mortality in Marine Demersal Fish

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We examine the hypothesis that population variability is created and regulated in the juvenile stage for demersal marine fish. Juvenile mortality is examined for 17 populations of Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*), plaice (*Pleuronectes platessa*), yellowtail flounder (*Pleuronectes ferrugineus*), and sole (*Solea vulgaris*) in the North Sea, Irish Sea, Barents Sea, Baltic Sea, and Northwest Atlantic. A latent variable covariance analysis of recruitment time series with measurement error is used to test hypotheses. We found strong evidence of density-dependent mortality within cohorts during the juvenile stage for cod, plaice, sole, and whiting; density-dependent mortality appears to be related to the log of juvenile abundance. There is evidence of negative autocorrelation between adjacent cohorts of cod; this pattern is consistent with density-dependent mortality between adjacent cohorts. The autocorrelations are positive for the flatfish examined. It is possible to obtain estimates of estimation error variances for populations if there are multiple research surveys of the same population. We conclude that the juvenile stage is very important for population regulation in most species but that the source of the variability in year class strength is in the larval stage or very early juvenile stage.

Nous examinons l'hypothèse que la variabilité des populations de poissons démersaux apparaît au stade juvénile et est régularisée au même stade. Nous examinons la mortalité juvénile dans 17 populations de morues franches (*Gadus morhua*), d'églefins (*Melanogrammus aeglefinus*), de merlans (*Merlangius merlangus*), de plies (*Pleuronectes platessa*), de limande à queue jaune (*Pleuronectes ferrugineus*) et de soles (*Solea vulgaris*) de la mer du Nord, de la mer d'Irlande, de la mer de Barents, de la mer Baltique et du N.-O. de l'Atlantique. Pour la vérification des hypothèses, nous nous sommes servis de l'analyse de covariance à variables latentes appliquée aux séries chronologiques du recrutement avec erreur de mesure. Nous avons constaté de forts indices que la mortalité dépend de la densité dans les cohortes du stade juvénile de la morue, de la plie, de la sole et du merlan. La mortalité dépendante de la densité semble reliée au logarithme de l'abondance des juvéniles. Il y a des signes d'autocorrélation négative entre les cohortes adjacentes de la morue; cette manifestation correspond à la mortalité dépendante de la densité entre les cohortes adjacentes. Les autocorrélations sont positives pour les poissons plats examinés. Il est possible d'obtenir des estimations de la variance des erreurs d'estimation pour les populations si la même population a fait l'objet de multiples relevés de recherche. Nous concluons que le stade juvénile est très important pour la régularisation des populations de la plupart des espèces, mais que la variabilité de l'effectif d'une classe d'âge trouve son origine au stade larvaire ou très tôt au stade juvénile.

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Our purpose is to examine density-dependent mortality within and between cohorts of marine fish during the juvenile stage. The approach taken is to consider populations for which multiple surveys are available. We use statistical methods that combine research surveys so that the underlying variability can be separated from the estimation error. We wish to identify the life-history stage in which density-dependent mortality is important. In spite of the crucial importance of this question (Ursin 1982; Shepherd and Cushing 1990), very little is known about the relative importance of density dependence in different life-history stages.

Density-dependent mortality during the juvenile stage has been most thoroughly studied in North Sea plaice (*Pleuronectes platessa*) (Rauck and Zijlstra 1978; Lockwood 1980; Veer 1986; Veer et al. 1990; Iles and Beverton 1991; Beverton and Iles 1992a, 1992b). Plaice is particularly amenable to study because the juvenile stage can be sampled. Sundby et al. (1989) presented evidence that juvenile mortality in northeast Atlantic cod (*Gadus*

morhua) is also density dependent. Although these studies are on the whole convincing, it usually cannot be excluded that the negative correlation between abundance and mortality is not a statistical artifact, i.e., abundance and mortality are usually not independent variables (Veer 1986). The approach taken here eliminates this statistical artifact that has plagued previous studies.

We have tried to assemble all time series of research survey estimates in which there are at least four independent, reliable estimates of juveniles for each cohort. The major limitation of our analysis is that the time series are relatively short. Thus, the reliability of the results for any one time series is limited. However, by analyzing many populations using identical methods, it is possible to arrive at conclusions with greater reliability. We test the sensitivity of our conclusions by analyzing alternative methods of estimation and by simulations to assess the effect of small sample size and violations of the model assumptions.

TABLE 1. Data for the North Sea cod stock from VPA in millions of fish, IYFS in numbers per hour fished, and EGFS in numbers per hour fished.

Year class	VPA 1-yr-olds	IYFS 1-yr-olds	IYFS 2-yr-olds	EGFS 0-yr-olds	EGFS 1-yr-olds	EGFS 2-yr-olds
1970	847	98.30	34.50			
1971	159	4.10	10.60			
1972	289	38.00	9.50			
1973	232	14.70	6.20			
1974	426	40.30	19.90			
1975	196	7.90	3.20			4.50
1976	726	36.70	29.30		62.70	12.50
1977	426	12.90	9.30	13.90	22.80	5.80
1978	449	9.90	14.80	12.60	24.20	6.70
1979	800	16.90	25.50	18.60	50.80	13.90
1980	271	2.90	6.70	10.20	11.40	2.90
1981	557	9.20	16.60	74.20	32.40	11.00
1982	269	3.90	8.00	2.50	15.40	4.70
1983	534	15.20	17.60	95.10	61.20	11.90
1984	108	0.90	3.60	0.40	4.30	1.20
1985	581	17.00	28.80	8.30	34.40	10.70
1986	257	8.80	6.10	1.20	14.20	4.10
1987	201	3.60	6.30	0.40	8.40	2.50
1988	324	13.10	15.20	16.80	22.80	5.10
1989		3.30		6.0	6.10	
1990				3.90		

There is an important secondary outcome of our work. We obtain independent (of the sampling design) estimates of the accuracy of abundance estimates obtained from research surveys.

In this paper, we examine only the component of juvenile mortality related to population abundance, i.e., the density-dependent component. For populations that have two independent, simultaneous surveys of population abundance, it is possible to estimate the variability of juvenile mortality unrelated to population abundance. This is done in Myers and Cadigan (1993).

An Example

Before presenting the statistical model, it is useful to discuss an example first. In Table 1, we show the results, presented to the ICES assessment working group (ICES 1991a), from research trawl surveys of cod in the North Sea. The English Groundfish Surveys (EGFS) take place in the autumn, while the International Young Fish Survey (IYFS) takes place in the late winter (February–March). Also included is the virtual population analysis (VPA) of the population (Pope 1972). Several things are immediately apparent from the data:

(1) Large and small year classes are consistent through all the surveys and the VPA.

(2) There is much greater variation in large and small year classes at early ages than at later ages. This appears not to be due to estimation error alone because the small and large year classes show up consistently throughout all the analyses.

(3) There is much greater variation in the research surveys than in the VPA.

(4) There appears to be density-dependent mortality, i.e., large year classes appear to have higher mortality. To illustrate this, we plot an index of survival (the difference between the log numbers at age 2 and 0 from the EGFS) against an independent index of abundance of that cohort (the log numbers at age 1 from the EGFS). There appears to be a significant decrease in survival

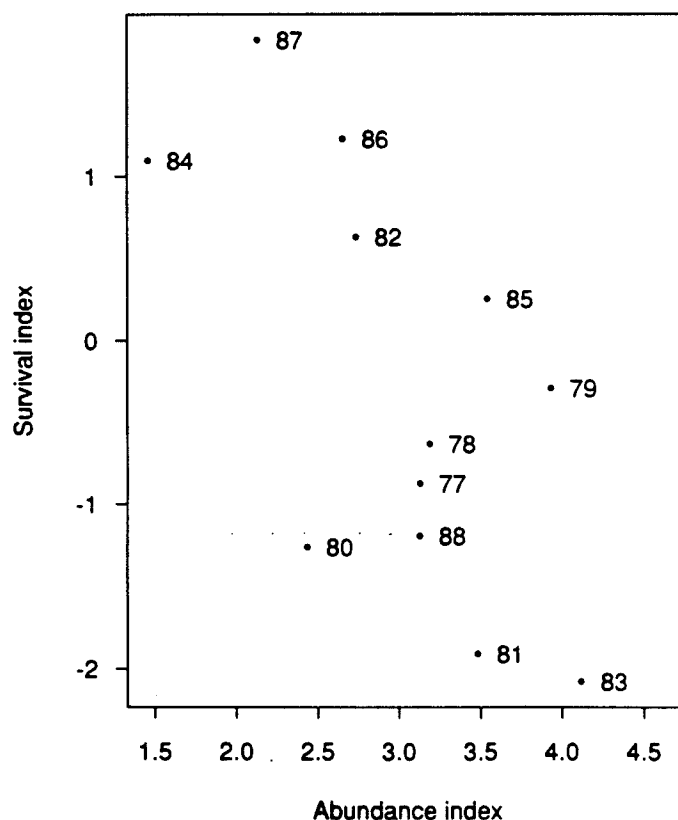


FIG. 1. Survival index versus abundance index for the EGFS of North Sea cod. The index of survival is the difference between the log index of numbers at age 2 and 0. The index of abundance is the log numbers at age 1. The correlation is -0.65 (p -value = 0.0054).

with log abundance. The estimation errors for the two variables in Fig. 1 are independent, and thus the negative slope is not caused by correlated errors.

(5) Recruitment appears to be low after large cohorts. This implies that there may be density-dependent mortality between adjacent cohorts.

In this paper, we examine the above points using stochastic models.

Methods

The Basic Model

Consider a population in which each cohort is surveyed several times in the juvenile stage. Let the number of fish in cohort t surveyed at age a be $N_{t,a}$. The surveys see the juveniles at different ages; the survey index of the youngest age is 0, and surveys that see the fish at later ages are labeled sequentially. Let the average mortality between the first survey and the survey at age a that is independent of density be m_a . The population dynamics during the juvenile stage are described by

$$N_{t,a} = N_{t,0} e^{-m_a}.$$

Here, $m_0 = 0$.

Now consider the case of density-dependent mortality. We examine the hypothesis that mortality is linearly related to the logarithm of the initial number of juveniles in the cohort (Fig. 1). Let $(1 - \lambda_a) \log N_{t,0}$ be the density-dependent mortality where $\lambda_0 = 1$. We now have that

$$N_{t,a} = N_{t,0} e^{-m_a - (1 - \lambda_a) \log N_{t,0}}.$$

Note that the density-dependent component of mortality is a function of the numbers of fish in the cohort at the first time they are seen in the surveys.

It is useful to work with log-transformed variables, e.g., $L_{t,a} = \log N_{t,a}$. Thus, the above equation becomes

$$L_{t,a} = \lambda_a L_{t,0} - m_a$$

Consider observational error in the log-transformed survey data, $l_{t,a,i}$. Let $c_{a,i}$ be the log catchability of survey i on age a and let $\delta_{t,a,i}$ be the observational error of survey i on age a of cohort t . Estimates of abundance are assumed to be proportional to the true abundance. We write $\lambda_{a,i}$ now instead of λ_a . The observed log-transformed abundance from age a and survey i is

$$(1) \quad l_{t,a,i} = c_{a,i} + L_{t,a} + \delta_{t,a,i} \\ = c_{a,i} - m_a + \lambda_{a,i} L_{t,0} + \delta_{t,a,i}.$$

The following assumptions are made about the stochastic nature of recruitment and estimation errors when estimating the parameters of Eq. 1:

(1) Relative year class strength is determined in the larval stage, and there is no interannual variation in mortality in the juvenile stage unrelated to density. This assumption is tested in Myers and Cadigan (1993).

(2) Log-transformed standardized recruitments are mutually independent, identically distributed random variables (i.e., independent of year) following a normal distribution with constant mean and variance, that is

$$L_{t,0} \sim N(\mu, \phi).$$

(3) Errors in estimating abundance from research surveys, $\delta_{t,a,i}$, are independent normal random variables with zero mean and

constant variance, that is

$$\delta_{t,a,i} \sim N(0, \theta_{a,i}).$$

Furthermore, the errors are independent of $L_{t,0}$. The variance is constant in that it does not depend upon year, but it does depend upon age and survey.

Note that $c_{a,i} - m_a$ is constant for each survey and age. We do not attempt to estimate these terms, but merely subtract the sample mean over time for each survey and age from the data. We concentrate on estimating the other parameters in Eq. 1.

Density-dependent mortality may also be a function of the numbers in the previous cohort abundance, $N_{t-1,0}$. In this case, we define between cohort density-dependent mortality such that

$$N_{t,0} = N_{t,l} e^{\beta \log N_{t-1,0}}.$$

$N_{t,l}$ is defined as the recruitment before the effects of density-dependent mortality have occurred. The subscript l refers to the larval stage. Taking logarithms yields

$$(2) \quad L_{t,0} = L_{t,l} + \beta L_{t-1,0}.$$

We assume that $L_{t,l}$ is independent of $L_{t-1,0}$. We also assume that $L_{t,0}$ is normal with constant variance. If the variance of $L_{t,0}$ is ϕ , as we assumed before, then the variance of $L_{t,l}$ is $(1 - \beta^2)\phi$.

In Eq. 2, adjacent cohorts are assumed to interact through increased mortality that occurs before the first juvenile survey. However, the results from many VPA estimates of recruitment are positively autocorrelated (Myers et al. 1990). This may be because recruitment is responding to autocorrelated environmental variable or because errors in aging commercial catch at age data used by VPA's induce autocorrelated errors (Myers and Drinkwater 1989; Bradford 1991). We eliminate the second problem by using only research vessel data on juvenile fish in which aging is thought to be very accurate because there is minimal size overlap between the youngest ages. Thus, the parameter β can be interpreted as the density-dependent mortality between adjacent cohorts, or as the autocorrelation between the log of adjacent cohorts.

When estimating β in Eq. 2 the above assumptions must be modified. Specifically, we modify the assumption that recruitment is independent between adjacent cohorts. We estimate the parameter β by estimating the covariance between the factors describing recruitment in year t and $t - 1$. In order to estimate β , we must examine the assumption that the errors in estimation are independent between surveys. A likely source of nonindependent errors occurs because the errors in estimating abundance of all ages in a survey often appear to be positively correlated. When the same survey is used to estimate the numbers at two age groups and lagged data are used, this could create spurious correlations. Let $l_{t,1,i}$ be an estimate of recruitment from survey i for age 1, and let $l_{t-1,2,i}$ be the estimate for age 2 lagged 1 yr from the same survey. Then $l_{t,1,i}$ and $l_{t-1,2,i}$ both are estimated during the same year, and it is not reasonable to assume that the estimation errors are independent. That is, the covariance between the estimation errors, i.e., $\text{cov}(\delta_{t,1,i}, \delta_{t-1,2,i})$, is positive. We estimate all such covariance parameters in the model. We present the estimated correlation, e.g., $\rho(\delta_{t,1,i}, \delta_{t-1,2,i})$ instead of the covariance because it is easier to understand. Note that because the estimated correlation is derived from covariance estimates, it may sometimes be estimated as being greater than 1. We present

TABLE 2. Parameters and estimates for the density dependence between cohorts model, North Sea (SE's in parentheses), ρ (•) denotes the correlation coefficient; p -values are two-sided probabilities that estimates are not zero; $P(\lambda > 1)$ is the joint probability that all the estimated λ 's are > 1 .

	Cod	Haddock	Whiting		Plaice	Sole
$l_{t,0,1}$	EGFS	EGFS	EGFS	$l_{t,0,1}$	INSHORE	INSHORE
$l_{t,1,2}$	IYFS	IYFS	IYFS	$l_{t,0,2}$	TRIDENSA	TRIDENSA
$l_{t,1,1}$	EGFS	EGFS	EGFS	$l_{t,1,3}$	TRIDENSS	TRIDENSS
$l_{t,2,2}$	IYFS	IYFS	IYFS	$l_{t,1,2}$	TRIDENSA	TRIDENSA
$l_{t,2,1}$	EGFS	EGFS	EGFS	$l_{t,1,1}$	INSHORE	INSHORE
n	18	18	18	n	21	21
$\lambda_{0,1}$	1.00	1.00	1.00	$\lambda_{0,1}$	1.00	1.00
$\lambda_{1,2}$	0.50 (0.07)	0.68 (0.12)	0.55 (0.23)	$\lambda_{0,2}$	1.00	1.00
$\lambda_{1,1}$	0.47 (0.06)	0.88 (0.12)	0.70 (0.18)	$\lambda_{1,3}$	0.69 (0.11)	0.72 (0.11)
$\lambda_{2,2}$	0.40 (0.06)	0.68 (0.12)	0.26 (0.23)	$\lambda_{1,2}$	0.60 (0.08)	0.22 (0.13)
$\lambda_{2,1}$	0.45 (0.06)	1.0 (0.15)	0.41 (0.17)	$\lambda_{1,1}$	0.57 (0.11)	0.52 (0.13)
$\theta_{0,1}$	0.99 (0.30)	0.39 (0.12)	0.31 (0.10)	$\theta_{0,1}$	0.15 (0.05)	0.10 (0.12)
$\theta_{1,2}$	0.13 (0.04)	0.15 (0.05)	0.29 (0.08)	$\theta_{0,2}$	0.16 (0.06)	0.91 (0.23)
$\theta_{1,1}$	0.02 (0.01)	0.07 (0.03)	0.01 (0.02)	$\theta_{1,3}$	0.30 (0.07)	0.58 (0.14)
$\theta_{2,2}$	0.05 (0.02)	0.16 (0.05)	0.36 (0.10)	$\theta_{1,2}$	0.18 (0.05)	0.90 (0.20)
$\theta_{2,1}$	0.01 (0.01)	0.12 (0.05)	0.15 (0.04)	$\theta_{1,1}$	0.28 (0.07)	1.06 (0.24)
$\rho(\delta_{t,0,1}, \delta_{t-1,1,1})$	0.48	0.28	-0.4	$\rho(\delta_{t,0,1}, \delta_{t-1,1,1})$	0.01	1.00
p -value	(0.12)	(0.43)	(0.49)	p -value	(0.96)	(0.02)
$\rho(\delta_{t,1,1}, \delta_{t-1,2,1})$	1.06	-0.14	0.60	$\rho(\delta_{t,0,2}, \delta_{t-1,1,2})$	0.56	0.22
p -value	(0.02)	(0.73)	(0.33)	p -value	(0.04)	(0.31)
$\rho(\delta_{t,1,2}, \delta_{t-1,2,2})$	0.50	-0.50	0.48			
p -value	(0.08)	(0.07)	(0.06)			
ϕ	2.69 (1.15)	0.93 (0.36)	0.27 (0.15)	ϕ	0.78 (0.21)	1.45 (0.35)
β	-0.59	0.19	-0.68	β	0.43	0.12
p -value	(0.12)	(0.52)	(0.16)	p -value	(0.11)	(0.61)
$P(\lambda > 1)$	0.000	0.508	0.061	$P(\lambda > 1)$	0.002	0.006

such estimates but make no inferences about them.

Using the above assumptions, it is possible to obtain maximum likelihood estimates of the model parameters. We defer more discussion of parameter estimation to Appendix 1.

Many readers may suspect that estimating density-dependent mortality from research surveys is not possible because of large biases due to the errors-in-variable regression problem (Hilborn and Walters 1992). We have addressed this problem using Monte Carlo simulations and have found that such biases do not appear to be a problem for our methods (Appendix 2).

Data

We examined data from regions where there are multiple surveys in each year and used the following criteria for selecting time series. First, we attempted to use surveys that covered the complete range of the population. Unfortunately, this was not always possible. Some surveys covered regions close to shore, while others, such as the North Wales Groundfish Survey (NWGS), covered only a portion of the region. We have identified such limitations of the data below. Second, we had to deal with the problem of zero catches in some years. We attempted to

use surveys that only had nonzero catches. If there were zero catches, we replaced the observation with one tenth the minimum of the nonzero catches. We performed the above procedure with one half the minimum and found that estimates were not very sensitive to the fraction of the minimum. The data from some surveys appeared to have so much estimation error that estimates were unrealistic. In analyzing the robustness of the methodology (Appendix 2), estimates from such surveys were considerably biased and had large standard errors. We have identified these cases below.

The North Sea gadoid populations were estimated from two surveys that cover the area very well (ICES 1991a). The EGFS (Table 2) take place in the autumn, while the IYFS takes place in the late winter (February–March). The eastern North Sea populations of sole (*Solea vulgaris*) and plaice were surveyed during the spring (April–May) and autumn (September–October) from the Dutch to the Danish coastal waters using the research vessel *Tridens* (ICES 1991b). The surveys are denoted by TRIDENSA and TRIDENSS for the age 0+ and 1+ surveys in the autumn and the age 1+ surveys carried out in the spring (Table 2). These surveys have been carried out since 1970. There are surveys carried out at approximately the same time in more

TABLE 3. Parameters and estimates for the density dependence between cohorts model, Irish Sea (SE's in parentheses). See Table 2 for details.

Cod			Whiting		Plaice
$l_{t,0,1}$	OCTOBER	$l_{t,0,1}$	GADOID	$l_{t,0,1}$	OCTOBER
$l_{t,1,2}$	MARCH	$l_{t,0,2}$	OCTOBER	$l_{t,1,2}$	MARCH
$l_{t,1,3}$	JUNE	$l_{t,1,3}$	JUNE	$l_{t,1,3}$	JUNE
$l_{t,1,1}$	OCTOBER	$l_{t,1,1}$	GADOID	$l_{t,1,4}$	ISMAY
n	14	n	11	n	14
$\lambda_{0,1}$	1.00	$\lambda_{0,1}$	1.00	$\lambda_{0,1}$	1.00
$\lambda_{1,2}$	0.75 (0.12)	$\lambda_{0,2}$	1.00	$\lambda_{1,2}$	0.93 (0.23)
$\lambda_{1,3}$	0.51 (0.11)	$\lambda_{1,3}$	0.45 (0.30)	$\lambda_{1,3}$	0.52 (0.18)
$\lambda_{1,1}$	0.65 (0.13)	$\lambda_{1,1}$	0.82 (0.38)	$\lambda_{1,4}$	0.26 (0.13)
$\theta_{0,1}$	0.56 (0.36)	$\theta_{0,1}$	0.74 (0.34)	$\theta_{0,1}$	1.05 (0.48)
$\theta_{1,2}$	0.58 (0.25)	$\theta_{0,2}$	1.15 (0.46)	$\theta_{1,2}$	0.20 (0.32)
$\theta_{1,3}$	0.78 (0.26)	$\theta_{1,3}$	0.44 (0.17)	$\theta_{1,3}$	0.88 (0.29)
$\theta_{1,1}$	0.89 (0.31)	$\theta_{1,1}$	0.42 (0.22)	$\theta_{1,4}$	0.55 (0.17)
$\rho(\delta_{t,0,1}, \delta_{t-1,1,1})$	0.57	$\rho(\delta_{t,0,1}, \delta_{t-1,1,1})$	-0.04		
p -value	(0.17)	p -value	(0.92)		
ϕ	3.72 (1.32)	ϕ	0.58 (0.36)	ϕ	1.93 (0.93)
β	-0.24	β	0.20	β	0.26
p -value	(0.48)	p -value	(0.68)	p -value	(0.47)
$P(\lambda > 1)$	0.019	$P(\lambda > 1)$	0.338	$P(\lambda > 1)$	0.382

inshore regions from the Belgium to the Danish coastal waters. These are autumn surveys (September–October) that are primarily aimed at estimating the numbers of 0+ recruits. These surveys are denoted by INSHORE0 and INSHORE1 for the age 0+ and 1+ fish.

The Irish Sea gadoid populations are estimated from the October, March, and June NWGS (Table 3) and the autumn (September–October) prerecruit gadoid surveys, denoted as GADOID (Brander and Symonds 1981; ICES 1991c). The NWGS take place at 16 fixed sites along the North Wales coast, and even though the coverage is only of a portion of the ranges of the populations, they are highly correlated with recruitment calculated from VPA (ICES 1991c). These surveys have taken place every year since 1976. The prerecruit gadoid survey is a 32-haul survey stratified by depth throughout the Irish Sea. This survey occurred from 1979 to 1987. The Irish Sea plaice population is also surveyed by the Irish May Survey, which took place from 1976.

Random stratified surveys of the Gulf of Maine, Georges Bank, and southern New England) populations have taken place in the offshore regions by the U.S. Northeast Fisheries Center (NEFC) in the spring since 1968 and in the fall since 1963 (Table 4). Abundance is estimated with few or no zero catches at age 1+ in the spring surveys (Anonymous 1991). Cod, haddock (*Melanogrammus aeglefinus*), yellowtail flounder (*Pleuronectes ferrugineus*), and silver hake (*Merluccius bilinearis*) have been aged in these surveys and are thus amenable for our analysis; however, the errors in estimating the numbers of silver hake were too large to obtain reliable estimates.

Surveys of cod on the southern Grand Banks of Newfoundland (Table 5) have taken place since 1972 by Canada (Baird et al.

1991) and since 1978 by the USSR (Kuzmin 1991). Both surveys are in the spring and cover the same region. However, the Russian surveys did not appear to give reliable estimates until age 3. There are surveys by Canada and France on the nearby St. Pierre Bank; however, the estimation errors for juveniles were too large to produce reliable results.

The Northeast Arctic haddock population has been surveyed in the Barents Sea by Norway using trawl surveys, denoted by NORWAYB, since 1983 and acoustic surveys, denoted by NORWAYA, since 1977 during winter (January–March) with only one year missing for the acoustic survey (Table 5). Young age groups of Northeast Arctic cod do not seem to be as well surveyed by the acoustic surveys; there are several years in which no age 1+ cod were caught. We therefore used the USSR bottom trawl surveys carried out during late autumn – early winter (November–December) which did not record zero catches for any juvenile age class (ICES 1991d and unpublished data). For the USSR trawl surveys for cod, we use the combined index for ICES subareas I, IIa, and IIb.

Survey Reliability

Two crucial assumptions in the analysis are that the research survey estimates of population abundance are proportional to the true abundance and that the populations are well defined. Estimates of abundance from a well-designed research survey should respond proportionally to changes in true population abundance if the total range of the population is surveyed. In most of the surveys considered here, this is the case. However, even if only a portion of the range is surveyed the estimates may be proportional to the true abundance.

TABLE 4. Parameter and estimates for the density dependence between cohorts model, United States (SE's in parentheses). See Table 2 for details.

	Cod Georges Bank	Cod Gulf of Maine	Haddock Georges Bank	Haddock Gulf of Maine	Yellowtail Georges Bank	Yellowtail Southern New England
$l_{1,1}$	SPRING	SPRING	SPRING	SPRING	SPRING	SPRING
$l_{1,2}$	FALL	FALL	FALL	FALL	FALL	FALL
$l_{2,1}$	SPRING	SPRING	SPRING	SPRING	SPRING	SPRING
$l_{2,2}$	FALL	FALL	FALL	FALL	FALL	FALL
n	26	26	26	26	26	26
$\lambda_{1,1}$	1.00	1.00	1.00	1.00	1.00	1.00
$\lambda_{1,2}$	1.08 (0.17)	0.79 (0.15)	0.91 (0.09)	1.06 (0.12)	0.88 (0.19)	0.94 (0.19)
$\lambda_{2,1}$	1.10 (0.18)	0.71 (0.15)	0.73 (0.07)	1.01 (0.09)	0.78 (0.13)	1.06 (0.18)
$\lambda_{2,2}$	0.88 (0.16)	0.53 (0.12)	0.71 (0.09)	1.05 (0.10)	0.60 (0.12)	1.18 (0.23)
$\theta_{1,1}$	0.74 (0.16)	1.99 (0.46)	1.71 (0.48)	1.55 (0.39)	3.00 (0.68)	2.54 (0.53)
$\theta_{1,2}$	0.19 (0.06)	0.74 (0.19)	2.02 (0.51)	2.31 (0.55)	1.31 (0.33)	1.05 (0.24)
$\theta_{2,1}$	0.10 (0.05)	0.59 (0.16)	0.71 (0.22)	0.60 (0.22)	0.51 (0.16)	0.57 (0.15)
$\theta_{2,2}$	0.26 (0.06)	0.57 (0.13)	2.31 (0.52)	1.17 (0.33)	0.25 (0.08)	0.29 (0.13)
$\rho(\delta_{1,1,1}, \delta_{1,2,1})$	0.79	0.87	0.05	-0.04	0.70	0.89
p -value	(0.00)	(0.00)	(0.86)	(0.89)	(0.49)	(0.00)
$\rho(\delta_{1,1,2}, \delta_{1,2,2})$	0.36	0.78	0.82	0.77	0.31	0.71
p -value	(0.13)	(0.00)	(0.00)	(0.00)	(0.76)	(0.00)
ϕ	0.68 (0.24)	1.45 (0.55)	7.33 (1.89)	6.09 (1.71)	2.37 (1.01)	1.18 (0.51)
β	-0.22	-0.00	-0.14	0.45	0.76	0.46
p -value	(0.33)	(1.00)	(0.55)	(0.07)	(0.45)	(0.14)
$P(\lambda > 1)$	0.784	0.085	0.164	0.836	0.257	0.821

Myers and Stokes (1989) examined the EGFS in the North Sea to determine if local population log abundance changed uniformly throughout the North Sea. They found that this was true for haddock, but not for cod and whiting (*Merlangius merlangus*). There are few instances where this needs to be considered in detail. In the plaice and sole survey on the continental side of the North Sea, we used two independent surveys, each of which covers a portion of the habitat. Jointly, these surveys cover much of the range of the population, and the estimates should be reliable because we have constrained both estimates to be proportional to each other, i.e., we have constrained both $\lambda_{0,1}$ and $\lambda_{0,2}$ to be 1.

The U.S. surveys do not cover the nearshore areas. This may present a problem for Gulf of Maine cod which has its juvenile nursery grounds close to shore. A portion of the inshore area is covered by the State of Massachusetts Inshore Surveys. In Myers and Cadigan (1993), we estimated density-dependent mortality using these data and found significant density-dependent mortality in this population whereas in the current analysis (Table 2), we did not.

In the Irish Sea, the NWS covers only a portion of the range of the populations. Thus the results for this region must be viewed with some reservation.

For any one of the above populations, density-dependent habitat utilization combined with surveys that do not cover the entire range of the populations could bias the results. In particular, if only the core area of the population was surveyed, density-dependent habitat utilization might appear as density-

dependent mortality. We conclude that this factor may be important in a few of the populations, but should have only limited influence on our overall conclusions.

Results

Density-Dependent Mortality within a Cohort

We initially estimated the model under the assumption that recruitment was independent between adjacent year classes ($\beta = 0$). We then estimated the model without the above assumption. Our results were similar in both cases. To save space, we present only the results for the case without the assumption because the parameter estimates (other than β , Tables 3–5) are very similar.

If there is density-dependent mortality within cohorts, we expect $\lambda_a < 1$ for older ages. For cod, λ_a decreases with age for all populations except the Georges Bank population (Fig. 2). This implies that the variability in recruitment is being reduced through density-dependent mortality or a process similar to density dependent mortality. Georges Bank cod is perhaps the most overexploited of the cod populations (Anonymous 1991). It may show no evidence of density-dependent mortality because the population abundance has never reached a level where density-dependent mortality would be important.

The density-dependent mortality parameter, λ , appears to be typically around 0.5 for cod. This would imply that a 100-fold increase in postlarval cod would result in only a 10-fold increase in abundance a year later. There appears to be strong density-

TABLE 5. Parameters and estimates for the density dependence between cohorts model, Newfoundland and Arctic (SE's in parentheses). See Table 2 for details.

	Cod Southern Grand bank		Cod Northeast Arctic	Haddock Northeast Arctic
$l_{t,1,1}$	CANADA	$l_{t,1,1}$	RUSSIA	NORWAYA
$l_{t,2,1}$	CANADA	$l_{t,1,2}$	NORWAYB	NORWAYB
$l_{t,3,1}$	CANADA	$l_{t,2,1}$	RUSSIA	NORWAYA
$l_{t,3,2}$	RUSSIA	$l_{t,2,2}$	NORWAYB	NORWAYB
n	18	n	9	11
$\lambda_{1,1}$	1.00	$\lambda_{1,1}$	1.00	1.00
$\lambda_{2,1}$	0.60	$\lambda_{1,2}$	0.87	0.81
	(0.15)		(0.17)	(0.24)
$\lambda_{3,1}$	0.45	$\lambda_{2,1}$	0.67	1.08
	(0.12)		(0.13)	(0.30)
$\lambda_{3,2}$	0.60	$\lambda_{2,2}$	0.57	0.97
	(0.18)		(0.12)	(0.29)
$\theta_{1,1}$	2.73	$\theta_{1,1}$	2.27	2.99
	(0.82)		(0.95)	(1.27)
$\theta_{2,1}$	0.18	$\theta_{1,2}$	0.80	1.33
	(0.13)		(0.43)	(0.62)
$\theta_{3,1}$	0.40	$\theta_{2,1}$	0.64	1.66
	(0.13)		(0.30)	(0.90)
$\theta_{3,2}$	0.97	$\theta_{2,2}$	0.53	1.89
	(0.29)		(0.24)	(0.89)
$\rho(\delta_{t,1,1}, \delta_{t-1,2,1})$	0.68	$\rho(\delta_{t,1,2}, \delta_{t-1,2,1})$	0.36	0.01
p -value	(0.07)	p -value	(0.39)	(0.98)
$\rho(\delta_{t,2,1}, \delta_{t-1,3,1})$	0.47	$\rho(\delta_{t,1,2}, \delta_{t-1,2,2})$	0.45	0.12
p -value	(0.24)	p -value	(0.32)	(0.98)
ϕ	2.28	ϕ	5.69	4.18
	(1.15)		(2.89)	(2.53)
β	-0.06	β	0.49	0.53
p -value	(0.85)	p -value	(0.26)	(0.28)
$P(\lambda > 1)$	0.015	$P(\lambda > 1)$	0.216	0.697

dependent mortality for sole and plaice. These observations are consistent with previous observations of density-dependent mortality in plaice from the analysis of other types of data. The results for yellowtail flounder are ambiguous. The Georges Bank population shows evidence of density-dependent mortality whereas the southern New England population does not.

Both populations of whiting show density-dependent mortality. Density-dependent mortality in haddock appears to be less important than in the two other gadoids considered. However, all haddock populations except Gulf of Maine show some evidence of density-dependent mortality.

Overall, there appears to be generally very high levels of density-dependent mortality in most populations examined. The consistency of the relationship implies that it is a general phenomenon. The results are robust to reasonable violations of the model assumptions (Appendix 2).

Density-Dependent Mortality between Cohorts

To test the assumption that recruitment is independent between adjacent cohorts, we estimated the parameter β , which is the first-order autocorrelation between cohorts. We did this by estimating the covariance between the factors describing recruitment and lag recruitment (Tables 2–5). Although the individual estimates of β are not statistically significant, consistent patterns are evident.

β is positive for all the flatfish and the haddock populations. For whiting, β is slightly positive in the Irish Sea and negative

in the North Sea. For cod, β is negative for five of the six populations examined. This is consistent with the hypothesis that there is density-dependent mortality between adjacent cohorts.

• For cod, the only exception is the Northeast Arctic population. The standard errors of the estimates of β are relatively large. Nevertheless, the strong pattern within the taxa indicates that density-dependent mortality between adjacent cohorts of cod may be a real phenomenon.

The autocorrelation between year classes is probably governed by two competing factors. The first is a negative correlation caused by density-dependent mortality due to competition and cannibalism between adjacent cohorts. The second is a positive correlation caused by autocorrelation in the environment. In some cases, i.e., Northeast Arctic cod, the second factor may dominate whereas the first factor may dominate for other populations.

Estimation Error Variances

There is a striking difference in the estimation error variance in different surveys (Fig. 3; Tables 2–5). The North Sea surveys for cod, whiting, and haddock have the smallest estimation error variance of all surveys. In particular, these surveys are much less variable than those conducted off New England, Canada, and in the Northeast Arctic. The relatively low estimation error for the North Sea surveys may be because these surveys usually employed fixed stations in contrast with the New England and Canadian stratified random surveys where rerandomization is

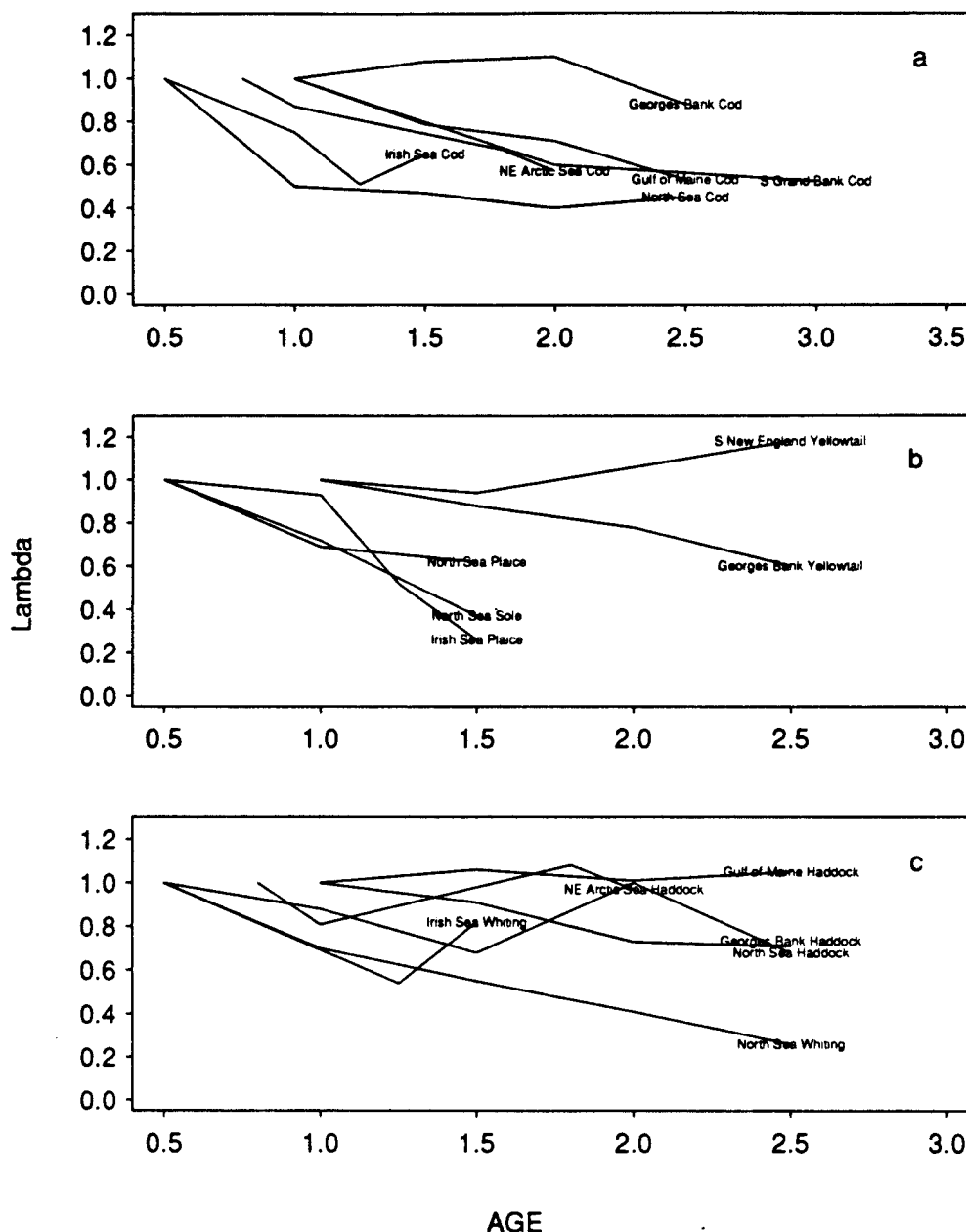


FIG. 2. Density-dependent mortality coefficient, λ , in relation to age for (a) cod, (b) plaice, sole, and yellowtail flounder, and (c) haddock and whiting.

performed each year. Note that the Irish Sea surveys have relative low estimation error variance even though these surveys have few sample trawls, i.e., either 16 or 32. The Irish sea surveys may owe their low estimation error to having fixed sample sites.

The estimation error usually decreases with age (Fig. 3). The source of the higher estimation error may be caused by the behavior of the younger fish. For example, younger fish may be more pelagic or may tend to school more, either of which would increase the sampling variability.

Note that $\text{cov}(\delta_{i,j,i}, \delta_{i-1,j+1,i}) > 0$ for 28 of 33 covariances estimated. Given the shortness of the series, this is good evidence of year effects in the surveys and that the standard errors calculated from survey design models will underestimate the true estimation errors. This underestimation probably occurs because the efficiency of the sampling gear is not constant. For example,

environmental conditions or differences in how the crew handle the fishing gear may affect the efficiency.

Density-Dependent Mechanisms

Our results are consistent with density-dependent mortality for most of the populations examined. There are several biological processes that could result in density-dependent mortality:

(1) Density-dependent mortality could be the consequence of competition for food. Mortality may result from starvation or from increased predation, i.e., fish with reduced specific growth rates would be exposed to predators for a longer time (Ricker and Foerster 1948; Shepherd and Cushing 1980). Density-dependent growth would usually be seen if there is increased competition for food; however, competition for food may increase mortality

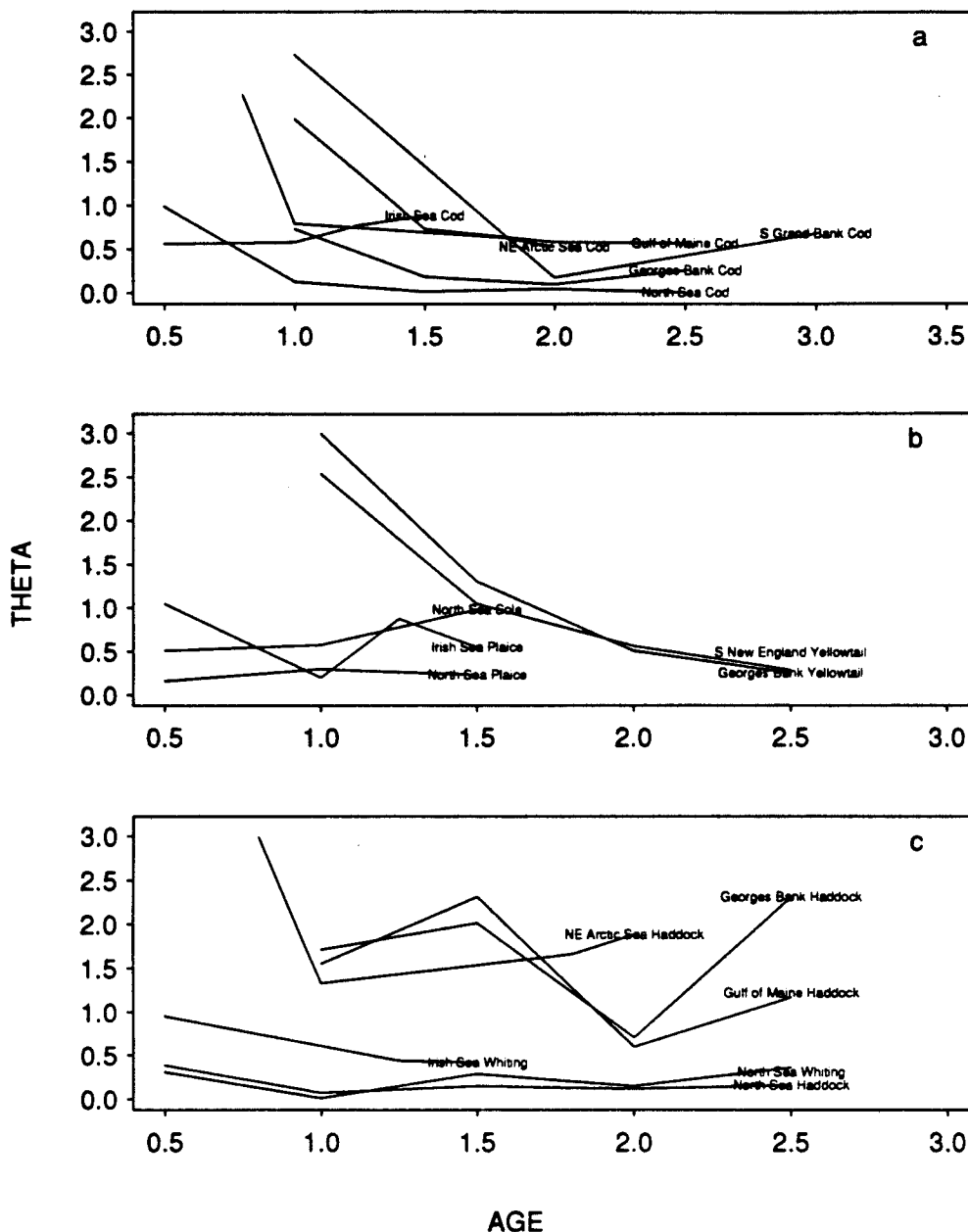


FIG. 3. Estimates of survey error variance, $\theta_{a,i}$, in relation to age for (a), cod, (b) plaice, sole, and yellowtail, and (c) haddock and whiting.

even if a change in growth rate is not seen. For example, at higher densities, fish may have to spend more time feeding and moving, which may increase exposure to predator.

(2) Cannibalism is a possible explanation for some piscivorous species such as cod and whiting. However, no evidence we know of suggests that cannibalism within a year class is an important source of mortality.

(3) Prey switching by predators to abundant year classes is a possible explanation that would be applicable to most species.

(4) Density-dependent mortality might result if there is only a fixed area of juvenile habitats, and the juveniles that settle there survive, while the others do not. In this case, a relatively fixed number of juveniles survive no matter what number was originally produced. This mechanism has been proposed to account for the relative small variation in recruitment seen in North Sea plaice (Ursin 1982). This mechanism may involve food limita-

tion or increased predation risk outside a nursery area; it assumes that there is a mechanism to maintain a relatively constant density within the favorable habitat, e.g., territorial behavior or some other form of density-dependent habitat utilization.

Density-Dependent Fishing Mortality

The above biological hypotheses cannot be distinguished with the present data. However, it is conceivable that there is density-dependent fishing mortality on young fish. If fishermen act in the same way as prey-switching predators which target abundant year classes, then this could result in the observed patterns. If fishermen set trawls when they detect fish on their sonar fish detectors, then these schools of young fish from abundant year classes would be preferentially caught. They also might largely be discarded. Conser et al. (1992) has found that

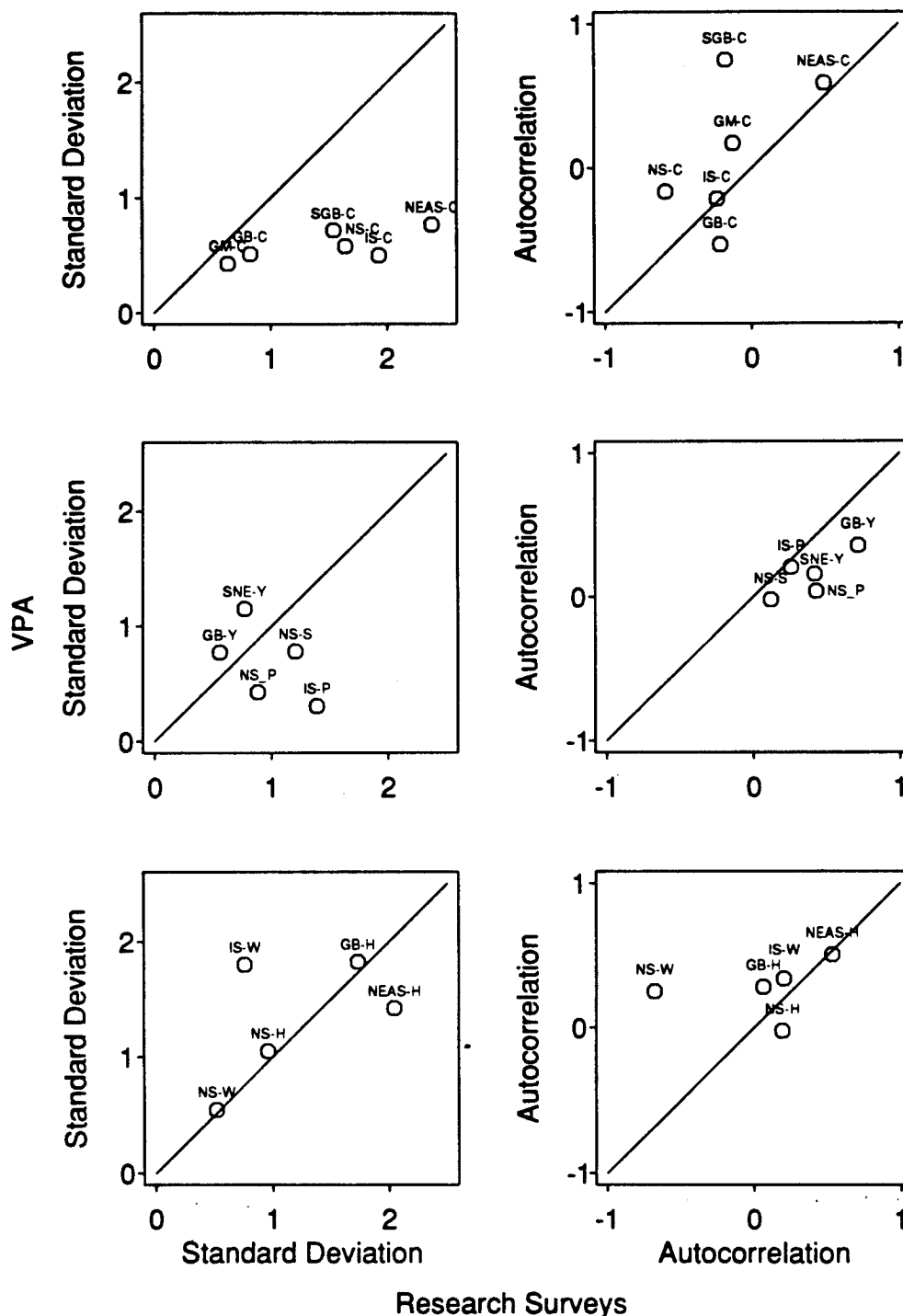


FIG. 4. Plots of estimated standard deviations of log recruitment from VPA's versus those estimated at the earliest age of the research survey used in the analysis. On the right is the first-order autocorrelation of log recruitment from VPA estimates and those obtained here (Tables 2–5). The population locations are abbreviated as follows: GB, Georges Banks; GM, Gulf of Maine; IS, Irish Sea; NS, North Sea; NEAS, Northeast Arctic Sea; SGB, southern Grand Banks; SNE, southern New England. The population names are abbreviated as follows: C, cod; H, haddock; P, plaice; S, sole; W, whiting; Y, yellowtail flounder. for example, IS-C is the Irish Sea cod population. The top panels show the results for cod, the middle panels for plaice, sole, and yellowtail flounder, and the bottom panels for haddock and whiting. The one-to-one reference lines are also shown.

discard rates of juveniles may increase with the strength of year class. If the density-dependent mortality is caused by fishing, it is then possible that production could be greatly improved if fishing pressure on young fish were reduced.

Discussion and Conclusions

This study is the first to demonstrate the general importance of density-dependent juvenile mortality in marine demersal fish. Our study confirms the results of density-dependent mortality in

plaice that have been conducted on a very restricted spatial-scale (Rauck and Zijlstra 1978; Lockwood 1980; Veer 1986; Veer et al. 1990; Iles and Beverton 1991; Beverton and Iles 1992a, 1992b).

An important result in our analysis is that density-dependent juvenile mortality appears to be significant in most of the populations we have examined. For example, haddock is usually characterized by having much more variable recruitment than cod (Ursin 1982; Myers et al. 1990; Myers 1991). However, our analysis of the North Sea and Barents Sea data demonstrates that this is true only for the postjuvenile stage. In both cases, the recruitment variability at the youngest age observed (ϕ) is greater for cod than for haddock, but density-dependent mortality is much stronger in cod so that this initial variability is greatly reduced.

Our results appear to be robust in that our conclusion that density-dependent mortality is important is not affected by reasonable violations of the model assumptions (Appendix 2). If anything, our methods underestimate the strength of density-dependent mortality. The estimates of observational error are negatively biased but usually not more than 10%. The estimates of the underlying variability of recruitment are positively biased but again usually not more than 10%.

It is useful to compare our results with those obtained from a VPA of the same populations (Fig. 4). Myers et al. (1990) estimated the variance and autocorrelation in recruitment for a large number of populations. We use their analysis when possible. For the New England populations in which a VPA was not used in Myers et al. (1990), we used the VPA from the latest assessment. We compare the standard deviation of log recruitment estimated at the earliest age of the research survey used in the analysis with that estimated from the VPA. In general the estimated standard deviation in log recruitment is larger in our analysis. This is consistent with density-dependent mortality, i.e., the variability in recruitment at the earlier ages is attenuated. Aging errors in the VPA also reduce the estimation variability in recruitment and induce autocorrelations. The autocorrelation estimated from the research surveys is usually less than that estimated by VPA (Fig. 4).

The degree of density-dependent mortality is so strong that the variation in abundance can be much less for older ages. For example, λ is estimated to be 0.41 for the age 1 whiting in October for the Irish Sea Surveys (Table 3). This would imply that a 10-fold increase in abundance during the first survey, at age 0, would result in only a 2.6-fold increase a year later. The presence of such strong density-dependent mortality within cohorts may explain why there is often little relationship between stock and recruitment, i.e., large year classes that occur when population size is large may suffer higher mortality during the juvenile stage.

The pattern of negative autocorrelation in cod is consistent with density-dependent mortality between adjacent year classes. This may also result if there is a negative autocorrelation between environmental factors causing recruitment variation. Myers et al. (1990) found that estimates of recruitment from VPA's were usually positively autocorrelated. Walters (1990) suggested that the autocorrelation in the residuals from a stock recruitment function was generally between 0.2 and 0.6. The autocorrelation in recruitment that we observed is less; our median autocorrelation was 0.15. Simulation studies indicate that the relative biases of our estimates of the autocorrelation are small (Appendix 2). This level of autocorrelation should be greater than that observed in the residuals from a fit of a stock and

recruitment function because some of the autocorrelation we calculated is caused by both autocorrelated population size and any functional relationship between stock and recruitment.

Our model assumes that density-dependent mortality is proportional to the log of the initial juvenile density. This is likely to be true only over a portion of the range of juvenile densities. At low juvenile densities, we would expect very little density-dependent mortality. This may be the reason that very over-exploited populations, e.g., most of the New England populations, show relatively little evidence of density-dependent mortality.

There is correlation between estimation errors in surveys of different cohorts taken in the same year of the same survey. This implies that there are strong year effects in the surveys and that the standard errors calculated from survey design models underestimate the true estimation errors. The methods described in this paper allow the true estimation errors of the surveys to be estimated by treating different surveys as replicates. Our study directly estimates the estimation error variance of surveys. These estimates can be used to assess the reliability of survey estimates when estimating population abundance (Rosenberg et al. 1992).

This study has clearly demonstrated the importance of density-dependent mortality in the juveniles. We do not understand why it is more important in some species, e.g. cod, and less important in others, e.g. haddock. Research studies of density-dependent habitat utilization of juveniles may clarify this difference.

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Appendix 1. Model Estimation

Recall that the model considered is

$$l_{t,a,i} = c_{a,i} - m_a + \lambda_{a,i} L_{t,0} + \delta_{t,a,i}$$

$$L_{t,0} = L_{t,l} + \beta L_{t-1,0}.$$

The parameters $c_{a,i} - m_a$ are removed by standardizing each $l_{t,a,i}$ (subtracting the sample mean, $\frac{1}{T} \sum_{t=1}^T l_{t,a,i}$, where T is the number of years in the research survey). Hence, $l_{t,a,i}$, $L_{t,0}$, and $L_{t-1,0}$ are all in terms of deviations from their means.

To illustrate the subscripts used in the model, consider the data in Table 1. Here, $n_{t,0,1}$, $n_{t,1,1}$, and $n_{t,2,1}$ denote recruitment estimates

of cohort t from estimates of 0, 1, and 2-yr-olds in years t , $t+1$, and $t+2$, respectively, from the EGFS. For example, $n_{1979,0,1} = 18.60$, $n_{1979,1,1} = 50.80$, $n_{1979,2,1} = 16.90$, etc. The a subscript denotes the age of fish (in years); it is a truncation of the actual age of the fish (in fraction years). Hence, the fish $l_{t,1,2}$ and $l_{t,1,1}$ are not necessarily of the same age. The actual ages are shown in Fig. 2 and 3. For this reason, we estimate separate λ 's for different surveys unless they actually are of the same age. The surveys are listed in order by age in Tables 2–5.

The above model is written in terms of realizations of random variables (observations), unknown parameters, and latent random variables. This suggests that a latent variable (i.e., confirmatory factor) analysis is appropriate. Using the assumptions presented in the Methods section, it is possible to estimate the above parameters using maximum likelihood methods. We write the model for the data in Table 1 in matrix form and translate our notation with common notation (LISREL, Bollen 1989) in the statistical literature.

Let l_t be a vector of standardized log recruitment estimates at time t and $t-1$:

$$l_t = [l_{t,0,1}, l_{t,1,2}, l_{t,1,1}, l_{t,2,2}, l_{t,2,1}, l_{t-1,0,1}, l_{t-1,1,2}, l_{t-1,1,1}, l_{t-1,2,2}, l_{t-1,2,1}]$$

$$t = 2, 3, \dots, T.$$

Also, let L_t be a latent vector variable of standardized log recruitment at time t and $t-1$:

$$L_t = \begin{bmatrix} L_{t,0} \\ L_{t-1,0} \end{bmatrix}.$$

Construct a matrix of λ 's as follows:

$$\Lambda = \begin{bmatrix} 1 & 0 \\ \lambda_{1,2} & 0 \\ \lambda_{1,1} & 0 \\ \lambda_{2,2} & 0 \\ \lambda_{2,1} & 0 \\ 0 & 1 \\ 0 & \lambda_{1,2} \\ 0 & \lambda_{1,1} \\ 0 & \lambda_{2,2} \\ 0 & \lambda_{2,1} \end{bmatrix}.$$

Let δ_t be a vector variable of observational errors at time t and $t-1$:

$$[\delta_{t,0,1}, \delta_{t,1,2}, \delta_{t,2,2}, \delta_{t,2,1}, \delta_{t-1,0,1}, \delta_{t-1,1,2}, \delta_{t-1,1,1}, \delta_{t-1,2,2}, \delta_{t-1,2,1}].$$

In matrix notation, the model may be written as

$$l_t = \Lambda L_t + \delta_t.$$

The distributional assumptions presented in the Methods section are $L \sim N(0, \Phi)$, $\delta_t \sim N(0, \Theta)$, and $E(L, \delta'_t) = 0 \cdot \Phi$.

and Θ are

$$\Phi = \begin{bmatrix} \phi_{1,1} & \phi_{1,2} \\ \phi_{2,1} & \phi_{2,2} \end{bmatrix}$$

and for this example

$$\Theta = \begin{bmatrix} \theta_{0,1} & 0 & 0 & 0 & 0 & 0 & 0 & \theta_{0,1}^{1,1} & 0 & 0 \\ & \theta_{1,2} & 0 & 0 & 0 & 0 & 0 & 0 & \theta_{1,2}^{2,2} & 0 \\ & & \theta_{1,1} & 0 & 0 & \theta_{1,1}^{1,1} & 0 & 0 & 0 & \theta_{1,1}^{2,1} \\ & & & \theta_{2,2} & 0 & 0 & \theta_{2,2}^{2,2} & 0 & 0 & 0 \\ & & & & \theta_{2,1} & 0 & 0 & \theta_{2,1}^{2,1} & 0 & 0 \\ & & & & & \theta_{0,1} & 0 & 0 & 0 & 0 \\ & & & & & & \theta_{1,2} & 0 & 0 & 0 \\ & & & & & & & \theta_{1,1} & 0 & 0 \\ & & & & & & & & \theta_{2,2} & 0 \\ & & & & & & & & & \theta_{2,1} \end{bmatrix}$$

We constrain $\phi_{1,1} = \phi_{2,2} = \phi$. The β parameter is estimated as $\beta = \frac{\phi_{2,1}}{\phi}$. The notation $\theta_{i,j}^{k,l}$ denotes the covariance between $\delta_{i,j}$ and $\delta_{k,l}$.

In the statistical literature (e.g., Bollen 1989), L_i would commonly be denoted as x_i and I_i as L_i . Our notation (except subscripts and superscripts) is otherwise standard.

The theoretical covariance matrix derived from this model is

$$\Sigma = \Lambda \Phi \Lambda' + \Theta$$

This is a 10×10 matrix with 14 parameters to estimate. The sample covariance matrix $S \left(\frac{1}{T} \sum_{t=1}^T l_t l_t' \right)$ is also a 10×10 matrix with 55 unique terms.

The basic estimation procedure is to fit the observed variance-covariance matrix with the theoretical one. The fitting function that is minimized in order to find the maximum likelihood estimates is

$$\log |\Sigma| + \text{tr}(S \Sigma^{-1}) - \log(|S|) - p$$

where tr is the matrix trace and p is the dimension of S . The models are estimated using SAS's PROC CALIS with the pairwise covariance matrix. If this matrix is not positive definite, the ridge option in PROC CALIS is used to perturb the matrix so that it is positive definite.

Maximum likelihood estimates do not always produce sensible results, i.e., negative θ 's are estimated, usually because the data series are relatively short. Any model whose estimation yielded negative θ 's is rejected. For this reason, the North Sea cod model is estimated only from data containing no missing values. Also, one θ in the North Sea sole and Northeast Arctic haddock data is constrained to have a small positive variance.

The unconstrained λ 's are multivariate normal in distribution (an asymptotic result from maximum likelihood theory). The mean of this distribution is estimated from the parameter estimates. The covariance matrix is estimated by the information matrix evaluated at the parameter estimates. As a test of whether the λ 's are <1 , the joint p -values that all λ 's are <1 are presented.

The p -values are approximated using 10000 Monte Carlo samples. This sampling procedure produced two-digit accuracy when applied to some known results. The p -values presented for $p(\cdot)$ in Tables 2–5 are based upon a normal approximation of the estimated covariance and not $p(\cdot)$ because of difficulties in obtaining standard errors for derived parameters.

An issue that must be addressed is model identification. Note that it is not necessary to understand what follows to understand the data analysis. A parameter in Σ is identified if it can be expressed as a function of one or more elements in S . A parameter is underidentified if it cannot be expressed only as a function of some elements in S (Bollen 1989). Let $\Sigma_{\hat{\omega}}$ be the covariance matrix constructed from a particular set, $\hat{\omega}$, of free parameters in the model. If a model is identified, then for $\hat{\omega}$, and another set, $\ddot{\omega}$,

$$\Sigma_{\hat{\omega}} = \Sigma_{\ddot{\omega}} \Rightarrow \hat{\omega} = \ddot{\omega}.$$

The theoretical covariance matrix of all models considered in this paper may be represented as follows:

$$\Sigma_{\hat{\omega}} = \dot{\Lambda} \dot{\Phi} \dot{\Lambda}' + \dot{\Theta}$$

where

$$\dot{\Lambda} = \begin{bmatrix} \dot{\lambda} & \mathbf{0} \\ \mathbf{0} & \dot{\lambda} \end{bmatrix}, \dot{\lambda}' = (1, \dot{\lambda}_1, \dots, \dot{\lambda}_{l-1}),$$

$\mathbf{0} = l \times 1$ vector of zero's,

$$\dot{\Phi} = \begin{bmatrix} \dot{\phi}_{1,1} & \dot{\phi}_{1,2} \\ \dot{\phi}_{1,2} & \dot{\phi}_{1,1} \end{bmatrix},$$

$$\dot{\Theta} = \begin{bmatrix} \dot{\Theta}_{1,1} & \dot{\Theta}_{1,2} \\ \dot{\Theta}_{1,2} & \dot{\Theta}_{1,1} \end{bmatrix}, \dot{\Theta}_{1,1} = \text{Diag } \dot{\Theta}_{1,1}, \dots, \dot{\Theta}_{l,l},$$

$$\dot{\Theta}_{1,2} = l \times l \text{ symmetric matrix.}$$

The r -rule (Bollen 1989) always holds for this model when $l > 1$. This is a necessary but not sufficient condition for the model to be identified. Our model does not fall within any of the classes of models in Bollen (1989) for which sufficient conditions for identification have been constructed. The sufficient condition is that one (i, j) pair in $\Theta_{1,2}$ be fixed. This follows by observing that

$$\Sigma_{\hat{\omega}} = \Sigma_{\ddot{\omega}} \Rightarrow$$

$$\dot{\phi}_{1,1} \dot{\lambda} \dot{\lambda}' + \dot{\Theta}_{1,1} = \ddot{\phi}_{1,1} \ddot{\lambda} \ddot{\lambda}' + \ddot{\Theta}_{1,1}$$

$$\dot{\phi}_{1,2} \dot{\lambda} \dot{\lambda}' + \dot{\Theta}_{1,2} = \ddot{\phi}_{1,2} \ddot{\lambda} \ddot{\lambda}' + \ddot{\Theta}_{1,2}.$$

From the first equation, it is easy to show that $\dot{\phi}_{1,1} = \ddot{\phi}_{1,1}$, $\dot{\lambda} = \ddot{\lambda}$, and $\dot{\Theta}_{1,1} = \ddot{\Theta}_{1,1}$. If $\dot{\lambda}$ is substituted for in the second equation above, and one (i, j) pair in $\dot{\Theta}_{1,2}$ is fixed, then $\dot{\phi}_{1,2} = \ddot{\phi}_{1,2}$ and hence, $\dot{\Theta}_{1,2} = \ddot{\Theta}_{1,2}$. With this constraint, we now have that $\Sigma_{\hat{\omega}} = \Sigma_{\ddot{\omega}} \Rightarrow \hat{\omega} = \ddot{\omega}$, that is, the model is identified. For the populations considered here, most of the elements in $\Theta_{1,2}$ are fixed as zero's.

TABLE A2.1. Simulation results to test the robustness of the estimation model. The number of years of data used to estimate the model is n . $D(\cdot)$ denotes distribution of (\cdot); L, lognormal; G, gamma; LG, loggamma. See text for details.

No.	n	$D(\xi)$	$D(\delta_i)$	θ/ϕ	$\theta_{1,1}/\theta$	Mean bias $\lambda_2 - \lambda_4$	Mean bias $\theta_1 - \theta_4$	Bias ϕ	% simulations converged with positive variances
1	100	L	L	1	1	0.013	-0.020	0.010	
2	100	L	L	0.2	1	0.005	-0.002	-0.002	100
3	20	L	L	1	1	0.186	-0.080	0.084	90.1
4	20	L	L	0.2	1	0.013	-0.014	0.002	98.3
5	10	L	L	1	1	0.137	-0.129	0.313	59.2
6	10	L	L	0.2	1	0.022	-0.021	0.078	79.4
7	20	G	L	1	1	0.196	-0.088	-0.131	82.8
8	20	G	L	0.2	1	0.013	-0.012	-0.185	98.3
9	20	L	LG ^a	1	1	0.145	-0.076	0.087	88.9
10	20	L	LG ^a	0.2	1	0.017	-0.011	0.008	87.5
11	20	L	LG ^b	1	1	0.128	-0.079	0.104	87.3
12	20	L	LG ^b	0.2	1	0.011	-0.010	0.027	86.2
13	20	L	L ^c	1	1	0.142	-0.069	0.118	90.3
14	20	L	L ^c	0.2	1	0.015	-0.008	0.025	98.2
15	20	L	L	1	4	0.216	-0.127	0.540	76.9
16	20	L	L	0.2	4	0.064	-0.019	0.042	95.3
17	20	L	L	1	9	-0.141	-0.250	0.979	72.0
18	20	L	L	0.2	9	0.123	-0.036	0.144	93.8

^aLeft-skewed.

^bRight-skewed.

^cCorrelated errors.

Appendix 2. Robustness

We examined three questions about the reliability of our results: (1) Could our results be an artifact of the sampling gear? (2) Are our results robust to violations of the model assumptions? (3) What are the small sample biases of our estimators?

First, it is possible that the catchability of the research gear is density dependent, i.e., that the efficiency of the trawl increases for small fish when the net becomes clogged. This is unlikely because the research surveys use mesh small enough to catch all or nearly all fish of the size considered here. However, catchability may still increase with age because catchability also depends upon behavior, e.g., smaller fish may have a different vertical distribution.

The second question is partially addressed by relaxing the parametric assumptions for the statistical distribution describing recruitment and the form of the estimation errors. The maximum likelihood estimation procedure used requires log recruitment and the estimation errors to be normally distributed. Although this is a reasonable assumption (Myers et al. 1990), it is possible to use estimation methods for which this assumption is not required. In particular, our results are tested by using weighted and unweighted least squares estimation. To save space the results are not presented, but for weighted least squares the basic pattern in the results is usually very similar. Although the unweighted least squares solution is not generally scale invariant and is not generally comparable with maximum likelihood or weighted least squares (Bollen 1989), it is in our case because the logarithmic transformation removes the effects of a scalar transformation of the sample covariance matrix. This solution again produced the same general results although the parameter estimates are sometimes of different magnitude.

Simulations are conducted to investigate the small sample properties of the estimators used and further test violations of the model assumptions. The model assuming independence between

adjacent cohorts is used (Eq. 1). The general simulation procedure is to (1) fix the sample size (n) to be investigated, (2) fix the distribution of the model latent recruitment ($L_{i,0}$) and the errors ($\delta_{i,a,i}$), (3) specify the parameters, (4) generate 1000 data sets each with n random observations of $L_{i,0}$ and $\delta_{i,a,i}$, (5) use these values to generate the standardized survey data, and (6) estimate parameters using the standard distributional assumptions given in the Methods section.

Our interest is to determine if statistical artifacts could cause the estimated λ 's to be less than 1; therefore, all λ 's are set at 1 to investigate this in the simulations. The error variances (θ) are equal to and one fifth of the variance of ϕ which is set as 1. These ratios of variances are rough bounds on estimates in Tables 2–5.

In the first six simulations the effect of sample size on the accuracy of parameter estimates at two levels of ϕ/θ (Table A2.1) is investigated. $L_{i,0}$ and δ are generated as standard normal random variables (rv's) with zero means and variances equal to 1 and θ , respectively. These normality assumptions are the same as used in the data analysis.

Simulation's 7 through 14 are conducted to investigate the robustness of the estimators to violations in distributional assumptions. In simulations 7 and 8 the distribution of $L_{i,0}$ over time was generated as a gamma rv with a mean and variance constrained to equal that of the log of a standard normal rv (i.e., $\phi = 1$). Left-skewed errors (δ 's) were generated from a gamma rv with shape and scale parameters 2 and $1/\sqrt{2}$, respectively; these are considered as reasonable parameters. A right-skewed gamma deviate is generated as the negative of a left-skewed deviate. In simulations 9–12, these rv's are centered to have mean 0 (they are error terms). In simulations 13 and 14, correlated errors are produced by adding 0.1 to the first half of the time series of errors ($\delta_{1,1}$) and -0.1 to the later half. $\delta_{2,1}$ is modified by the same procedure except 0.1 is added to the first half + 1 of the errors. This is done to simulate a change in the efficiency of a survey half way through the survey series.

In the last four simulations, the effect of unequal estimation error variance is investigated. of particular concern is that larger estimation error variances at younger ages might lead to biased results for small sample sizes. We considered an estimation error variance of the younger age, $\theta_{1,j}$, equal to 4 or 9 times the variance of the other error terms, which are all equal (θ).

The analyses indicate that most of the potential biases in parameter estimates result from small sample sizes and not deviations in model assumptions. Generally the biases resulting from deviations in distributional assumptions do not differ substantially compared with those obtained (at the same sample size) when the distributional assumptions are exact. The simulations indicate that our estimates of density-dependent mortality are not generally artifacts of violations in model assumptions because the simulated biases are too small and are of the wrong sign, except if the estimation error variance is large.

If the estimation error variance for the youngest age is much larger than for older ages and the estimation error variances of the older ages are similar to ϕ , then very large biases may result. In particular, density-dependent mortality may be estimated to exist when there is none. The estimates of variance parameters in Tables 2–5 for most populations are similar to the parameters in simulations 3, 4, and 16 in Table A2.1. The biases here are not substantial, particularly for Nos. 4 and 16. Five populations have variance estimates somewhere between those considered in

simulations 3 and 15. These populations are Irish Sea whiting, Gulf of Maine cod, Georges Bank yellowtail flounder, southern New England yellowtail flounder, and southern Grand Bank cod. While one might consider these biases as being substantial, they would not result in false conclusions. The variance estimates from all populations are not in the range of simulation 15; hence, we conclude that estimates of density-dependent mortality are not statistical artifacts.

A referee pointed out that there is a potential for the estimate of autocorrelation of recruitment, β , to be negatively biased. As part of ongoing research into the small sample properties of maximum likelihood estimates for latent variable models, further analyses (simulations) have been conducted in which the bias of the autocorrelation is investigated. The results are too bulky to report here in detail but for $n = 10$, it was found that when the ratio of the estimation error variance (θ) to the latent variable variance (ϕ) was small (0.1) the %bias in the estimate of the correlation was between -2 and 7% depending upon if the actual correlation was small (0.1) or large (0.9); when the θ/ϕ ratio was 1 the %bias ranged between 2 and 17% . These biases are small and not a cause for great concern. Although the model in the unreported simulations is essentially the same as the one in Appendix 1, more parameters were estimated; however, the fact that the correlation between latent variables (i.e., underlying recruitment) is estimated relatively accurately should still apply.