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Is juvenile natural mortality in marine demersal fish variable?

R.A. MYERS AND N.G. CADIGAN

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Is Juvenile Natural Mortality in Marine Demersal Fish Variable?

Ransom A. Myers and Noel G. Cadigan

Department of Fisheries and Oceans, Northwest Atlantic Fisheries Centre, Science Branch, P.O. Box 5667, St. John's, NF A1C 5X1, Canada

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We test the hypothesis that the interannual variability of the density-independent component of juvenile natural mortality is a major source of variability in abundance of marine demersal fish. Our tests use data on populations for which there are research surveys consisting of two simultaneous estimates of abundance of young juveniles soon after settlement and two more simultaneous estimates of the same cohort a year later. We applied our test to 14 populations of Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*), plaice (*Pleuronectes platessa*), and sole (*Solea vulgaris*). We conclude that, in all populations examined except North Sea sole, there was very little or no interannual variability in the density-independent component of juvenile mortality.

Nous vérifions l'hypothèse que la variabilité interannuelle de la composante indépendante de la densité de la mortalité naturelle chez les juvéniles est la principale cause de la variabilité de l'abondance des poissons démersaux. Pour nos vérifications nous utilisons des données sur les populations pour lesquelles il existe des relevés de recherche constitués de deux estimations simultanées de l'abondance des jeunes juvéniles, peu après la sédentarisation, et deux autres estimations simultanées de la même cohorte une année plus tard. Nous avons appliqué notre épreuve à 14 populations de morues franches (*Gadus morhua*), d'églefins (*Melanogrammus aeglefinus*), de merlans (*Merlangius merlangus*), de plies (*Pleuronectes platessa*) et de soles (*Solea vulgaris*). Nous concluons que, dans toutes les populations examinées, sauf la sole de la mer du Nord, il n'y avait presque pas de variabilité interannuelle de la composante de la mortalité juvénile qui est indépendante de la densité.

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The variability of year class strength is a fundamental problem in the population biology of marine fish. Hjort (1914, 1926) hypothesized that the principle life stage in which interannual variability in survival occurred was the larval planktonic stage. Recently, it has been suggested that the life stage in which interannual variability in survival is most important is the juvenile stage (May 1984; Smith 1985). Although there are many estimates of the interannual variability in recruitment (Myers et al. 1990), there have been very few estimates of the interannual variability in juvenile survival. This hypothesis is difficult to test because variable survival cannot usually be separated from errors in estimating abundance. Peterman et al. (1988) argued that the major source of variability in recruitment in the northern anchovy (*Engraulis mordax*) was variable survival between 19-d-old larvae until age 1. However, Peterman et al. (1988) had no estimates of the errors in estimating either quantity.

Here, we attack this problem by analyzing populations in which there are two simultaneous estimates of abundance during age 0+ and two more simultaneous estimates a year later. The independent, simultaneous surveys were not usually carried out as part of a designed research program, but because two nations had overlapping claims to the same fish population. If there are multiple estimates of abundance, it is possible to separate variable survival from errors in estimation. To fix ideas, consider a population in which there are two simultaneous surveys to estimate abundance at age 0 and two more a year later at age 1. Assume in this simple example only that the variance in estimating abundance is the same for all surveys. If there is no

interannual variability in survival between ages 0 and 1, then the correlations between the survey estimates should be the same at the same age as between ages. However, if there is large interannual variability in survival between the ages then there should be higher correlations in the surveys at the same age than between ages. The analysis below is an elaboration of this simple idea to the general case in which the variance of the survey errors is unknown and unequal.

Our approach here is to (1) develop a statistical model of variable juvenile mortality, (2) compile a large number of data sets that would allow this hypothesis to be tested, (3) apply the model systematically to each data set, and (4) investigate the power of our statistical test.

We consider two components of interannual variability in survival: (1) the density-dependent component and (2) the density-independent component. In the companion paper to this one (Myers and Cadigan 1993), we used similar methods and data to examine density-dependent survival.

An Example: North Sea Sole

Before we develop a formal model, it is useful to consider an example. On the continental side of the North Sea, there are inshore and offshore surveys for juvenile flatfish (Table 1). The index used for the INSHORE surveys was weighted by area and corrected for differences in efficiency between the survey gear. The units for the TRIDENS surveys are the number of fish caught per 100 h of fishing.

The correlation between the age 0 surveys is high ($r = 0.81$, $p < 0.001$) (Fig. 1). Similarly the correlations between the age 1

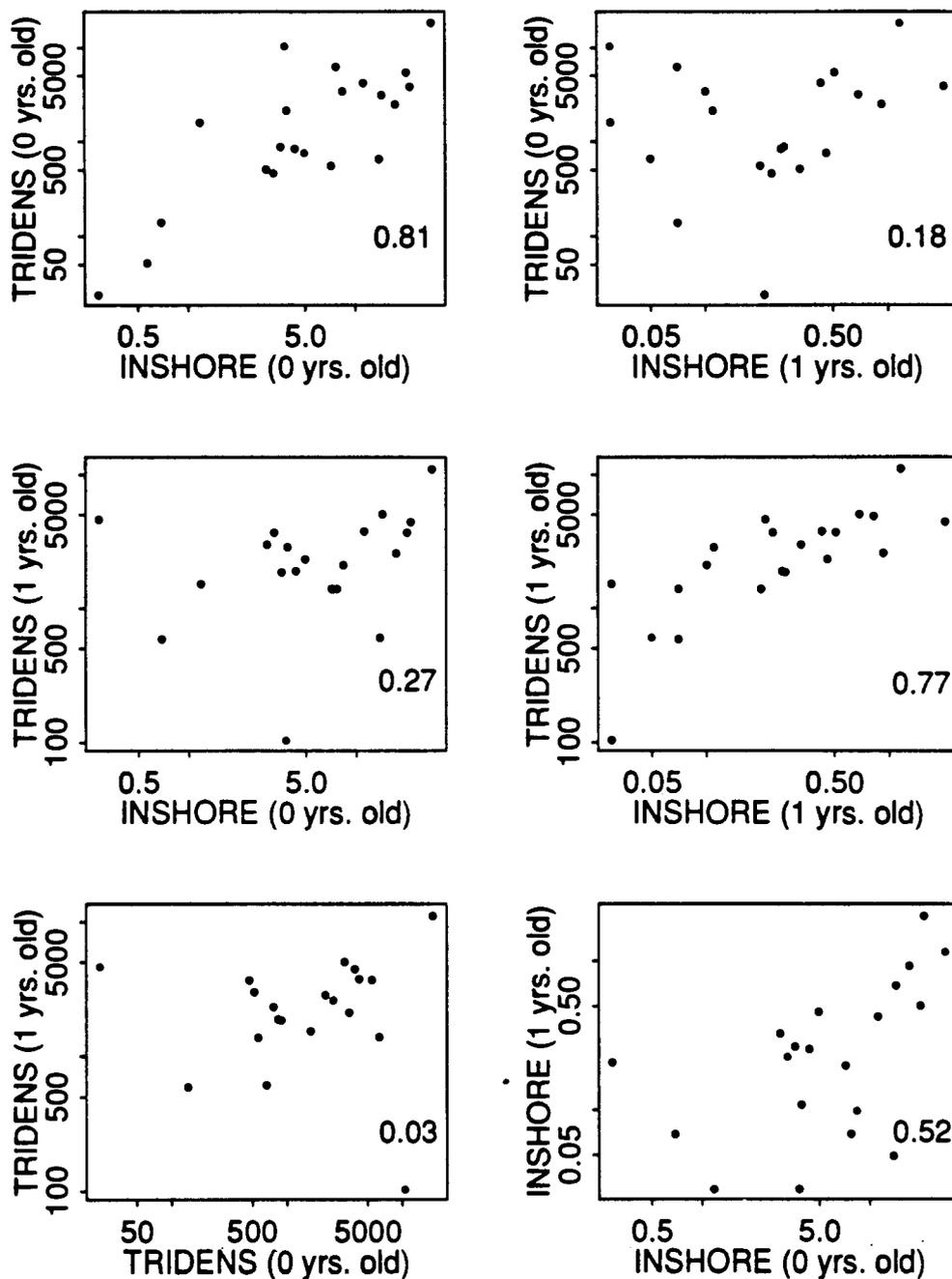


FIG. 1. Pairwise plots of abundance estimates for North Sea sole (Table 1). The estimates are log transformed. The correlation coefficient is presented in the lower right corner.

surveys is high ($r = 0.77$, $p < 0.001$); however, the correlation between the surveys at different ages is much lower, ranging from 0.03 to 0.52. One explanation for this result is that both surveys are reasonable estimates of abundance but that variable survival takes place during the year between surveys. There is also evidence that density-dependent survival is a linear function of the abundance (Fig. 2). Abundance is taken as the log numbers at age 1 and survival is taken as the difference in log numbers at ages 2 and 0. Note that the 1972 year class is very low in both 0+ surveys but appears to be close to normal in the 1+ surveys. Thus, we include density-dependent survival in the model in a manner similar to Myers and Cadigan (1993).

The Model

Consider a population in which each cohort is surveyed simultaneously at two different ages. Let the number of fish in cohort i surveyed at age a be $N_{i,a}$. The surveys see the juveniles at two ages; the survey index of the youngest age is 0 and surveys that see the fish at later ages are labeled 1. The natural mortality is divided into three components: (1) the average mortality between the two ages that is independent of density, m , (2) the density-dependent component which is assumed to be proportional to the logarithm of the initial density, $(1 - \lambda) \log N_{i,0}$, and (3) the variable component unrelated to abundance, ϵ_i . It is

TABLE 1. Data for the North Sea sole population from the TRIDENS (in units of numbers per 100 h of fishing) and INSHORE surveys (in units of numbers per 1000 m²).

Year class	TRIDENS 0-yr-olds	TRIDENS 1-yr-olds	INSHORE 0-yr-olds	INSHORE 1-yr-olds
1969		4 938		0.82
1970	669	613	13.88	0.05
1971	6 327	1 410	7.72	0.07
1972	24	4 686	0.29	0.21
1973	847	1 924	4.35	0.26
1974	140	597	0.69	0.07
1975	565	1 413	7.14	0.20
1976	475	3 724	3.23	0.23
1977	1 620	1 552	1.18	0.03
1978	10 529	104	3.80	0.03
1979	3 908	4 483	21.24	2.03
1980	5 518	3 739	20.17	0.51
1981	3 194	5 098	14.40	0.69
1982	2 528	2 640	17.36	0.93
1983	769	2 359	4.96	0.46
1984	3 473	2 151	8.39	0.10
1985	4 268	3 791	11.19	0.43
1986	901	1 890	3.58	0.27
1987	18 690	11 227	28.66	1.16
1988	523	3 052	2.93	0.33
1989	2 171	2 900	3.89	0.11
1990	53		0.57	

mathematically convenient to estimate the density-dependent survival rate, λ , rather than mortality. The population dynamics is described by

$$(1) N_{t,1} = N_{t,0} e^{-m - (1-\lambda) \log N_{t,0}}$$

Note that we assumed in Eq. 1 that recruitment was independent between adjacent cohorts. In Myers and Cadigan (1993), we examined autocorrelated recruitment and found that there was little effect on the estimation of the other parameters if the autocorrelation was assumed to be zero.

$$\begin{bmatrix} \text{VAR}(l_{t,0,1}) & \text{COV}(l_{t,0,1}, l_{t,0,2}) & \text{COV}(l_{t,0,1}, l_{t,1,1}) & \text{COV}(l_{t,0,1}, l_{t,1,2}) \\ & \text{VAR}(l_{t,0,2}) & \text{COV}(l_{t,0,2}, l_{t,1,1}) & \text{COV}(l_{t,0,2}, l_{t,1,2}) \\ & & \text{VAR}(l_{t,1,1}) & \text{COV}(l_{t,1,1}, l_{t,1,2}) \\ & & & \text{VAR}(l_{t,1,2}) \end{bmatrix}$$

Note that the above matrix has seven unknown parameters to estimate and there are 10 terms in the upper triangular portion of the matrix. Also note that we do not attempt to estimate m , or the $c_{a,i}$. These parameters cannot be estimated without independent data or by making unreasonable assumptions. We estimate the other parameters in Σ by matching the observed var-

It is useful to work with log-transformed variables, e.g. $L_{t,a} = \log N_{t,a}$. Thus, (1) is written as

$$(2) L_{t,1} = -m + \lambda L_{t,0} + \epsilon_t$$

The observed log-transformed data from survey i at age a is $l_{t,a,i}$. We assume that the estimates of abundance at age in each survey are proportional to the true abundance at that age. Let $c_{a,i}$ be the log catchability of survey i at age a , and let $\delta_{t,a,i}$ be the observation error of survey i at age a from cohort t . The observed log-transformed abundance from survey i is

$$(3) l_{t,a,i} = c_{a,i} + L_{t,a} + \delta_{t,a,i}$$

Estimation

We are primarily interested in determining the interannual variability in juvenile survival. In order to estimate the parameters of the above model, we make the following assumptions:

(1) Log-transformed standardized recruitments are independent random variables from a normal distribution with constant mean and variance (i.e., independent of year and also (2) and (3) below). That is:

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

(2) The variable components of mortality are independent random variables from a normal distribution with zero mean and constant variance (i.e., independent of year, (1) above, and (3) below). That is:

$$\epsilon_t \sim N(0, \psi)$$

(3) Errors in estimating abundance of each age group from each research survey are independent random variables from a normal distribution with zero mean and constant variance (i.e., independent of year and also (1) and (2) above). That is:

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

$$= \begin{bmatrix} \phi + \theta_{0,1} & \phi & \lambda\phi & \lambda\phi \\ & \phi + \theta_{0,2} & \lambda\phi & \lambda\phi \\ & & \lambda^2\phi + \psi + \theta_{1,1} & \lambda^2\phi + \psi \\ & & & \lambda^2\phi + \psi + \theta_{1,2} \end{bmatrix}$$

iance covariance matrix (S) as close as possible. By inspection, we see that each model parameter can be uniquely written as a function of one or more elements in S ; that is, the model is identified. We use maximum likelihood methods to obtain the estimates. Details of the estimation methods are described in Bollen (1989).

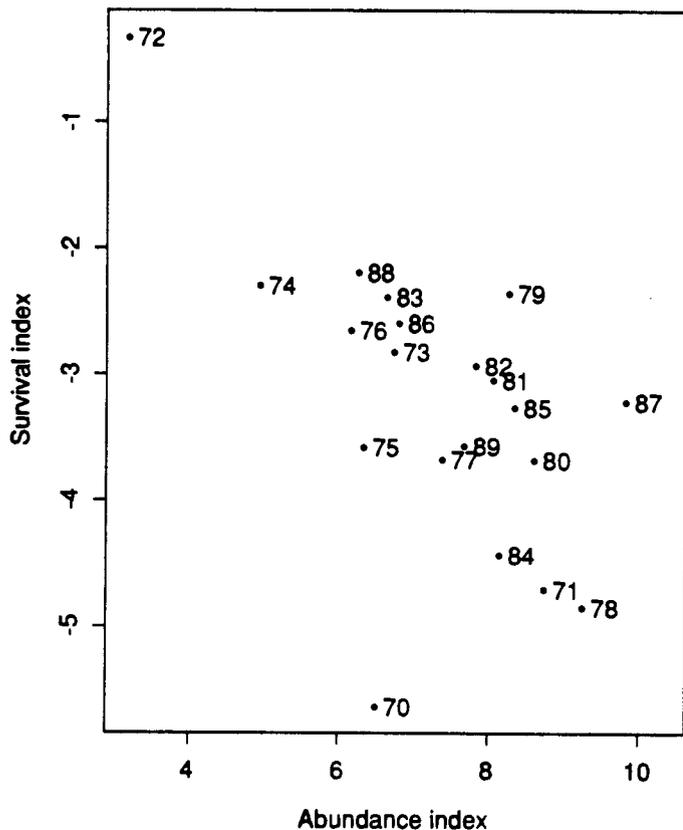


FIG. 2. Survival index versus abundance index for North Sea sole. The index of survival is the difference between the log numbers at age 0 and 1 from the INSHORE survey. The index of abundance is the log numbers at age 1 from the TRIDENS survey. Note that the estimation errors in the two surveys are independent.

With the above assumptions, it is possible to calculate the variance of each survey at age and the covariance between surveys. The theoretical variance-covariance matrix, Σ , is

Data

We attempted to compile and analyze all data sets in which there were two reliable, simultaneous research survey estimates of juvenile fish abundance. We had several criteria before a data set could be included in our analysis. First, the data series had to have estimates for at least 10 years. Second, 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 Surveys (NWGS), covered only a portion of the region. We have identified such limitations of the data below. Third, we had to deal with the problem of zero catches in some years. We attempted to use data series that only had positive catches. In several cases, we replaced zeros with one tenth the minimum estimate for that age. Fourth, the data sets had to be simultaneous or nearly simultaneous. Most of the surveys took place within a month of each other. The major exception is the southern Baltic survey for cod. We have used the data sets described in Myers and Cadigan (1993) when possible; however, the requirement that the surveys be simultaneous has led us to modify some of the data sets used. The sources of the data sets can be found in Myers and Cadigan (1993) unless otherwise stated.

The North Sea gadoid populations (Table 2) are estimated from three autumn surveys: the English Groundfish Surveys (EGFS) cover the whole North Sea, the Scottish Groundfish Surveys (SGFS) have better coverage in the north, and the Dutch Groundfish Survey (DGFS) have better coverage in the south. The EGFS has taken place since 1977, the DGFS since 1980, and the SGFS since 1982. Atlantic cod (*Gadus morhua*), which has its maximum abundance in the southern part of the North Sea, is well estimated by the EGFS and DGFS, while haddock (*Melanogrammus aeglefinus*), which has its maximum abundance in the north, is best estimated by EGFS and SGFS. Whiting (*Merlangius merlangus*) is covered by all three surveys. We use the EGFS and DGFS for this population because they are the longest.

The eastern North Sea populations of sole (*Solea vulgaris*) and plaice (*Pleuronectes platessa*) (Table 2) were surveyed during the autumn (September–October) from the Dutch to the Danish coastal waters using the research vessel *Tridens*. There are surveys carried at approximately the same time in more inshore regions during the same time period 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.

The Irish Sea gadoid populations (Table 3) are estimated from the October NWGS and the autumn (September–October) prerecruit gadoid surveys, denoted as GADOID. The Irish Sea plaice population is surveyed by the NWGS and the Irish September survey. In the Irish Sea prerecruit gadoid survey, there were two years when no age 0+ cod were caught. In these years the zeros were replaced by one tenth the lowest catch in the series for 0+ cod.

Random stratified surveys of the Gulf of Maine (Table 4) and Georges Bank cod populations have taken place in the offshore regions in the spring (since 1968) and the fall (since 1963) and in the inshore regions by the State of Massachusetts in the spring (since 1978) and autumn (since 1978). There was no age in which cod from the Georges Bank population was caught effectively in both surveys, so only the analysis for the Gulf of Maine population is given. We use the fall 0+ and spring 1+ surveys in the analysis. There was no other species in the region that was reliably estimated simultaneously from both surveys.

Surveys of cod (Table 4) on the southern Grand Banks of Newfoundland have taken place since 1972 by Canada and since 1978 by the USSR. Both surveys are in the spring and cover the same region. Random stratified surveys of cod (Table 4) on the St. Pierre Bank south of Newfoundland have taken place since 1972 by Canada (Bishop et al. 1991) and since 1978 by France (Moguedet 1991). Both surveys are in the spring and cover the same region with the exception that the Canadian surveys extend into deeper water.

The Northeast Arctic haddock population (Table 5) has been surveyed in the Barents Sea by the USSR since 1948 during late autumn–early winter (November–December) using trawl surveys and since 1977 during winter (January–March) by Norway using acoustic surveys. We examined survival for one year from the 0+/early 1+ stage. The Northeast Arctic cod population does 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 use the bottom trawl survey for cod carried out from January to March in the Barents Sea since 1983 which did not record zero catches for any age class. For the USSR trawl surveys for cod, we use the combined index for ICES subareas I, IIa, and

TABLE 2. Parameters and estimates for the variable juvenile mortality model, North Sea (SE's in parentheses). n is the median number of cohorts used in the analysis.

	Cod	Haddock	Whiting	Plaice	Sole
$l_{t,0,1}$	EGFS	EGFS	EDGS	TRIDENS	TRIDENS
$l_{t,0,2}$	DGFS	SGFS	DGFS	INSHORE	INSHORE
$l_{t,1,1}$	EGFS	EGFS	EGFS	TRIDENS	TRIDENS
$l_{t,1,2}$	DGFS	SGFS	DGFS	INSHORE	INSHORE
n	12	12	12	19	21
λ	0.90 (0.11)	0.89 (0.06)	0.51 (0.23)	0.57 (0.11)	0.28 (0.17)
ϕ	1.76 (0.91)	0.82 (0.44)	0.43 (0.31)	0.77 (0.26)	1.58 (0.55)
$\theta_{0,1}$	0.85 (0.40)	0.10 (0.06)	0.33 (0.23)	0.23 (0.10)	0.97 (0.39)
$\theta_{0,2}$	0.36 (0.20)	0.13 (0.07)	0.67 (0.35)	0.05 (0.07)	0.00 (0.25)
$\theta_{1,1}$	0.31 (0.15)	0.06 (0.03)	0.05 (0.06)	0.12 (0.07)	0.19 (0.17)
$\theta_{1,2}$	0.03 (0.05)	0.04 (0.02)	0.43 (0.20)	0.22 (0.09)	0.40 (0.20)
ψ	-0.14 (0.11)	-0.06 (0.03)	-0.02 (0.07)	0.08 (0.06)	0.73 (0.27)

TABLE 3. Parameters and estimates for the variable juvenile mortality model, Irish Sea (SE's in parentheses). n is the median number of cohorts used in the analysis.

	Cod	Plaice	Whiting
$l_{t,0,1}$	OCTOBER	OCTOBER	OCTOBER
$l_{t,0,2}$	GADOID	GADOID	GADOID
$l_{t,1,1}$	OCTOBER	OCTOBER	OCTOBER
$l_{t,1,2}$	GADOID	GADOID	GADOID
n	12	14	11
λ	0.61 (0.11)	0.48 (0.24)	1.78 (5.45)
ϕ	3.70 (1.75)	0.75 (0.47)	0.03 (0.10)
$\theta_{0,1}$	-0.02 (0.26)	0.53 (0.36)	2.39 (1.08)
$\theta_{0,2}$	0.88 (0.49)	0.40 (0.32)	0.04 (0.10)
$\theta_{1,1}$	0.61 (0.37)	0.83 (0.44)	1.15 (0.52)
$\theta_{1,2}$	0.99 (0.52)	0.58 (0.34)	0.05 (0.08)
ψ	-0.05 (0.26)	-0.14 (0.21)	-0.05 (0.32)

TABLE 4. Parameters and estimates for the variable juvenile mortality model, western North Atlantic (SE's in parentheses). n is the median number of cohorts used in the analysis.

	Cod Gulf of Maine	Cod Southern Grand Banks	Cod St. Pierre Bank
$l_{t,0,1}$	FALL	$l_{t,1,1}$ CANADA	CANADA
$l_{t,0,2}$	FALLMA	$l_{t,1,2}$ RUSSIA	FRANCE
$l_{t,2,3}$	SPRING	$l_{t,2,1}$ CANADA	CANADA
$l_{t,2,4}$	SPRINGMA	$l_{t,2,2}$ RUSSIA	FRANCE
n	18	n 17	17
λ	0.21 (0.18)	λ 1.90 (4.13)	0.33 (0.45)
ϕ	2.26 (1.57)	ϕ 0.39 (0.95)	1.32 (1.54)
$\theta_{0,1}$	6.33 (2.86)	$\theta_{1,1}$ 3.37 (1.50)	3.16 (1.88)
$\theta_{0,2}$	0.82 (1.27)	$\theta_{1,2}$ 2.90 (1.35)	5.22 (2.48)
$\theta_{2,3}$	1.24 (0.56)	$\theta_{2,1}$ 0.01 (0.20)	1.11 (0.61)
$\theta_{2,4}$	0.34 (0.28)	$\theta_{2,2}$ 0.78 (0.36)	1.82 (0.83)
ψ	0.15 (0.26)	ψ -0.43 (2.90)	0.03 (0.48)

Ib. This is a shorter time series than we use for haddock, it begins in 1982, but cod is more widespread than haddock and it appears to give better estimates.

The southern population of cod in the Baltic Sea (Table 5) was surveyed since 1980 by the Federal Republic of Germany (ICES 1991). We treat the cod in Baltic ICES region 22 as a unit population. Although there are surveys in November, January, and March, we use the 0+ November survey and the 1+ survey in January as "simultaneous" measures of 0+ recruit numbers. Similarly, we use the November 1+ and January 2+ surveys as measures of the abundance a year later. That is, we assume that most mortality occurs during the spring, summer, and autumn.

Results

The model was fit to data from 14 populations (Tables 2-5). In only one case, North Sea sole (Table 2), was the interannual variance in juvenile mortality significant at the 0.05 nominal level. Overall it is clear that the estimates of the variability in the density-independent component of juvenile mortality (ψ) are small compared with recruitment variability (ϕ). The estimates of ψ are positive for only 5 of the 14 populations.

We can obtain estimates less than zero because the variance is a component of a larger model. If the interannual variance in juvenile mortality is zero, we would expect about half the estimates to be negative with relatively small sample size.

TABLE 5. Parameters and estimates for the variable juvenile mortality model, Arctic (SE's in parentheses). n is the median number of cohorts used in the analysis.

	Cod Northeast Arctic	Haddock Northeast Arctic		Cod Southern Baltic Sea
$l_{i,1,1}$	RUSSIA	RUSSIA	$l_{i,0,1}$	NOVEMBER
$l_{i,1,2}$	NORWAY	NORWAY	$l_{i,1,2}$	JANUARY
$l_{i,2,1}$	RUSSIA	RUSSIA	$l_{i,1,1}$	NOVEMBER
$l_{i,2,2}$	NORWAY	NORWAY	$l_{i,2,2}$	JANUARY
n	10	23	n	10
λ	1.09 (0.32)	0.91 (0.15)	λ	1.76 (0.78)
ϕ	2.76 (1.87)	4.38 (1.78)	ϕ	3.14 (2.51)
$\theta_{1,1}$	1.57 (0.91)	0.13 (0.34)	$\theta_{0,1}$	4.24 (2.07)
$\theta_{1,2}$	3.08 (1.55)	1.17 (0.57)	$\theta_{1,2}$	4.08 (2.01)
$\theta_{2,1}$	1.15 (0.64)	0.37 (0.27)	$\theta_{1,1}$	1.96 (1.07)
$\theta_{2,2}$	1.55 (0.81)	0.20 (0.24)	$\theta_{2,2}$	1.44 (0.89)
ψ	-1.16 (0.77)	0.92 (0.51)	ψ	-3.60 (3.35)

The density-dependent component of survival appears to be important for most populations. For cod, λ is less than 1 for most populations. An exception is southern Grand Banks cod and southern Baltic Sea cod. In both of these cases the observational error variance is quite high, and none of the estimates are reliable.

Power and Bias Analysis

Our interest here is to quantify the power of the test that interannual variance in juvenile mortality, ψ , is 0, i.e., $H_0: \psi = 0$ versus $H_a: \psi > 0$ (Peterman 1990). Specifically, for a given value of ψ (we choose $\psi = 0, 0.1, 0.25, 0.5$, and 0.9), we are interested in the small sample probability that the test rejects H_0 at different levels of the estimation error variance (θ) in favor of H_a (indicating significant interannual variance in juvenile mortality).

The power analysis is performed by generating 1000 realizations of the model with $\phi = 1$, $\lambda = 0.8$, θ as defined in Fig. 3, and the number of years of data used, n , to be either 10 or 20. Thus, we generate 1000 data sets, each with n observations of four variables, for each of the 15 models considered. For each data set and for each particular model, we estimate the parameters and test H_0 . For each model, we then count the number of times H_0 is rejected in the 1000 realizations; the simulated power of the test is this number divided by 1000.

There are two ways we considered testing the two-sided alternative of the above hypothesis. In the likelihood ratio test the model is fit twice: first with ψ estimated and second with ψ constrained to be zero. If the reduction in the estimated log-likelihood in the second case is greater than $X^2_{(1)}/2$, the parameter is considered significant (Cox and Hinkley 1974). The second approach is to test the significance of ψ by using the estimated standard error and the assumption that the estimate of ψ follows a normal distribution — an asymptotic result. We found the power of both tests to be virtually identical. Because the

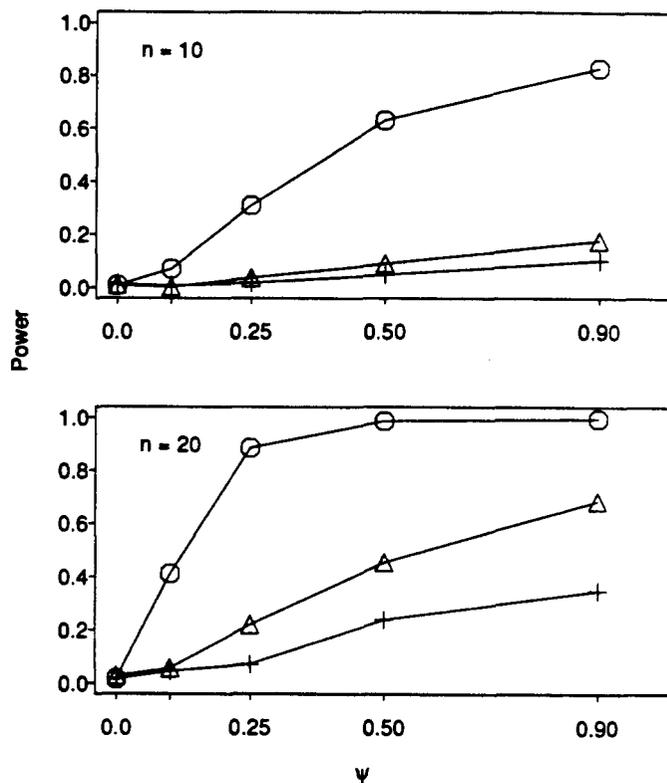


FIG. 3. Power curves for the test $H_0: \psi = 0$ for $\theta = 0.1$ (O), $\theta = 0.5$, and $\theta = 1.0$ (+) where θ is the estimation error variance and ψ is the interannual variance of the density-independent juvenile mortality. See text for details.

TABLE 6. Simulated %bias of the maximum likelihood estimate of ψ . Eighteen sets of simulations were conducted with data generated in a $2 \times 3 \times 3$ factorial experiment with two sample sizes (n), three values of the estimation error variance (θ), and three values of the variance in juvenile mortality unrelated to abundance (ψ). The variance in recruitment (ϕ) is always equal to 1 and the density-dependent survival rate (λ) is always equal to 0.8.

n	θ	ψ		
		0.25	0.50	0.90
20	0.01	-12.1	-11.6	-8.4
	0.50	-20.6	-12.4	-18.9
	1.00	-60.4	-31.0	-31.5
10	0.01	-30.9	-23.3	-30.5
	0.50	-101.8	-41.3	-41.9
	1.00	-163.3	-79.5	-79.7

likelihood ratio test is difficult to apply for the one-sided alternative, we only use and present the results from the second test.

The hypothesis was tested with a type I error (α) of 0.05. When $\psi = 0$ the simulated α is less than 0.05 (see Fig. 3), indicating that the test is conservative at the sample sizes studied. Otherwise, if the estimation error (θ) decreases the power of the test increases. Also, the test is not very powerful at rejecting H_0 when ψ is small and when θ is large in comparison with ϕ . In conjunction with the power analysis, the biases in parameter estimates were also investigated. The results for density-

dependent mortality parameters and the estimation error variances are similar to those obtained in Myers and Cadigan (1993) and are thus not discussed here. The bias in the maximum likelihood estimate of ψ is generally negative (Table 6). The %bias decreases with sample size and the true ψ and increases with the error variances. This negative bias results in a reduced statistical power in detecting significant ψ . If the estimation error variance is less than half the ϕ for sample sizes of around 10 the results cannot be interpreted because of the large bias in the estimated ϕ .

Considerable effort has been invested into producing a bias reduced estimator for the type of model considered here. A resampling procedure (the jackknife) and an analytic procedure have been used and simulations conducted to assess their usefulness. The simulation results are too extensive to report but they do not suggest that either bias-reduced estimator works well. Hence, we have no better estimator of ψ than the maximum likelihood estimator used.

Violations of the Model Assumptions

A violation of the model assumptions could bias our results. An environmental factor that simultaneously influenced the efficiency of the survey gear in capturing fish in both surveys would result in an overestimate of variability of juvenile mortality, ψ . Given the general absence of evidence for positive ψ , this factor is probably not of general importance, but it cannot be eliminated for North Sea sole.

It is possible that other violations of the model assumptions could have biased our results. In Myers and Cadigan (1993), we tested the bias in a similar model that would result if recruitment and the estimation errors followed other distributions than assumed. In no case were the resulting biases important. We therefore believe that reasonable violations of these assumptions are not important for our conclusions.

Discussion and Conclusions

We have provided a systematic test of one portion of Hjort's hypothesis: we estimated the proportion of recruitment variability caused by variable juvenile survival.

Our results (Tables 2–5) should be interpreted in light of the simulation studies. The average estimation error variance is more than half of ϕ for the following populations: North Sea whiting, Irish Sea plaice, Irish Sea whiting, Gulf of Maine cod, southern Grand Banks cod, St. Pierre Banks cod, Northeast Arctic cod, and southern Baltic Sea cod. The bias in estimating the interannual variance in juvenile mortality appears to be too large for the results to be interpreted because of the relatively large estimation error variance.

The results for the other six populations appear to be reliable because the estimation error variance is relatively small. The estimates of ψ are positive for only two of these populations. Overall the results indicate that we would have detected an effect in more populations than one if the density-independent component of juvenile mortality was highly variable.

The results for North Sea sole appear to be reliable. There is previous evidence of interannual variability in postlarval survival in this flatfish, particularly related to extreme cold or freezing (Woodhead 1964; de Veen 1969). The strong correlations between the surveys at age 0 and at age 1 (Fig. 1) appear to be reliable in the sense that they would remain strong even if the most influential points were removed from the analysis. For this

population the interannual variability in juvenile survival appears to be the most important source of variability in abundance. The log variance of numbers at age 1 will be $\lambda^2\phi + \psi$. By substituting the estimates from Table 2, we can estimate for North Sea sole that approximately 85% of the interannual variance in log abundance at age 1 is caused by variable density-independent mortality in the juvenile stage.

The only other population with evidence of density-independent variability in juvenile survival is Northeast Arctic haddock. Although the estimate of the ψ was close to being statistically significant, it does not appear to account for a large portion of the interannual variance at age 1.

Our results indicate that it is very difficult to detect density-independent variability in juvenile survival. Research programs that attempt to investigate this portion of the life history would need to have low estimation error variance and must be long term, i.e., 20 yr. The value of short-term studies for estimating the importance of the juvenile stage in recruitment studies must be questioned.

Fisheries scientists often have access to a plethora of population dynamics data. Too often these data are not examined to ask fundamental ecological questions. In this paper and in Myers and Cadigan (1993), we have shown how modern statistical methods can be used to address these questions.

Our results suggest that the variability of relative year class strength is usually determined in the larval stage for marine demersal species (see also Bradford 1992) but that this variability is attenuated by density-dependent juvenile mortality (Myers and Cadigan 1993). For North Sea sole, variable mortality of juveniles may also contribute to recruitment variability. This study represents one of a few attempts to directly test Hjort's hypothesis that the variability in year class strength is determined in the larval stage. Although our results support Hjort's hypothesis in general, our results indicate two important modifications: (1) variable mortality of juveniles may be important in some flatfish species and (2) variability in recruitment created in the larval stage is attenuated by density-dependent mortality in the juvenile stage.

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