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Northwest Atlantic Fisheries Organization

Serial No. N2355 NAFO SCR Doc. 94/2

SCIENTIFIC COUNCIL MEETING - FEBRUARY 1994

Temporal Variability in Estimates of Population Sustainability for 3NO Atlantic Cod from 1959 to 1994

by

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Introduction

The objective of this analysis is to provide estimates of population sustainability for Atlantic cod, *Gadus morhua*, in NAFO Divisions 3N and 3O. A population that is sustainable is one in which each individual's lifetime survivorship and fecundity allow that individual to replace itself. In theory, sustainable populations are at equilibrium and, as such, do not change in abundance through time. The goal of this analysis is to determine those years from 1959 to 1993 (and forecasts for 1994) when the age-specific values of survival and fecundity for 3NO cod were sufficiently high to permit the stock to replace itself through time.

Methods

The instantaneous rate of change of the 3NO cod stock was estimated as r, the intrinsic rate of natural increase, as given by the discrete-time version of the Euler-Lotka equation

(1) $$1 = \Sigma\, l_x\, m_x\, e^{-rx} \quad ,$$

where l_x represents survival from the zygote to the beginning of the breeding season at age x and m_x is the number of female zygotes produced by a female breeding at age x (Cole 1954; Schaffer 1974). The intrinsic rate of natural increase is frequently used as a measure of genotypic fitness (Charlesworth 1980; Stearns 1992; Hutchings 1993). As a measure of the rate of change in population abundance, population size at time t+1 can be estimated from population size at time t from the equation $N_{t+1} = N_t\, e^r$ (Caughley 1977). Thus, r=0 for a population that is neither increasing nor decreasing, i.e., able to sustain itself through time.

Age-specific rates of survival, l_x, and fecundity, m_x, for 3NO cod from 1959 to 1994 were estimated from data provided in assessment documents for this stock (or forecasted in the case of 1994) and summarized in Tables 1 and 2. Fishing mortality estimates for ages 3-13 yr are available in Davis et al. (1993). Natural mortality per annum for all ages was assumed to be 18% (i.e., M=0.2; Davis et al. 1993). Age-specific fecundities were estimated from the fecundity vs. weight regressions calculated by May (1967). Weight-at-age data from the commercial fishery are available in Davis et al. (1993) for ages 3-12 yr and from the yearly assessment documents for this stock for ages 13-20 yr. Data for cod aged 3-12 yr from 1959 to 1971 were approximated by the average weight-at-age from 1972 to 1992. Data for cod aged 13-20 yr from 1959 to 1982 were estimated to be the average weight-at-age from 1983 to 1992. Based on empirical data available in NAFO (1993), it was assumed that 4% of females reproduce at age 4 yr, 22% at age 5, 64% at age 6, 94% at age 7, 99% at age 8, and 100% at all subsequent ages until death following reproduction at age 15.

To estimate survival from birth to age 3 yr (ages for which survival data are not available), it was assumed that female cod replace themselves in the absence of fishing, i.e., the population is at equilibrium, and that females live on average to an age of 20 yr. Thus, the product of age-specific rates of survival and fecundity from ages 5 through 20 yr were constrained to equal 2, the expected lifetime number of offspring produced by a sexual organism that replaces itself (Charlesworth 1980). Survival from birth to age 3 yr, $s_{0\text{-}3}$, was estimated to be 2.6×10^{-7}. To allow for 50% under-estimation error in this parameter, two values of $s_{0\text{-}3}$ were used to estimate r. These were 2.6×10^{-7} and 5.2×10^{-7}. Although an implicit assumption of this analysis is that survival to age 3 yr is density-independent, these two survival estimates should encompass a sufficiently large range of values concordant with the assumption that juvenile survival is negatively associated with population abundance.

Results

Temporal changes in the estimates of r were in broad agreement with observed changes in harvestable abundance, i.e., numbers of cod aged 3 yr and older (as determined from Virtual Population Analysis) (Fig. 1).

Values of r estimated using $s_{0\text{-}3}=5.2\times10^{-7}$ (middle panel of Fig. 1) provided a close fit to the harvestable abundance data from 1959 to 1978. The increase in population size from the late 1950s to the mid 1960s was generally associated with values of r equal to or greater than zero (i.e., indicative of annual increases in population size). The large decline in stock size from 1967 to the mid 1970s was associated with negative values of r (indicative of annual declines in population size). The small rise in population size from 1976 to 1978 was associated with values of r greater than zero.

From 1978, changes in harvestable abundance closely approximated changes in r estimated from the lower survival probability from birth to age 3 yr, i.e., $s_{0\text{-}3}=2.6\times10^{-7}$ (upper panel of Fig. 1). The intrinsic rate of natural increase was slightly greater than or slightly less than zero from 1978 to 1985. This corresponds to a period during which the population changed little in size. The decline in harvestable abundance from 1985 to 1992 was associated with a continuous decline in r (with the exception of 1991) from -0.04 to -0.35.

Discussion

Age-specific survival probabilities, and corresponding age-specific fecundities, experienced by 3NO cod since 1959 may have been sufficiently high for cod to sustain themselves (i.e., $r\geq0$) during the late 1950s and early 1960s and from the late 1970s to the mid 1980s (Fig. 1). However, since 1988, r has declined to values similar to those experienced during the marked decline of 3NO cod from the mid 1960's to the mid 1970's (Fig. 1). The time-dependent associations between r and harvestable abundance suggest that survival from birth to age 3 yr was significantly lower throughout the 1980s than it was during the two previous decades. Importantly, the 1992 estimates of r (-0.26 and -0.35, depending on $s_{0\text{-}3}$) are among the lowest for this stock. Given these extremely low values of r, and given the historically low size of the harvestable component of the stock (as estimated from VPA and research surveys since 1971; data in Davis et al. 1993), fishing mortality on cod in Divisions 3N and 3O should be reduced significantly. Estimates of r based on the conservative and more reliable (see above) estimate of survival from birth to age 3 indicate that 3NO cod would not be able to sustain themselves at the Total Allowable Catch forecasted for 1994 (i.e., 6,000 t).

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Table 1. Age-specific survival values for 3NO cod from 1959 to 1994. Survival probabilities are given from age x to age $x+1$. Values estimated from F values given in Davis et al. (1993) and in unpublished data (1993 data and 1994 forecast) and were calculated under the assumption of constant, age-independent natural mortality of M=0.2.

Year	Age (years)											
	3	4	5	6	7	8	9	10	11	12	13	14
59	0.7905708	0.6941967	0.5886050	0.5091564	0.5593387	0.5939263	0.6941967	0.6736800	0.5677921	0.7363866	0.7363866	0.7363866
60	0.7913618	0.6831779	0.5158187	0.5798418	0.5786833	0.5241381	0.6596803	0.7268755	0.6101808	0.7312499	0.7312499	0.7312499
61	0.8097741	0.7356506	0.4630131	0.4123017	0.5504605	0.5272924	0.6281351	0.7378609	0.8105842	0.7261490	0.7261490	0.7261490
62	0.8105842	0.7679735	0.7618543	0.7146231	0.5862553	0.6325475	0.5980984	0.6636503	0.6921172	0.7319815	0.7319815	0.7319815
63	0.8154624	0.7595721	0.6287636	0.6550786	0.6408243	0.3957391	0.3745612	0.4823911	0.6453258	0.6518114	0.6518114	0.6518114
64	0.7702809	0.6047138	0.5565490	0.6053188	0.7011734	0.6596803	0.5992958	0.4848091	0.7764679	0.7254233	0.7254233	0.7254233
65	0.8130196	0.7423013	0.6453258	0.4985756	0.3790830	0.4639400	0.5833313	0.2383536	0.4747343	0.6120141	0.6120141	0.6120141
66	0.8154624	0.6955864	0.5515626	0.4021219	0.4081992	0.2931708	0.5288767	0.1873082	0.5810026	0.5689288	0.5689288	0.5689288
67	0.7203630	0.4916442	0.3342052	0.3627650	0.3993169	0.2671353	0.7239739	0.7649078	0.6777343	0.6683121	0.6683121	0.6683121
68	0.6736800	0.4312790	0.3008932	0.2862184	0.3882911	0.4686027	0.5945205	0.7203630	0.7834876	0.6872893	0.6872893	0.6872893
69	0.7610928	0.6485605	0.3921935	0.4223166	0.6083530	0.5752216	0.5757971	0.6004956	0.7153381	0.7182052	0.7182052	0.7182052
70	0.7953285	0.6369908	0.5992958	0.4360493	0.5127330	0.5482631	0.6537698	0.6969790	0.5363330	0.7225274	0.7225274	0.7225274
71	0.8089647	0.4421969	0.3790830	0.4218945	0.4950978	0.4094256	0.6683121	0.7254233	0.7018750	0.7032801	0.7032801	0.7032801
72	0.8179124	0.5638314	0.4295574	0.3048303	0.3461095	0.5035864	0.7046881	0.7210837	0.7687419	0.6962824	0.6962824	0.6962824
73	0.5740723	0.3389170	0.4737858	0.3771924	0.5712091	0.5933327	0.5559928	0.6811314	0.7327139	0.7225274	0.7225274	0.7225274
74	0.6784123	0.4160291	0.2597593	0.2949351	0.3790830	0.3471494	0.4218945	0.3675117	0.4625503	0.6010964	0.6010964	0.6010964
75	0.7961243	0.5363330	0.4593237	0.3243280	0.3188610	0.2722594	0.2359819	0.3914099	0.3605949	0.5471677	0.5471677	0.5471677
76	0.7124824	0.4985756	0.4625503	0.5786833	0.6900439	0.6969790	0.7356506	0.7196430	0.7882027	0.7733682	0.7733682	0.7733682
77	0.8089647	0.7276028	0.6035056	0.6243776	0.5998954	0.6629869	0.6649789	0.6511599	0.6656442	0.7437874	0.7437874	0.7437874
78	0.8057353	0.7297889	0.6914254	0.7032801	0.7452765	0.7535198	0.7415594	0.7626165	0.7874149	0.7905708	0.7905708	0.7905708
79	0.8162782	0.7535198	0.5604585	0.3464558	0.6414654	0.7452765	0.7695110	0.7882027	0.8017167	0.7834876	0.7834876	0.7834876
80	0.8089647	0.7702809	0.7327139	0.7046881	0.7283308	0.7490122	0.7842715	0.7842715	0.8009154	0.7953285	0.7953285	0.7953285
81	0.8049300	0.7702809	0.7430440	0.7482636	0.6838614	0.7254233	0.7385991	0.7741420	0.7610928	0.7819222	0.7819222	0.7819222
82	0.8089647	0.7497616	0.7268755	0.7371234	0.7557837	0.6636503	0.6852305	0.6997725	0.7189237	0.7687419	0.7687419	0.7687419
83	0.7929461	0.7929461	0.7305190	0.7232502	0.7437874	0.7557837	0.6976763	0.7408182	0.7535198	0.7834876	0.7834876	0.7834876
84	0.8179124	0.7913618	0.7475157	0.6703200	0.6852305	0.7124824	0.7527666	0.6955864	0.7718230	0.7741420	0.7741420	0.7741420
85	0.8170949	0.7482636	0.6047138	0.6144670	0.5792622	0.6914254	0.7239739	0.7679735	0.7349153	0.7633795	0.7633795	0.7633795
86	0.8049300	0.7319815	0.6126264	0.5689288	0.6531163	0.6629869	0.6900439	0.7117703	0.7749165	0.7595721	0.7595721	0.7595721
87	0.7497616	0.7718230	0.6736800	0.6382661	0.6969790	0.7089289	0.6095709	0.6537698	0.6583622	0.7535198	0.7535198	0.7535198
88	0.7993151	0.7618543	0.5980984	0.4274149	0.4946029	0.6730067	0.6845456	0.6459714	0.6914254	0.7319815	0.7319815	0.7319815
89	0.6866023	0.6293926	0.4681343	0.5147881	0.5466208	0.6059244	0.7146231	0.7378609	0.7131953	0.7452765	0.7452765	0.7452765
90	0.5746466	0.3667775	0.2195885	0.3726931	0.6206425	0.6287636	0.6596803	0.6872893	0.7482636	0.7460221	0.7460221	0.7460221
91	0.6120141	0.5499104	0.5466208	0.4766370	0.4417549	0.5406409	0.5804219	0.6107913	0.6518114	0.6928096	0.6928096	0.6928096
92	0.7124824	0.2783155	0.1912832	0.4448581	0.3910187	0.4714228	0.5666576	0.6453258	0.6175471	0.6879769	0.6879769	0.6879769
93	0.8025188	0.7572968	0.6935028	0.6616623	0.6459714	0.6225073	0.6059244	0.5833313	0.5874289	0.6138529	0.6138529	0.6138529
94	0.8065414	0.7725952	0.7239739	0.6990731	0.6872893	0.6683121	0.6550786	0.6376282	0.6408243	0.6623243	0.6623243	0.6623243

Table 2. Age-specific fecundity estimates for 3NO cod, as calculated from weight-at-age data given by Davis et al. (1993) and using fecundity-size equations given by May (1967).

Year	Age (years)							Age (years)			
	4	5	6	7	8	9	10	11	12	13	14	15
59	501939.3	676032.6	942501.9	1312005.9	1798756	2470259	3052939	3301643	4069074.8	4459896	4783212	5348127
60	501939.3	676032.6	942501.9	1312005.9	1798756	2470259	3052939	3301643	4069074.8	4459896	4783212	5348127
61	501939.3	676032.6	942501.9	1312005.9	1798756	2470259	3052939	3301643	4069074.8	4459896	4783212	5348127
62	501939.3	676032.6	942501.9	1312005.9	1798756	2470259	3052939	3301643	4069074.8	4459896	4783212	5348127
63	501939.3	676032.6	942501.9	1312005.9	1798756	2470259	3052939	3301643	4069074.8	4459896	4783212	5348127
64	501939.3	676032.6	942501.9	1312005.9	1798756	2470259	3052939	3301643	4069074.8	4459896	4783212	5348127
65	501939.3	676032.6	942501.9	1312005.9	1798756	2470259	3052939	3301643	4069074.8	4459896	4783212	5348127
66	501939.3	676032.6	942501.9	1312005.9	1798756	2470259	3052939	3301643	4069074.8	4459896	4783212	5348127
67	501939.3	676032.6	942501.9	1312005.9	1798756	2470259	3052939	3301643	4069074.8	4459896	4783212	5348127
68	501939.3	676032.6	942501.9	1312005.9	1798756	2470259	3052939	3301643	4069074.8	4459896	4783212	5348127
69	501939.3	676032.6	942501.9	1312005.9	1798756	2470259	3052939	3301643	4069074.8	4459896	4783212	5348127
70	501939.3	676032.6	942501.9	1312005.9	1798756	2470259	3052939	3301643	4069074.8	4459896	4783212	5348127
71	501939.3	665373.8	942501.9	1312005.9	1798756	2470259	3052939	3301643	4069074.8	4459896	4783212	5348127
72	498386.4	665373.8	892760.9	1180547.7	1418594	2267742	2978327	3109785	3756417.5	4459896	4783212	5348127
73	509045.2	661820.9	931843.1	1443464.1	1798756	2374330	3550348	4122369	5124293.1	4459896	4783212	5348127
74	413116.2	580103.6	850125.8	1169889.0	1812968	2754493	2093649	3138209	775514.4	4459896	4783212	5348127
75	469963.0	608527.0	910525.5	1269370.8	1631769	2118520	2548423	2026144	2672775.7	4459896	4783212	5348127
76	477068.8	654715.0	981584.0	1308453.0	1585581	2523553	3259008	3401125	4591354.6	4459896	4783212	5348127
77	509045.2	679585.5	1034877.9	1400829.0	1837839	2701199	3283879	4310674	4228956.3	4459896	4783212	5348127
78	526809.8	704456.0	953160.6	1482546.3	1791651	2353013	2722517	3521925	4726365.7	4459896	4783212	5348127
79	501939.3	647609.2	896313.8	1173441.9	1468335	1841392	2694093	2988986	3745758.7	4459896	4783212	5348127
80	523256.8	754196.9	1041983.7	1464781.6	2104308	2988986	3429548	3919852	4633989.6	4459896	4783212	5348127
81	604974.1	807490.7	1109489.3	1415040.7	2047461	2686987	3386913	3354937	3759970.4	4459896	4783212	5348127
82	569444.9	686691.3	935396.0	1514522.6	2022591	2814893	3280326	3642724	4516743.2	5351680	4832953	6090688
83	569444.9	818149.5	1088171.7	1503863.8	2001273	2381436	3024515	3347831	4065521.8	3727994	4353309	4641095
84	555233.2	690244.3	963819.4	1233841.6	1592687	2200237	2718964	3322961	4633989.6	5007047	5511562	6179511
85	459304.2	640503.3	882102.1	1308453.0	1805862	2505788	3109785	3109785	4108156.9	4442132	4328438	5913042
86	512598.1	693797.2	921184.3	1393723.2	2075885	2978327	3642724	3642724	3664041.5	4022887	4559378	4637543
87	445092.5	615632.9	803937.8	1180547.7	1844944	2733175	3333620	3333620	4626883.8	3962487	4861377	5493797
88	509045.2	644056.3	789726.1	946054.8	1493205	1972850	2598164	2598164	4086839.4	4683731	5209563	5383657
89	498386.4	722220.6	949607.7	1315558.8	1791651	2669223	3106232	3106232	4506084.4	4427920	4705048	5010600
90	512598.1	672479.6	1045536.6	1123701.0	1624663	1937321	3127550	3127550	4150792.0	2928586	4495426	4783212
91	455751.3	718667.7	970925.2	1514522.6	2129178	2829104	3365596	3365596	5120740.2	4321332	4797424	5088764
92	384692.8	533915.6	821702.4	1191206.5	1930215	2210896	2850422	2850422	3934063.7	4665966	4946647	5625255
93	501939.3	676032.6	942501.9	1312005.9	1798756	2470259	3052939	3301643	4069074.8	4459896	4783212	5348127
94	501939.3	676032.6	942501.9	1312005.9	1798756	2470259	3052939	3301643	4069074.8	4459896	4783212	5348127

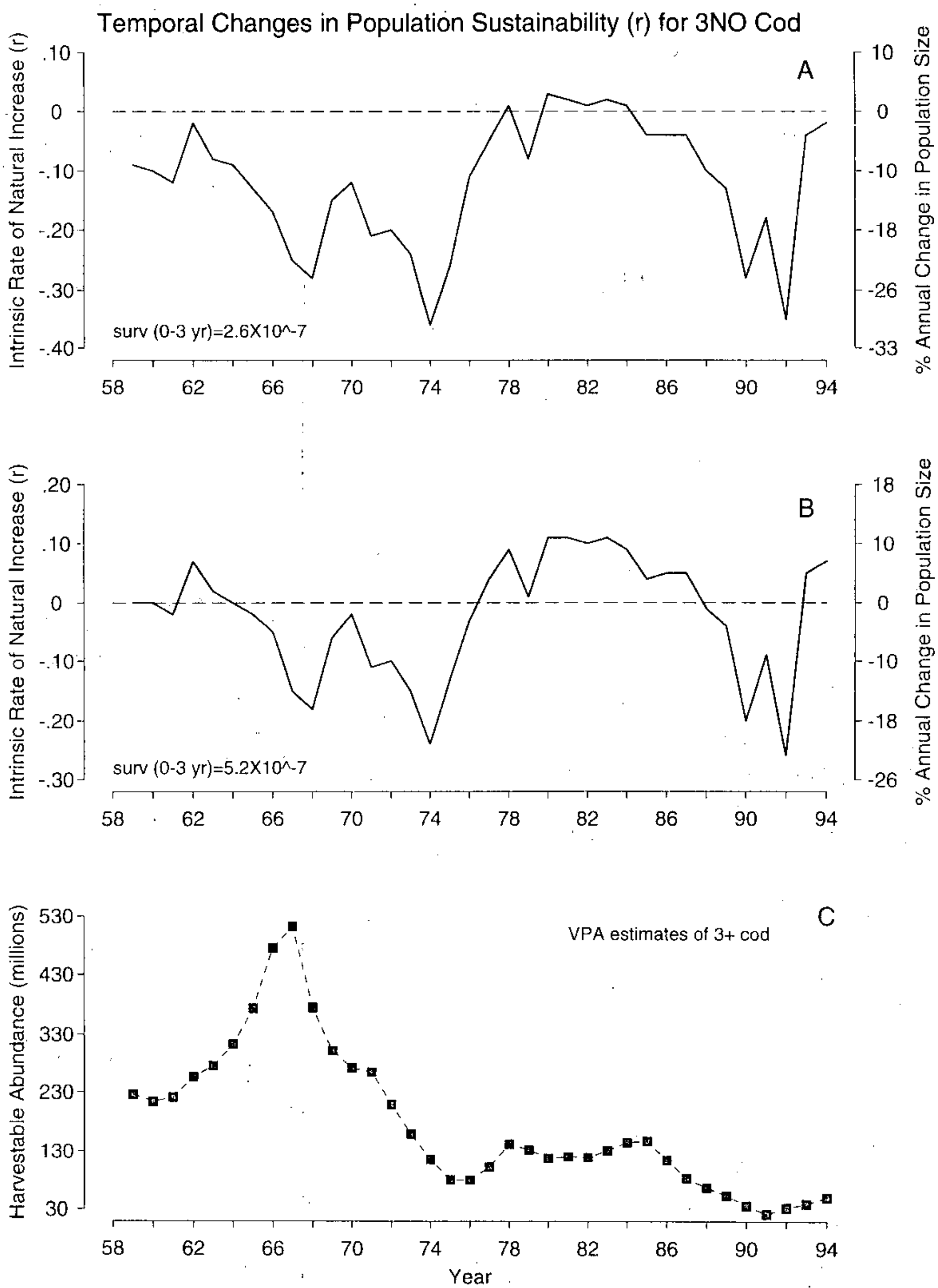

Figure 1. Temporal variation in *r*, the intrinsic rate of natural increase (as indicated on the left ordinate) and harvestable abundance (cod aged 3 yr and older) from 1959 to 1994. At *r*=0, the population replaces itself through time. When *r* is greater or less than 0, the population increases or decreases, respectively, at the annual rates of change indicated on the right ordinate. A. Survival from birth to age 3 yr estimated to be 2.6×10^{-7}. B. Survival from birth to age 3 yr estimated to be 5.2×10^{-7}. C. Temporal change in harvestable abundance as estimated by VPA (1959-1992 data in Davis et al. 1993; 1993-1994 data are unpublished).