

Coherence of Atlantic Cod Stock Dynamics in the Northwest Atlantic Ocean

BRIAN J. ROTHSCHILD*

School for Marine Science and Technology, University of Massachusetts Dartmouth,
706 South Rodney French Boulevard, New Bedford, Massachusetts 02744-1221, USA

Abstract.—The stocks of Atlantic cod *Gadus morhua* in the Northwest Atlantic Ocean declined in abundance from 1965 to 2003; the declines in spawning stock biomass (SSB) have been temporally coherent. A coherent, sharp increase in SSBs from 1975 to 1985 and a subsequent decrease from 1985 to 1992 are superimposed on the general decline. The coherence suggests that cod stock variability in the Northwest Atlantic Ocean is driven by a common set of causes or that the linkages among the nominal stocks are stronger than was previously thought. The coherent increases in cod SSB from the mid-1970s to 1985 occurred under relatively low fishing mortalities. The declines in SSB beginning in 1985 began during a period of low fishing mortalities. During the 1985–1992 period the declines in Atlantic cod abundance were coupled with greatly reduced growth rates, increased natural mortality rates, and a lack of response to reduced fishing mortality. This suggests that the 1985–1992 decreases were driven by a strong negative environmental signal, implying that the environment had a stronger role in affecting cod abundance than had been previously thought. It appears that the decline in SSB over most of the range of the cod was coupled with a major perturbation in the forage available to cod. Inasmuch as this perturbation involved seemingly disparate groups, such as capelin *Mallotus villosus*, euphausiids, and Atlantic herring *Clupea harengus*, it appears that the change in the environment was associated with the dynamics of the plankton.

The abundance of nominal stocks of Atlantic cod *Gadus morhua* in the Northwest Atlantic Ocean has generally decreased during the past half century. The decreases, which began in the 1960s, resulted in historically low levels of cod in the mid-1970s. However, in 1975 stocks generally increased in abundance until 1985. Thereafter, abundances plummeted to even lower levels, reaching nadirs in the early 1990s.

Analyses of variations in abundance have generally focused on individual nominal stocks of Atlantic cod. For example, the declines in abundance that began in the 1960s, the increases from 1975 to 1985, and the second decline in abundance from 1985 to 1992 were described principally for the northern cod stock (Northwest Atlantic Fisheries Organization [NAFO] Division 2J3KL) by deYoung and Rose (1993), Rice (2002), and Lilly and Murphy (2004). Working in another location of the Northwest Atlantic Ocean, Chouinard and Fréchet (1994) focused on the Gulf of St. Lawrence cod.

In contrast to studies of single nominal stocks, there have been only a few analyses of the ensemble of nominal cod stocks. Koslow (1984) studied the recruitment pattern of Northwest Atlantic Ocean fish stocks (including cod). Sinclair (1996) reviewed the

few studies of the ensemble of Atlantic cod stocks and provided an analysis of temporal changes in biomass, recruitment (R), prerecruitment survival, weight at age, fishing mortality (F), and biomass.

Further, analysis is facilitated by the recent publication of spawning stock biomass (SSB) data for all 11 stocks (Shelton et al. 2006). This data set enables an exploration of the interrelationships among nominal stocks, between stocks and environmental forcing, and between stocks and the effects of fishing.

The 11 stocks identified by Shelton et al. (2006) are listed in Table 1 (see Figure 1 for stock locations) along with annual estimates of SSB normalized by standard deviation (SD) units. The stocks are defined in terms of NAFO stock assessment boundaries. The normalized SSB data are plotted as a function of time in Figure 2.

The normalized SSB data follow a pattern across nearly all stocks: the relative measures of SSB declined from the 1960s to the mid-1970s, then increased to the mid-1980s, and thereafter declined precipitously to the mid-1990s, remaining at very low levels in the early 2000s (Figure 2).

This paper is intended to investigate the temporal pattern and its associated variability. This involves (1) computing the correlation matrix that contains the magnitude of the correlations implied in Figure 1; (2) decomposing the correlation matrix into its principal components to identify “natural” groupings of Atlantic cod stocks; (3) comparing the temporal trajectories of weight at age with SSB trajectories to infer the agents

* E-mail: brothschild@umassd.edu

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TABLE 1.—Normalized spawning stock biomass (SSB; SD units) data for 11 nominal Atlantic cod stocks in the Northwest Atlantic Ocean (see Figure 1 for stock codes). Note that data are available for all stocks only for the years 1983–1999. Supplemental data were provided by Shelton et al. (2006), who note that there is no consensus on the 2J3KL stock data.

Year	3NO	3M	3Ps	2J3KL	4RS3Pn	4TVn	5Z	5Y	4VsW1	4X	4VNMO
1965	2.290			1.806		-0.233					
1966	1.771			1.398		-0.520					
1967	0.570			1.415		-0.522					
1968	0.329			1.431		-0.403					
1969	0.748			1.221		-0.221					
1970	0.632			0.672		-0.079			-0.504		
1971	0.567			0.502		-0.404			0.012		
1972	0.473	2.655		0.437		-0.533			-0.152		
1973	0.306	0.641		0.142		-0.789			0.780		
1974	0.360	-0.099		0.058	0.454	-0.998			-0.816		
1975	-0.498	-0.752		-0.276	0.404	-1.118			-0.837		
1976	-1.147	-0.568		-0.592	0.632	-1.133			-0.597		
1977	-1.060	0.783	-1.516	-0.781	0.615	-1.001			-0.108		
1978	-0.964	1.272	-1.402	-0.727	0.761	-0.398	1.010		0.109		
1979	-0.722	0.578	-1.199	-0.501	1.005	0.138	1.337		0.694		
1980	-0.282	-0.405	-0.694	-0.229	1.339	0.353	1.457		0.827		
1981	0.690	-0.532	-0.113	-0.046	1.528	0.511	1.234		0.994		1.565
1982	1.199	-0.052	-0.036	-0.078	1.764	0.515	1.353	1.758	1.399		1.269
1983	1.181	-0.037	0.155	-0.227	2.090	0.568	0.929	0.647	2.330	1.964	1.257
1984	1.186	0.300	0.940	-0.169	0.956	0.640	0.522	-0.312	2.856	1.535	1.436
1985	1.006	0.698	1.253	-0.113	0.668	1.153	0.086	0.009	1.371	0.743	1.538
1986	0.944	-0.209	0.785	-0.240	0.957	1.645	0.157	0.246	0.140	0.478	1.092
1987	0.921	-0.351	0.217	-0.230	0.174	1.004	0.560	-0.141	0.871	0.275	0.628
1988	0.305	0.010	-0.330	-0.131	-0.148	0.472	0.759	0.110	0.290	0.554	0.183
1989	0.015	1.586	-0.573	-0.180	-0.201	0.009	0.698	1.462	0.001	0.881	-0.218
1990	-0.258	1.273	-0.633	-0.425	-0.651	-0.422	0.556	1.822	0.016	1.528	-0.495
1991	-0.547	0.768	-0.642	-0.582	-0.894	-0.799	-0.026	1.139	-0.253	0.690	-0.468
1992	-1.020	0.776	-0.857	-0.697	-0.955	-1.080	-0.516	-0.617	-0.694	0.033	-0.659
1993	-1.227	-0.627	-1.434	-0.997	-1.043	-1.276	-0.883	-0.990	-0.132	-0.715	-0.916
1994	-1.297	0.120	-1.473	-1.065	-1.157	-1.224	-1.264	-0.607	-0.896	-1.036	-0.963
1995	-1.264	0.312	-0.749	-1.062	-1.101	-1.168	-1.325	-0.289	-0.769	-0.913	-0.899
1996	-1.209	-1.290	-0.006	-1.054	-1.033	-1.106	-1.274	-0.659	-1.043	-0.754	-0.884
1997	-1.197	-1.327	0.651	-1.049	-0.928	-1.038	-1.229	-1.218	-1.118	-0.794	-0.863
1998	-1.194	-1.320	1.018	-1.037	-0.885	-1.015	-1.169	-1.309	-0.770	-1.070	-0.866
1999	-1.194	-1.413	1.102	-1.035	-0.777	-1.053	-1.081	-1.050	-0.832	-1.146	-0.881
2000	-1.221	-1.419	0.655	-1.046	-0.830	-1.080	-1.003		-1.068	-1.104	-0.858
2001	-1.216	-1.369	0.297	-1.052	-0.873	-1.074	-0.888		-0.984	-0.776	
2002	-1.242		0.849		-0.941	-1.158			-1.115	-0.374	
2003	-1.285		1.891		-0.928	-1.193					
2004			1.845								
2005											

associated with the increase followed by the decline of the stocks; and (4) comparing the trajectories of normalized SSB, fishing mortality, and recruitment.

Correlations of SSBs

The magnitude of coherence among stocks is calculated by computing simple pairwise correlations of normalized SSBs. Because data were not equally available for each stock for all years (see Table 1), correlations were calculated two ways: (1) by using the maximum number of observations available for each pair of stocks and (2) by using only the 17 years of observations (1983–1999) for which data were available for all stocks. The following subsections consider (1) correlations for all possible pairs of stocks (there are 55 possible pairs) and (2) correlations based on the 17 years for which a complete data set is

available. The latter set of data comprises a 17×11 data matrix.

The 55 pairwise comparisons based on the maximum number of years for which SSB data were available for each stock pair are shown in Figure 3. Bivariate-normal ellipses were fit to the data and plotted at a probability level of 0.5 in each plot. The scatterplot shows the correlations in qualitative terms. Inspection reveals that most ellipses are fairly narrow and oriented in a positive direction, indicating that the correlations among the nominal stocks are fairly high and positive.

This is supported by Table 2, which exhibits the 55 correlation coefficients computed for each pair of stocks. Approximate 1% significance levels are indicated by the use of bold italics. Table 2 is remarkable because of the number of high correlation

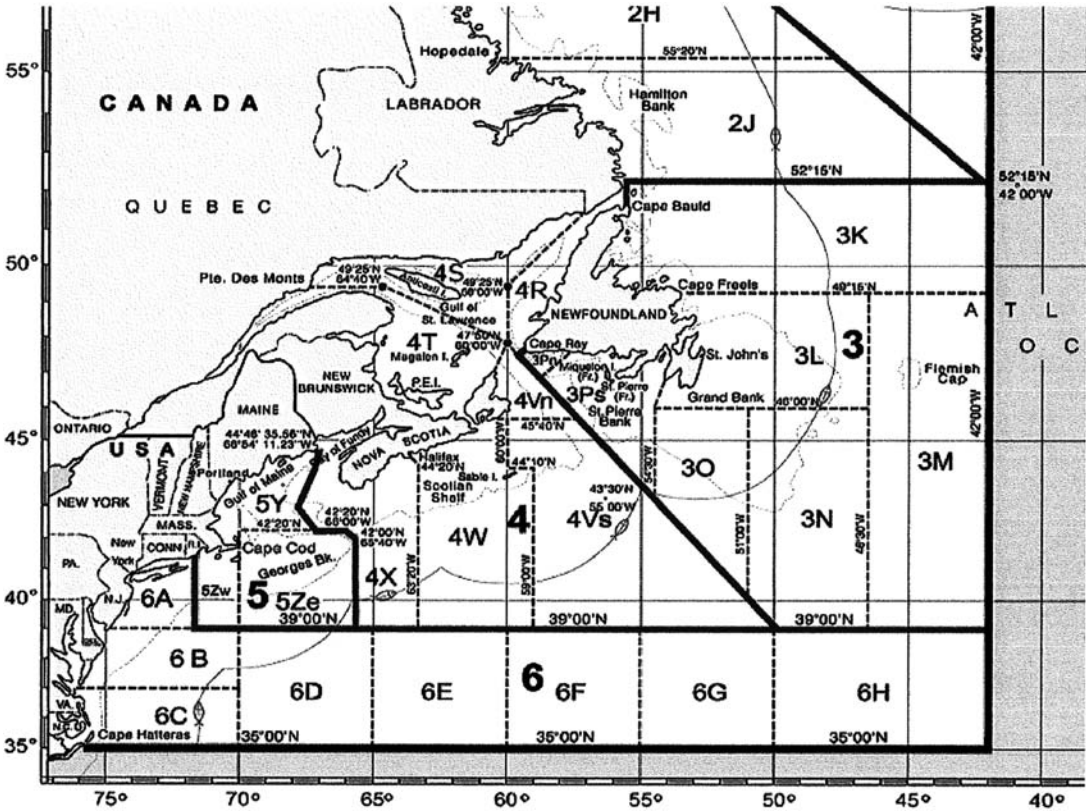


FIGURE 1.—Areas associated with nominal Atlantic cod stocks in the northwestern Atlantic Ocean as defined by the North Atlantic Fisheries Organization.

coefficients. The 3M stock appears to be related to the 4X, 5Z, 5Y, and 2J3KL stocks but not to the 4RS3Pn, 4TVn, 4Vn, and 4VsW stocks. In other words, the Flemish Cap stock covaries with most of the stocks except those in the Gulf of St. Lawrence and the adjacent southern Newfoundland–St. Pierre stock. The Gulf of Maine (5Y) stock appears most correlated with the Georges Bank (5Z) stock, while the southern Scotian Shelf–Bay of Fundy stock (4X) also appears most correlated with the Georges Bank stock. The one stock that appears independent of the other stocks is the 3Ps stock.

Decomposition of the Correlation Matrix

The relatively high correlation among SSB trajectories suggested that further insights into possible natural groupings of the stocks would be obtained from a principal components analysis (PCA) of the correlation matrix. Because data are complete for only 17 out of the 41 years, natural groupings could be explored only for the years 1983–1999 (Table 1).

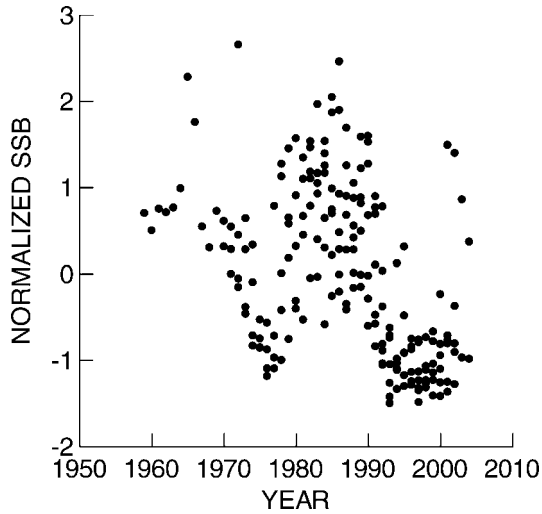


FIGURE 2.—Normalized spawning stock biomass (SSB) data from Table 1. The ordinate is in standard deviation units. Note the depression in 1975, the peak in 1985, and the general decline after 1985.

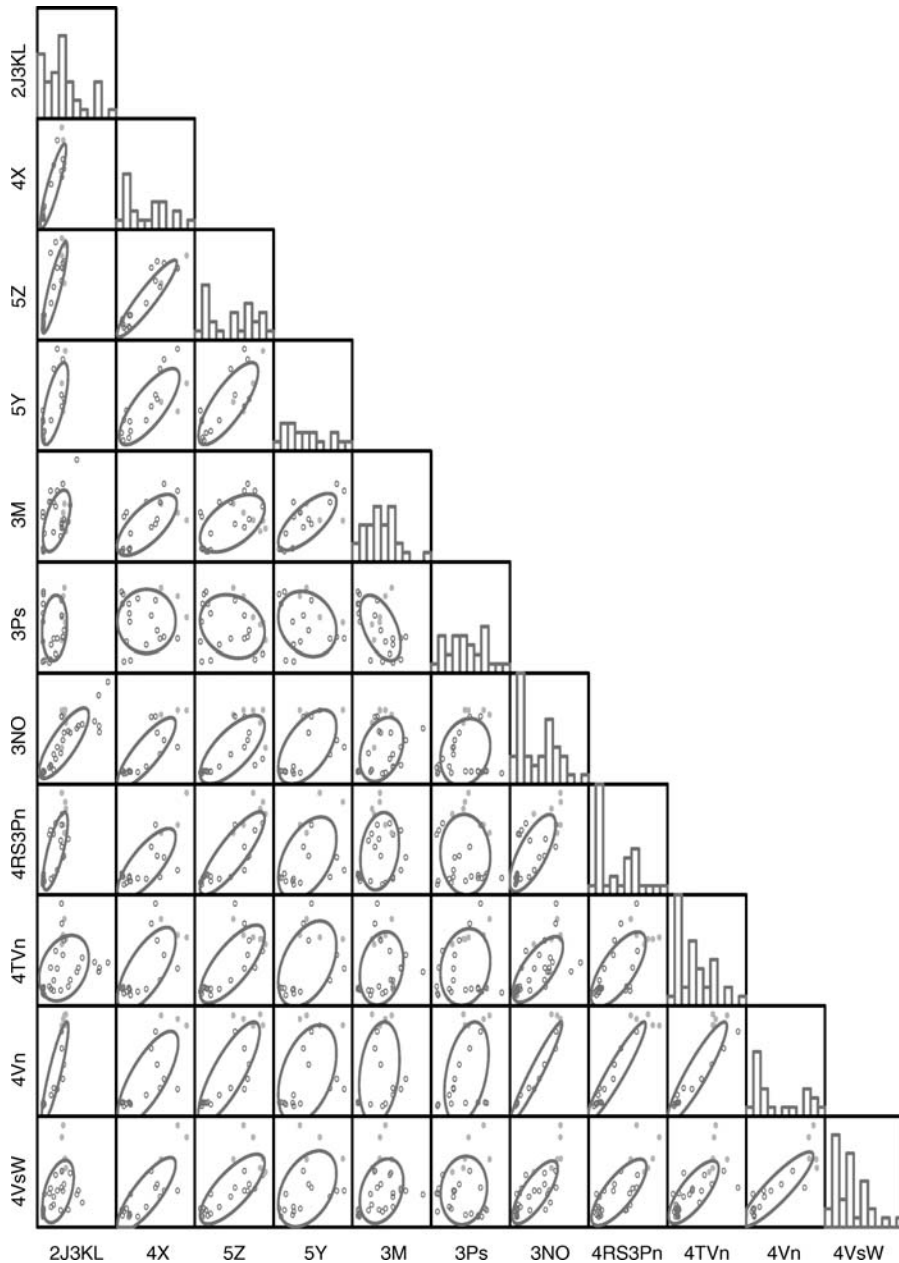


FIGURE 3.—Scatterplots of cod spawning stock biomass (SSB) by pairs of stocks (see Figure 1 for stock codes). The number of observations per plot varies according to the available number of matching years. The ellipse is centered on the centroid of the observations, and the axis of the ellipse is proportional to the x and y standard deviations. The slope of the main axis is dependent on the correlation coefficients. The bar graphs represent the marginal distribution for each nominal stock.

The PCA analysis resulted in two factors that accounted for about 80% of the variation. The factor loadings plot (Figure 4) suggests five groups of Atlantic cod stocks in the Northwest Atlantic Ocean, namely,

- (1) the southern Newfoundland–St. Pierre Bank stock (3Ps);
- (2) a complex of the southern Grand Bank (3NO) and Gulf of St. Lawrence stocks (4RS3Pn, 4TVn, 4Vn, and 4VsW);

TABLE 2.—Correlation coefficients between normalized spawning stock biomass values for each pair of stocks (see Figure 1 for codes). Significance ($P \leq 0.01$) is indicated by bold italics.

	2J3KL	3NO	3M	3Ps	4RS3Pn	4TVn	4Vn	4VsW	4X	5Z	5Y
2J3KL	1.0										
3NO	0.80	1.0									
3M	0.54	0.32	1.0								
3Ps	0.12	0.19	-0.53	1.0							
4RS3Pn	0.75	0.74	0.22	-0.05	1.0						
4TVn	0.31	0.70	0.21	0.16	0.70	1.0					
4Vn	0.88	0.96	0.25	0.38	0.91	0.91	1.0				
4VsW	0.46	0.76	0.30	0.1	0.76	0.76	0.89	1.0			
4X	0.89	0.83	0.69	0.0	0.76	0.70	0.75	0.81	1.0		
5Z	0.87	0.69	0.52	-0.2	0.85	0.74	0.81	0.75	0.93	1.0	
5Y	0.69	0.55	0.72	0.2	0.47	0.43	0.42	0.40	0.77	0.79	1.0

- (3) the southern Labrador–northern Grand Bank or “northern cod” stock (2J3KL);
- (4) the Georges Bank (5Z) and southern Scotian Shelf–Bay of Fundy stocks (4X);
- (5) the Gulf of Maine (5Y) and Flemish Cap stocks (3M).

The temporal trajectories of the standardized SSB for each of the five stock groups are plotted in Figure 5a–e.

With the exception of the Gulf of Maine–Flemish Cap group, the stock boundaries in groups 4 (Georges Bank plus southern Scotian Shelf–Bay of Fundy) and 2 (Gulf of St. Lawrence divisions and southern Grand Bank) are contiguous in space, lending support to the possibility that these nominal stocks are somehow interrelated. That the Gulf of Maine stock (5Y) was not grouped with group 2 perhaps relates to the shortened time series used in the PCA, as pairwise correlations using the maximum data were slightly higher between 5Y and 5Z (0.79) and 5Y and 4X (0.77) than between 5Y and 3M (0.72).

The SSB trajectories in each group can be summarized as follows:

- (1) The northern cod SSB (2J3KL; Figure 5a) time series initially declined, increased somewhat in the mid-1980s, and then continued to decline.
- (2) The southern Newfoundland–St. Pierre SSB (3Ps; Figure 5b) peaked in 1985, declined to 1994, and then in contrast to all other stocks, increased sharply into 2004, the last year data were collected.
- (3) The most typical pattern in SSB occurs in the Gulf of St. Lawrence–southern Grand Bank group (4RS3Pn, 4TVn, 4VsW, 4Vn, 3NO; Figure 5c). The characteristic features of these stocks are relatively low SSB in the 1970s (with the possible exception of 4Vn), peaks in early to mid-1980s, declines to the mid-1990s, with sustained low values into the 2000s. For the period 1974–1993, Chouinard and Fréchet (1994) pointed out the

similarity in trends between the SSBs (and population biomass) of northern (4RS3Pn) and southern (4TVn) stocks of the Gulf of St. Lawrence, noting the increase in SSBs from the mid-1970s to the mid-1980s with declines thereafter.

- (4) The Georges Bank (5Z)–southern Scotian Shelf–Bay of Fundy (4X) SSB trends appear to be concordant (Figure 5d), exhibiting small peaks in 1990 within a downslide to the mid-1990s and small upturns in abundance thereafter.
- (5) The Gulf of Maine (5Y)–Flemish Cap (3M) SSB time series (Figure 5e) exhibits peaks in 1990 with declines thereafter.

Thus, all stock complexes exhibited peaks in either the mid-1980s (a, b, and c) or the early 1990s (d and e),

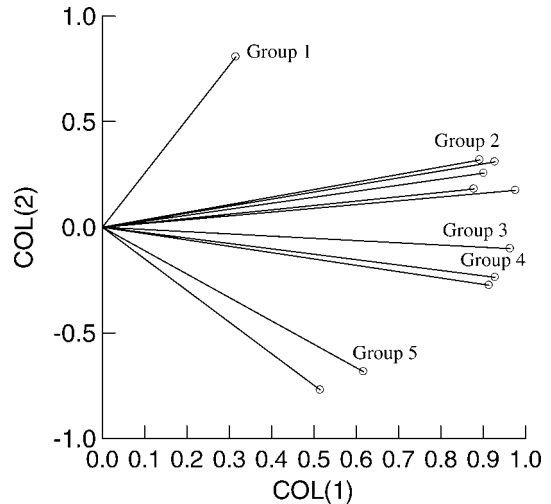


FIGURE 4.—Factor loadings of the standardized spawning stock biomass time series extracted from the subset of years 1983–1999. The “natural” groupings or affinities (reading clockwise) are as follows: (1) 3Ps; (2) 3NO, 4RS3Pn, 4TVn, 4Vn, and 4VsW; (3) 2J3KL; (4) 5Z and 4X; and (5) 5Y and 3M (see Figure 1 for stock codes).

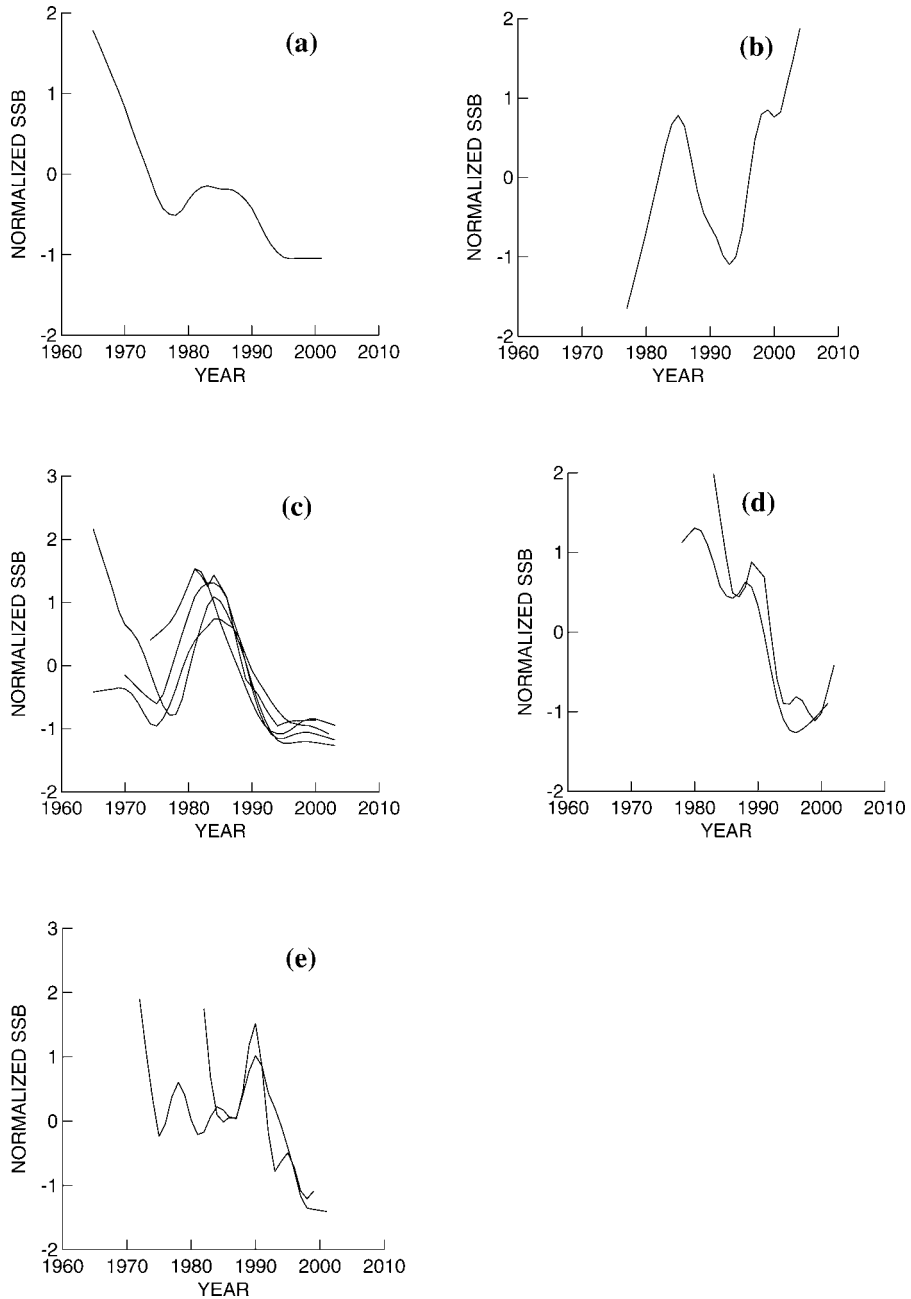


FIGURE 5.—Temporal trajectories of normalized spawning stock biomass (SSB) for five complexes of Atlantic cod in the Northwest Atlantic Ocean identified by principal components analysis (PCA) on a 17-year (reduced) matrix, 1983–1999: (a) southern Labrador–northern Grand Bank or “northern cod” stock (2J3KL), (b) southern Newfoundland–St. Pierre Bank stock (3Ps), (c) southern Grand Bank (3NO) and Gulf of St. Lawrence stocks (4RS3Pn, 4TVn, 4Vn, and 4VsW), (d) southern Scotian Shelf–Bay of Fundy (4X) and Georges Bank (5Z) stocks, and (e) Gulf of Maine (5Y) and Flemish Cap stocks (3M). The ordinates are standard deviation units (see Figure 1 for stock codes).

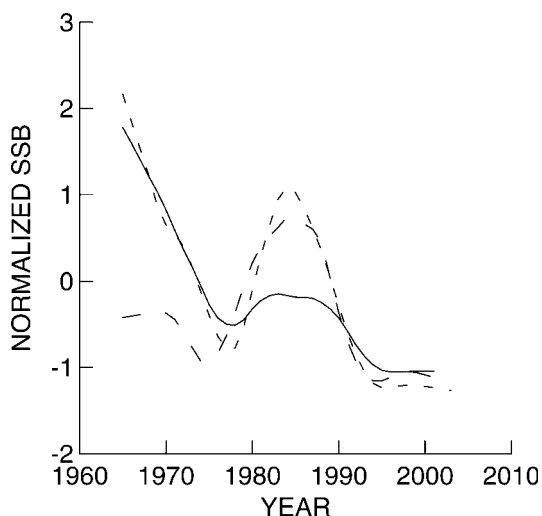


FIGURE 6.—Normalized spawning stock biomass (SSB) trajectories with long time series in complexes (a) (northern cod [2J3KL]; solid line) and (c) (Grand Bank [3NO]; large dashes) in Figure 5 and the Gulf of St. Lawrence stock (4TVn; small dashes).

and all stocks declined after their peaks. The decline was sustained in complexes a, b, and e. In complex d, SSB increased slightly; in complex b, the 3Ps stock increased rapidly.

The PCA clustering resulted in loss of information for the three stocks for which long-time series of data are available: 2J3KL (complex a), 3NO, and 4TVn (within complex c). These three time series are replotted in Figure 6 for further comparison. Initially 3NO and 2J3KL are highly correlated; but from 1980 onward, 4TVn and 3NO became more correlated. In other words, the two southern stocks increased or recovered relatively more into the mid-1980s compared with their historic levels, while the northern stock recovered only minimally. This could be indicative of a southerly shift in production during this time (see deYoung and Rose 1993). However, all three stocks reached equivalent relative levels in SSB from the mid-1990s into the 2000s.

Weight at Age

Changes in Atlantic cod weight at age have been identified in a number of instances. For example, Chouinard and Fréchet (1994) stated that the southern cod stock in the Gulf of St. Lawrence (4TVn) exhibited the most pronounced change in size at age of all the stocks in Canadian waters. Their data for the average weight of cod at age 7 from 1960 to 1992 show that fish in 1992 (~1.2 kg) weighed 45–50% less than in

1975–1979, a period of high weight (~2.3–2.5 kg), and about 10% less than in 1985 (1.4 kg).

Time series of weight at age of Atlantic cod were contoured for four stocks: Georges Bank (5Z), northern Gulf of St. Lawrence (4R53Pn), southern Gulf of St. Lawrence (4TVn), and western Scotian Shelf (4VsW) (Figure 7a–d). As with the changes in relative SSB, the variability in weight at age of these cod stocks also appears to be coherent, particularly among the stocks found in the northern and southern Gulf of St. Lawrence and the eastern Scotian Shelf. The pattern shown by the cod on Georges Bank is not as similar.

To compare the temporal patterns in weight at age for the four stocks shown with the major changes in SSB, vertical lines marking the SSB minima in 1975 and 1992 and the SSB maximum in 1985 were superimposed in Figures 7a through 7d. A coherent pattern emerges showing that after the 1975 minimum there was about a 2-year burst in growth. Following this, weight at age declined sharply until 1985. The increase and decline could be interpreted as a density-dependent change in growth rate. Between 1985 and 1992 when the population was decreasing, size at age continued to decrease, suggesting that an unfavorable environmental signal existed, at least superficially and independent of density. After 1992, the size at age begins to increase, once again reflecting a probable density-dependent response.

Taggart et al. (1994) compared average body condition indices (calculated as gutted weight/length³) for Atlantic cod age-groups (3–5, 6–8, and 9–11 years) in NAFO Divisions 2J, 3K, and 3L from 1979 to 1992. Their data indicate that the condition of these age groups of cod in 2J and 3K was 10–20% poorer in 1992 than in 1986–1988 or 1981, though no particular trends were evident in 3L. Rice (2002) and Lilly et al. (1998a, 1998b) present graphs that show similar changes in weight at age for the northern cod stocks. For example, Lilly et al. (1998b; Figure 6) shows for 2J, 3K, and 3L combined that the weights of 8-, 9-, and 10-year-old cod doubled from 1975 to 1980, declined by 1993 to weights a little above those seen in 1975, and then began to increase to 1997, the last year data were collected. Weights of 4-, 5-, and 6-year-old cod increased from 1971 to 1983, declined to 1992, and increased to 1997, showing an overall doubling in weight during the period. Mean lengths and weight of age-6 cod shown separately for each division (Figure 8; 1979–1997) declined from 1979 to 1992, then increased to 1997. Age-4 fish show more variability among areas and generally declined from 1979 to the early 1990s, with an upswing to 1997. The northern cod (Lilly et al. 1998a, 1998b; Rice 2002) had growth dynamics similar to the cod in what might be called the

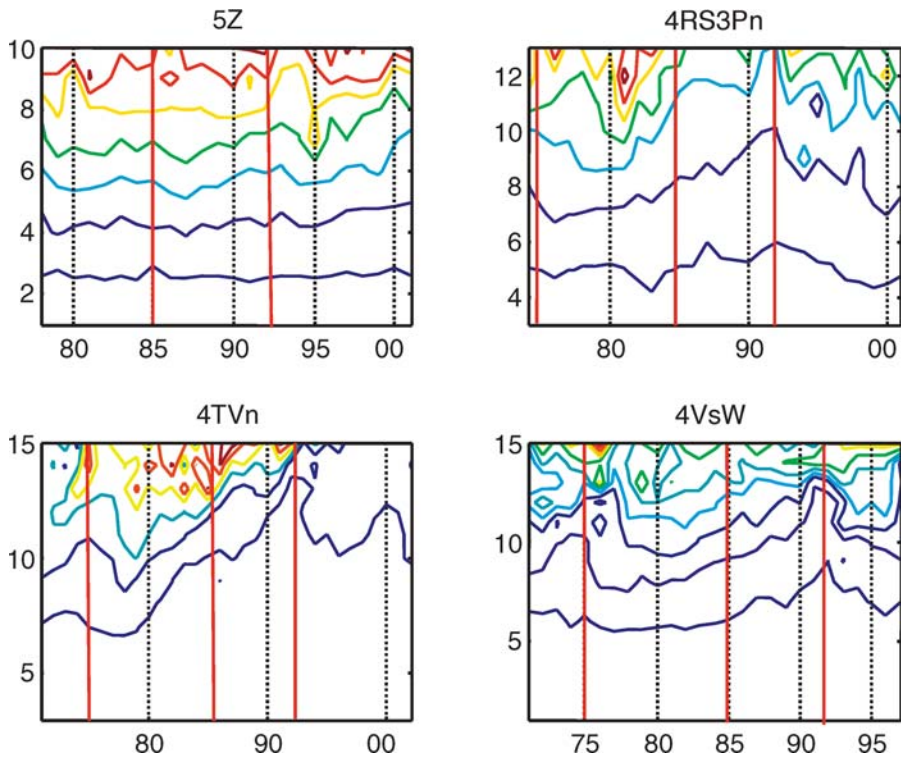


FIGURE 7.—Weight-at-age contours for four stocks of Atlantic cod (see Figure 1 for stock codes). The y-axis is age, the x-axis is year, and the contoured z-axis is weight. An upward movement in a contour indicates a reduction in weight at age. The vertical red bars mark the 1975 and 1992 minima and the 1985 maximum in spawning stock biomass. Because early data are lacking for the 5Z stock, the year scale is different. Contour intervals are in 2-kg units except for the 4RS3Pn stock, which is in 1-kg units.

Laurentian complex (i.e., 3NO, 4RS3Pn, 4TVn, 4VsW, and 4VNMO) for the period 1975–1992.

Frank et al. (1994) present time series of weight at age for age-6 Atlantic cod on Georges Bank (5Z; 1978–1991), western Scotian Shelf (4X; 1948–1991), and eastern Scotian Shelf (4VsW; 1966–1992). Their data show the average weight of age-6 cod on Georges Bank increased from 1978 to 1987, with peaks in 1980–1981 and in 1986–1987, during which time weights were about 20% and 25%, respectively, heavier than in 1991, the last year data were collected. The longer time series of data available for western Scotian Shelf actually suggests an overall increasing weight at age 6 punctuated by notable peaks in 1958–1959, 1970, 1975, and 1980, the average weight in 1980 also being 20% higher than that observed in 1991 and within the average positive trend. The time series for age-6 cod on the eastern Scotian Shelf from 1966 to 1992 shows fish weights were highest at the beginning of the series, declined about 25% until 1973, increased to the previous high by 1977–1982, and thereafter

continuously declined, such that fish weight in 1992 was about 50% less than that in 1978–1982.

Dynamics of SSB, F , and R

The causal mechanisms that drive the dynamics illustrated in Figures 5, 6, and 7 are of central interest. Most authors describe the declines as a result of overfishing while acknowledging at least some environmental forcing (see, e.g., Sinclair and Murawski 1997; Myers et al. 1996). As data accumulated, reductions in growth, increases in natural mortality, and a lack of recovery despite reduced fishing, accompanied by historically low stock size, point to the operation of a strong negative environmental signal affecting the cod stocks.

The problem can be reduced to separating the environmental forcing from fishing mortality. A plausible model is that environmental forcing modulates the abundance of the fish stocks. However, fishing mortality is superimposed on the environmental forcing to either enhance or suppress the positive (density-dependent factors) or negative effects of fishing. In

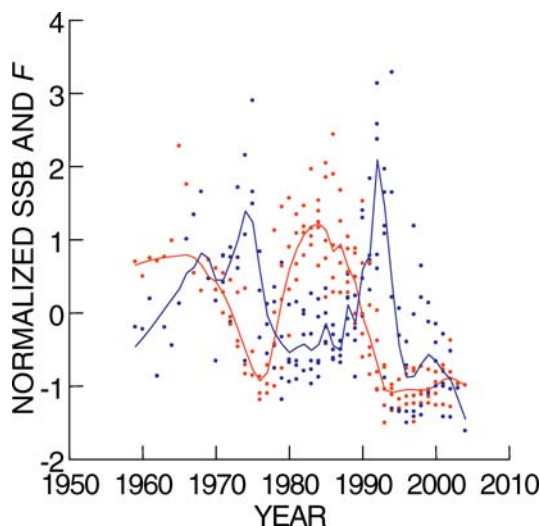


FIGURE 8.—Ensemble of normalized spawning stock biomass (SSB; red circles) and fishing mortality (F ; blue circles) data from nominal stocks 3NO, 4TVn, 4VsW, 4X, and 5Z (see Figure 1). LOWESS smoothers (tension = 0.1) are fit through the data (red and blue lines).

other words, if the environment is favorable, intense fishing mortality may not reduce the stock (this is evidently the case in the so-called gadoid outburst—North Sea Atlantic cod increased in abundance for a decade despite intense and increasing fishing mortality [Rothschild 1998]). On the other hand, if environmental conditions are not favorable, then fishing mortality will only accelerate the effects of the environment.

Separating environmental forcing from fishing mortality continues to be a major challenge, which is amplified by a lack of data on relevant temporal and spatial scales, the difficulty in separating recruitment and SSB forcing, and the nonlinear nature of fish stock dynamics. In the case of the Atlantic cod there is an additional layer of complexity that relates to the fact that the linkage between SSB and fishing mortality for various individual nominal stocks may be estimated incorrectly because the nominal stocks are not closed systems.

While the full treatment of the dynamics of the stock units is beyond the scope of this analysis, it is worth developing some heuristic observations. In this context, ensemble trajectories for most stocks are developed. These are based on time series of SSB, F , and R data (ICES 2005; K. Brander, International Council for the Exploration of the Sea, personal communication). Examination of the data set reveals that the data for 3NO, 4TVn, 4VsW, 4X, and 5Z nominal stocks are reasonably coherent. The normalized SSB and F data for these stocks are plotted in Figure 8. A LOWESS

smoother is fit through the data (tension = 0.1). The smoothed curves are plotted in phase space in Figure 9; three different stanzas are used to remove the visual overlap in the trajectories.

The smoothed curves might be thought of as the dynamics of the SSB- F interaction. The SSB and F curves appear to be negatively correlated and have, as expected, different phases. The most interesting part of the dynamics is in the 1985–1989 period of time when SSB began to decline during a period of low fishing mortality. The simplest explanation is that the cod population continued to increase in abundance in the early 1980s until it reached its carrying capacity and then began to decrease. Because F was relatively low, the decrease in SSB can be interpreted as a response to an environmental signal. In 1989 the decline in SSB per unit F decreased until 1992, at which time F and SSB reached their lowest levels. Whether the increase in fishing mortality was the result of removing a more or less fixed quantity of fish from a rapidly declining stock or whether the increasing fishing mortality actually forced the decline is not known. The time-phase difference between the SSB and F curves is important. Sinclair (1996), in examining individual stocks, noted that F could increase after SSB decreased. He reasoned that this was the result of increased fishing to attain quotas. However, a simpler explanation is that nominal effort remained relatively constant, the stock declined faster than the change in nominal effort, and, as a result, the stock decline caused an increase in fishing mortality.

Part of the explanation of the dynamics needs to take into account recruitment dynamics. These are plotted in Figure 10 where the dynamics of SSB and R are contrasted. Figure 10 can be interpreted as elevated recruitment beginning in the early 1970s and contributing to the buildup of spawning stock biomass, which reached its peak in 1985. However, as the SSB continued to build in the late 1970s and early 1980s, recruitment leveled, possibly as a density-dependent response (as in Ricker or Beverton–Holt recruitment–stock theory when SSB is at a relatively high level). A pulse of recruitment initiating in 1985 probably contributed to sustaining the right-hand shoulder of the SSB curve after 1985. It is not known whether the post-1985 decline in SSB contributed to the increase in recruitment. Nevertheless, it is clear from Figure 8 that this pulse of recruitment essentially did not enter the population. The pre-1985 buildup in the SSB occurred under relatively low fishing mortality, while the lack of buildup post-1985 was in a setting of high fishing mortality.

These data serve to emphasize that the interactions among SSB, R , and F are indeed complicated,

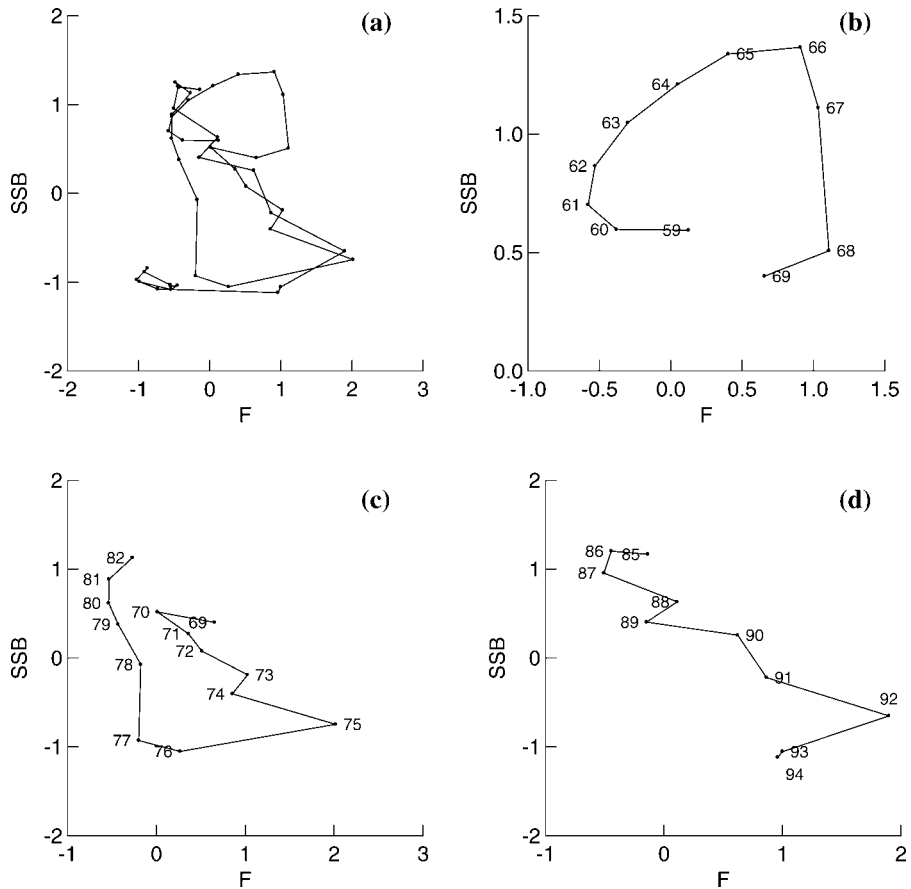


FIGURE 9.—Trajectories from Figure 8 plotted in phase space (a). For clarity, individual years (represented by two-digit numbers) are identified in panels (b), (c), and (d), and some points are omitted.

particularly when there is the possibility of multiple interacting stocks, predators (Atlantic cod), possibly “overfishing” prey (Atlantic herring *Clupea harengus*, capelin *Mallotus villosus*, and euphausiids), that operate both on the adult fish and recruitment time-and-space scales (see Hanson and Chouinard 2002; Rose and O’Driscoll 2002).

Chouinard and Fréchet (1994) came to a similar conclusion regarding the declines of both the southern (4TVn) and northern (4RS3Pn) cod stocks in the Gulf of St. Lawrence, based on their observations of SSB and F (ages 7 and older) from 1950 to 1993 (4TVn) and from 1974 to 1993 (4RS3Pn), respectively. For the northern cod stock (2J3KL), the time series of SSB (age 6 and older) and F (ages 5, 7, 9, 11, and 13) from 1973 to 1992 provided in Taggart et al. (1994) also show that SSB declined beginning in 1989, with dramatic increases in F from 1988 to 1991 followed by a sharp decline in 1992.

Discussion

The SSB and weight-at-age data suggest that the nominal Atlantic cod stocks have common linkages. The coherence in SSBs supports homogeneity among most nominal stocks. There are four striking characteristics of these data: (1) the temporally coherent SSB dynamics among the stocks in what might be called the Laurentian complex—the stocks occupying the Gulf of St. Lawrence, the eastern Scotian Shelf, and the southern Grand Bank; (2) the presence in all stocks over the entire range of the nominal populations of a peak in SSB in 1985 and a sharp depression by 1992 (except for 3Ps); (3) the sharp post-1992 increase in the southern Newfoundland–St. Pierre Bank stock (the mechanisms associated with the difference between the southern Newfoundland–St. Pierre stock are beyond the scope of this study); and (4) the coherent changes in weight at age, at least for the northern Gulf of St. Lawrence (3Pn4RS), southern Gulf of St. Lawrence (4TVn), and the eastern Scotian Shelf (4VSW) stocks.

As indicated in the introduction, either the nominal stocks mix to a greater extent than previously thought or some environmental influence is pervasive over a very large area, affecting most stocks simultaneously. These contrasting, purposely rhetorical conjectures, have important implications in understanding the causality of the dynamic changes in Atlantic cod populations in the Northwest Atlantic Ocean. Extant explanations of the dynamic changes in cod stocks are based on linking particular nominal stock-specific causes with nominal-stock-specific effects. But to what extent are the explanations dependent upon the assumed stock structure? Any change in assumed stock structure implies a need to reconsider linkages between SSB, F , and recruitment.

There are basically two types of studies that relate to stock structure: (1) those that infer stock structure from dynamic changes such as changes in SSB or recruitment patterns and (2) those that infer stock structure from genetic analyses. These approaches, while having different end points, are not necessarily inconsistent. The inferential approaches yield information on a lack of homogeneity in the dynamics of the nominal populations taken as a whole. The genetic approaches attempt to underpin the inferential approaches to define interbreeding units both at the time of reproduction and at subsequent times when the interbreeding units may be intermixed to varying degrees.

The coherence among SSB trajectories and coupled changes in growth rates leads to the conjecture of fewer and spatially more extensive stocks. However, genetic studies tend to imply that there may be more stocks (in this case, genetically distinct stocks) with ranges that are less extensive than the nominal NAFO stocks. In particular, the genetic studies tend to differentiate more inshore and offshore units than do the inferential studies.

The published inferential studies on stock structure are not inconsistent with the present analysis. The paper by Sinclair (1996) is the most recent and comprehensive of these inasmuch as Sinclair considered all nominal stocks. Sinclair's (1996) paper is more a consideration of each stock rather than a consideration of a "megastock" and how it can be partitioned into management units, genetic units or subunits, or both. Although, Sinclair (1996) considered adult biomass, recruitment, prerecruitment survival, weight at age, and fishing mortality, his assessment of stock differences focused on recruitment. Recruitment time series are difficult to use to discriminate among possible stocks. Recruitment time series are challenging to interpret statistically because they contain internal nonlinearities that challenge stationarity assumptions. The differencing and detrending used by

several investigators are respectively high- and low-pass filters that suppress the decadal variability that is most evident in the cod time series. The SSB is a natural filter that integrates or averages recruitment, which is notoriously variable. It is for these reasons that SSB seems to be a better stock differentiator than recruitment.

Continuing with inferential studies that focus more on single nominal stocks, Chouinard and Fréchet (1994) recognized the correlation between the dynamic properties in the northern and southern Gulf of St. Lawrence. A complex structure for northern Atlantic cod is described by deYoung and Rose (1993). Smedbol and Wroblewski (2002) developed the notion of "metapopulations" within the range of *northern cod*. Tagging results pertain not only to the southwestern stocks but also to exchanges between the northern cod and 3Ps cod. Templeman (1962) used tagging results to identify the NAFO areas. Templeman (1981) also used vertebral numbers to identify stock units (the vertebral counts are probably related to temperature). Hunt et al. (1998) reviewed tag returns for cod tagged and released on Georges Bank (5Zj) and on adjacent Browns Bank (4Xp). They found clear evidence of cod interchange between these areas, with a net movement from Georges Bank to southern Nova Scotia. Cod tagged on Browns Bank also moved to inshore areas of Nova Scotia, including the Bay of Fundy. They observed less movement between Georges Bank (5Z) and the Gulf of Maine (5Y). Myers et al. (1995) found that the correlation length scale for recruitment was about 500 km, which is not inconsistent with the groupings depicted in Figures 4 and 5.

From the point of view of genetic analysis, Ruzzante et al. (1998) examined the genetic affinities of Atlantic cod from 14 locales in the Northwest Atlantic Ocean based on five microsatellite DNA loci and related their findings to the results of previous tagging and biological studies. Their samples ranged from NAFO Division 2J (southern Labrador) to 5Z (Georges Bank) and were collected variously from 1992 to 1995. Though they found that genetic differences among most of the populations were small and genetic distances quite variable, they were able to suggest population structuring at basin-level scales. Offshore samples from 2J3K were genetically distinct from those from offshore 3L3N, both of which were also distinct from inshore samples (Trinity Bay) in 3L, all collected in winter. Cod from the Flemish Bank were genetically distinct from other locations. Genetic divergence patterns and consideration of other data led the authors to conclude that cod on Georges Bank (5Z), the Bay of Fundy and Browns Bank (4X), and locales farther east on the Scotian Bank and south of

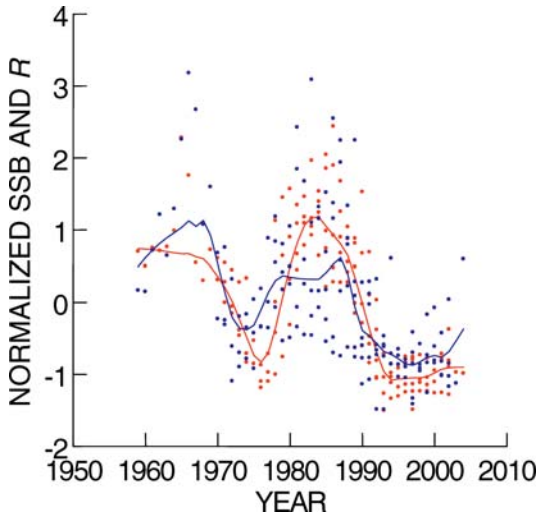


FIGURE 10.—Ensemble of spawning stock biomass (SSB; red circles) and recruitment (R ; blue circles) data from nominal stocks 3NO, 4TVn, 4VsW, 4X, and 5Z. LOWESS smoothers (tension = 0.1) are fit through the data (red and blue lines).

the Laurentian Channel (Scatarie Bank, 4Vn; Western Bank, 4W; Banquereau Bank, 4Vs) formed three separate stocks. They speculated that cod sampled inshore in Placentia Bay (3Ps) seasonally intermingled with cod migrants from offshore areas of 3Ps (St. Pierre and Burgeo banks) and locales from the west and northeast. The inshore movements of offshore cod to feed in summer appeared to mitigate interpretations of stock distinctness owing to nonwinter sampling times in some areas.

Beacham et al. (2002) extended the genetic analysis of Atlantic cod from 14 locales around Newfoundland and Labrador using additional microsatellite loci and the pantophysin locus. From 1996 to 2000 (but mostly 1998–1999), they sampled inshore areas during the spring spawning season and offshore areas in the autumn and confined their analyses to fish with ripe, running, or partly spent gonads. They confirmed the previous results of Ruzzante et al. (1998), which showed that the most northern inshore and offshore cod populations off the northeast coast of Newfoundland were distinct and suggested that the offshore cod in 2J3KL consists of three spawning stocks. They found no genetic differentiation between inshore cod from Trinity Bay and the northern Grand Bank (3L) and also confirmed the distinctiveness of the Flemish Cap cod stock. Finally, they found no evidence to suggest that the abundance of cod in Placentia Bay (3Ps) was the result of postulated inshore migration of offshore stocks from 2J3KL and concluded that it was due to

local recruitment. Samples from four locales in 3Ps—Burgeo Bank, Halibut Channel, Fortune Bay, and Placentia Bay—showed no consistent genetic differences and were deemed a single spawning population. Comparisons also showed that cod from Placentia Bay did not differ significantly from cod sampled from Conception or Trinity bays. These authors concluded that genetic isolation by distance accounted for the patterns in genetic differentiation they observed, in that cod from nearby locations were more similar to each other than to those in more distant locales.

All of the discussions of stock structure tend to be based on the assumption that the geographical bounds of inferential or genetic stocks are constant. In a number of stocks the range of the stock is positively and dramatically correlated with stock abundance (Rothschild 2000). Thus, the common peak in SSB in about 1985 could result from common environmental forcing on all stocks or the expansion of a few nominal stocks into the range of other nominal stocks.

The discussion of the state of knowledge on inferential stocks and genetic stocks continues to support the notion of fewer inferential nominal stocks in the Northwest Atlantic Ocean than are indicated in Table 1. At the same time, the genetic studies imply that any reconfiguration of stock structure needs to be modulated by new information on the genetic structure of Atlantic cod.

The discussion of stock structure sets the stage for considering the remarkable increase in SSB in the early 1980s and decreases in the late 1980s. As the stocks increased in the early 1980s individual fish growth declined sharply. This is easily explained as density-dependent growth. However, as the stocks declined after 1985 the growth rate continued to decline. A simple basic explanation is that the cod stocks experienced a positive environmental signal before 1985 and a negative signal after 1985.

What are these signals and how are they modulated by or related to the effect of fishing? There are differing points of view. To oversimplify, some investigators believe that the change in Atlantic cod growth is the effect of food limitation. Others seem to say that the changes in growth are the effect of temperature changes on cod per se. Yet, others suggest or imply that temperature had changed in the entire ecosystem and this is reflected in the growth of cod. In fact, the changes are probably the result of a mixture of these causes and the different points of view represent shades of meaning.

Chouinard and Fréchet (1994) related differences in weight to density-dependence, citing small year-classes associated with the peak weight years and large year-classes with low-weight years. In a later paper,

Chouinard and Swain (2002) examined weight at age and condition relative to depth, water temperature, and the population density of Atlantic cod (30–60 cm in length) on their feeding grounds in the Gulf of St. Lawrence. They concluded that at high population densities, more fish as a result of competition occupied colder (intermediate depth) less favorable habitats and exhibited poor condition. During low population densities, more fish occupied the favorable habitats and fish condition was high in both shallow, favorable habitats and in the less favorable ones. They attributed strong declines in length-at-age of cod occupying intermediate depths during the 1990s to unusually cold water temperatures. It is important to note that variability in growth is particularly noticeable in small fish, yet the declines in growth appear to affect larger fish as well.

Frank et al. (1994) linked the changes in Atlantic cod weights on the eastern Scotian Shelf to changes in near-bottom summer temperatures. These temperatures from 1970 to 1991 are illustrated by Page and Losier (1994; Figure 7), which showed increasing temperatures from 1973 to 1977–1982 and declines thereafter to 1991. Data for the western shelf seem open for interpretation. Page and Losier's (1994; Figure 7) data for the western Scotian Shelf area showed declines in water temperature from 1970–1971 to 1975 and a slow warming trend through 1990 that is perhaps linked to the gradual increase in the lowest weights of age-6 fish observed in this time period. However, the lack of correlation between water temperature trends and declines in peak weights may be a result of the effects of the actual water temperature on growth physiology. Taylor (1958) found a linear relationship between the logarithmic value of the von Bertalanffy growth parameter (k) and that of water temperature estimated for cod populations, indicating that the effect of temperature difference is related to the temperature level in explaining cod growth. Brander (1995) obtained reasonable predictions of weight at age of 4-year-old cod on Faroe Plateau and West Greenland, respectively, in relation to lifetime average local water temperatures.

Sinclair et al. (2002) argued that declines in the length at age of Atlantic cod in the late 1970s and early 1980s observed in the southern Gulf of St. Lawrence were primarily a result of size-selective fishing mortality and density-dependence (not temperature), both of which operated to increase growth in the earlier period and decrease growth in the later period. They attributed the continuation of slow fish growth after the fishing moratorium was imposed in 1993 to the depression of growth potential by size selection, implying that slow-growing fish had been at a selective

advantage. The models that Sinclair et al. (2002) constructed used back-calculated lengths at age of cohorts to estimate the effects of size-selective fishing, but omitted direct estimates of fishing mortality on cohorts, which would seem a more direct method of estimating fishing pressure.

The image of the negative influence of growth on Atlantic cod populations is enhanced by large increases in natural mortality (see Shelton et al. 2006). Significant depressions in condition indices are also evident (Lambert and Dutil 1997). Increases in natural mortality may relate to increased predation by gray seals *Halichoerus grypus* on cod at least in the southern Gulf of St. Lawrence over the period 1975–1995 (Chouinard et al. 2005).

Shelton et al. (2006) attributed the warmer ocean bottom temperatures experienced by the Atlantic cod stocks on Flemish Cap (3M), the western Scotian Shelf–Bay of Fundy (4X), Georges Bank (5Z), and Gulf of Maine (5Y) to be related to their greater productivity, greater persistence, and more gradual declines than for stocks inhabiting colder waters. However, according to Petrie et al. (2006), bottom temperature in 4X, 4W, 4Vn, and 4Vs all declined sharply in the 1985–1992 period. Sharp declines in temperature were also evident in the 200–300-m layer of Cabot Strait. An almost more striking variable reported by Petrie et al. (2006) is the decline of the stratification index during the 1985–1992 period.

Garrod and Schumacher (1994) compiled Atlantic cod landings for several decades from all North Atlantic Ocean stocks and concluded that the widespread concordances in landings and their shear magnitudes of change had to be reflective of changing environmental conditions irrespective of fishing effort. They showed that the trend in combined northeastern Arctic and Icelandic cod landings was well matched with average surface air temperatures in the northern hemisphere from 1900 to the mid-1970s.

Taking yet another point of view emphasizing the role of temperature, Campana et al. (1996) stated: “the question is not whether temperature has a major influence on cod growth in time and space, the question is how large will its effect be?” This is somewhat answerable by inspecting, for example, the work of Björnsson and Steinarsson (2002). Björnsson and Steinarsson's (2002) work on Icelandic cod suggests that relative temperature changes of about 2°C might not have an important effect on growth of food-satiated fish. The interaction between Atlantic cod abundance and cod growth and temperature (in addition to a host of other environmental variables) remains unresolved. This is because while temperature obviously affects growth, it is also confounded with

activity. In a natural environment, the relative abundance of predator and prey is related to the activity required to acquire the ration, possibly overriding a temperature effect. It is likely that the temperature effect is more important in terms of it influencing the accumulation of energy along the various pathways in the food web rather than on growth of cod per se. The effects of temperature on fish growth expressed as weight at age are most pronounced on young fish. The effect of temperature and ration on the spawning biomass of fish may be underestimated by considering only the somatic weight of the fish stocks. As discussed by Rothschild (1986), considerable variability in growth of mature fish is expressed in variations in reproductive capacity, rather than in variations in somatic biomass.

The linkages between temperature and various components of the food web are very complicated. For example, time series presented by Zwanenburg et al. (2002) for the eastern (4W) and western Scotian Shelf (4) indicate biotic changes linked to cooling water temperatures. In the period 1991–1994 compared with 1961–1969, the phytoplankton color index intensified, the abundance of krill declined, and the prevalence of coldwater *Calanus* spp. increased while seasonal shifts were also seen in which phytoplankton, krill, and copepod abundance peaked a month earlier in the spring. Bottom temperatures on the eastern Scotian Shelf expressed in 5-year running averages were 0.2–0.5°C above average from 1976 to 1983 and 0.6–0.8°C below average from 1986 to 1996. This decline in water temperature was tracked by a 30% decline in mean size (length) of age-7 haddock *Melanogrammus aeglefinus* and appeared linked to much increased catch rates of the coldwater snow crab *Chionoecetes opilio* on Misaine and Banquereau banks in Division 4Vs. The shift in cod from spring spawning to autumn spawning on the Scotian Shelf must be a major perturbation and must have resulted from a change in environmental conditions.

Frank et al. (1996) related the strong correlation in time series of capelin abundance in Divisions 4VW and 4T to abnormally low water temperatures. Biomass estimates from fall surveys from 1971 to 1995 in 4T show exponential increases in the period 1985–1995, when extreme anomalies occurred. During this time, capelin also appeared on Flemish Cap in conjunction with similar conditions. Other coldwater species that appeared on the Scotian Shelf during this abnormal period were the Arctic–boreal Greenland halibut *Reinhardtius hippoglossoides* and checker eelpout *Lycodes vahliei*.

The use of the interacting dynamics of Atlantic cod and its prey and predators in interpreting stock trends is

emerging. Capelin, an important forage item for many cod stocks, seems particularly important (see Rose and O'Driscoll 2002). In the northern region, capelin year-class strength increased and standard length decreased substantially (Carscadden et al. 2001; Figure 6) as the cod population declined in the late 1980s. In the Laurentian region, the capelin stock increased by 100-fold as the cod began to decline in the mid-1980s (Carscadden et al. 2001; Figure 9). Northern sand lance *Ammodytes dubius*, another important forage fish for cod, were abundant only before and after cod peaked in abundance in the mid-1980s (Zwanenburg et al. 2002). Worm and Myers (2003) examined the relationship between cod and pandalid shrimp biomass in the North Atlantic and concluded that increase in shrimp biomass was related to release of predation pressure by declining cod stocks and not to a regime-shift response to climate variability. Swain and Sinclair (2000) point to the important role that pelagic fish may have in contributing to counterintuitive dynamics of cod in the southern Gulf of St. Lawrence considering the role that the pelagic fish might have in reducing the recruitment of cod in this region. They examined the relationship between cod recruit survival, calculated as the ratio of recruits (R) to spawning stock biomass (SSB), and biomass of herring (age 2 and older) and of Atlantic mackerel *Scomber scombrus* during the period 1960–1995. The use of ratios such as R :SSB as indicators of productivity is complicated because bias can be introduced since the relation between R and SSB is not generally linear. Hence the R :SSB ratio is not constant but varies as a function of SSB. Swain and Sinclair (2000) suggest that the reduced biomasses of these pelagic fish and cod contributed to the recruitment success (it is important to recognize that a high level of R :SSB is not equivalent to a high R [see Myers et al. 1995] for cod in the mid-1970s but reduced cod recruit survival in the 1990s and 1950s). These events were due to high pelagic–low cod biomass and low pelagic–high cod biomass, respectively. However, Myers et al. (1997) found no differences in recruitment levels of 1-, 2-, and 3-year-old cod between 1992 or 1993 compared with those in previous years for Labrador and northeastern Newfoundland, St. Pierre Bank, the Gulf of St. Lawrence, or eastern Scotian Shelf stocks. They attributed the lower recruitment of age-3 cod to the southern Grand Bank stock at the time of the stock collapse (1993) compared with earlier years to foreign fishing during the early 1990s, which targeted young cod (ages 2 and 3) in the portion of the stock outside Canadian waters. They attributed stock collapses to overfishing that occurred due to underestimated fishing mortality levels caused by high discarding rates of young cod and misreporting of

catches of older fish. These factors resulted in overestimates of stock abundances determined by virtual population analysis (VPA) during the critical years from 1988 to 1991. Myers et al. (1997) documented how VPA estimates of F on young ages increased with subsequent assessments, and, indeed, the revised F s and SSBs analyzed here incorporate the magnitude of these changes.

The dynamic nature of the changes in diet (involving changes in capelin in the north and herring and invertebrates in the south; e.g., Hanson and Chouinard 2002) and the apparent lack of reversibility in the system are reminiscent of dynamic systems that are deterministically coupled but at the same time uncorrelated. The disappearance of capelin in the north and replacement of invertebrates by herring in the south certainly seems to be an important indicator of environmental change at lower trophic levels. As pointed out earlier the increase in herring in diets was coincident with both a decline in recruitment as might be caused by herring grazing on cod eggs. However, it is more difficult to explain the failure of cod growth to increase when feeding on seemingly more nutritious herring. The simplest explanation appears to be that the energetic advantage of feeding on herring is not as good as their feeding on invertebrates.

The influence of fishing mortality is important to the analysis. The stocks increased under favorable conditions from 1975 to 1985. The 1975–1985 period was one of relatively low fishing mortality. By 1985 the Atlantic cod stocks reached their carrying capacity and began to decline precipitously. This decline was also initiated at a time when fishing mortality was relatively low. Fishing mortality did increase sharply after the decline began, and it is conceivable that this resulted from the stock's declining at a faster rate than any change in nominal effort. The fact that growth declined and natural mortality increased (see Shelton et al. 2006), possibly as a result of increased gray seal predation (Chouinard et al. 2005), low or poor food availability, or both after 1985, strengthens the notion that the decline was caused by a negative environmental signal rather than fishing. The remarkable lack of recovery of the cod stocks under a fishing moratorium coupled with the biological nonfishery induced changes in growth rates unrelated to the fishery and changes in the ecosystem suggests that the effects of fishing that exist may not be as important as previously thought.

While most authors emphasize the role of fishing in the decline of the Atlantic cod, substantial basinwide changes in the Northwest Atlantic Ocean environment are well known. Among these, the Great Salinity Anomalies (GSA) are particularly striking. The GSAs are large masses of low-salinity, low-temperature water

that are evidently advected over the surface of the North Atlantic on decadal time scales. Belkin et al. (1998) reviewed the GSA of the 1970s and the GSA of the 1980s. The fresh, cold water associated with the GSA of the 1970s appeared off the Canadian Maritimes in the early 1970s. The fresh, cold water that was associated with the GSA of the 1980s appeared off the Canadian Maritimes in the mid-1980s. The lowest temperatures persisted in Newfoundland and Labrador waters into the early 1990s. Colbourne (2004) observed that the reduction of salinity in the 1990s was comparable in magnitude to the GSA of the 1970s (see also Belkin 2004; Greene and Pershing 2007). It is tempting to speculate that the dynamics of the Atlantic cod populations were coupled in some way to these anomalies. Of course, as Colbourne (2004) points out, the coupling would be nonlinear, so conventional statistical tests would not be informative.

In summary, this study suggests that Atlantic cod exist in complexes (relative to the traditional nominal stock boundaries used by Shelton et al. 2006). These complexes are responding to signals that are operating over most of the range of the cod in the Northwest Atlantic Ocean. That these are environmental signals that operate over wide areas is reflected by the fact that the major 1975–1992 perturbation in SSB (increase and decrease) appears to have been initiated during a period of low fishing mortality. The decreases in SSB are coupled with reduced growth and increased natural mortality. An intriguing aspect of the underlying causation of nominal stock–environmental interaction is that the ranges of the nominal stocks may not be static but that they expand and contract over large areas as the respective stock units increase and decrease in abundance. It appears that both the increase and decline of the cod, particularly the latter, are the result of a complex interaction with the environment, but this interaction must be driven by other complex factors (e.g., the influence of stratification on the eastern Scotian Shelf) that have yet to be resolved. It appears that the food web on which Atlantic cod rely differs over the range of the cod stocks, and yet the distinctly different components of the “traditional” food webs were all affected in a negative way at the same time. This suggests that the negative characteristic of the signal was associated with the dynamics of the plankton community.

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