Abstract.–A population model incorporating temporal and spatial detail revealed that the majority of eastern Georges Bank haddock, *Melanogrammus aeglefinus,* were found on the Canadian side of the Canada-U.S. boundary. During spring they were more widespread across the top of the bank and subsequently migrated eastward so that by fall almost all haddock were found in the deeper waters on the Canadian side. There is a return migration to the top of the bank during the winter. The seasonal distribution and migration of haddock has remained stable since 1985 and migration rates do not appear to be related to the observed range of abundance. The distribution pattern since 1985 appears similar to that observed between 1972 and 1984. In contrast, during 1963–71 haddock were more widespread throughout the area in both spring and fall. Abundance of haddock in the Georges Bank and Gulf of Maine area was exceptionally high in the earlier period, and haddock from the spawning component in the Great South Channel area may have accounted for a greater augmentation to the eastern Georges Bank population. In implementing strategies for managing this transboundary resource, scientists will need to evaluate the nature of haddock distributions in order, in turn, to evaluate the implications of their strategies.

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Movements of haddock, *Melanogrammus aeglefinus*, on eastern Georges Bank determined from a population model incorporating temporal and spatial detail

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The haddock, *Melanogrammus aeglefinus*, on Georges Bank have supported a commercial fishery since the early 1900s. Since 1977, with the extension of jurisdiction by coastal states, only Canada and the United States have conducted haddock fisheries on Georges Bank. In October 1984 the International Court of Justice (ICJ) established a maritime boundary between Canada and the United States in the Gulf of Maine area. Subsequently, fishing by Canada and the United States on Georges Bank has been restricted to these respective jurisdictions (Fig. 1). The new boundary line, referred to as the ICJ line in our study, lies over an established grid of statistical unit areas that has been used to summarize landings data since the 1930s. These areas have been based on, among other factors, considerations of biological stock structure (principally cod, *Gadus morhua*, and haddock), political boundaries, and practicalities of data collection (Halliday and Pinhorn, 1990). Aggregates of unit areas are used to determine the boundaries of fisheries "management units"—geographic areas defined for regulatory purposes.

Prior to establishment of the maritime boundary, regulation of the haddock fishery was based on a management unit encompassing all of subarea 5, although it was recognized that this unit included at least two major spawning concentrations (Walford, 1938; Bigelow and Schroeder, 1953). Historical evidence indicates that the most important spawning concentration was on the eastern part of Georges Bank whereas the spawning was variable among years over the Great South Channel and the southern part of the bank (Walford, 1938). Tagging studies and other biological data have shown that little mixing occurs between haddock on Georges Bank and those in surrounding areas, e.g. 4X (Fig. 1), which is situated north and east of Georges Bank (Schuck and Arnold, 1951; Grosslein, 1962; Clark et al., 1982). Tagging studies have also indicated limited east–west movement within subdivision 5Ze, which is the eastern portion of division 5Z and includes unit areas g, h, j, m, n, and o (Fig. 1), as only about 5% of returns from haddock tagged off Cape Cod were reported from areas east of 68°W and 95% of returns from haddock tagged on eastern Georges Bank were reported from areas east of 69°W (Grosslein, 1962). In 1990, Canada adopted unit areas 5Zj and 5Zm,

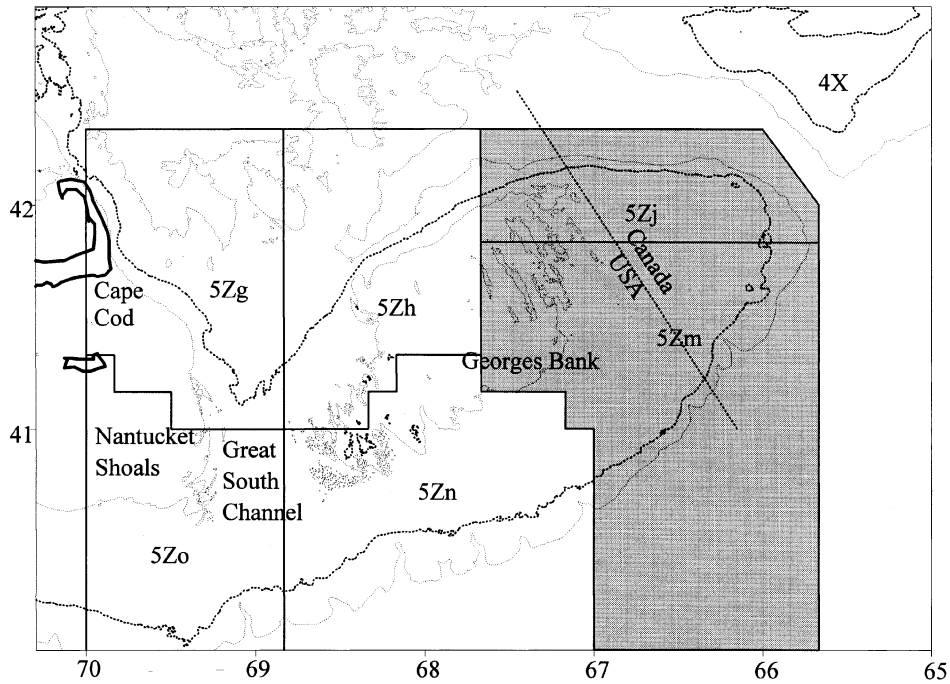

Figure 1

Fisheries statistical unit areas in NAFO subdivision 5Ze (includes 5Zg,h,j,m,n,o). The Canadian management unit for haddock comprises unit areas 5Zj and 5Zm (shaded).

eastern Georges Bank, as a management unit. Gavaris and Van Eeckhaute (1990) summarized the considerations on which the management unit boundaries are based. The ICJ line bisects this management unit and imposes additional complexity for resource management considerations in the absence of consistent practices by the two jurisdictions. A prerequisite to investigation of harvest strategies for the transboundary haddock resource is an understanding of haddock distribution and migration on eastern Georges Bank in relation to the ICJ line.

Earlier studies have described spatial distribution of Georges Bank haddock and patterns in relation to season, topography, time, and hydrographic conditions (Colton, 1955; Grosslein, 1962; Overholtz, 1985, 1987). Our study focuses on the relative distribution and net migration rates of haddock within the 5Zj,m Canadian management unit in relation to the ICJ line. Our objectives were to describe the relative abundance of haddock on the Canadian and U.S. sides of eastern Georges Bank since 1963 and to estimate rates of migration for haddock across the ICJ line since 1985 when fishery statistics first became available at a resolution sufficient to be summarized with respect to the ICJ line. These results are necessary for the evaluation of the effects of regulatory measures, whether unilateral or bilateral.

Methods

Relative abundance

Results from research vessel bottom trawl surveys were used to estimate haddock abundance on the Canadian and U.S. sides of the ICJ line on eastern Georges Bank and to subsequently derive ratios of abundance on the Canadian side to total 5Zj,m abundance. Annual surveys have been conducted by the U.S. National Marine Fisheries Service (NMFS) during the fall since 1963 and during the spring since 1968 and by the Canadian Department of Fisheries and Oceans (DFO) during the spring since 1986. Ratios of relative abundance were calculated to 1993 for the NMFS surveys and to 1994 for the DFO surveys, but survey data beyond those years were used to illustrate haddock distribution patterns as the data became available. All surveys used a stratified random design but the strata boundaries differed (Fig. 2). The strata boundaries for the DFO survey were modified to incorporate the ICJ line as a border in 1987. The results from the DFO survey in 1986, which used a different strata design, were not considered in our study owing to the complication that such a design would introduce and to the limited additional information that would result.

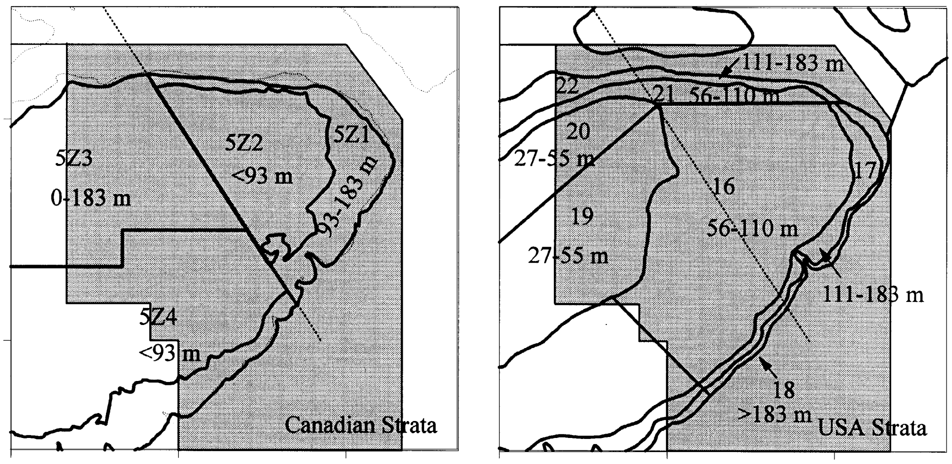

Figure 2

Strata for DFO and NMFS bottom trawl surveys with depth ranges. Several NMFS strata are bisected by the Canada-U.S. boundary line. Some strata for both countries are bisected by the 5Zj and 5Zm unit area boundaries.

The DFO surveys have been conducted by the RV *Alfred Needler* and for one year, by its sister ship, the RV *Wilfred Templeman*, with a Western IIA trawl. The NMFS surveys have been conducted by the RV *Albatross IV* and the RV *Delaware II* with a BMV door until 1984 and a polyvalent door subsequently. A further gear alteration occurred with the replacement of the standard Yankee 36 trawl by a modified Yankee 41 trawl during the spring surveys in 1973–81 (Hayes and Buxton[1]). Conversion factors to account for these differences were not considered in this study because the analysis involved only within-year comparisons. In the autumn of 1985, 1986, and 1988, both NMFS vessels made tows in the 5Zjm area but there was only one instance out of the three years, 1988, which would have resulted in slightly different ratios. The boat conversion factor was therefore not applied in our study.

Abundance of haddock on each side of the ICJ line was obtained by summing the estimates of abundance for the strata in the respective jurisdictions. This method can be applied directly to the Canadian side for the DFO survey results because the strata boundaries incorporate the ICJ line; however, the strata on the U.S. side, 5Z3 and 5Z4, are bisected by the 5Zj,m unit area lines (Fig. 2). Several strata in the NMFS surveys are bisected by the ICJ line or the 5Zj,m unit area lines, or by both (Fig. 2). We refer to the parts of the bisected strata as strata sections. Because the tow locations were selected at random, we computed the abundance of haddock in the strata sections in the same manner as was done for entire strata according to the method in Smith (1988). Total abundance on either side of the ICJ line was then obtained by summing the respective abundances from strata or strata sections, or from both. Abundance for each stratum or stratum section was obtained as the average catch per tow for tows within it multipied by the number of possible tow units within it, thereby weighting the average catch per stratum or stratum section by its area.

This approach could be applied in most instances; however, there were cases in the NMFS surveys where no tows were made in a stratum section (Tables 1 and 2). Missing observations were handled in three ways; by estimation using the multiplicative model, by assumption of a zero value, or by assigning the mean per tow obtained for the whole stratum. The multiplicative model (Gavaris, 1980) was the preferred method but it requires a ln transformation of the catch per tow from the surveys which precludes the use of "0" values in the model; therefore, for strata sections with low abundance, this model was inappropriate. The U.S. sections of strata 17 and 18 in both spring and fall surveys, the U.S. section of stratum 19 in the fall, and the Canadian section of stratum 18 in the spring had a predominance of "0" values, suggesting that it would be reasonable to assume a zero value for missing observations in those strata sections. Missing observations for U.S. stratum section 20 within 5Zj,m were assumed to be equal to the mean catch per tow obtained for the entire stratum that extends west of 5Zjm, and the age composition for the whole stratum was extrapolated to that portion lying within 5Zj,m. This procedure was first followed for the 1991 eastern Georges

[1] Hayes, D., and N. Buxton. 1992 Assessment of the Georges Bank haddock stock in 1991. Northeast Fisheries Science Center, Res. Doc. SAW 13/1. [Appendix to CRD-92-02.]

Table 1

Estimated abundance (numbers in thousands) of haddock by stratum on the Canadian and U.S. side of the ICJ line in unit areas 5Zj and 5Zm (eastern Georges Bank) from fall NMFS bottom trawl surveys. When a stratum section was not sampled, as indicated by "( )", a multiplicative model was used to estimate abundance except for the U.S. side of strata 17, 18, and 19 which were assigned an abundance of "0" and stratum 20 where the mean for the whole stratum was used. The last two columns show the percentage of the total abundance that came from nonsampled strata or strata sections, or from both.

	Stratum												Total abundance		% from non sampled	
	16		17		18		19	20	21		22					
Year	Can.	U.S.	Can.	U.S.	Can.	U.S.	U.S.	U.S.	Can.	U.S.	Can.	U.S.	Can.	U.S.	Can.	U.S.
1963	38,652	32,353	2148	0	(12,942)	0	30,950	4313	16,462	1942	(21,761)	3772	91,964	73,330	38	0
1964	31,485	45,050	667	62	358	0	45,126	8627	2095	(627)	(4535)	(555)	39,140	100,048	12	1
1965	11,434	7102	914	(0)	198	0	16,341	1849	2091	113	923	126	15,560	25,530	0	0
1966	7999	574	123	16	57	0	7034	3817	204	8	137	175	8521	11,624	0	0
1967	3543	344	131	0	102	5	1118	154	105	(50)	137	(45)	4018	1716	0	6
1968	4831	0	97	0	119	(0)	0	34	0	8	156	(16)	5203	58	0	27
1969	387	168	87	0	21	(0)	325	548	21	(12)	50	0	566	1052	0	1
1970	483	47	392	19	128	(0)	5005	0	242	8	125	(31)	1369	5111	0	1
1971	451	836	319	0	13	0	758	0	32	315	87	(39)	902	1948	0	2
1972	2313	3300	312	(0)	13	0	0	0	189	8	(375)	11	3202	3319	12	0
1973	11,515	230	735	0	19	0	0	0	347	(71)	(511)	(63)	13,128	363	4	37
1974	387	72	58	0	13	0	0	(0)	284	8	0	66	742	145	0	0
1975	6212	9756	602	(0)	64	0	108	5512	21	(92)	175	(81)	7073	15,549	0	1
1976	58,353	143	580	0	102	0	0	(0)	11,452	(236)	(1708)	55	72,195	435	2	54
1977	2641	42	421	0	(789)	0	22	0	13,809	129	1614	(162)	19,275	355	4	46
1978	6035	2374	4571	0	543	0	3809	126	821	0	271	55	12,240	6364	0	0
1979	7173	451	416	8	1465	0	22	9	491	(362)	6595	448	16,140	1299	0	28
1980	1643	112	3727	0	192	0	433	154	453	1200	1143	55	7157	1954	0	0
1981	3704	1865	1558	210	172	0	81	23	274	(180)	648	66	6356	2425	0	7
1982	591	36	1228	(0)	511	0	0	17	21	(29)	6	33	2358	115	0	25
1983	1369	947	735	(0)	192	0	0	0	158	(104)	(749)	77	3202	1127	23	9
1984	414	0	2133	(0)	141	0	0	0	116	(43)	(311)	55	3114	98	10	44
1985	5315	7231	588	(0)	324	0	0	0	568	(139)	25	(123)	6819	7493	0	3
1986	6845	0	892	(0)	358	0	0	0	2274	40	12	0	10,381	40	0	0
1987	81	179	271	(0)	115	0	135	103	316	0	312	0	1094	417	0	0
1988	2537	143	493	(0)	741	0	0	0	1179	(78)	362	0	5311	222	0	35
1989	852	47	1190	(0)	(311)	5	0	103	1379	16	573	16	4447	176	7	0
1990	564	915	1204	0	345	(0)	0	0	1165	(120)	170	(106)	3448	1141	0	20
1991	483	245	609	(0)	(124)	0	(0)	0	0	315	274	0	1491	560	8	0
1992	709	2869	1219	50	64	(0)	0	228	147	0	75	(39)	2214	3188	0	1
1993	1519	0	667	(0)	0	(0)	0	34	8041	(35)	162	(31)	10,390	99	0	66

Bank haddock assessment (Gavaris and Van Eeckhaute, 1991) and therefore the method used then was followed in our study. For all other missing observations that occurred in strata which did not have a predominance of zero values, a multiplicative model employing strata and years as factors influencing the mean catch per tow was used to derive predicted values:

$$\ln I_{s,y} = \ln I'_{s'y'} \sum_{s} (\ln P_s) X_s + \sum_{y} (\ln P_y) X_y + \varepsilon_{s,y},$$

where s = stratum;

y = year;

I = survey catch/tow;

P = relative power for stratum or year;

X = dummy variables indicating the stratum and year of observation; and

ε = independent identically distributed normal error.

Strata sections 17u, 18c, and 18u in the spring and strata sections 17u, 18u, and 19 in the fall were not included in the multiplicative model analysis because of the prevalence of zeros in these strata sections.

Table 2

Estimated abundance (numbers in thousands) of haddock by stratum on the Canadian and U.S. sides of the ICJ line in unit areas 5Zj and 5Zm (eastern Georges Bank) from spring NMFS bottom trawl surveys. When a strata section was not sampled, as indicated by "()", a multiplicative model was used to estimate abundance except for stratum 18 and the U.S. side of stratum 17 which were assigned an abundance of "0" and stratum 20 where the mean for the whole stratum was used. The last two columns show the percentage of the total abundance which came from nonsampled strata or strata sections, or from both.

	Stratum												Total abundance		% from non sampled	
	16		17		18		19	20	21		22					
Year	Can.	U.S.	Can.	U.S.	Can.	U.S.	U.S.	U.S.	Can.	U.S.	Can.	U.S.	Can.	U.S.	Can.	U.S.
1968	3318	1506	595	(0)	43	0	1515	274	32	(55)	(200)	77	4186	3427	5	2
1969	2164	1119	445	0	0	0	397	34	11	(25)	87	(21)	2707	1596	0	3
1970	713	7221	218	0	0	0	252	(21)	21	(26)	75	(21)	1027	7540	0	1
1971	139	430	194	0	0	5	271	0	14	73	374	(19)	720	797	0	2
1972	1002	215	310	0	0	0	144	0	91	1534	0	(20)	1403	1913	0	1
1973	2462	1052	443	(0)	0	0	685	46	21	186	1322	0	4248	1968	0	0
1974	9582	0	116	0	4	0	2841	0	416	(19)	(70)	0	10,189	2860	1	1
1975	4134	538	65	(0)	0	(0)	577	0	42	16	12	(17)	4254	1148	0	2
1976	3818	1052	629	(0)	0	(0)	406	(154)	358	16	(128)	0	4933	1628	3	9
1977	3221	502	48	0	0	0	681	1061	13,115	16	0	5	16,384	2266	0	0
1978	5738	2905	48	8	6	0	606	0	4652	(60)	33	(50)	10,479	3629	0	3
1979	7043	6743	319	23	0	(0)	401	(28)	253	0	594	87	8209	7284	0	0
1980	6120	27,212	254	54	6	(0)	24,863	(1124)	3694	0	112	(114)	10,187	53,367	0	2
1981	14,387	8704	638	3	(0)	(0)	6125	2659	1905	(246)	87	230	17,017	17,967	0	1
1982	5411	3945	416	233	6	0	397	251	1179	(113)	898	22	7910	4962	0	2
1983	1933	538	735	39	0	0	0	171	(1119)	16	87	109	3874	874	29	0
1984	2623	1255	305	(0)	0	0	433	17	105	8	37	33	3071	1746	0	0
1985	9133	574	252	31	38	0	108	0	1937	(50)	87	(41)	11,447	804	0	11
1986	6313	1521	29	0	0	0	433	0	1305	4	0	(18)	7647	1975	0	1
1987	5991	115	136	0	6	0	0	1872	126	(11)	25	(9)	6284	2007	0	1
1988	1417	1894	15	0	0	(0)	54	0	284	0	0	0	1716	1948	0	0
1989	4168	5022	392	93	153	(0)	27	0	1631	0	798	(40)	7142	5182	0	1
1990	4268	9756	44	0	(0)	(0)	0	0	1291	16	12	(23)	5615	9795	0	0
1991	9341	2254	48	(0)	0	(0)	0	0	74	0	0	0	9463	2254	0	0
1992	966	369	165	(0)	0	(0)	65	11	379	(10)	0	(8)	1510	464	0	4
1993	2791	841	551	(0)	0	(0)	0	0	365	(30)	237	(25)	3944	896	0	6

Treatment of missing observations is summarized in Table 3.

The multiplicative model requires a ln transformation of the catch per tow from the surveys. This necessitated some treatment of remaining "0" values in the data. To reduce the influence of "0" values, the strata means rather than individual tow data were used because there are frequent occurrences of "0" catch in the individual tow data. Consequently, a test for the significance of interaction between years and strata was not possible. Because a logarithmic transformation of the mean catch per tow is required, a constant less than the minimum catch was added to "0" values. To examine the impact of adding a constant to the zero observations, analyses using three different constants, 0.1, 0.01, and 0.001, were considered. It was found that smaller constants exerted a greater influence on the model's output as seen by increases in Cook's *D* statistic (Cook, 1977). Moreover, the frequency distribution of the residuals showed greater departure from a normal distribution when 0.01 was added and particularly when 0.001 was added, displaying a marked skew toward negative values. Consequently, 0.1 was added to zero values for multiplicative model computations. The smallest observed value greater than "0" was 0.2.

For each survey, an age-length key combining all strata on eastern Georges Bank was applied to the length composition in each stratum or stratum section to derive the age structure. The age structures to which the estimated mean number per tow for missing values were applied were taken from the

Table 3

Treatment of missing observations in the NMFS spring and fall surveys to estimate abundance on the U.S. side and the Canadian side of unit areas 5Zj and 5Zm. c = Canadian side of stratum; u = U.S. side of stratum; *M* and **M** = used in multiplicative model; **M** = missing observations estimated from multiplicative model; 5Z = 5Z stratum mean used to fill in missing observations; 0 = missing observations assigned a value of 0.

Stratum	Spring	Fall
16c	*M*	*M*
16u	*M*	*M*
17c	*M*	*M*
17u	0	0
18c	0	**M**
18u	0	0
19	*M*	0
20	5Z	5Z
21c	**M**	**M**
21u	**M**	**M**
22c	**M**	**M**
22u	**M**	**M**

adjacent stratum section of the same stratum. When both strata sections of a stratum had missing observations, the age composition from an adjacent stratum was used. Haddock abundance at age on the Canadian and U.S. sides of the ICJ line were obtained by applying the age compositions of strata and strata sections to their respective total abundance and then summing the results within each jurisdiction. A ratio of relative abundance for the Canadian side was calculated by dividing the estimate on the Canadian side by the sum of the estimates on Canadian and U.S. sides.

Instantaneous rates of net migration

The availability of fisheries statistics, since 1985, at a resolution sufficient to be summarized with respect to the ICJ line, in conjunction with the relative abundance information described above, made it possible to derive estimates of net migration rates. Catch-at-age by quarter which was required for this analysis is reported in Gavaris and Van Eeckhaute (1997).

Net migration rates were estimated by using a model that follows from one originally proposed by Beverton and Holt (1957). Terminal population abundance for each cohort at the beginning of 1994 for the 1986 to 1993 year classes and at age 8 for the 1968 to 1985 year classes was taken from Gavaris and Van Eeckhaute (1994). Population abundance in all of 5Zj,m at time y, expressed in units of years, e.g. 1991.75, for ages 1–8, a, was calculated by using virtual population analysis with a three-month time period, i.e. t=0.25, according to the following algorithm. The annual instantaneous natural mortality rate, M, was assumed constant and equal to 0.2. In all equations N refers to numbers of fish and, if preceded by a subscript letter, indicates the source of the loss so that ${}_FN$ is the number dying from fishing, ${}_MN$ is the number dying from natural mortality, and ${}_EN$ is the number lost or gained from migration. If not preceded by a subscript, N refers to population abundance. The method assumes an exponential decay model:

$$N_{y,a} = N_{y+t,\,a+t}\,e^{(F_{y,a}+M)t},$$

where the fishing mortality, $F_{y,a}$, for ages 1 to 7 is obtained by solving the catch equation using a Newton-Raphson algorithm with the three-month commercial catch-at-age data, ${}_FN_{y,a}$.

$$N_{y,a} = \frac{{}_F N_{y,a}(F_{y,a}+M)t}{F_{y,a}t\left(1-e^{-(F_{y,a}+M)t}\right)}.$$

The total number of fish dying due to natural mortality in each quarterly period, y, was obtained by applying the quarterly rate of natural mortality to the average population abundance during the period:

$${}_M N_{y,a} = Mt\overline{N},$$

where $\overline{N}$, the average population abundance during the period, is defined as

$$\overline{N}_{y,a} = \frac{N_{y,a}\left(1-e^{-(F_{y,a}+M)t}\right)}{(F_{y,a}+M)t}.$$

DFO surveys were conducted between 10 February and 19 March, whereas NMFS spring surveys were conducted from 23 March to 26 April. The NMFS fall surveys were conducted between 3 October and 25 October. The distributions of haddock obtained from the spring and fall survey results were considered to be representative of 1 April and 1 October, respectively. For each year, six-month net migration rates were calculated for the spring–summer period (1 April–30 September) and the fall–winter period (1 October–31 March).

Since proportions of haddock on the Canadian side of the ICJ line, as indicated from DFO and NMFS survey results, were available for only two points in time, spring and fall, subsequent calculations were done on a half-year basis to coincide with the survey timing. The 5Zj,m population numbers at the beginning of quarters 2 and 4 as obtained from the quarterly VPA were used. Numbers of haddock dying from natural mortality and from fishing were summed for quarters 2 and 3 to give 1 April numbers and for quarters 4 and 1 to give 1 October numbers. The proportions of haddock at ages 1 to 8 on the Canadian side of the ICJ line were averaged for the two spring surveys for 1987 to 1993. These were then combined with the 1985 and 1986 proportions from the NMFS spring survey and, along with the NMFS fall proportions, were applied to the 5Zj,m population abundance at the beginning of quarters 2 and 4 to obtain population abundance on the Canadian side:

$$N_{Can,y,a} = N_{y,a} R_{Can,y,a},$$

where $R_{Can,y,a}$ = the proportion occurring on the Canadian side.

The number of fish dying from natural mortality on the Canadian side of the ICJ line was assumed proportional to the fraction of the population occupying the Canadian side on average during the period:

$$_M N_{Can,y,a} = \frac{_M N_{y,a} \overline{N}_{Can,y,a}}{(\overline{N}_{Can,y,a} + \overline{N}_{USA,y,a})},$$

where $\overline{N}_{Can,y,a}$ and $\overline{N}_{USA,y,a}$ = the average population abundances on the Canadian and USA sides, respectively, during the period.

The net number of fish migrating from the Canadian side to the U.S. side of the ICJ line was obtained by subtracting the number of fish caught by the Canadian fishery at age, $_F N_{Can,\,y,\,a}$, and the number of fish dying from natural mortality on the Canadian side from the difference between population abundance on the Canadian side at the beginning of the two six month periods:

$$_E N_{y,a} = N_{Can,y,a} - N_{Can,y+t,a+t} - {}_F N_{Can,y,a} - {}_M N_{Can,y,a}.$$

Instantaneous rates of migration were calculated in relation to the average abundance in 5Zj,m as follows:

$$E_{y,a} = \frac{_E N_{y,a}(Z_{y,a})}{N_{y,a}\left(1 - e^{-(Z_{y,a})}\right)},$$

where the total mortality

$$Z_{y,a} = -\ln \frac{N_{y+t,a+t}}{N_{y,a}}.$$

By convention, $_E N_{y,a}$ and $E_{y,a}$ is positive when the net direction of migration is towards the U.S. side and negative when it is towards the Canadian side.

Results

Ratios of relative abundance

Although the ICJ line was not established until October 1984, to provide a historical perspective of haddock relative abundance with respect to the line, we make reference to Canadian and U.S. sides of eastern Georges Bank for all surveys conducted since 1963. Because relative abundances of older haddock, greater than age 8, are difficult to interpret because of the small numbers caught, an aggregated age grouping of 9+ was used.

Fall season The multiplicative model accounted for about half of the total variation in catch per tow (multiple R^2=0.47). The stratum influence with an F-value of 7.245 and P<0.001 accounted for most of the variation, but the year effect also accounted for some with an F-value of 3.247 and P<0.001. The frequency distribution of residuals approximated a normal distribution. The strata coefficients from the multiplicative model give an indication of the relative abundances between strata sections, i.e. the higher the value, the higher the abundance. For those strata sections that were used in the model, the shading in Figure 3 was scaled to the magnitude of the strata coefficients. All Canadian sections of strata had higher coefficients than the corresponding U.S. sections. The four sections on the U.S. side that were not used in the model were dominated by zero catch per tow. Canadian strata sections having depth zones of 56 to 183 m exhibited the highest coefficients. The model results indicate that the strata on the Canadian side had higher abundance than those on the U.S. side.

For each stratum the abundances by stratum or stratum section are contained in Table 1. The dominant strata were 16c, 16u, and 17c. Abundance in 19u and 20u used to be quite high but in recent times almost no haddock have been caught there. In contrast, 17c has shown an increase in its relative abundance in recent years in comparison to early catches, although that abundance since the 1960s has dropped substantially. Total fall abundance showed that more haddock were caught on the U.S. side during the 1960s and early 1970s, after which haddock became more abundant on the Canadian side. Numbers estimated by the multiplicative model accounted for a significant amount of the abundance on the U.S. side

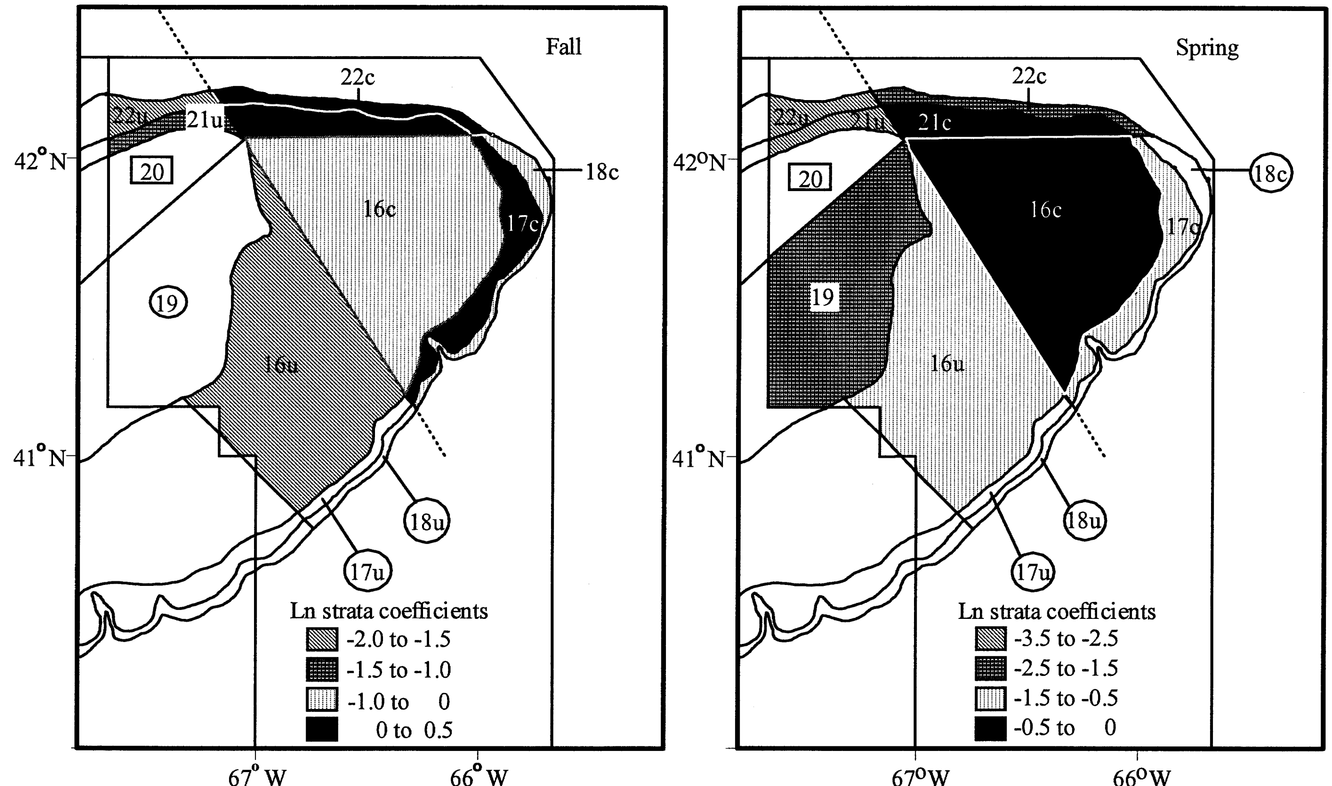

Figure 3

The relative abundances between strata as characterized by the ln strata coefficients from the multiplicative model for the NMFS fall and spring surveys. Strata which have a circle (○) around them, e.g. 17u , were not used in the multiplicative model and missing observations were given a value of "0." Stratum 20 was also not used in the model because the 5Z stratum means were used for missing observations. Strata depth zones are as follows: 19 and 20, 27–55 m; 16 and 21, 56–110 m; 17 and 22, 111–183 m; 18, >183 m.

in several years but, in those years, the total abundance on the U.S. side was usually small. For the Canadian side, in most instances, very little of the abundance was estimated from the multiplicative model.

An examination of the fall ratios of relative abundance, (Fig. 4), revealed two distribution patterns in haddock age 1 and older. Between 1963 and 1972, haddock were highly variable in their relative abundance and were found throughout the bank. After 1971, the majority of haddock ages 1 and older were found on the Canadian side as indicated by the predominance of ratios ≥0.75. The ratios of relative abundance indicated that age-0 haddock were very variable throughout 1963–93 and were often more abundant on the U.S. side.

Friedman's nonparametric test revealed that the ratios for ages 1–9+ during the period 1972–93 were similar but the ratios for age 0 differed from these. During the period 1963–71, the ratios for all ages, 0–9+, did not show persistent patterns (Table 4).

We conclude then that the relative abundance of age-0 haddock across the ICJ line is different from that for ages 1–9+ but only during the period 1972–93. Therefore, for further analysis of time trends, ages 1–9+ were combined (Fig. 5). From 1963 to 1971 haddock of ages 1+ were distributed throughout 5Zj,m but were generally found in greater numbers on the U.S. side. Since 1972, however, very few haddock at these ages have been found on the U.S. side. Between 1963 and 1971, there was one anomolously high value, 1968 with a ratio of 0.99, but all other ratios were lower than any of the values after 1971. In contrast to ages 1+, the ratios of relative abundance of age-0 haddock were very variable and indicated a less patterned distribution, being distributed throughout 5Zj,m. All except one of the stronger year classes, 1972, 1975, 1978, 1983, 1985, 1987, and 1992, with relative abundance ratios at age 0 of 0.34, 0.28, 0.47, 0.62, 0.40, 0.21, and 0.08, respectively, were more abundant on the U.S. side. Interestingly, the weak year classes that followed these (1973, 1976, 1979, 1984, 1986, 1988, and 1993) were found in greater abundance on the Canadian side with ratios of 0.85, 0.85, 0.64, 1.0, 1.0, 1.0, and 0.93, respectively. A likely mechanism has not been determined.

The distribution of age-1+ haddock determined by using the catch-per-tow data from the NMFS fall survey, pooled over 1985–95, are shown in Figure 6. As

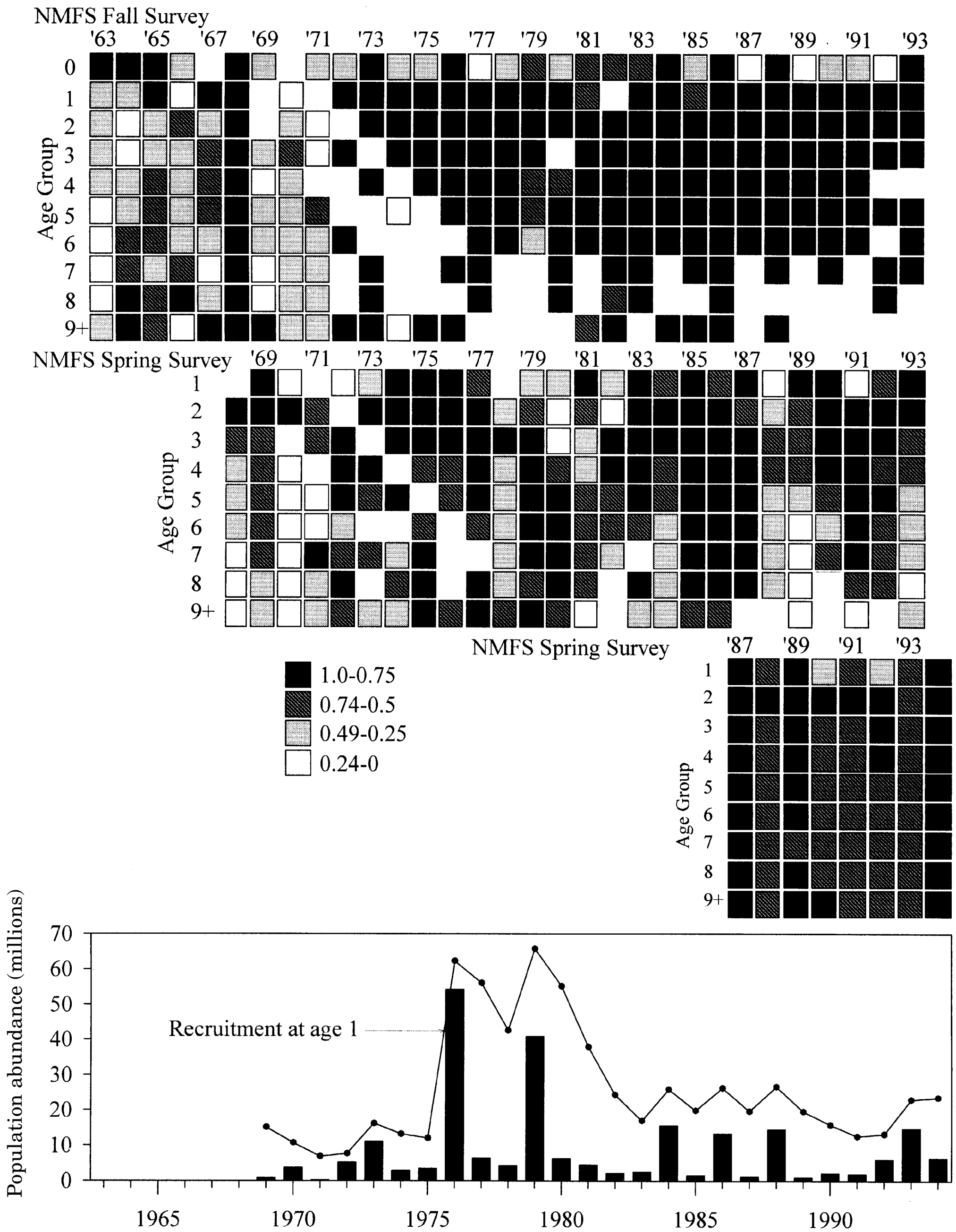

Figure 4

Ratios of relative abundance for haddock on eastern Georges Bank aggregated into four categories from the DFO and NMFS surveys and (below) population abundance and recruitment at age 1 in 5Zj,m as estimated by sequential population analysis by Gavaris and Van Eeckhaute (1995).

noted from the analyses of ratios of relative abundance, in recent times few haddock have been found on the U.S. side during the fall. For comparison purposes the 1963–71 distribution determined by using NMFS fall survey data are also shown. It is evident that the 1963–71 distribution pattern is markedly different from the 1985–95 patterns. The wide spread abundance observed west of the ICJ line in the 1963–71 period is no longer present in recent times and the aggregations on the northeast peak that were apparent from 1985 to 1995 were not evident in the earlier period.

Spring season As with the fall results, the multiplicative model accounted for about half of the total

Table 4

Probability estimates of Freidmans's nonparametric test for randomness within ages from the National Marine Fisheries Service (NMFS) and Canadian Department of Fisheries and Oceans (DFO) survey ratios of relative abundance for two age groupings.

Age groups	Years	*F*-value	Degrees of freedom	Probability of test criterion
NMFS fall sSurvey				
0–9+	1963–71	8.424	9	0.5 > *P* > 0.25
0–9+	1972–93	25.185	9	0.005 > *P* > 0.001
1–9+	1972–93	0.8	8	*P* > 0.999
NMFS spring survey				
1–9+	1968–93	28.292	8	0.001 > *P*
DFO spring survey				
1–9+	1987–94	6.058	8	0.75 > *P* > 0.5

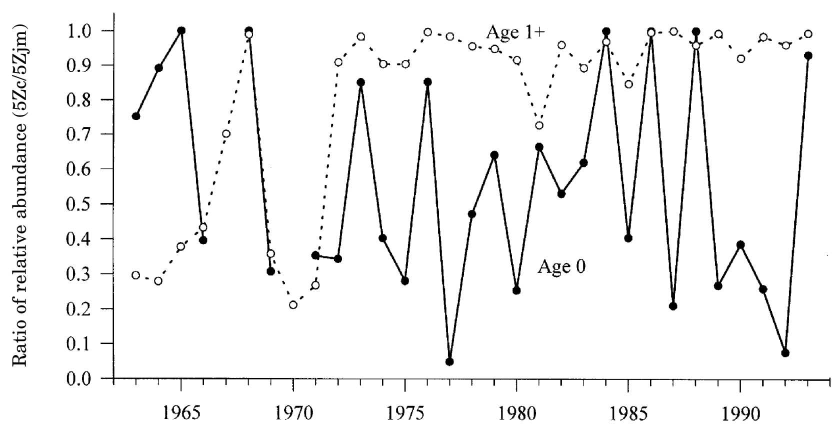

Figure 5

The distribution of haddock across the ICJ line in 5Zjm during the fall as indicated by the ratios of relative abundance from the NMFS fall survey.

variation in catch per tow (multiple R^2=0.41). The stratum influence accounted for most of the variation with an F-value of 8.389 and P<0.001 but the year effect was not as strong for the spring survey as it was for fall (F-value of 1.647, 0.1<P<0.2). The frequency distribution of residuals approximated a normal distribution, although not as well as those of the fall survey. An outlier from stratum 21u in 1972 influenced the model's estimates of abundances for that stratum; estimates were 60% greater than they would have been had this value been excluded from the analysis. A higher proportion of haddock on the Canadian side would have resulted if this value had been excluded. This stratum, however, does not contribute substantially to the overall abundance; therefore its impact was not studied further. The relative abundances between strata as characterized by the strata coefficients from the multiplicative model are shown in Figure 3. Two Canadian strata sections, 21c and 16c, which have a depth range from 56 to 110 m, had the highest coefficients. Three strata sections with a high number of zero values, 17u, 18c and 18u, were not used in the model.

The stratum and stratum section abundances from NMFS spring surveys are given in Table 2. Stratum section 16c, and 16u (secondarily), were again the highest contributors to total abundance. The relative contribution of stratum section 21c increased after 1976, whereas the contribution from stratum section 17c remained stable over time. As in fall, 19u in spring also declined in relative abundance from earlier times; very few haddock were caught there after 1981. The highest numbers in 19u were caught during 1980 and 1981. Haddock were virtually absent from 18c in spring but in the fall there were almost always some to be found there. Total abundance on the Canadian side was augmented by estimated numbers only four times, whereas most years were augmented for the U.S. side. The contribution made by these values to abundance on the U.S. side, however, was negligible.

Abundances by stratum for the DFO spring survey are given in Table 5. Haddock were always more abundant on the Canadian side than on the U.S. side; the Canadian side had 61–99% of the abundance in 5Zjm. Except for two occasions, haddock were more abundant in the shallower 5Z2 stratum than in the deeper 5Z1 stratum. Stratum 5Z2 and 5Z4 have the

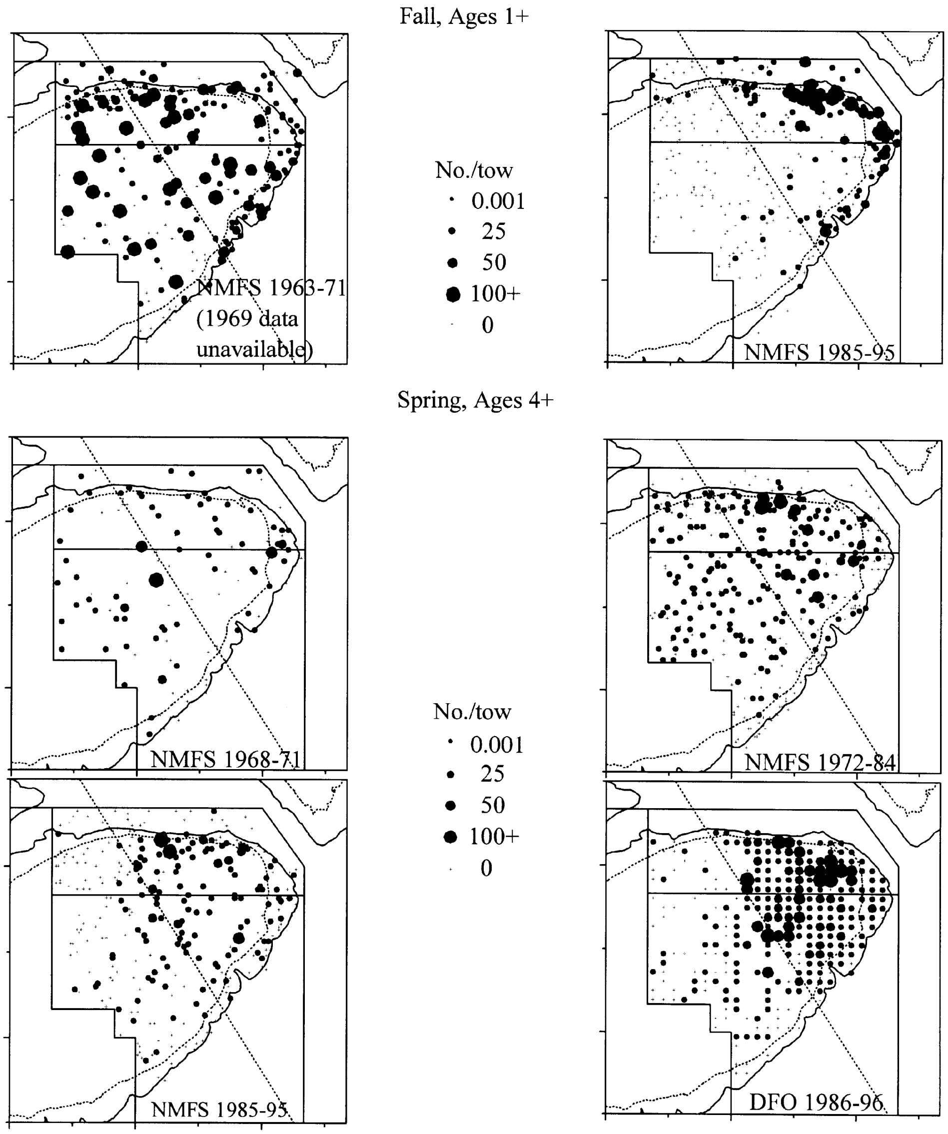

Figure 6

Fall distributions of ages 1+ haddock and spring distributions of ages 4+ haddock on eastern Georges Bank from the NMFS and DFO bottom-trawl surveys. The DFO data points are aggregated due to the high density of sets.

same depth range but, except for 1993, haddock were much more abundant in 5Z2.

The ratio of relative abundance trends from both the NMFS spring survey and the DFO spring survey indicated that haddock abundance is generally greater on the Canadian side of the ICJ line, though not as high as during the fall (Fig. 4). There was no obvious pattern by age in the ratios of abundance. The results of Friedman's test confirmed that there was not a significant age effect in the DFO spring survey but indicated that there were significant differences by age in the NMFS survey (Table 4). There was a tendency for lower ratios as age increases but the relationship was very weak (r^2=0.083 for ages 4–9+). Similarities in ratios of relative abundance among ages were examined with a correlation test of arcsine-transformed NMFS survey ratios. This revealed that age 1 did not correlate with any other ages (r<0.5), ages 2 and 3 showed some correlation with adjacent age classes, and ages 4–8 were highly correlated (r>0.5; Fig. 7). The ratios were plotted as three groups in Figure 8. For ages 4–8, there was

Table 5

Estimated abundance (numbers in thousands) of haddock by stratum on the Canadian and U.S. sides of the ICJ line in unit areas 5Zj and 5Zm (eastern Georges Bank) from spring Canadian Department of Fisheries and Oceans bottom trawl surveys.

	Canadian side		U.S. side		Total abundance	
Year	5Z1	5Z2	5Z3	5Z4	Canadian side	U.S. side
1987	3794	7162	103	40	10,956	143
1988	1398	12,444	5344	483	13,842	5827
1989	1874	9117	279	120	10,991	399
1990	4038	9903	1814	4214	13,941	6028
1991	2243	7961	3674	2429	10,204	6103
1992	4694	5540	2508	1507	10,234	4015
1993	2946	1879	37	2988	4825	3025
1994	15,424	11,091	167	180	26,515	347

more variability in the ratios from year to year than in the fall survey, but high values predominated except from the 1968–71 period when the ratios were lower. Ratios for age 1 were variable with no obvious tendency but most ages 2 and 3 ratios were greater than 0.5. The short length of the DFO survey series precluded investigation of this feature for these data.

The effect of total 5Zj,m abundance on the spring ratios of relative abundance was examined for this period because the greatest amount of dispersion onto the bank occurs during spring. This was evaluated by plotting the NMFS spring survey ratios of relative abundance against the beginning of year population numbers aggregated into three age groupings: age 1, ages 2 and 3, and ages 4–8. Population numbers were obtained from the 1995 eastern Georges Bank haddock assessment (Gavaris and Van Eeckhaute, 1995). No relation between abundance and ratios of relative abundance was apparent. The DFO time series was not investigated for this effect because of its short time span.

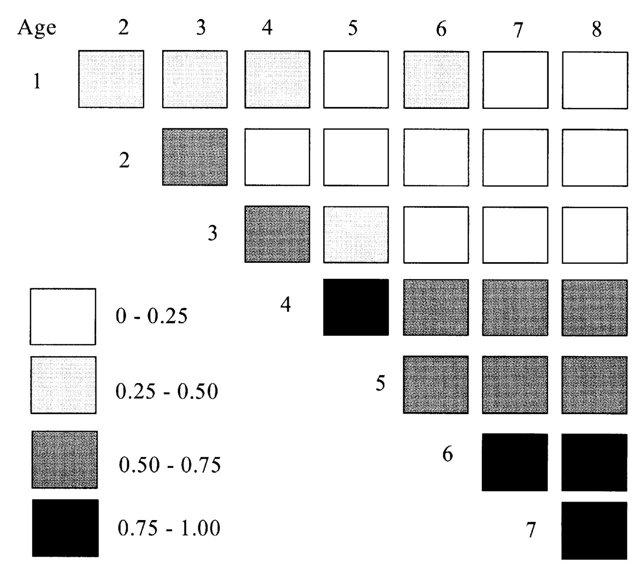

Figure 7

Age by age correlation of haddock ratios of relative abundance from the NMFS spring survey.

The distribution of age 4+ haddock determined by using the catch-per-tow data from the DFO spring survey pooled over 1986 to 1996 and the NMFS spring survey pooled over 1968–71, 1972–84, and 1985–95 are shown in Figure 6. During the 1972–84 and 1985-95 period (1986–96 for the DFO survey) there were aggregations throughout the Canadian side of 5Zj,m, especially in the area of the northeast peak, whereas the U.S. side showed lower abundance. This was especially evident for the 1985–95 period, but there were a number of occurrences of haddock along the southern flank of the bank in this period also. The spring distribution from 1968 to 1971 was markedly different from the recent distribution pattern. The northeast peak aggregations were not seen, and haddock seemed to be distributed uniformly throughout 5Zj,m. The distribution pattern during this period was strongly influenced by the exceptionally abundant 1963 year class.

Instantaneous rates of net migration

Haddock landings by the U.S. and Canadian fisheries have been affected by the spawning closure area

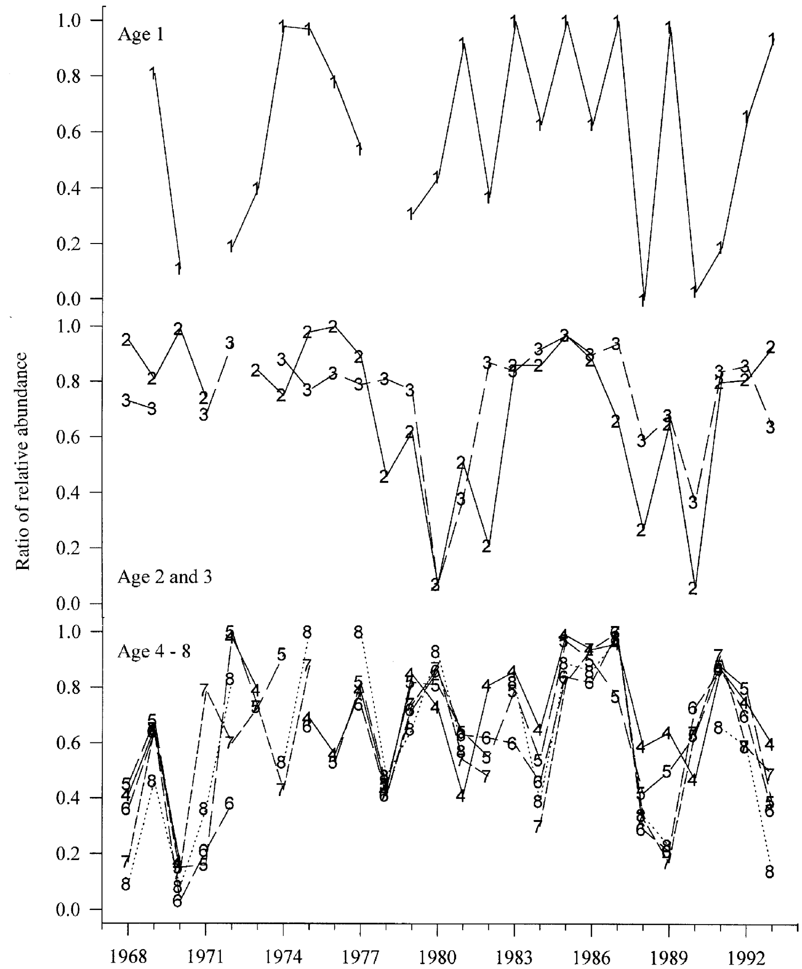

Figure 8

Relative abundance of haddock on the Canadian side of 5Zj,m by age group from the NMFS spring survey. Ratios were determined as abundance on Canadian side to total abundance in 5Zjm.

which was first instituted in 1970 by the International Commission for the Northwest Atlantic Fisheries and which was retained by both countries following extension of jurisdiction in 1977 (Halliday, 1988). The closure, which was put into effect from March to April during 1970–71, was extended to include May in 1972 and at that time an exemption for hook fisheries was introduced. In 1987 the United States extended the period to include February and in 1993, it was further extended to include January through June. The Canadian bottom trawl fishery has traditionally had limited activity during January and February except during 1991–93. Since 1985, when Canada and the United States have conducted haddock fisheries only on their respective sides of the ICJ line, the U.S. monthly catch of haddock in unit areas 5Zj,m (Fig. 9) generally have increased from January to June, but a sharp decline in landings occurred in July and the months following. Canadian landings peaked in June and July, the first two months following the spawning closure period, and decreased gradually to November.

The 6-month net migration rates calculated for three age groups (age 1, ages 2 and 3 combined, and ages 4 to 8 combined) displayed a persistent seasonal pattern indicating net movement towards the U.S. side between October and April followed by a return to the Canadian side between April and October (Fig. 10). Age-1 haddock had the greatest net migration rate to the Canadian side from April to September but also the

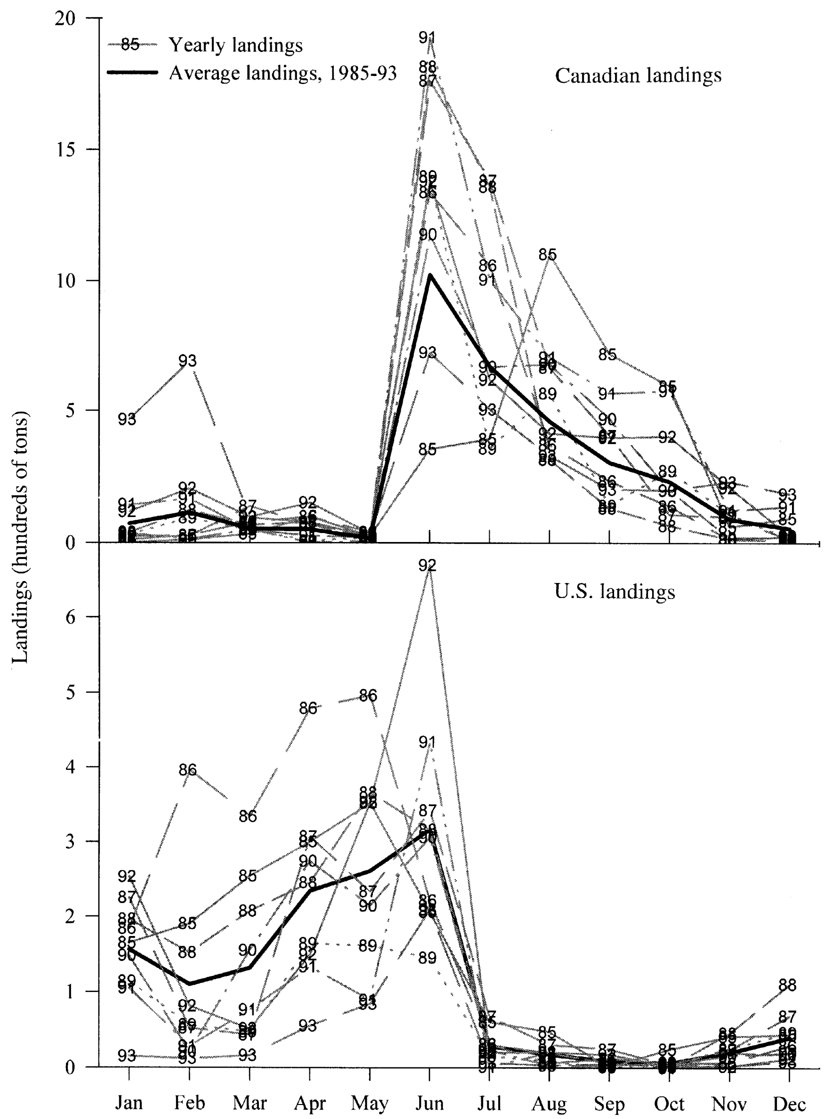

Figure 9

Monthly haddock landings in 5Zj,m from 1985 to 1993.

most variable. The net migration rate towards the U.S. side from October to March was often lowest at age 1, intermediate at ages 2 and 3, and greatest at ages 4 and older. By ages 4+ net migration back and forth seemed to be balanced. This general pattern was supported by the migration rates for the entire period examined, but the trend was less distinct from April 1985 to October 1987 than from April 1988 to October 1993. Examination of the spring ratios of relative abundance showed very high values during 1985–87 for ages 4–8 haddock (Fig. 8), indicating that there was not much movement across the ICJ line during that period.

Figure 11, which shows the movement and removals of a weak and a strong year class, the 1984 and 1985, respectively, for ages 1 and older, illustrates the migratory nature of the 5Zj,m stock across the ICJ line. The migratory pattern is well illustrated; a portion of the stock moved to the U.S. side from October to March and most of the stock moved back to the Canadian side from April to September. In spring the abundance on the Canadian side remained higher than on the U.S. side. The U.S. catch often consisted primarily of fish that had moved across the ICJ line from the Canadian side to the U.S. side and is indicated in the figure by the arrows pointing to the left.

No obvious pattern between net migration rates and population abundance was found. The range of abundance, however, for this period was very limited.

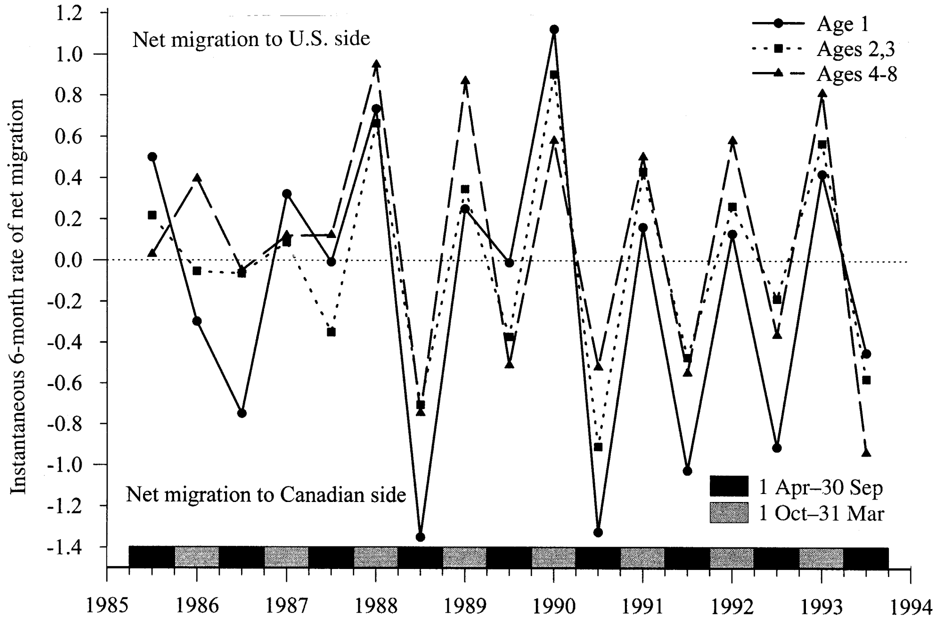

Figure 10

Net migration rates (expressed as annual rates) across the ICJ line for 6-month time periods for 5Zj,m haddock. These rates show that from April to September, net haddock migration was towards the east resulting in almost all haddock in 5Zj,m residing on the Canadian side in the fall. There was then a migration westward and across the ICJ line from October to March, a migration associated with spawning activities.

Discussion

Observations regarding haddock spatial distribution on Georges Bank during an earlier period (Colton, 1955) and for two dominant year classes more recently (Overholtz, 1985) have indicated that adult haddock are more abundant off the bank in deeper waters during the fall but are found on the bank in shallower waters during the spring. Colton (1955) reported that during spring, the greatest concentrations of larger haddock occur in water less than 110 m and presumed this was related to spawning activities. Migration from shallower water in spring to deeper water in the fall appears to occur by the end of July. Colton (1955) reported that few haddock of any age were found between 110 m and 165 m during the July–August surveys undertaken in 1949 and 1950. Older haddock, age 5+, could be found in waters deeper than 165 m in unit areas 5Zg,h and j. Overholtz (1985) also suggested that survey distributions of age-2 haddock indicated a movement by summer to deeper water in relation to the shallower depths generally occupied in spring. Colton (1955) and Overholtz (1985) reported some segregation of ages as fish moved into deeper water, i.e. older fish occupied deeper water than did younger fish, but Colton (1955) observed that in spring there appeared to be less segregation of age groups.

Although we observed two distinct distribution patterns over time within 5Zj,m, our analysis indicates that the depth-related patterns described above were persistent. The 1963–71 distribution pattern will be discussed more fully later in this section. Patterns observed from 1972 to recent times show that adult haddock in 5Zj,m were broadly dispersed over the bank during the spring period, their distribution extending westward of the ICJ line especially along the southern flank of Georges Bank. The NMFS strata with the highest densities in the spring were the Canadian portions of 21 and 16 which have a depth range from 56 to 110 m. The ratios of relative abundance, especially those from the DFO survey, clearly show that the majority of age-2+ haddock occupied waters within the Canadian jurisdiction at that time. Both NMFS and DFO spring surveys exhibit similar distribution patterns with similar areas of concentration. During the fall, haddock distribution shifted to the east onto the deeper bank slopes and few haddock remained on the U.S. side of the ICJ line. The ratios of relative abundance indicate that virtually all age 1+ haddock within 5Zj,m are on the Canadian side of the ICJ line in the fall.

The net migration results suggest that the westward migration of age-2 and older haddock in the winter–spring period is matched by a corresponding eastward migration during the summer–fall period of roughly similar magnitude. The net result is that roughly 20% to 25% of the adult haddock move across the ICJ line during a cycle. There may be a tendency for older haddock to migrate back and forth across the boundary line in greater numbers than for younger haddock because the instantaneous rates of net migration during the winter period for ages 4–8 are often greater than for younger ages, i.e. six out of nine times (Fig. 10). No relationship was found between stock abundance and the 1985–93 spring net migration rates, or the 1968–93 spring ratios of relative abundance, when a greater range in stock abundance occurred. The variability seen in the magnitude of movement to the U.S. side in spring from year to year (Figs. 8 and 10) may reflect variation in the timing of migration, variation in the magnitude of migration, sampling variation, or immigration from another source. Improved understanding of the source of this variability and better estimates of the magnitude and extent of migration may be possible from repeated surveying during the winter–spring period.

Distribution and migration show differences by age. The distribution of age-0 haddock was found to be different from that of older haddock, as has been previously described (Overholtz, 1985; Lough and Boltz, 1989; Polacheck et al., 1992). Haddock eggs and larvae spawned on the northeast peak may be distributed as far south as the Middle Atlantic Bight (Polacheck et. al., 1992). The ratios of relative abundance of age-0 haddock during fall are very variable and abundance often favors the U.S. side. There was a pattern of strong year classes being more abundant on the U.S. side whereas the weak year classes that followed were more abundant on the Canadian side. Additional research is needed to determine whether there is a mechanistic explanation for this observation. Our results suggest that the distribution and movement of age-1, -2 and -3 haddock differ from those of older haddock. In spring there was some correlation of ratios of relative abundance such that age-4 and older haddock had similar patterns and age-2 and age-3 haddock were similar whereas age-1 haddock did not correlate with any other ages. The differences likely reflect different migration patterns of immature and mature haddock. Maturity rates increase from ages 1 to 3 and by age 4 all haddock are mature (O'Brien and Brown, 1996; Trippel et al., 1997).

Haddock biomass (age 2 and older) on all of Georges Bank from 1935 to 1960 averaged 153,000 meteric tons (t). In

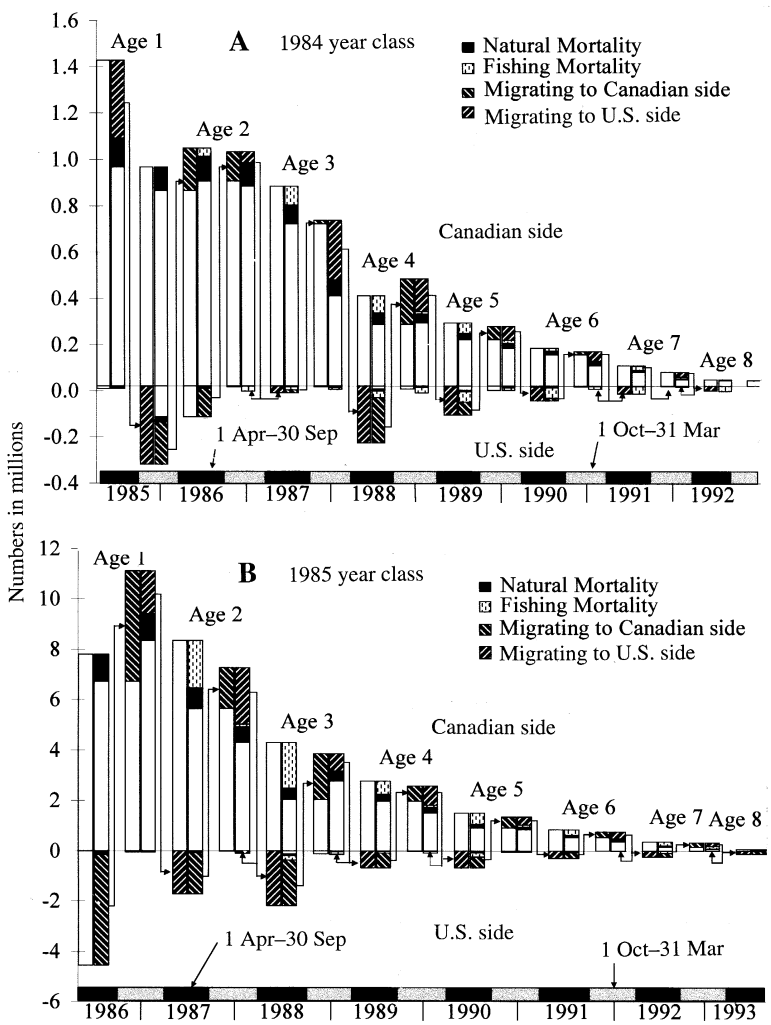

Figure 11

History of the (**A**) 1984 and (**B**) 1985 haddock year classes in unit areas 5Zj,m. The first bar of each pair represents the population size at the beginning of each 6-month period with the numbers gained from migration, if any. The second bar indicates the numbers lost to natural mortality, fishing mortality and migration to the other side of the ICJ line. The number of haddock left over at the end of the time period is represented by the unshaded portion of the second bar. The haddock that migrated across the ICJ line are added to the population or contribute to fishing mortality on the side they are migrating to during the same time period.

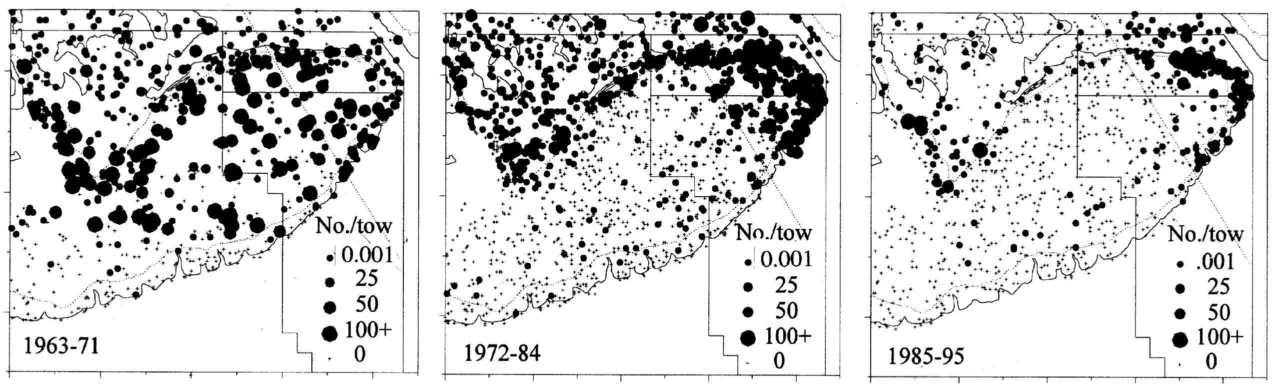

Figure 12

Fall distribution of age 1+ haddock on Georges Bank from NMFS bottom-trawl surveys. Data have been aggregated for the three time periods shown. Note that 1969 data are not included as these data were unavailable.

1965, biomass peaked at 427,000 t due to the recruitment of the "very strong" 1962 and the "outstanding" 1963 year classes that continued to dominate the population during the late 1960s and early 1970s (Clark et al., 1982). There was a large decline, by an order of magnitude, in the biomass of haddock on Georges Bank during the late 1960s and the early 1970s to a low of 14,000 t in 1973 (Clark et al., 1982). The fall distribution pattern during this period of exceptionally high but rapidly decreasing abundance indicates that haddock within 5Zj,m were more widely dispersed over the bank from 1963 to 1971 (Fig. 6) than that which was observed subsequently. Moreover, the ratios of relative abundance did not strongly favor the Canadian side of the ICJ line during 1963–71 (Figs. 4 and 5). This difference in distribution was also evident in the spring distribution pattern for ages 4 to 8 (Fig. 6) and in the spring ratios of relative abundance that were generally less than 0.5 during 1968–71 (Fig. 8). After this period, the ratios, though variable, were usually above 0.5. Polacheck[2] noted that haddock, since the late 1960s, were almost never caught in research survey tows in the southern and central portions of Georges Bank, areas where they had been caught regularly during the mid-1960s.

The post-1971 ratio of relative abundance trends for haddock persist to the present. During the late 1970s and early 1980s, the 1975 and 1978 year classes dominated the population and since then there have been several moderately strong year classes, i.e. the 1983, 1985, 1987, and 1992 (O'Brien and Brown, 1996; Gavaris and Van Eeckhaute, 1997). Despite accompanying fluctuations in haddock abundance, the relative abundance pattern has not reverted to that observed from 1963 to 1971. Polacheck,[2] using percent zero tows and patchiness to explore spatial distribution of Georges Bank haddock, also observed that when abundance increased with the 1975 and 1978 year classes, the patterns in spatial distribution did not resemble those observed from 1963 to the late 1960s. The distribution pattern during that time period was influenced strongly by the exceptionally large 1963 year class and may not be typical of the stock when it was in a more stable state as during the 1935–60 period. Recognizing the two spawning components and the likelihood that haddock may display different spatial affinities depending on their origin, we hypothesize that the 1963–71 distribution patterns may have been the result of an unusually greater contribution of recruitment from the southwestern spawning component. On the other hand, since 1985, the southwestern spawning component has probably been depleted to a greater extent and may not be contributing to Georges Bank production to the degree that it did from the mid-1970s to mid-1980s. The depletion of the southwestern spawning component is well illustrated by the fall distribution in 5Ze of ages 1+ haddock for three time periods, 1963–71, 1972–84, and 1985–95 (Fig. 12). Note that the almost continuous distribution of haddock seen along the northern edge of the bank during the first two time periods is not apparent during the later time period.

Since 1985, the relative abundance across the ICJ line and the net migration rates have likely not been strongly affected by variations in the abundance of the eastern Georges Bank spawning component. However, these attributes may get distorted by dis-

[2] Polacheck, T. 1995. CSIRO, Division of Fisheries, P.O. Box 1538, Hobart, Tasmania 7001, Australia. Personal commun.

tributional overlap of the two spawning components if the abundance of the southwestern component increases. This overlap effect may be responsible for the higher abundance at ages 2 and 3 of the strong 1978 year class on the U.S. side in spring (Fig. 8). Note, however, that at ages 4 and older, abundance shifts to being higher on the Canadian side of 5Zj,m.

From the temporal and spatial patterns of distribution, ratios of relative abundance with respect to the ICJ line, net migration rates, and monthly landings statistics, we can infer then that a seasonal migration, probably associated with spawning behavior, occurs in 5Zj,m. This migratory behavior may be influenced by temperature conditions but, although temperature data is collected during surveys, the time range of this information is too limited to investigate the effect on migration timing. The westward movement of haddock onto the bank into shallower water probably begins around November and reaches its greatest extent to the west during the peak of spawning in March–April, after which the return migration eastwards begins. Most haddock have probably migrated eastward across the ICJ line by July and by October; haddock are found far east of the line preferring the deeper waters of the northeast slopes of the bank.

An understanding and appreciation of the distribution and migration patterns on eastern Georges Bank in relation to the ICJ line are important prerequisites for investigation of sustainable harvest practices for this transboundary resource. The pattern of migration described in our study does not alter sustainable levels for the area as a whole but because of the seasonal nature of exploitation by Canada and the United States, this information can provide guidance on the exploitable biomass available on each side during different seasons so that consistent and equitable harvest rates can be determined. After establishment of the international boundary, Canada and the United States have managed the resources in their respective territories with little attention to what was being done in adjacent waters. Though it has been suggested that sustainable fisheries could be maintained through independent management (Gavaris et al., 1993), it is likely that the greatest potential would be achieved through consistent management. Knowledge of temporal and spatial distribution patterns can form the basis upon which consistent management practices are explored.

Acknowledgments

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Literature cited

Beverton, R. J. H. and S. J. Holt.
1957. On the dynamics of exploited fish populations. Fish. Invest. Minist. Agric. Fish. Food UK (series 2) 19, 533 p.

Bigelow, H. B., and W. C. Schroeder.
1953. Fishes of the gulf of Maine. U.S. Fish Wildl. Serv. Bull. 74, vol. 53, 577 p.

Clark, S. H., W. J. Overholtz, and R. C. Hennemuth.
1982. Review and assessment of the Georges Bank and Gulf of Maine haddock fishery. J. Northw. Atl. Fish. Sci. 3: 1–27.

Colton, J. B.
1955. Spring and summer distribution of haddock on Georges Bank. Special Scientific Report of the U.S. Fish and Wildlife Service—Fisheries 156, 65 p.

Cook, R. D.
1977. Detection of influential observation in linear regression. J. Statistical Society 74:169–174.

Gavaris, S.
1980. Use of a multiplicative model to estimate catch rate and effort from commercial data. Can. J. Fish. Aquat. Sci. 37:2272–2275.

Gavaris, S., and L. Van Eeckhaute.
1990. Assessment of haddock on eastern Georges Bank. Canadian Atlantic Fisheries Scientific Advisory Committee (CAFSAC) Res. Doc. 90/86, 37 p.
1991. Assessment of haddock on eastern Georges Bank. CAFSAC Res. Doc. 91/86, 30 p.
1994. Assessment of haddock on eastern Georges Bank. Canadian Dep. Fisheries and Oceans (DFO) Res. Doc. 94/31, 38 p.
1995. Assessment of haddock on eastern Georges Bank. DFO Res. Doc. 95/6, 36 p.
1997. Assessment of haddock on eastern Georges Bank. DFO Res. Doc. 97/54, 72 p.

Gavaris S., and L. Van Eeckhaute, M. I. Buzeta, and J. Hunt.
1993. Yield projections for the transboundary cod and haddock resources on eastern Georges Bank. Canadian Dep. Fisheries and Oceans (DFO) Res. Doc. 93/71, 19 p.

Grosslein, M. D.
1962. Haddock stocks in the ICNAF Convention Area. International Commission for the Northwest Atlantic Fisheries (ICNAF) Redbook Part III: 124–131.

Halliday, R. G.
1988. Use of seasonal spawning area closures in the management of haddock fisheries in the Northwest Atlantic. Northwest Atlantic Fisheries Organization (NAFO) Sci. Coun. Studies 12:27–36.

Halliday, R. G., and A. T. Pinhorn.
1990. The delimitation of fishing areas in the northwest Atlantic. J. Northwest Atl. Fish. Sci. 10:1–51.

Lough, R. G., and G. R. Bolz.
1989. The movement of cod and haddock larvae onto the shoals of Georges Bank. J. Fish Biol. 35(suppl. A):71–79.

O'Brien, L., and R. W. Brown.
1996. Assessment of the Georges Bank haddock stock for 1994. New England Fisheries Steering Committee (NEFSC) Ref. Doc. 95–13.

Overholtz, W. J.
1985. Seasonal and age-specific distribution of the 1975 and 1978 year-classes of haddock on Georges Bank. Northwest Atlantic Fisheries Organization (NAFO) Sci. Coun. Studies 8:77–82.
1987. Factors relating to the reproductive biology of Georges Bank haddock (*Melanogrammus aeglefinus*) in 1977–83. J. Northwest Atl. Fish. Sci. 7:145–154.

Polacheck, T., D. Mountain, D. McMillan, W. Smith, and P. Berrien.
1992. Recruitment of the 1987 year class of Georges Bank haddock (*Melanogrammus aeglefinus*): the influence of unusual larval transport. Can. J. Fish. Aquat. Sci. 49: 484–496.

Schuck, H. A., and E. L. Arnold.
1951. Comparison of haddock from Georges and Browns bank. Fish. Bull. 52:177–185.

Smith, S. J.
1988. Abundance indices from research survey data. *In* D. Rivard (ed.), Collected papers on stock assessment methods, p. 16–40. CAFSAC Res. Doc. 88/61.

Trippel, E. A., M. J. Morgan, A. Fréchet, C. Rollet, A. Sinclair, C. Annand, D. Beanlands, and L. Brown.
1997. Changes in age and length at sexual maturity of northwest Atlantic cod, haddock and pollock stocks, 1972–1995. Can. Tech. Rep. Fish. Aquat. Sci. 2157:xii +120 p.

Walford, L. A.
1938. Effects of currents on distribution and survival of the eggs and larvae of haddock (*Melanogrammus aeglefinus*) on Georges Bank. Bull. U. S. Bur. Fish. 49:1–73.