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Dynamics of Yellowtail Flounder and American Plaice Populations on the Grand Bank

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Abstract

On the basis of recent analytical analyses and other data for yellowtail flounder (*Limanda ferruginea*) and American plaice (*Hippoglossoides platessoides*) stocks on the Grand Bank, effort *vs* catch-per-unit-effort regressions, stock-recruitment relationships, yield-per-recruit and total yield curves, and production rates were calculated. Yellowtail flounder seemed to be less dependent on environmental variations than American plaice. The latter species showed two levels in the stock recruitment relationship, total-yield curve and production rate, which were presumed to be related to ecological succession. For both species, the value of $F_{0.1}$ from the total-yield curve was greater than from the yield-per-recruit curve. American plaice seemed to be more sensitive to overfishing than yellowtail flounder, the latter being more resistent to collapse at the presently-used partial recruitment-at-age values. From a comparison of variations in year-class strength of the two flatfish stocks on the Grand Bank (NAFO Div. 3LNO) with that for Atlantic cod (*Gadus morhua*) in Div. 3NO, cod and yellowtail flounder appear to be r-strategists and American plaice is more of a k-strategist.

Introduction

The major fisheries of the Northwest Atlantic have been monitored and sampled for many years through the coordinated efforts of the International Commission for the Northwest Atlantic Fisheries (ICNAF) during 1951-79 and subsequently by the Northwest Atlantic Fisheries Organization (NAFO). Cohort analysis, catch projection and other statistical methods have been routinely used for stock assessments, and long annual series (20 years or more) of fishing mortality rates and other vital statistics are now common. However, these basic studies follow a set routine and do not often take account of ecological events. In addition to these statistical studies, extensive environmental data have been collected, but the two data series frequently cannot be correlated.

It may be better to explore the existence of stages in the dynamics of fish populations, which correspond to environmental events, such as warm and cold periods, than to attempt rough correlations of the biological and environmental data. If two or more biological stages in the dynamics of a stock can be identified, they might indicate the mechansims which govern the key parameters, such as those of the stock-recruitment relationship. If so, the correlation of biological and environmental data would have to be done separately for each stage or period. Another debatable question is the use of yield-per-recruit curves instead of yield curves, because fishery managers deal with yield rather than yield-per-recruit. Thus, the realistic optimum and maximum fishing mortality levels ($F_{0.1}$ and F_{max}) should be those of the yield curve instead of the yield-per-recruit curve. Some of these problems are examined in this paper for two flatfish populations of the Grand Bank off Newfoundland, namely yellowtail flounder (*Limanda ferruginea*) and American plaice (*Hippoglossoides platessoides*).

Methods

Larraneta (1981) described a method of using catch-per-unit-effort (CPUE) data in the ecological analyses of fisheries. When the points in the plot of CPUE against fishing effort fall consistently into two groups, ecological changes of the following types are indicated:

a) If the regression lines are parallel or diverge to the right (high effort values), the changes pertain to (i) physical environment (temperature, pollutants, settling surfaces, etc.), (ii) niche (relative abundance of prey, competitors and predators), and (iii) genotype composition.

b) If the regression lines converge to the right, the changes pertain to (i) fecundity, and (ii) larval food availability (normally changes in primary productivity).

If an effort-CPUE regression line is identified for a period of several years, the parameters of the general production model (Schaefer, 1954) for the period can be estimated from the equation

$$Y = af - bf^2$$

where Y is yield, f is effort, and a and b are specific constants of the regression line.

To study the stock-recruitment relationships of the two populations, the equations of Ricker (1975) and Beverton and Holt (1957) were used. These are respectively

$$R = aSe^{-bS} \quad \text{and} \quad R = 1/(a + b/S)$$

where R is number of recruits, S is stock size (numbers) and the constants (a, b) are specific parameters of each stock-recruitment relationship. The parameters of these equations were estimated by the following regressions:

$$\ln(R) - \ln(S) = \ln(a) - bs \quad \text{and} \quad 1/R = a + b/S$$

where *ln* refers to natural logarithms.

Empirical yield-per-recruit curves for yellowtail flounder and American plaice, based on the method of Thompson and Bell (1934), were reported by Brodie and Pitt (MS 1983a, MS 1983b). In the present paper, the yield function (eg. 4.4 of Beverton and Holt, 1957) was used to obtain a generalized curve, which provides estimates of total yield from the data for each species. Because $Y = (Y/R)R$, it was necessary to calculate recruitment as a function of fishing mortality (F).

Cohort analysis of a fish population gives average annual biomass ($\bar{B}$). The biomass at the beginning of year *t* is

$$B_t = (\bar{B}_{t-1} + \bar{B}_t)/2$$

and the biomass increment ($\triangle B$) during year *t* is

$$\triangle B_t = B_{t+1} - B_t + C_t$$

where C_t is the catch in year *t*. From the Schaefer (1954) equation,

$$\triangle B = aB(B_\infty - B) = AB - aB^2$$

so that $B_\infty = A/a$, and $B_{max} = A/2a$

where B_∞ is the biomass when $\triangle B = 0$, and B_{max} is the biomass when $\triangle B$ is maximum.

Yellowtail Flounder

CPUE-effort relationship

Data from Brodie and Pitt (MS 1983a) on total catch, effort and CPUE for yellowtail flounder in 1968–82 are listed in Table 1. The relationship between CPUE and effort is shown in Fig. 1. A regression line was not calculated because there was no observable trend in the data.

Stock-recruitment relationship

Data for calculating the stock-recruitment relationships were from the cohort analysis of Brodie and Pitt (MS 1983a). Recruitment (R) was defined as the number of age 4 fish in the population, and the parental stock (S) was considered in two ways: (i) as the spawning biomass (tons) of age 6 and older fish (S_B), and (ii) as an index of the number of eggs spawned (S_E) which was calculated for each year from the age composition (age 6+) of the population (Brodie and Pitt, MS 1983a) and the fecundity-age relationship of Pitt (1971), i.e.

$$\log F = 4.31 + 2.10 \log A$$

where A is age in years and *log* refers to base 10 logarithms. The estimated values of recruitment, spawning biomass and egg-number index are given in Table 2.

Both sets of data were used to calculate stock-recruitment relationships according to the Beverton and Holt (1957) and Ricker (1975) models, and the specific values of the parameters (a, b) for each are given in Table 3. In the case of the Beverton-Holt model, the negative values of *b* implies that the model may not be suitable for analysis of the yellowtail flounder population, although the correlation coefficients (0.64 and 0.57) were reasonable. For the Ricker model, the correlation coefficients were much higher

TABLE 1. Yellowtail flounder catch and effort data for the otter-trawl fishery on the Grand Bank, 1968–82. (Data from Brodie and Pitt, MS 1983a.)

Year	Catch (tons)	Effort (hours)	CPUE
1968	13,340	18,921	0.705
1969	15,708	25,750	0.610
1970	26,426	44,191	0.598
1971	37,342	62,236	0.600
1972	39,259	64,677	0.607
1973	32,815	50,876	0.645
1974	24,318	57,762	0.421
1975	22,894	56,950	0.402
1976	8,057	24,268	0.332
1977	11,638	27,513	0.432
1978	15,466	31,181	0.496
1979	18,351	35,495	0.517
1980	12,377	19,939	0.640
1981	14,580	23,745	0.614
1982	11,631	22,154	0.525

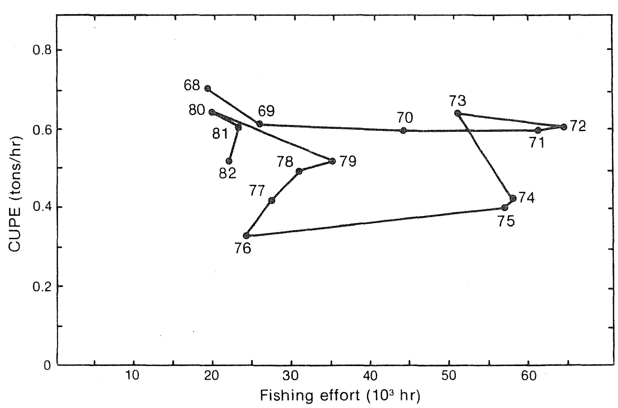

Fig. 1. Yellowtail flounder: relationship between catch-per-unit effort and fishing effort, 1968–82.

TABLE 2. Yellowtail flounder: estimates of spawning stock (age 6+) as egg number, biomass (age 6+) and recruitment at age 4.

Year	Egg number (10^{10})	Biomass (tons)	Recruits (10^3)
1964	—	—	156,799
1965	—	—	147,013
1966	—	—	119,893
1967	—	—	110,608
1968	7,375	25,926	121,788
1969	11,237	40,372	113,159
1970	14,686	50,199	75,826
1971	15,610	48,747	71,914
1972	12,794	33,846	82,921
1973	9,006	24,050	102,114
1974	7,165	21,035	131,122
1975	6,827	18,164	125,633
1976	5,071	19,200	122,718
1977	6,549	18,901	80,055[a]
1978	7,388	22,586	93,617[a]
1979	8,500	21,567	—
1980	9,992	41,608	—
1981	13,431	41,419	—
1982	15,679	49,396	—

[a] Recruitment values for the 1977 and 1978 year-classes are dependent on the input values of partial recruitment and terminal F in the last year of the cohort analysis, and are probably underestimated.

TABLE 3. Yellowtail flounder: parameters (a, b) of the stock-recruitment curves, and correlation coefficients (r) of the regression lines.

Stock-recruit curve	Parameters a	Parameters b	r
	Ricker model		
S_E–R	44.4114	1.460×10^{-4}	0.96
S_B–R	12.8381	4.294×10^{-5}	0.95
	Beverton-Holt model		
S_E–R	1.45×10^{-5}	-3.55×10^{-2}	0.64
S_B–R	1.42×10^{-5}	-10.08×10^{-2}	0.57

(0.96 and 0.95), and the resultant stock-recruitment relationships were considered further.

The relationships between ln(R/S_B) and S_B and between ln(R/S_E) and S_E are shown in Fig. 2. In the first case where S_B represents the spawning biomass (tons) of age 6 and older fish (Fig. 2A), two regression lines are implied, but they are not sufficiently distinct to be treated separately. In the second case where the parental stock (age 6+) is represented by S_E in terms of egg number (Fig. 2B), a linear trend is clearly indicated. Although only the S_E–R relationship, with 95% confidence limits, is illustrated in Fig. 3, the predicted recruitment values from both the S_E–R and S_B–R curves for wide ranges of S_E and S_B levels respectively are given in Table 4. Maximum recruitment is indicated when the spawning biomass is about 25,000 tons.

Yield

The rather distinct stock-recruitment relationship for yellowtail flounder allows an examination of the

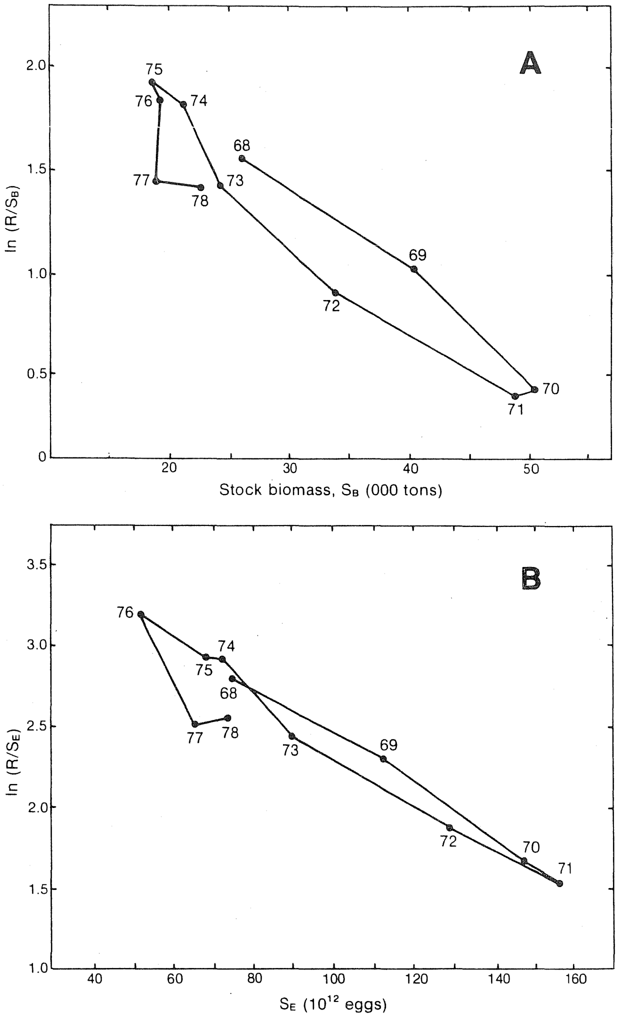

Fig. 2. Yellowtail flounder: relationship between ln (R/S) and parental stock size, where (**A**) stock size is expressed as biomass S_B and (**B**) stock size is expressed as egg number index S_E (from Table 2).

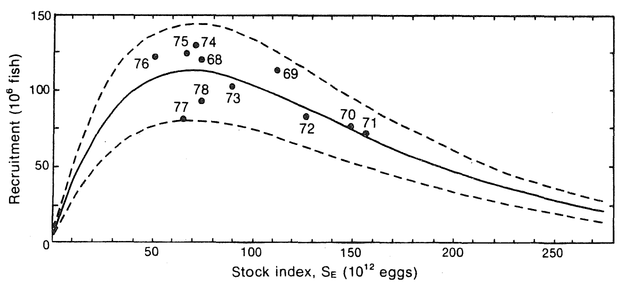

Fig. 3. Yellowtail flounder: stock-recruitment curve with 95% confidence limits, based on the Ricker model.

difference between a yield-per-recruit curve and a total yield curve. To draw the yield-per-recruit curve according to the yield equation of Beverton and Holt (1957), the following parameters were chosen:

W_∞ = 1.1 kg (deduced from Brodie and Pitt, MS 1983a)

M = 0.3 (according to Brodie and Pitt, MS 1983a)

K	= 0.28	(according to Pitt, 1974)
t_o	= 0.63 yr	(according to Pitt, 1974)
t_c	= 6.0 yr	(deduced from Brodie and Pitt, MS 1983a)
t'_λ	= 11 yr	(according to Brodie and Pitt, MS 1983a)

Specific values of F and Y/R from the yield-per-recruit curve of Brodie and Pitt (MS 1983a), which was based on the method of Thompson and Bell (see Ricker, 1975, page 236), and from this study are as follows:

Source	$F_{0.1}$	$Y/R(F_{0.1})$	F_{max}	$Y/R(F_{max})$
Brodie-Pitt	0.518	0.186 kg	0.616	0.216 kg
This study	0.628	0.312 kg	∞	0.383 kg

Estimates of F_{max} are very sensitive to small changes in the parameters, but F_{max} of a yield-per-recruit curve does not have great descriptive value. The curve better describes $F_{0.1}$, which was determined in this study as the point where the increment is 10% of the yield when F is 0.01.

To estimate the steady-state recruitment of the reproduction curves, the following partial recruitment values (Brodie and Pitt, MS 1983a) were used: 0.01 for age 4, 0.13 for age 5, 0.46 for age 6 and 1.00 for age 7 and older fish. Fecundity indices at age (I_t) were calculated from Pitt's (1971) expression relating fecundity (Fe) and age (t), where $I_t = Fe \times 10^{-7}$, as follows:

$I_6 = 0.087962$ $\quad I_9 = 0.206020$

$I_7 = 0.121536$ $\quad I_{10} = 0.257040$

$I_8 = 0.160876$ $\quad I_{11} = 0.313996$

TABLE 4. Yellowtail flounder: predicted recruitment from the stock-recruitment relationships for wide ranges of egg number and biomass, based on the Ricker (1975) model.

S_E–R		S_B–R	
Egg number (10^{10})	Recruits (10^3)	Biomass (tons)	Recruits (10^3)
500	20,642	5,000	51,787
2,000	66,330	10,000	83,561
3,500	93,248	15,000	101,123
5,000	107,011	20,000	108,778
6,500	111,754	25,000	109,699
8,000	110,491	30,000	106,203
9,500	105,403	35,000	99,963
11,000	98,042	40,000	92,168
12,500	89,499	45,000	83,654
14,000	80,524	50,000	74,983
15,500	71,617	55,000	66,549
17,000	63,099	60,000	58,571
18,500	55,162	65,000	51,192
20,000	47,905	70,000	44,477
21,500	41,370	75,000	38,446
23,000	35,552	80,000	33,085
24,500	30,422	85,000	28,361
26,000	25,935	90,000	24,225

Recruitment (age 4) and stock biomass (age 4+) curves, as functions of fishing mortality (F), are shown in Fig. 4, and the yield-per-recruit and total-yield curves are shown in Fig. 5. Furthermore, a series of population and fishery parameters were calculated under the assumption that the age at first capture (t_c) is 6 years (Table 5). Of course, all fishing parameters will vary with changes in t_c except those which pertain to the "virgin" population.

Productivity

The rate of production of a stock is the ratio of the increment between successive annual biomass values and the average biomass ($\triangle B/\bar{B}$). Average biomass values for age 4 and older yellowtail flounder were obtained from cohort analysis of Brodie and Pitt (MS 1983a). The relationship between rate of production ($\triangle B/\bar{B}$) and average biomass ($\bar{B}$) is shown in Fig. 6. It is evident from the linear regression that, if $\triangle B/\bar{B} = 0$, B_∞ = 173,614 tons and consequently B_{max} = 86,807 tons. Actually, this value of B_{max} is very similar to the value of $B_{4+}(F_{max})$ in Table 5 (84,119 tons), the first value being derived from the Schaefer (1954) general production equation and the latter from the Beverton and Holt

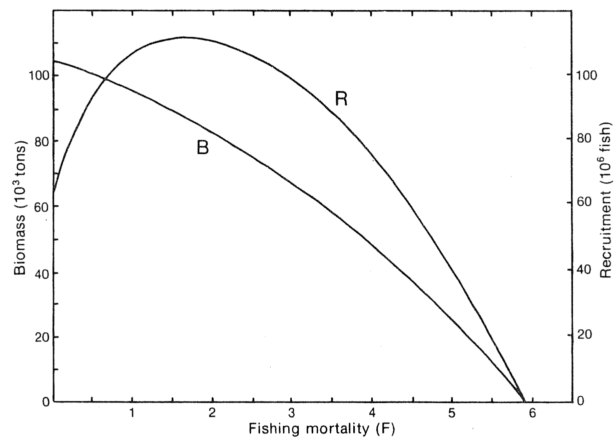

Fig. 4. Yellowtail flounder: recruitment and biomass as functions of fishing mortality.

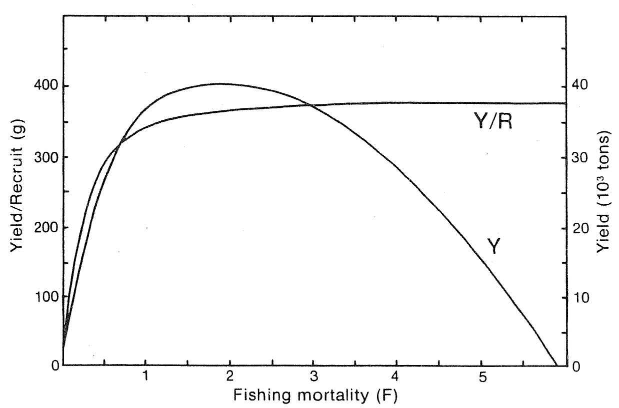

Fig. 5. Yellowtail flounder: yield-per-recruit and yield curves as functions of fishing mortality.

TABLE 5. Yellowtail flounder: resultant population and fishery parameter values, with the age at first capture as 6 years.

Parameter	Value	Parameter	Value
R(virgin)	= 62,598,000	F_{max}(Y)	= 1.87
B_{4+}(virgin)	= 105,341 tons	R(F_{max})	= 111,450,000
B_{6+}(virgin)	= 75,735 tons	B_{4+}(F_{max})	= 84,119 tons
B_{4+}(max)	= virgin	B_{6+}(F_{max})	= 31,876 tons
F_{ext}(R = 0)	= 5.914	Y(F_{max})	= 40,633 tons
$F_{0.1}$(Y)	= 1.08	R_{max}	= 111,904,400
R($F_{0.1}$)	= 108,585,000	B_{4+}(R_{max})	= 87,331 tons
B_{4+}($F_{0.1}$)	= 94,463 tons	B_{6+}(R_{max})	= 34,816 tons
B_{6+}($F_{0.1}$)	= 43,372 tons	F(R_{max})	= 1.637
Y($F_{0.1}$)	= 37,623 tons	Y(R_{max})	= 40,427 tons

(1957) analytical production equation. Because both equations are theoretically independent of each other, it may be concluded that these estimates of about 85,000 tons provide an indication of the equilibrium biomass level. It must not be forgotten, however, that the production curves of both equations depend critcally on the age at first capture or on the partial recruitment pattern and that the estimate of 85,000 tons is based on t_c being 6 years.

American Plaice

CPUE-effort relationship

Data from Brodie and Pitt (MS 1983b) on total catch, fishing effort and CPUE for 1965-82 are listed in Table 6. A plot of the CPUE and fishing effort values (Fig. 7) implied the use of two regression lines: one for the 1965-71 period, and the other for the 1973-82 period, with 1972 being a transitional year. The corresponding general production curves are shown in Fig. 8. The relevant fishery parameters for the 1965-71 and 1973-82 periods are listed in Table 7. Comparison of catches in Table 6 with the maximum sustainable yield

TABLE 6. American plaice catch and effort data for the otter-trawl fishery on the Grand Bank, 1965-82. (Data from Brodie and Pitt, MS 1983b.)

Year	Catch (tons)	Effort (hours)	CPUE
1965	51,304	56,836	0.905
1966	53,273	60,813	0.876
1967	62,875	76,864	0.818
1968	59,164	94,060	0.629
1969	67,322	122,850	0.548
1970	60,379	117,013	0.516
1971	60,724	126,772	0.479
1972	50,708	105,422	0.481
1973	40,986	79,276	0.517
1974	37,727	86,929	0.434
1975	36,479	87,689	0.416
1976	43,735	101,709	0.430
1977	40,306	99,275	0.406
1978	43,588	94,756	0.460
1979	43,420	87,717	0.495
1980	46,835	78,451	0.597
1981	47,897	84,030	0.570
1982	44,703	79,542	0.562

(MSY) levels in Table 7 indicates that yields were generally close to the MSY levels during 1967-82.

Stock-recruitment relationship

Data for calculation of the stock-recruitment relationships for American plaice were from the cohort analysis of Brodie and Pitt (MS 1983b). Annual recruitment (R) was defined as the number of age 6 fish in the population, and the parental stock (S) was judged to consist of age 11 and older fish, on the basic of Pitt's (1974) age-at-maturity data. Two aspects of the parental stock were considered: (i) as the stock biomass (tons) of age 11 and older fish (S_B), and (ii) from an index of the number of eggs spawned (S_E), which was calculated for each year from the age composition (age 11+) of the population (Brodie and Pitt, MS 1983b) and a fecundity-at-age relationship (Pitt, 1964), i.e.

$$\log F = 1.3367 + 1.1781 \log A$$

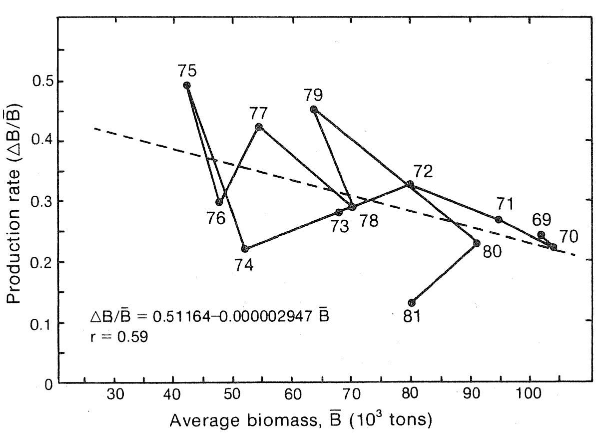

Fig. 6. Yellowtail flounder: relationship between rate of production ($\Delta B/\bar{B}$) and average biomass ($\bar{B}$), 1969-81.

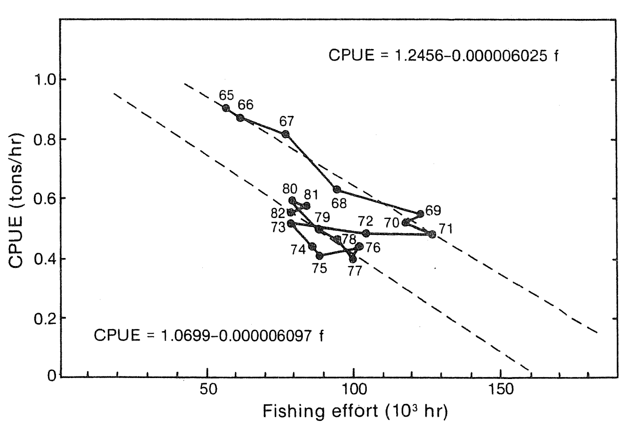

Fig. 7. American plaice: relationship between catch-per-unit-effort and fishing effort, 1965-82.

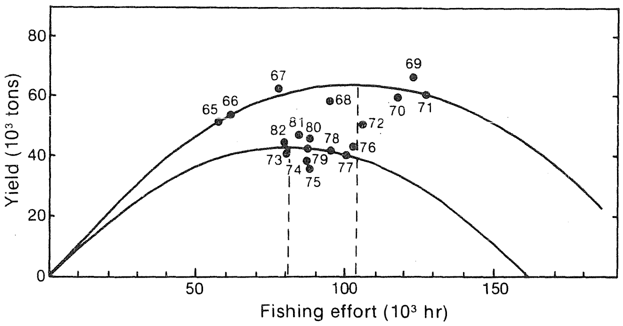

Fig. 8. American plaice: general production curves for the 1965–71 and 1973–82 periods.

TABLE 7. American plaice: fishery parameters from the general production model analyses in Fig. 7 and 8.

Parameter	1965–71	1973–82
f_{MSY} (hours)	103,350	80,900
MSY (tons)	64,372	43,296
2/3 f_{MSY} (hours)	68,900	53,933
Y(2/3 f_{MSY}) (tons)	57,217	38,477
CPUE (f_{MSY}) (tons)	0.62	0.54
CPUE (2/3 f_{MSY}) (tons)	0.83	0.71

where A is age in years. The estimated values of recruitment, spawning biomass and egg number index are given in Table 8.

The distribution of points in Fig. 7 implies that there may be two stages in the stock-recruitment relationship. From the trends in recruitment of the 1954–76 year-classes and in spawning stock during 1960–82 (Fig. 9), the increase in spawning stock during 1960–65 coincided with a decrease in strength of the 1960–65 year-classes, and there was a reversal of the trends during 1965–70, with the 1970 year-class being the largest on record. If the average level of recruitment is considered to be 200 million fish, the 1967–73 year-classes were above average strength. In Fig. 10, these points exhibit a linear trend, with those for 1960–66 and 1974–76 falling below the line. Therefore, it is hypothesized that there were two ecological states: one for the 1960–66 and 1974–76 year-classes and the other for the 1967–73 year-classes.

Both sets of stock and recruitment data (Table 8) were used to calculate the parameters of stock-recruitment relationships by the Ricker (1975) and Beverton and Holt (1957) models for the two ecological states separately and for the entire period (Table 9). The correlation coefficients (r) indicate that the Ricker model is much more appropriate for analysis of the American plaice data than the Beverton-Holt model. Because both S_E (egg number index) and S_B (age 11+ biomass) are equally highly correlated with recruitment, only one set of stock-recruitment curves is illustrated, namely those for spawning biomass (Fig. 11.)

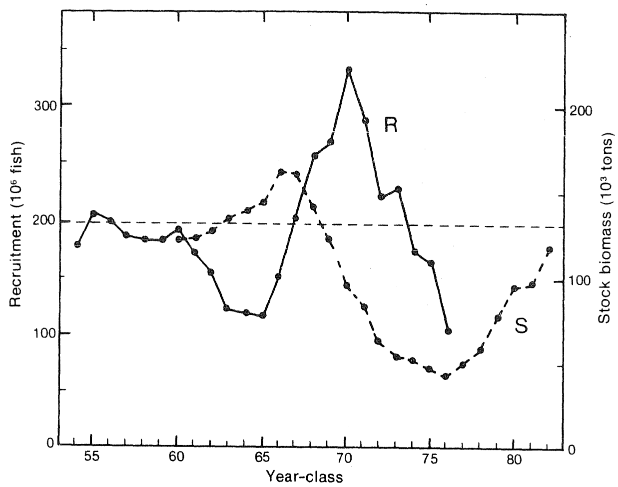

Fig. 9. American plaice: trends in recruitment (age 6) and stock biomass (age 11+) for the 1954–76 year-classes.

TABLE 8. American plaice: estimates of spawning stock (age 11+) as egg number, biomass (age 11+) and recruitment at age 6.

Year	Egg number (10^{10})	Biomass (tons)	Recruits (10^3)
1954	—	—	177,500
1955	—	—	206,613
1956	—	—	200,181
1957	—	—	186,373
1958	—	—	184,119
1960	6,680	123,002	183,930
1961	6,623	123,437	193,320
1962	6,851	127,650	171,843
1963	7,239	135,947	157,020
1964	7,376	140,707	122,383
1965	7,427	144,590	120,957
1966	7,644	163,135	116,195
1967	7,769	161,241	152,962
1968	6,920	141,917	203,439
1969	6,150	122,730	258,434
1970	5,432	96,212	269,084
1971	4,725	82,727	334,262
1972	3,984	63,180	289,648
1973	3,044	54,060	222,749
1974	2,394	52,035	229,788
1975	2,257	47,542	173,950
1976	2,263	41,927	165,626[a]
1977	2,497	50,108	106,931[a]
1978	3,300	58,998	—
1979	4,264	79,420	—
1980	5,803	95,728	—
1981	7,530	98,154	—
1982	7,473	118,665	—

[a] Recruitment values for the 1976 and 1977 year-classes are dependent on the input values of partial recruitment and terminal F in the last year of the cohort analysis and are probably underestimated.

Predicted recruitment values for the S_B–R curves over a wide range of S_B levels are given in Table 10. Maximum recruitment is indicated when the spawning biomass is 95,000 tons for curve A and about 85,000 tons for curves B and C.

Yield

The Beverton and Holt (1957) yield equation was

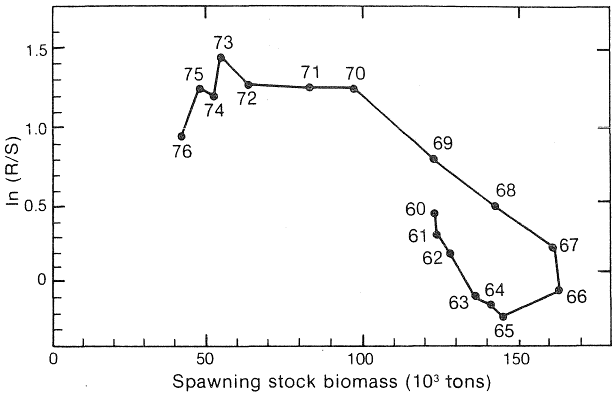

Fig. 10. American plaice: relationship between ln (R/S) and spawning stock biomass (S_B), 1960–77 (from Table 8).

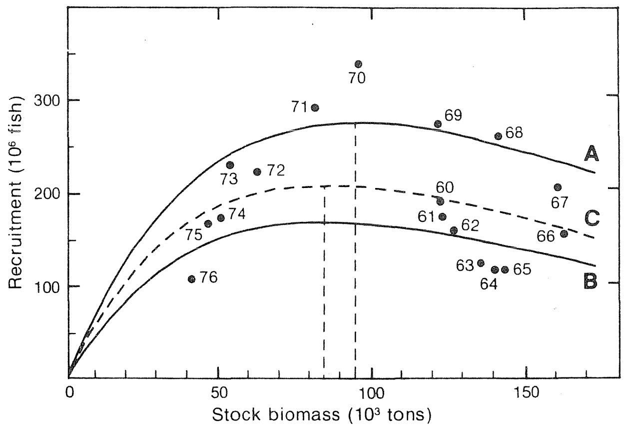

Fig. 11. American plaice: stock-recruitment curves, based on the Ricker model, with curve **A** for 1967–73, curve **B** for 1960–66 and 1974–76, and curve **C** for the entire 1960–76 period.

used to calculate the yield-per-recruit curve for American plaice with the following parameters:

W_∞	= 2.5 kg	(deduced from Brodie and Pitt, MS 1983b)
M	= 0.2	(according to Brodie and Pitt, MS 1983b)
K	= 0.065	(deduced from Pitt, 1975)
t_o	= 0.45 yr	(deduced from Pitt, 1975)
t_c	= 10.3 yr	(deduced from Brodie and Pitt, MS 1983b)
t_λ	= 20 yr	(according to Brodie and Pitt, MS 1983b)

Specific values of F and Y/R from the yield-per-recruit curve of Brodie and Pitt (MS 1983b), which was based on the method of Thompson and Bell (see Ricker, 1975, p. 236), and from this study are as follows:

Source	$F_{0.1}$	$Y/R(F_{0.1})$	F_{max}	$Y/R(F_{max})$
Brodie-Pitt	0.262	0.178 kg	3.136	0.214
This study	0.305	0.189 kg	3.150	0.217

The two curves were very similar and the F and Y/R values may be considered as being equivalent.

Under the hypothesis of two ecological states, two curves of steady-state recruitment as functions of fishing mortality can be calculated. The following partial recruitment (PR) values of Brodie and Pitt (1983b) were used: 0.025 for age 6, 0.10 for age 7, 0.22 for age 8, 0.30 for age 9, 0.47 for age 10, 0.58 for age 11, 0.73 for age 12, and 1.00 for age 13 and older fish. The following weight-at-age values from Brodie and Pitt (MS 1983b) were taken as fecundity indices (I_t):

I_{11} = 0.700	I_{14} = 1.250	I_{17} = 2.022	I_{20} = 2.428
I_{12} = 0.880	I_{15} = 1.524	I_{18} = 2.233	
I_{13} = 1.020	I_{16} = 1.803	I_{19} = 2.401	

Recruitment (age 6) and stock biomass (age 6+) curves as functions of fishing mortality for the two ecological periods (1967–73, and 1960–66, 74–76) are shown in Fig. 12. The overall yield-per-recruit curve and the total-yield curves for the two periods are shown in Fig. 13. Furthermore, a series population and fishery parameters were calculated under the assumption that the mean age at first capture (t_c) was 10.3 years (Table 11).

It is worth noting in Fig. 12 that the maximum biomass may not necessarily occur when the stock is

TABLE 9. American plaice: parameters (a, b) of the stock-recruitment curves, and the correlation coefficient (r) of the regression lines, for the two ecological periods and for the entire period.

		Ricker model			Beverton-Holt model		
Curve	Period	a	b	r	a	b	r
S_E–R	1960–66, 74–76	111.385	2.398×10^{-4}	0.95	7.038×10^{-6}	-2.160×10^{-5}	0.002
	1967–73	146.912	2.020×10^{-4}	0.93	3.742×10^{-6}	1.128×10^{-3}	0.119
	1960–76	134.249	2.377×10^{-4}	0.85	5.392×10^{-6}	1.745×10^{-3}	0.002
S_B–R	1960–66, 74–76	5.4212	1.187×10^{-5}	0.95	6.807×10^{-6}	1.737×10^{-2}	0.082
	1967–73	7.9402	1.064×10^{-5}	0.96	3.796×10^{-6}	1.555×10^{-2}	0.109
	1960–76	6.7450	1.196×10^{-5}	0.86	5.462×10^{-6}	2.587×10^{-2}	0.079

TABLE 10. American plaice: predicted numbers of recruits in relation to biomass from the stock-recruitment relationships for two ecological periods and for the entire period.

Biomass (tons)	Predicted recruitment (10^3) 1960-67, 74-76	1967-73	1960-76
10,000	48,142	71,389	59,849
20,000	85,505	128,369	106,210
30,000	113,897	173,122	141,361
40,000	134,860	207,535	167,242
50,000	149,701	233,238	185,494
60,000	159,528	251,641	197,509
70,000	165,279	263,954	204,461
80,000	167,741	271,219	207,338
90,000	167,581	274,329	205,969
100,000	165,354	274,049	204,051
110,000	161,525	271,033	199,163
120,000	156,480	265,834	192,785
130,000	150,540	258,924	185,315
140,000	143,969	250,701	177,080
150,000	136,982	241,501	168,349
160,000	129,755	231,605	159,336
170,000	122,430	221,246	150,217
180,000	115,118	210,620	141,130
190,000	107,908	199,885	132,183
200,000	100,870	189,172	123,460
210,000	94,055	178,585	115,025
220,000	87,502	168,209	106,923
230,000	81,237	158,108	99,186
240,000	75,279	148,333	91,836
250,000	69,636	138,920	84,882

unexploited (e.g. the 1967–73 biomass curve indicates a maximum at F = 0.36). This anomaly may be due to some density-dependent factor. Theoretical formulations for the general production model are based on the assumption that maximum biomass (B_∞) occurs when the stock is unexploited and that the act of fishing reduces the biomass from its "virgin" level. For the same reason and because CPUE is considered to be a linear index of stock biomass, it is also assumed that the B–F and CPUE-F curves have the same shape. However, if fishing mortality varies due to partial recruitment of some age-groups and if the CPUE-F relationship is linear, the B–F relationship will not be so. Nevertheless, for a specific pattern of partial recruitment, the empirical CPUE-F relationship is useful for practical purposes. The contradiction between the 1967–73 biomass curve of Fig. 12 and those derived from the general production model is due to the fact that the latter does not take into account the effects of fishing mortality on recruitment.

Productivity

Annual average biomass values for age 6 and older fish, that were used in illustrating the relationship between rate of production ($\Delta B/\bar{B}$) and biomass (Fig. 14), were obtained from the cohort analysis of Brodie and Pitt (MS 1983b). This relationship is quite unexpected, because theory indicates that it should be a negative linear regression, similar to that for yellowtail flounder (Fig. 6). In fact, the points tend to follow a cyclic pattern.

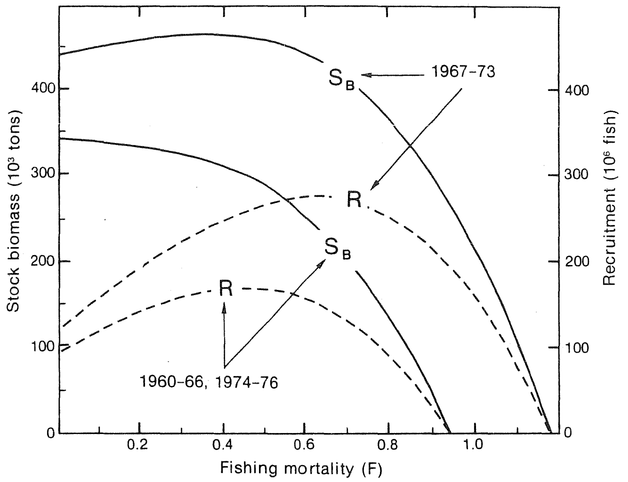

Fig. 12. American plaice: recruitment and biomass as functions of fishing mortality for the ecological periods 1967–73 and 1960–66, 74–76.

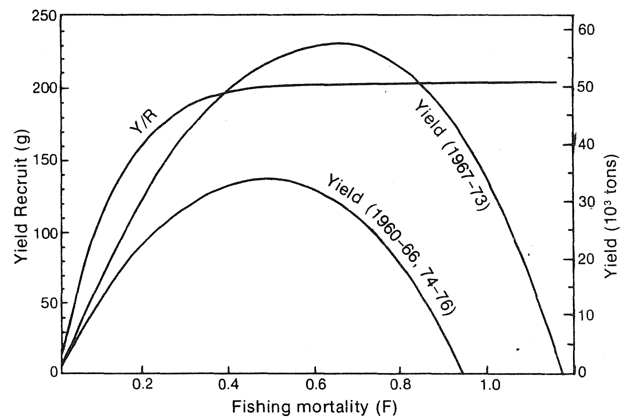

Fig. 13. American plaice: yield-per-recruit, and total yield curves for the 1967–73 and 1960–66, 74–76 periods.

Biological productivity of a fishery resource depends on recruitment, growth and natural mortality, the most variable factor being recruitment, which is considered to occur at age 6 in this American plaice stock. If the high biomass increments for 1973–78 (Fig. 14) are indicative of a high stock-recruitment relationship, they are related to the ecological state of the population 6 years earlier (i.e. the 1967–72 period), which is consistent with the linear trend for these years in Fig. 10. From Fig. 14, it seems that the cycle has a period of 13–14 years.

Year-class Prognosis

The initial intention of this study was to test the value of the method in predicting year-classes. Recruitment (age 4) to the yellowtail flounder stock during 1983–86 will depend on the sizes of the spawning stock during 1979–82 (Table 2), and recruitment (age 6) to the American plaice stock during 1983–88

TABLE 11. American plaice: resultant population and fishery parameter values for two ecological periods, with 10.3 yr as the age at first capture.

Parameter	1960-66 1974-76	1967-73
R(virgin)	93,033,000	119,577,000
B_{6+}(virgin)	342,905 tons	440,742 tons
B_{11+}(virgin)	211,647 tons	272,036 tons
$F_{ext}(R = 0)$	0.946	1.179
$F_{0.1}(Y)$	0.429	0.569
$R(F_{0.1})$	167,760,000	273,245,000
$B_{6+}(F_{0.1})$	303,702 tons	444,335 tons
$B_{11+}(F_{0.1})$	88,389 tons	103,614 tons
$Y(F_{0.1})$	33,901 tons	57,032 tons
$F_{max}(Y)$	0.486	0.641
$R(F_{max})$	167,223,000	274,225,000
$B_{6+}(F_{max})$	298,892 tons	433,121 tons
$B_{11+}(F_{max})$	86,813 tons	96,056 tons
$Y(F_{max})$	34,353 tons	57,762 tons
R_{max}	167,959,200	274,585,100
$B_{6+}(R_{max})$	298,891 tons	433,121 tons
$B_{11+}(R_{max})$	84,210 tons	75,840 tons
$F(R_{max})$	0.448	0.617
$Y(R_{max})$	34,158 tons	57,681 tons
B_{6+}max	virgin	464,113 tons
$F(B_{6+}$max)	0.00	0.361
$R(B_{6+}$max)	virgin	240,389,000
$B_{11+}(B_{6+}$max)	virgin	151,447 tons
$Y(B_{6+}$max)	0.0	47,191 tons

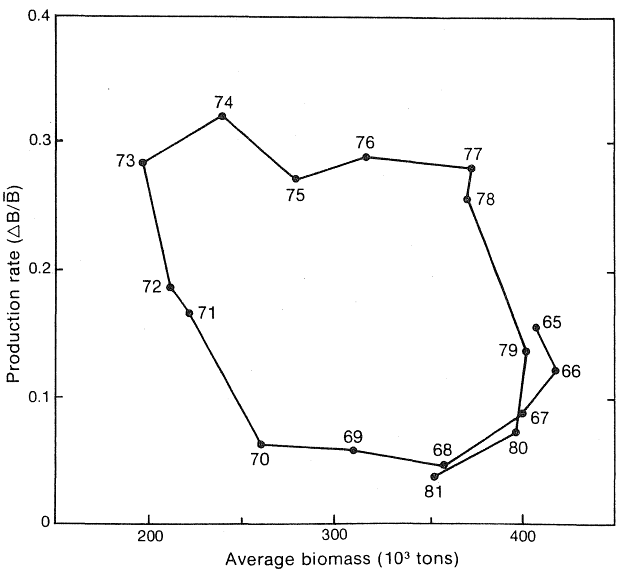

Fig. 14. American plaice: relationsip between rate of production ($\Delta B/\bar{B}$) and average biomass ($\bar{B}$), 1965–81.

will depend on the sizes of the spawning stock during 1977–82 (Table 8). The Ricker equation was used for these prognoses, and both the egg number index (S_E) and spawning biomass (S_B) were taken as the parental stocks (age 6+ for yellowtail flounder and age 11+ for American plaice).

According to the prognosis for yellowtail flounder (Table 12), recruitment is expected to decrease significantly from 1983 to 1986, because the spawning biomass (age 6+) in the early 1980's (Table 2) exceeded the $B_{6}+(R_{max})$ level of 34,816 tons (Table 5). From the prognosis for American plaice (Table 12), recruitment is expected to be relatively stable during 1983–88 if no ecological change occurs, although the spawning biomass (age 11+) in the early 1980's (Table 8) exceeded the $B_{11}+(R_{max})$ level of 84,210 tons (Table 11).

TABLE 12. American plaice: prognoses of recruitment (age 6), based on the Ricker model, with parental stock size represented by egg number index (S_E) and spawning biomass (S_B) of age 11+ fish.

Stock-recruit curve	Year	No. of recruits (10^3) S_E	S_B
	Yellowtail flounder		
Fig. 3	1983	109,132	109,672
	1984	103,177	89,484
	1985	83,943	89,804
	1986	70,576	76,037
	American plaice		
Fig. 11(A)	1983	221,523	233,272
	1984	248,925	250,090
	1985	264,730	270,919
	1986	264,013	274,539
	1987	241,692	274,325
	1988	242,641	266,636
Fig. 11(B)	1983	152,826	149,832
	1984	166,597	158,742
	1985	170,834	167,676
	1986	160,743	166,526
	1987	137,854	165,898
	1988	138,693	157,212
Fig. 11(C)	1983	185,165	185,655
	1984	202,190	196,552
	1985	207,752	207,267
	1986	196,114	205,570
	1987	168,799	204,754
	1988	169,807	193,707

Ecological Cycles

Variations in recruitment to yellowtail flounder and American plaice stocks of the Grand Bank (Div. 3LNO) are compared with the variation in recruitment to the Atlantic cod (*Gadus morhua*) stock in Div. 3NO (Fig. 15), the latter data being taken from Bishop and Gavaris (MS 1983). It is evident that the cod and yellowtail flounder year-classes vary synchronously, whereas the trend in American plaice recruitment tends to follow the opposite pattern. This observation is confirmed by the high positive correlation between cod and yellowtail flounder and the negative correlations for the other comparisons (Table 13). It seems, therefore, that the population dynamics of cod and yellowtail flounder in the area respond to the same ecological stimuli and that the response is different for American plaice. Examination of the stock-recruitment curves

TABLE 13. Correlation coefficients for relationships between recruitment of cod, American plaice and yellowtail flounder, based on data plotted in Fig. 15.

Comparison	r	Sign.
Cod-American plaice	–0.54	0.01<P<0.02
Cod-Yellowtail flounder	0.74	P<0.01
Yellowtail-American plaice	–0.80	P<0.01

indicates that the curve for yellowtail flounder (Fig. 4) is more skewed to the left than that for American plaice (Fig. 11). According to Cushing and Harris (1973), it is generally accepted that recruitment to flatfish populations is almost constant over a wide range of parental stock size, and thus the more appropriate model should be that of Beverton and Holt (1957). However, for the yellowtail flounder and American plaice stocks of the Grand Bank, a better fit was obtained with the Ricker (1975) model, especially for yellowtail flounder. Because one of the determinants of the Beverton-Holt model is spatial limitation of the prerecruit habitat, it seems that these flatfish species are not affected by space limitation.

Very skewed stock-recruitment curves are usually characteristic of highly fecund species which are able to produce large generations of young at relatively low levels of parental stock size. Thus, yellowtail flounder is considered to be more of an r-strategist than American plaice. The stock-recruitment curve for cod is characteristically skewed to the left (Cushing and Harris, 1973; Larraneta, 1983), like that of yellowtail flounder.

According to Larraneta and Vasquez (MS 1982), the largest year-classes of cod in the Arctic seas appear at the beginning of a polar ecological cycle. It is surprising that cod (a large and long-lived fish) can be considered as an r-strategist, but ecological cycles occur in the regions that are inhabited by cod in the North Atlantic. The longevity of cod allows it to survive from one favorable period to another, and its high fecundity allows it to behave as an "opportunistic" species at the beginning of such periods.

American plaice shows a stock-recruitment relationship that is better fitted to the Ricker model than to the Beverton-Holt model, but the former is not very different from the latter. Thus, American plaice can be considered to be more of a k-strategist than yellowtail flounder. This can also be deduced from the later age at maturity (up to 11 yr) for female American plaice. The concept of American plaice being a k-strategist agrees with the observation in Fig. 7 that the regression lines diverge to the right. According to Larraneta (1981), this indicates that density-independent factors, such as ecological succession, may play an important role. It also agrees with the data in Fig. 14, where the points could be interpreted as a sequential ecological cycle.

With respect to yellowtail flounder, the problem is knowing what roles are played by the environment and the precise form of the stock-recruitment relationship in determining variations in year-class strength. The stock-recruitment relationship in Fig. 3 seems to be quite clear, but the data in Fig. 1 does not show a definite trend, indicating the existence of an environmental signal. Pitt (1970) related the apparent increase in abundance of yellowtail flounder on the Grand Bank during 1961–68 to a general upward trend in bottom temperatures and the drastic reduction in the haddock population. It was noted previously that year-class variation in yellowtail flounder was positively correlated with year-class variation in cod (Fig. 15, Table 13), but the variation in year-class strength of cod was much greater than that for yellowtail flounder. Thus, the effect of environmental factors on the stock-recruitment pattern for yellowtail flounder may have been much less than that for cod.

From the foregoing analysis, the following ecological cycle can be inferred for the period under study. The early 1960's was the beginning of a favorable period, which allowed production of a few very large year-classes of cod. As the ecosystem matured during the late 1960's and 1970's, the cod year-class became smaller and smaller. The yellowtail flounder year-classes showed a similar evoluation but in a less pronounced way. Maturation of the ecosystem favored the development of some large year-classes of American plaice, but the "favorable" period ended in the 1970's with a consequent reduction in the year-class strengths of all three species.

According to Pitt (1975), the age at 50% maturity of American plaice in Div. 3L and 3N during 1969–72 was significantly lower than in earlier years. Beacham (1983) reported that the median length and age at sexual maturity of Atlantic cod on the Scotian Shelf declined by about 50% for most stocks between 1959

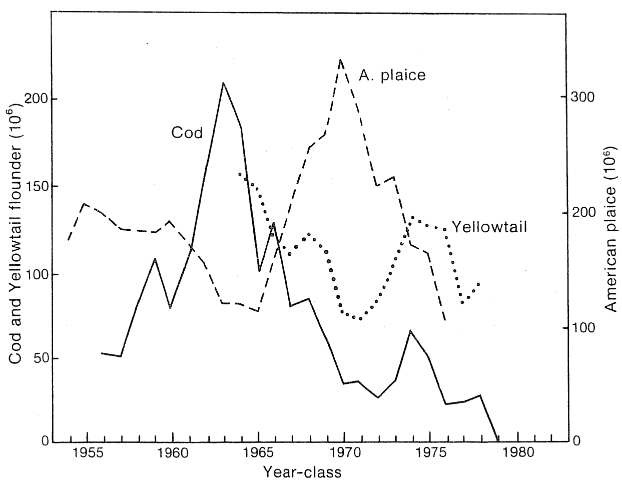

Fig. 15. Variations in year-class strengths of cod, yellowtail flounder and American plaice, 1954–79 year-classes.

and 1979. He speculated that these changes may have resulted from removal of larger, older immature fish by the commercial fishery, or a general decline in stock biomass during 1960–75 due to overexploitation, or to a combination of both processes. Long-lived species, which are heavily exploited, frequently suffer a decline in median age at maturity. This implies that fishing may result in genetic selection by favoring r-strategist genotypes. A change in genetic composition of a stock produces a change in the density-independent parameter A of the Ricker equation (Larraneta, 1979, 1981). Thus, exploitation may result in the selection of genotypes which generate more dome-shaped stock-recruitment curves (i.e. populations which are more resistent to overfishing and collapse.)

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