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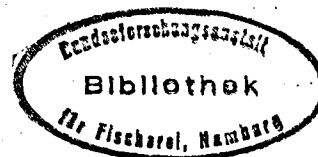
CM 1968/F:14

Demersal Fish (Northern Committee)

Stock and recruitment relationships in four north Atlantic cod stocks

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Introduction

Readers will be familiar with a widely held dogma of fisheries biology, that the size of a year-class is independent of spawning stock size over the wide range of spawning stock sizes that have been observed in exploited fisheries. The presumption is that the pelagic environment of the larval fish can support only a finite number of young fish and that this capacity can be satisfied by relatively few adult fish. Larval fish produced in excess of this requirement die as a result of a density-dependent process; models are at present being constructed that will show how such a mechanism could be mediated through the feeding behaviour of the components of the pelagic environment (Cushing, pers. comm.). The little evidence that supports the "classical" concept of stock and recruitment has been reviewed by Beverton and Holt (1957). In more recent years the interpretation has been challenged using data for the southern North Sea herring and Arcto-Norwegian cod stocks which demonstrate a trend of decreasing recruitment with decreasing spawning stock size (i.e. increased fishing) (Garrod 1966; Cushing 1968). The arguments in favour of this dependent relationship have been countered by the fact that the decline in recruitment that has been observed falls in a time series associated with a trend in increasing fishing effort and might equally be explained by some undetected trend in environmental conditions. The association in time between these four variables - spawning stock, recruitment, fishing effort and environmental trend - cannot be avoided in the methods so far used to demonstrate the stock/recruitment relation, by plotting some index of recruitment or another index of stock size, because fishing effort and climatic variations develop as trends over a period of years. This paper reports a slightly different approach, based on the assumption that if the stock is to remain stable the spawning stock should on average produce enough young to replace the average of its constituent year-classes.

## Method

Data for a long series of year-classes give the initial size at recruitment of the year-classes present in the spawning stock in any one year. These can then be compared with the year-class produced in that year to give a replacement rate. Thus, for the Arcto-Norwegian cod, the year-classes of 1937-1943 made up the major part of the spawning stock as 7-13 year-old fish in 1950. The mean number of 3 year-old recruits per year-class 1937-1943 was  $772 \times 10^{-6}$ . The resultant 1950 year-class numbered  $2252 \times 10^{-6}$  recruits, giving a replacement rate of  $2252 \times 10^{-6} / 772 \times 10^{-6} = 2.99$ .

If the unexploited stock is stable the replacement rate will average 1.00 and under these circumstances it can be assumed that the natural mortality and fecundity/survival relationships are in equilibrium. In the exploited stock, however, the year-classes are subject to an extra mortality caused by fishing which reduces the size of the spawning stock to some proportion of its original size. This proportion can be calculated if the fishing and natural mortality and growth rates are known. In practice, recent values of the latter two parameters have been used as constants, ignoring probable density-dependent changes.

When the potential spawning stock is being reduced recruitment can only be held constant by a proportionate increase in the survival of the eggs spawned. The computations described above give an index of this change in survival as the ratio of the replacement rate to the biomass of the spawning stock itself expressed as a proportion of its potential size in an unexploited stock. Referring again to the 1950 year-class of Arcto-Norwegian cod the mean fishing mortality in the 1937-1943 year-classes up to the year of spawning, 1950, was  $F = 0.88$  per year-class (0.13 per year, assuming knife-edge recruitment at 3 years old). This level of  $F$ , combined with a natural mortality ( $M$ ) of 0.3, would reduce the potential biomass of the spawning stock to 0.43 of its original potential. If the 1950 spawning were to produce a year-class equal to its parent year-classes (replacement = 1.00) survival would need to increase by a factor of  $1.00/0.43 = 2.33$ . The observed replacement was 2.99 (see above), so the total index of survival compared with the requirement of the stable unexploited stock would be  $2.99/0.43 = 6.95$ .

The trends in this index of survival have been examined for four cod stocks (Arcto-Norwegian, Iceland, West Greenland and Gulf of St. Lawrence), for each of

which estimates of year-class strength and fishing mortality can be derived from existing data by the 'virtual population' method (Gulland 1965). For the Arcto-Norwegian and Icelandic cod stocks the data have been based on calculations of the respective I.C.E.S. Working Groups (I.C.E.S. 1968 a, b). For the West Greenland cod year-class strength data are given by Hørsted (1967), and estimates of fishing mortality have been recalculated by the virtual population method using age composition data constructed by Hørsted, from data published in the I.C.N.A.F. Sampling Yearbooks. Data for the Gulf of St. Lawrence cod are derived from the statistics given by Paloheimo and Kohler (1967). For each stock the fishing mortality and the associated survival indices have been smoothed by a moving average of five years. An example of the computation of the survival indices is given for the Arcto-Norwegian cod in Table 1.

### Results and Discussions

The chronological series of variations in year-class strength is shown in Figure 1. Note the long-known higher variability of recruitment to the West Greenland fishery. Figure 2 shows the plots of  $\log_e$  survival index against fishing mortality per year-class, computed as described. Three calculated relationships have been superimposed on this figure to represent the requirements if survival is to vary so as to satisfy particular hypotheses concerning the stock and recruitment relationship.

If recruitment is proportional to year-class strength then the replacement rate will equal the reduction of spawning stock and the survival index will be 1.0,  $\log_e$  0.0000; this is shown as line 1. Line 2 represents the progressive increase in survival that is required to maintain a constant year-class strength (this is the assumption upon which assessments are currently based). There is a third possibility (line 3), that survival would increase to ensure full utilization of the available food resources, i.e. that the biomass would remain constant, and recruitment would be inversely proportional to the biomass. This concept is inherent in the 'energetic' approach to population dynamics being developed by Paloheimo and Dickie (1968).

In Figure 2 the points have been joined to follow the time series, and in two of the stocks, the Arcto-Norwegian and the West Greenland, the survival index/fishing mortality relations are quite clear, but different. The West Greenland stock follows a linear increase in the survival index, close to that required

if recruitment is to be maintained at a constant level. For the Arcto-Norwegian stock, however, the relation shows the increase in survival tending to an asymptotic level: the lower part of this 'curve' approximates to that required to maintain the biomass of the stock as a whole. There is no indication at any point that survival is adjusted to maintain constant recruitment. The relation for Iceland cod is indeterminate; data for the pre-war years do not conform to any pattern and in post-war years an early increase in survival, as though to maintain the biomass, has been subsequently modified to a trend which would maintain year-class strength. Overall there is a suggestion that the total change in survival will prove to be asymptotic, as with the Arcto-Norwegian stock. The time series for the Gulf of St. Lawrence cod is much shorter, but so far as it goes there is again a suggestion that it would follow the 'asymptotic' Arcto-Norwegian pattern, but at a higher level. The difference in level would be related to the lower age of maturity for this stock, which has been taken into account in the original computations of fishing mortality and proportional change in size of the spawning stock.

These results cover the period (up till about 1960) for which estimates of year-class strength and fishing mortality can be obtained from virtual population analysis. In more recent years, though comparative data are not available, recruitment is known to have declined in at least the Arcto-Norwegian, Icelandic and West Greenland stocks, although in the first of these there are two exceptionally good year-classes of 1963 and 1964.

The values plotted are not equilibrium values. However, one might suppose that in tending to a new equilibrium survival would increase rapidly at first and then more slowly, and that a continuous increase in fishing mortality, such as has occurred in the Arcto-Norwegian stock, would promote a continuous upward trend in survival towards some upper equilibrium level. Quite clearly this has not occurred in the Arcto-Norwegian cod! An asymptotic level of survival has been reached in this stock, and possibly in the Icelandic and Gulf of St. Lawrence stocks. This suggests there may be an upper maximum to the potential survival. Such a level must exist if interspecific variation in fecundity is to have any evolutionary significance: if survival were infinitely variable, as required by the dogma, why produce so many eggs?

It will also be noted that the relationships follow the inevitable time series. However, looking again at the Arcto-Norwegian stock, for which the

asymptotic level is reasonably established, it is clear there has been no trend with time. Hitherto the suggestion has been that reduction in year-class strength may have been caused by poorer conditions for survival. These data show the average survival to have remained approximately constant. This means that the reduction in recruitment must bear some relation to the decreased spawning stock. However, it remains probable that over and above this basic relation the survival will be modulated by environmental fluctuations.

The contrast between the Arcto-Norwegian and West Greenland stocks is also significant: it implies that stock/recruitment relations may be unique to each stock.

The implications of these results are shown in the more usual stock/recruitment relation plotted in Figure 3, where the straight lines represent equilibrium recruitment and biomass of the spawning stock at different levels of fishing mortality (see Gulland, 1968, for further explanation of this type of plot). Where the relationship lies above the equilibrium lines the stock will more than replace itself and will tend to increase in size. If the relation lies below the equilibrium line replacement does not occur and fishing will induce a progressive decline in the stock. The full curves of the relations reflect that part for which the results are available in these data. The relation for the Gulf of St. Lawrence cod is not sufficiently well established to place much reliance on its precise form, and at West Greenland replacement has been maintained at the levels of fishing observed up to 1960, although in view of the increases in fishing effort since 1960 there may well be doubt concerning the present situation. For the Arcto-Norwegian stock the data span a much wider range of fishing mortality (and hence spawning stock size), and show the stock failing to replace itself at disturbingly low levels of fishing mortality; in fact, from Figure 2 it is immediately obvious that since the early 1950s recruitment has been on average proportional to the size of the spawning stock.

Under these circumstances for the Arcto-Norwegian stock the concept of an equilibrium yield disintegrates when the fishing mortality ( $F$ ) per year-class in the period between recruitment to the fishery and 10 years old exceeds 1.4. This corresponds to an annual value of  $F$  of 0.3 for the fully recruited age groups, and is below the currently reduced levels of fishing mortality reported by the North-east Arctic Working Group (I.C.E.S. 1968 a). This reinforces the

advice currently being presented to the N.E.A.F.C., that economic benefit, and possibly increased catches, would accrue from a limitation of effort. It also necessitates a careful reappraisal of mesh assessments, to see how the distribution of fishing mortality with age varies with mesh size, in order to preserve the spawning stock. The alternative is a protracted decline in recruitment and stock abundance in at least the Arcto-Norwegian stock. For the other stocks the situation was less critical at the end of the period reviewed here.

#### Acknowledgement

I wish to thank Mr. S. A. Hørsted for the use of his data on the age composition of international catches in the West Greenland fishery.

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Table 1. Calculation of survival and fishing mortality indices for Arcto-Norwegian cod

Year	Number of recruits at 3 years old $\times 10^{-6}$	Mature year-classes (ages 7-13)	Average number of recruits to (2) $\times 10^{-6}$	Replacement rate (1)/(3)	Fishing mortality (F) per year-class in (3)	% Potential biomass of (3)*	Total survival (S) per year-class in (3)	Log <sub>e</sub> (7)	5-year moving average of		Log <sub>e</sub> (10)
									F (5)	S (7)	
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)
1931	555										
1932	536										
1933	818										
1934	786										
1935	581										
1936	714										
1937	1412										
1938	390										
1939	298										
1940	445										
1941	716										
1942	942										
1943	1067										
1944	642	1931-37	772	0.83	1.02	0.38	2.18	0.779			
1945	678	1932-38	748	0.91	0.27	0.78	1.17	0.157			
1946	680	1933-39	714	0.95	0.16	0.87	1.09	0.086	0.44	1.98	0.683
1947	947	1934-40	661	1.43	0.26	0.79	1.81	0.593	0.37	2.43	0.888
1948	1516	1935-41	651	2.33	0.48	0.64	3.64	1.292	0.49	3.59	1.278
1949	1685	1936-42	703	2.40	0.66	0.54	4.44	1.491	0.68	4.17	1.428
1950	2252	1937-43	753	2.99	0.88	0.43	6.95	1.939	0.88	4.24	1.445
1951	906	1938-44	643	1.41	1.10	0.35	4.03	1.394	1.11	4.27	1.452
1952	430	1939-45	684	0.63	1.27	0.30	2.10	0.742	1.32	4.57	1.519
1953	620	1940-46	739	0.84	1.66	0.22	3.82	1.340	1.52	3.95	1.374
1954	1011	1941-47	811	1.25	1.71	0.21	5.95	1.783	1.67	4.06	1.401
1955	672	1942-48	925	0.73	1.84	0.19	3.84	1.345	1.81	4.59	1.524
1956	860	1943-49	1031	0.83	1.89	0.18	4.61	1.528	1.88	4.92	1.593
1957	963	1944-50	1200	0.80	1.95	0.17	4.71	1.550	1.95	4.66	1.539
1958	1152	1945-51	1238	0.93	2.00	0.17	5.47	1.699	2.01	4.51	1.506
1959	906	1946-52	1202	0.75	2.09	0.16	4.69	1.545	2.08	3.85	1.348
1960	544	1947-53	1194	0.46	2.14	0.15	3.07	1.122	2.17	3.42	1.230
1961	220	1948-54	1203	0.18	2.24	0.14	1.29	0.255			
1962	340	1949-55	1083	0.31	2.39	0.12	2.58	0.948			

\* The biomass of the spawning stock under mean mortalities at (5) expressed as a proportion of the unexploited mature stock

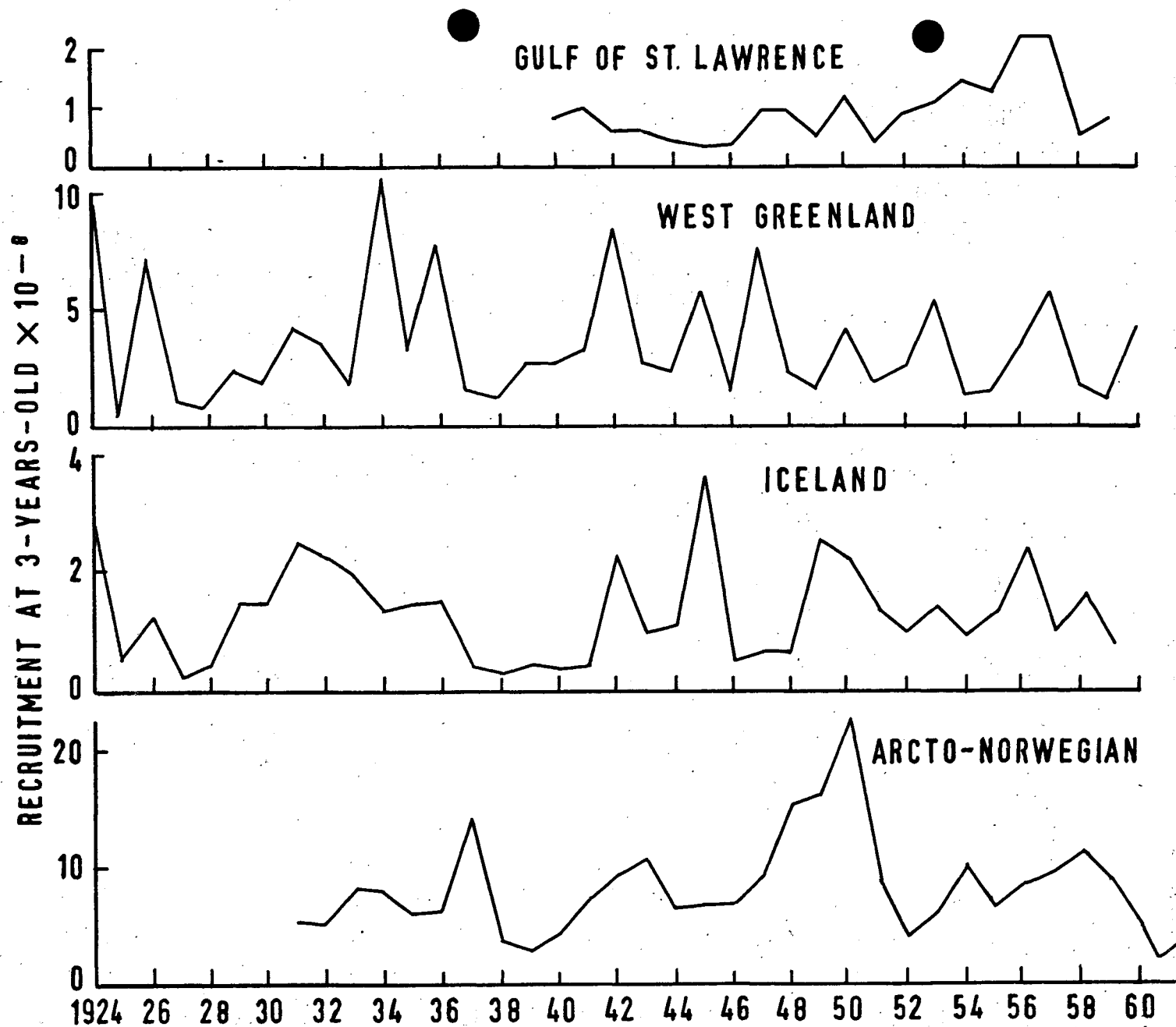


Figure 1 Absolute recruitment in numbers of 3-year-old fish in each year-class of the Arcto-Norwegian, Icelandic, West Greenland and Gulf of St. Lawrence cod stocks.



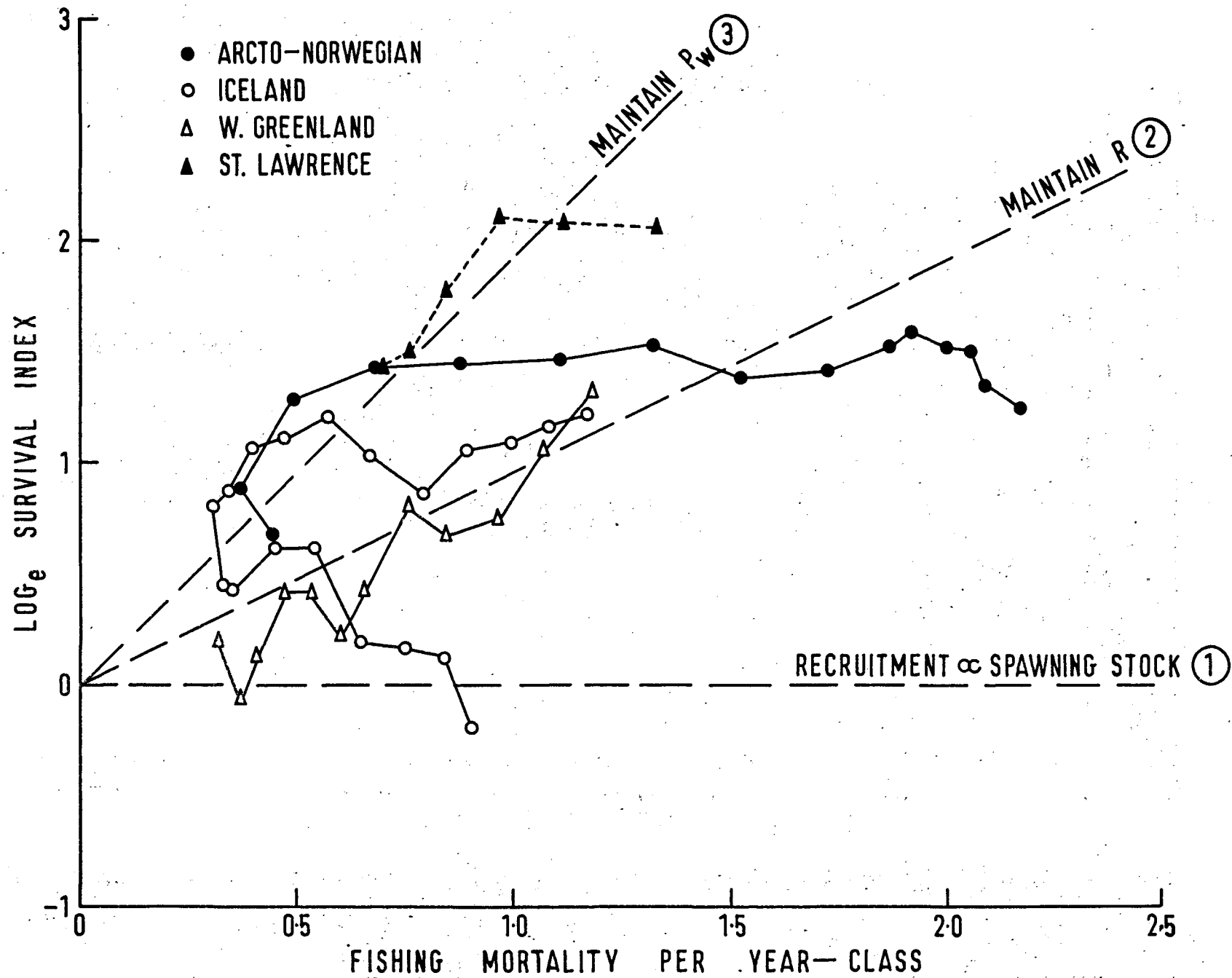


Figure 2 The relation between  $\log_e$  survival index and the fishing mortality per year-class.

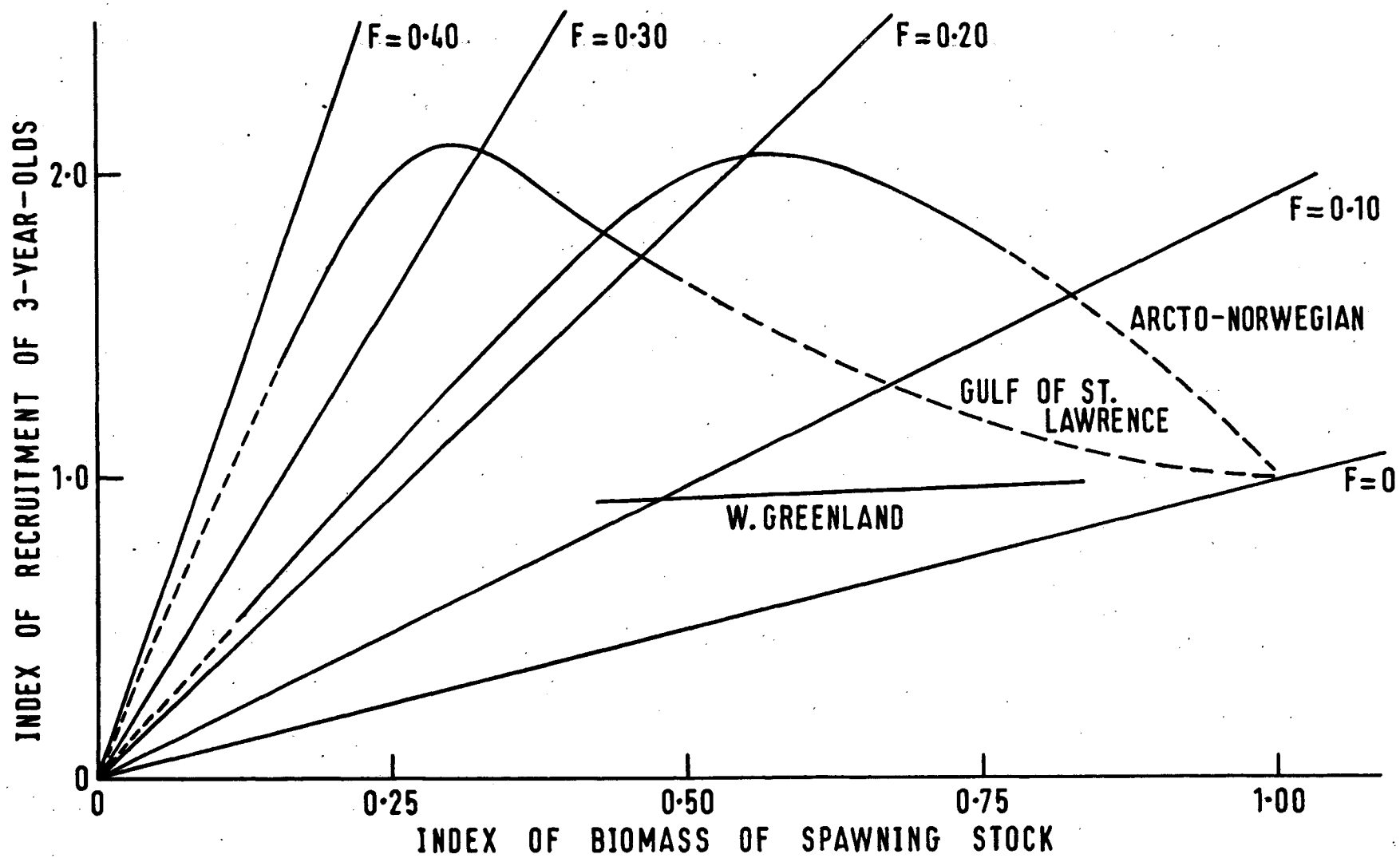


Figure 3 Stock/recruitment relationships for Arcto-Norwegian, West Greenland and Gulf of St. Lawrence cod.