Recruitment variability and oceanographic stability

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ABSTRACT

We examine the hypothesis that recruitment is more variable in populations on isolated offshore banks than nearby shelf populations. Recruitment of cod (*Gadus morhua*) and American plaice (*Hippoglossoides platessoides*) on Flemish Cap is more variable than in any comparable population. Recruitment of haddock (*Melanogrammus aeglefinus*) on Rockall Bank is also more variable than in surrounding populations. These results are confirmed both by estimates obtained by virtual population analysis and by research surveys. Recruitment of haddock and herring (*Clupea harengus*) on Georges Bank is also more variable than in surrounding populations; however, the results for two other groundfish populations, cod and yellowtake flounder (*Limanda ferruginae*), on Georges Bank are ambiguous. We conclude that marine fish populations on isolated banks are more variable than those on nearby shelf regions.

Key words: recruitment, spawning, stability, environment, cod, haddock, herring

INTRODUCTION

Most species of commercially important fish have a portion of the life cycle during which offspring are planktonic. It has been suggested that an important element of the planktonic phase is either the successful drift from spawning to nursery areas (Harden Jones, 1968) or the retention in suitable habitats (Sinclair, 1988). Whichever of these concepts is the more appropriate descriptor for the requirements of the planktonic period, the key similarity between them is the necessity for the eggs and larvae to remain within a specified distributional area in order not to be expatriated from the population's evolutionary stable range. It has been suggested that banks may represent potential retention zones for the early life stages of fish (review: Sinclair, 1988). Such topographic features often have circulation patterns, e.g. gyres, which can serve to limit dispersion away from the area (Loder *et al.*, 1988). The integrity of water masses above different banks is determined by a combination of factors that influence the intensity of the gyral circulation around them (Loder *et al.*, 1988). However, a breakdown or perturbation in the circulation pattern above a bank can lead to strong advection of water and particles out of the region (Myers and Drinkwater, 1989). Such events could be highly detrimental to the survival of planktonic eggs or larvae through expatriation. The magnitude of such events would depend on the relative strength of the mean circulation pattern and of the perturbing force (e.g. storms, meanders in boundary currents).

Populations that spawn on isolated banks may exhibit more variable recruitment than those which release their offspring on continental shelves because in an isolated system, when larvae are advected off into the open ocean, they are unlikely to return (Myers and Drinkwater, 1989), whereas on a shelf the larvae advected onto another portion of the shelf may be able to return. The purpose of this paper is to test such a hypothesis, i.e. that recruitment variability is larger on isolated offshore banks, which should be subject to more interannual variability in water mass replacement, than nearby shelf regions. For example, Polacheck *et al.* (1992) have convincingly demonstrated that haddock larvae can be transported off Georges Bank onto adjacent banks where they can survive and return as juveniles to Georges Bank. However, Sale (1982) has argued that dispersal into the open ocean may enhance survival of larvae by reducing predation mortality. Sale's argument was originally made for reef fish on the spatial scale of a coral reef; it is not clear if the argument applies to temperate banks.

Does the nature of the environment influence recruitment variability of commercial fish populations? The answer to this issue has almost always been assumed to be positive. The association between environmental factors and recruitment variability has formed the basis for a suite of studies (review: Shepherd *et al.*, 1984) but the validity of the resulting relationships has often been questioned because of their ad hoc premise. It is reasonable to expect that variation in population abundance is related to the degree of variation in the physical en-

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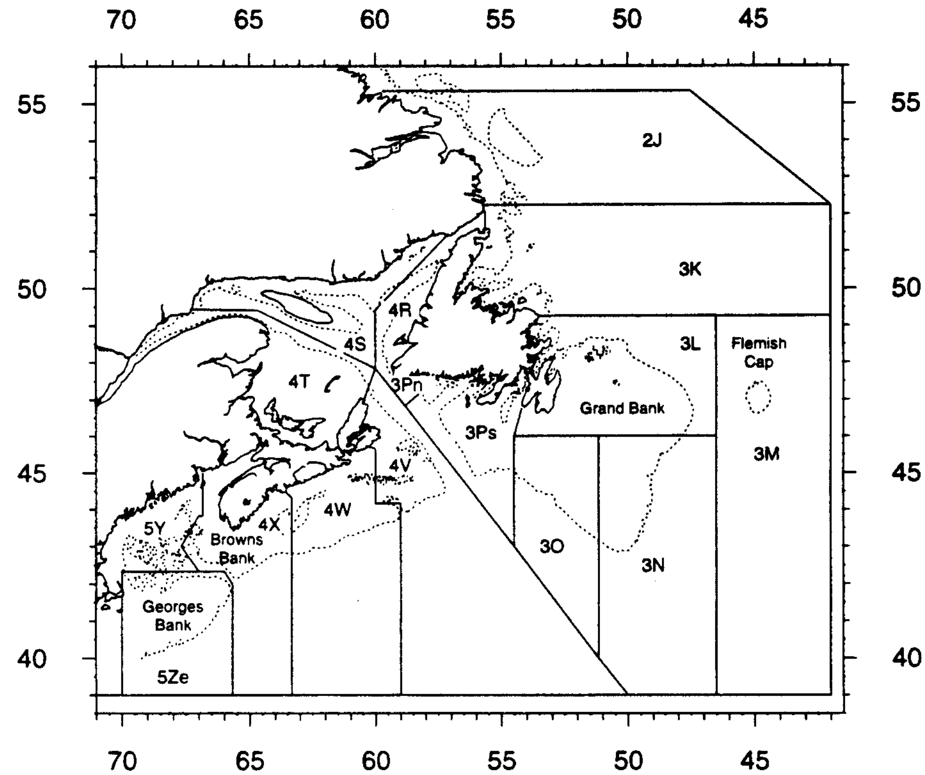
Figure 1. (a) Map of the North-west Atlantic. The 200 m (——) and 800 m (· · · · ·) depth contours are shown. Areas 2J, 3K etc. are NAFO regions. (b) Map of the North-east Atlantic around Rockall Bank. The 200 m (——) and 800 m (· · · · ·) depth contours are shown.

(a)



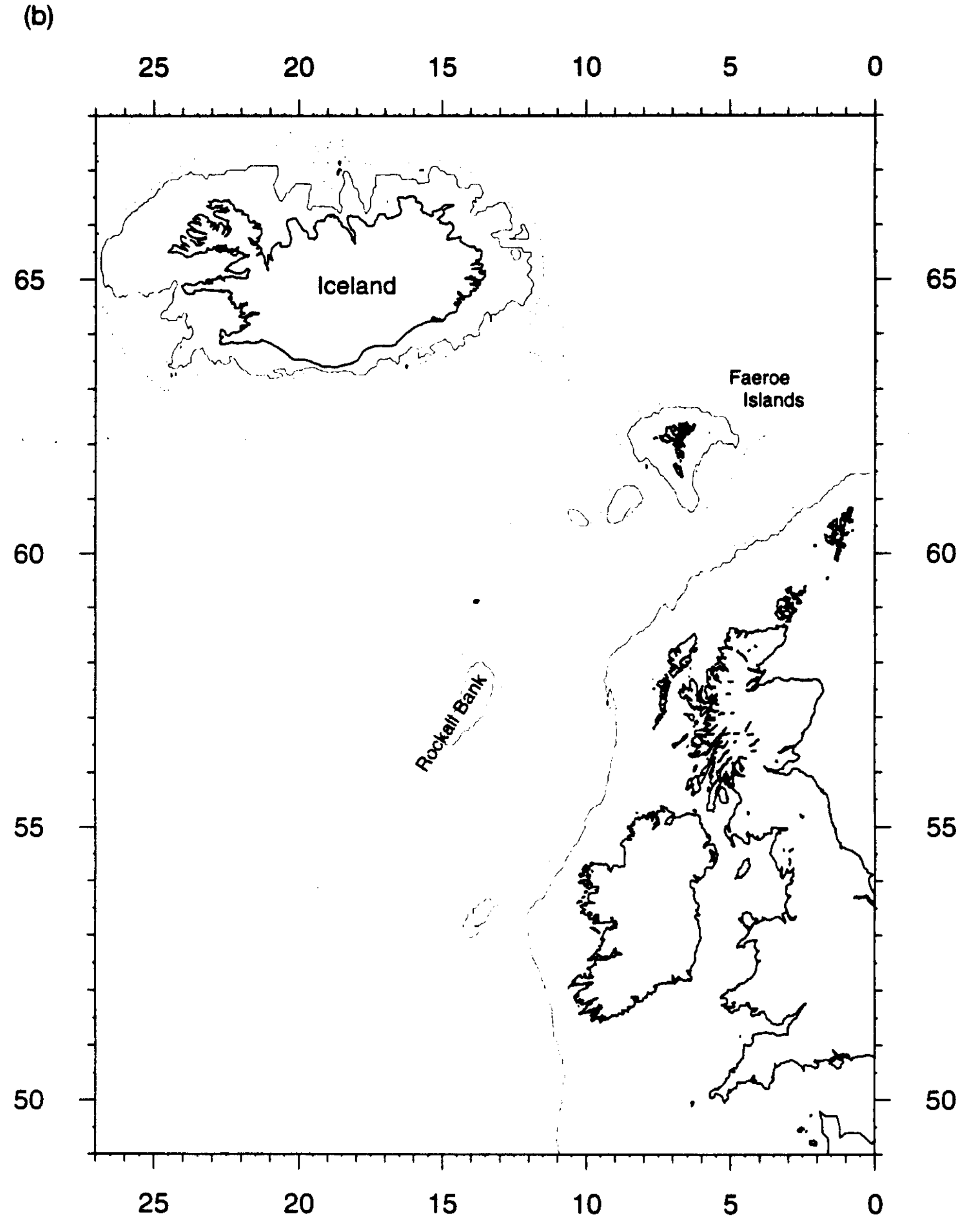
vironment; however, such links have rarely been made in a predictive manner (Pimm, 1991, p. 84). Two examples for marine fish are Myers' (1991) demonstration that three marine demersal species were more variable at the northern and southern limits of their ranges, and Mertz and Myers' (1994) demonstration that cod populations with more restricted seasonal spawning periods have more variable recruitment. A more suitable approach to study the effects of 'environmental factors' on recruitment variability would be to compare recruitment patterns from several populations of a species in different environments. A key point of such comparisons is to clearly define the environments which characterize the habitats being compared.

The approach we take here is to examine the recruitment variability of species found on two isolated banks that are separated from the adjacent continental shelves (Rockall Bank and Flemish Cap), and one bank that is surrounded by deep water on three sides (Georges Bank) (Fig. 1). These separate topographic features generally have gyral circulation patterns (Hansen, 1985; Loder *et al.*, 1988) which may serve as retention mechanisms for early life stages spawned in the vicinity of these banks. We hypothesize that these environments are unstable compared with continental shelves adjacent to a coastline, because perturbations in adjacent current fields can lead to significant advection of water from the inner portion of the gyre in which eggs and larvae occur (Myers and Drinkwater, 1988, 1989), which would reduce the average residence times. We will compare recruitment among populations at the same age and similar latitudes and temperature regimes using similar methods to estimate population size in order to eliminate the problem of changing recruitment variability in response to these features (Myers, 1991).

METHODS AND DATA

In the region encompassing the Flemish Cap and the Newfoundland shelf, cod (*Gadus morhua*) and American plaice (*Hippoglossoides platessoides*) are the only two species for which there is sufficient information to estimate recruitment. There are four commercially important species in the Georges Bank/Gulf of Maine area

Figure 1. *Continued.*



(cod, haddock (*Melanogrammus aeglefinus*), herring (*Clupea harengus*), and yellowtail flounder (*Limanda ferruginea*)) for which there are lengthy time series. Haddock is the only species in the north-eastern Atlantic for which bank and shelf comparisons were possible.

Virtual population analysis

Recruitment variability can be estimated from analyses of commercial catch-at-age data, e.g. virtual population analysis (VPA), or from research surveys. These different estimation methods may have different levels of measurement error. Because of the effect which this may have on a comparative study, the analysis for a given species and region will be restricted to cases where recruitment variability is measured using similar methods.

VPA reconstructs populations using commercial catch-at-age data; research surveys are used in VPA to estimate the number of 'survivors', i.e. the numbers-at-age in the last year of the analysis. Thus, the errors in the VPA and research survey estimates will be independent in cohorts for which recruitment is estimated only using commercial catch-at-age data, but may not be independent in the most recent years in the analysis.

The sources for the recruitment estimates obtained from virtual population analysis are described in Myers *et al.* (1990, 1994). The data series for Rockall Bank haddock is very short. We reconstructed the numbers-at-age for the 1981–83 cohorts by applying the fishing and natural mortality of the first year of the analysis, 1984, to the numbers-at-age for 1984.

In some cases, a management area may constitute several spawning components, e.g. this may be a problem for the Georges Bank and Gulf of Maine groundfish stocks. For cod, there often appears to be spawning inshore, which may constitute separate populations (Hutchings *et al.*, 1993). Unfortunately, it is not possible to reliably estimate the abundance of subpopulations.

Research surveys

In order to minimize statistical biases we used data from surveys carried out by the same ship using the same sampling design and sampling intensity when possible. In all cases, we used fish of the same age for comparison.

The recruitment variability estimated from research surveys includes the variance of the estimation error. The estimation error variance can be estimated from sampling considerations in a properly designed survey; however, this method will usually underestimate the true error variance because the sampling efficiency of the survey gear is likely to change over time because of year-to-year environmental variability, changes in ship or gear design, and changes in personnel. Another difficulty is that mortality may be density dependent in many populations (Myers and Cadigan, 1993). Thus, variability of recruitment for fish the same age must be compared because the variability at age 1 may be different from the variability a year later.

For cod and American plaice on the Flemish Cap and nearby regions the surveys were from Canadian vessels using stratified random design from 1978 to 1985. We compared Flemish Cap recruitment with data from the Southern Grand Banks (NAFO Div. 3NO), the Northern Grand Banks (NAFO Div. 3L), Funk Island Banks (NAFO Div. 3K) and Hamilton Bank (NAFO Div. 2J). The American plaice data for the Newfoundland Region was obtained from Brodie (1991), Brodie and Baird (1991), and Brodie and Bowering (1992).

The robustness of the results for cod on Flemish Cap based on Canadian research surveys can be checked with those carried out by the Soviet Union from 1960 to 1980 (Konstantinov, 1983). Although the estimation error variance of these surveys appears to be greater than that of the Canadian surveys (Myers and Cadigan, 1993), the sampling of Flemish Cap has been conducted over a longer period. We compare the surveys for age 3 cod (American plaice was not aged in the Soviet surveys).

For groundfish stocks from the Georges Bank and adjacent areas we used the stratified random trawl surveys carried out by the US National Marine Fisheries Service. We used the stock boundaries used in the surveys, and the survey estimates are available in the Reports of the Northeast Regional Stock Assessment Workshop Reports available from the NOAA/National Marine Fisheries Service, Northeast Fisheries Center, Woods Hole, MA 02543, USA. We used the youngest age at which there were few or no zero catches. For cod and yellowtail flounder we used the fall surveys for age 1 and for haddock we used the spring surveys. For the adjacent Canadian populations on Browns Bank we used surveys at the same age. These surveys were also random stratified design with similar sampling intensity.

Haddock is the only species for which there were research vessel catch-at-age data on Rockall Bank. The data for Rockall Bank were from five Scottish research vessels (Anon., 1993a). The Rockall haddock will be compared with haddock data from the North Sea, west of Scotland (ICES Div. VIa), the Faeroe Plateau, and Iceland. For Rockall Bank and adjacent regions it was not possible to obtain directly comparable surveys. The surveys of the West of Scotland population were carried out by Scotland. Recruitment estimates for the North Sea were obtained from the International Young Fish Surveys (Anon., 1993b), and those for the Faeroe Plateau were obtained from the Faeroe Goundfish surveys (Anon., 1993c).

Analysis

Our estimate of recruitment variability is the standard deviation of the logarithmically transformed (base 10) numbers-at-age. The recruitment time series are approximately normal after log-transformation (Myers *et al.*, 1990). An alternative measure of recruitment variability, the coefficient of variation, was also used to test the robustness of our results. The results were very similar in all cases so these results will not be reported here. See Pimm (1991, p. 54) for a discussion of alternative methods for measuring recruitment variability. We tested the *a priori* hypothesis that the recruitment variability is greater for isolated or semi-isolated banks by using a one-sided F-test, which is the standard method for testing if variances are equal.

RESULTS AND DISCUSSION

Recruitment of cod on Flemish Cap is more variable than in nearby shelf populations for all comparable estimates of recruitment: from the VPA, the Canadian surveys, and the Soviet Surveys (Fig. 2, Table 1). The results are statistically significant at the 0.05 level except for three of the comparisons using Soviet surveys, and in these cases the direction is that predicted from our hypothesis.

Recruitment of American plaice on Flemish Cap is more variable than in the nearby shelf regions for all comparisons (Table 1). These comparison are statistically significant at the 0.05 level even though the survey of Flemish Cap is relatively short.

Recruitment of haddock on Rockall Bank is also more variable than in surrounding populations for all comparisons for the VPA and the research surveys. The significance tests have relatively low power because of the short time series available for Rockall Bank haddock; nevertheless, the difference is statistically significant at the 0.05 level for three out of the seven comparisons. Flemish Cap and Rockall Bank are relatively small isolated offshore banks with weak gyral circulation. It is in these areas that we expect our hypothesis, that recruitment is more variable on isolated banks, is most applicable. We believe these conclusions to be robust; examination of alternative data sources (Newton and Jermyn, 1986) supports our conclusions.

Note that recruitment of haddock on Faeroe plateau does not appear to be more variable than in other nearby regions, even though the Faeroe Plateau population is more isolated than the other populations. This may be because the Faeroe Plateau is connected to Iceland and the European shelf above the 800 m isobath, which may allow migration back to the Faeroe Plateau, or may be caused by local currents that strongly retain larvae.

The time series for the Flemish Cap and Rockall Bank are relatively short; this should cause the true variability of the recruitment time series to be underestimated because of the characteristic low-frequency variability found in all time series of abundance (Pimm and Redfern, 1988; Myers *et al.*, 1990). That is, the bias caused by the relatively short time series available for Flemish Cap and Rockall Bank should cause a bias in the opposite direction predicted by our hypothesis.

Herring on Georges Bank was also found to be more variable than surrounding populations (Table 1 and Fig. 2). The variability on Georges Bank has probably been underestimated by the VPA, because the large recruitment that began a large increase in the commercial fishing effort on Georges Bank was not estimated because commercial catch-at-age data were not collected (Anthony and Waring, 1980). Similarly, at the end of the time series shown in Fig. 2 there were no commercial catch-at-age data to use in a VPA because recruitment was so low that the fishery was closed. Part of the variability in recruitment for this stock is caused by the reduction in spawners due to overfishing; however, this population is clearly very variable even when the effect of spawners is considered. Myers *et al.* (1994) provide estimates that show that although the effect of spawners is statistically significant, it only accounts for about one-fourth of the variance in log recruitment.

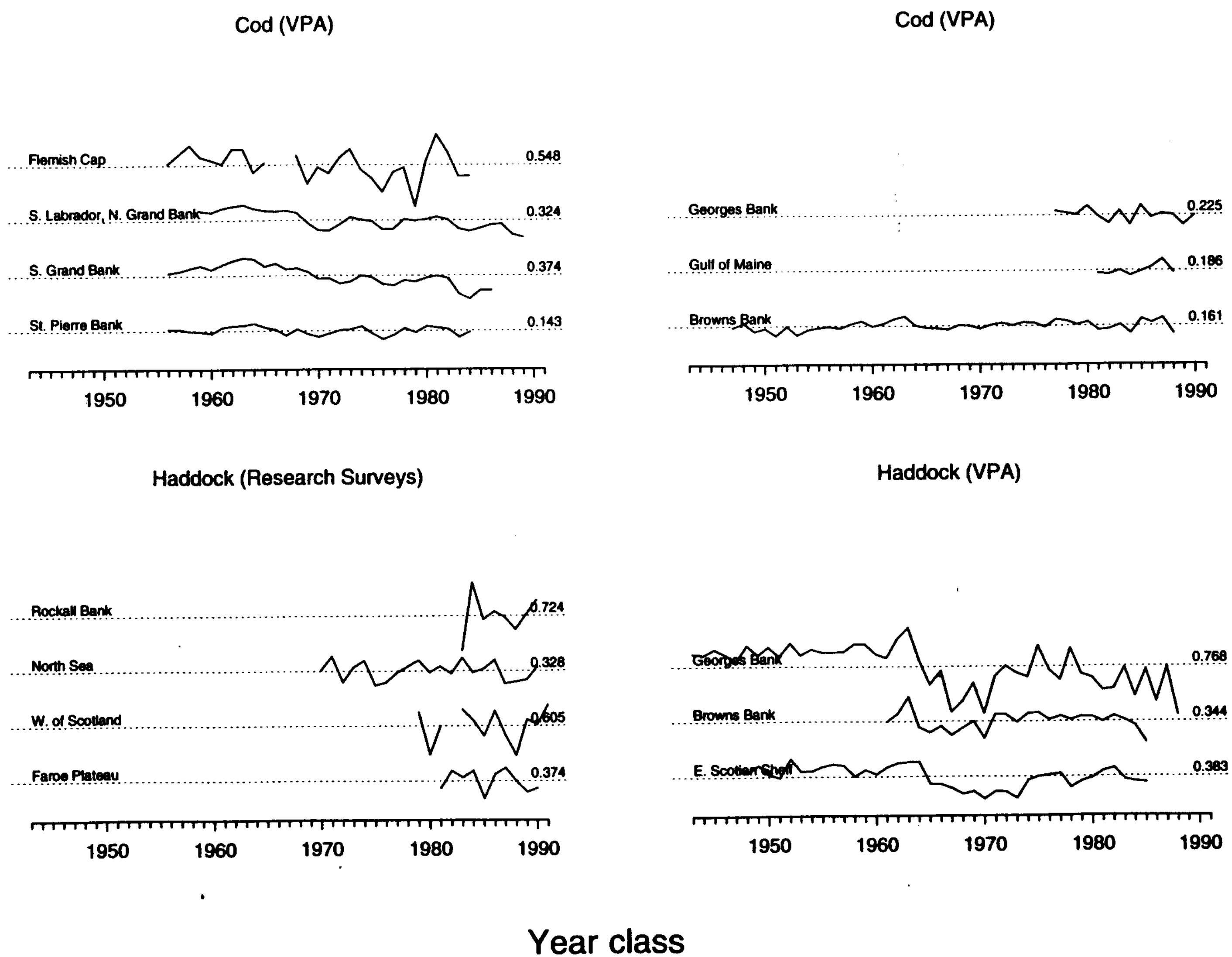
Haddock on Georges Bank was more variable than the surrounding populations (Table 1). The results for cod and yellowtail flounder on Georges Bank were ambiguous. Cod was more variable in the VPAs but not in the comparisons of Georges Bank and the Gulf of Maine research surveys. Given the high sampling variability of these research surveys (Myers and Cadigan, 1993), our inability to detect differences in recruitment variability among adjacent stocks in this region should not be totally unexpected. Yellowtail flounder on Georges Bank was more variable in the research surveys than the southern New England population, but was not more variable in the VPA. The reason for this ambiguity for the cod and yellowtail is not clear because in each case the Georges Bank population is more variable than nearby Canadian populations. The simplest explanation is that Georges Bank is not as isolated as Flemish Cap and Rockall Bank. The operational description of shelf and bank regions is determined using the 200 m isobath. However, when a deeper criterion is applied (Fig. 1a), it becomes evident that Georges Bank is an integral part of the New England shelf region. It is possible that larvae advected off Georges Bank onto nearby shelves may survive after settlement. Similarly, recruits may migrate into the region from nearby populations. In the case of Flemish Cap and Rockall Bank, vagaries in the current regime that may transport eggs and larvae off those banks are more likely to move these particles away from nearby shelves, thus limiting exchange among populations.

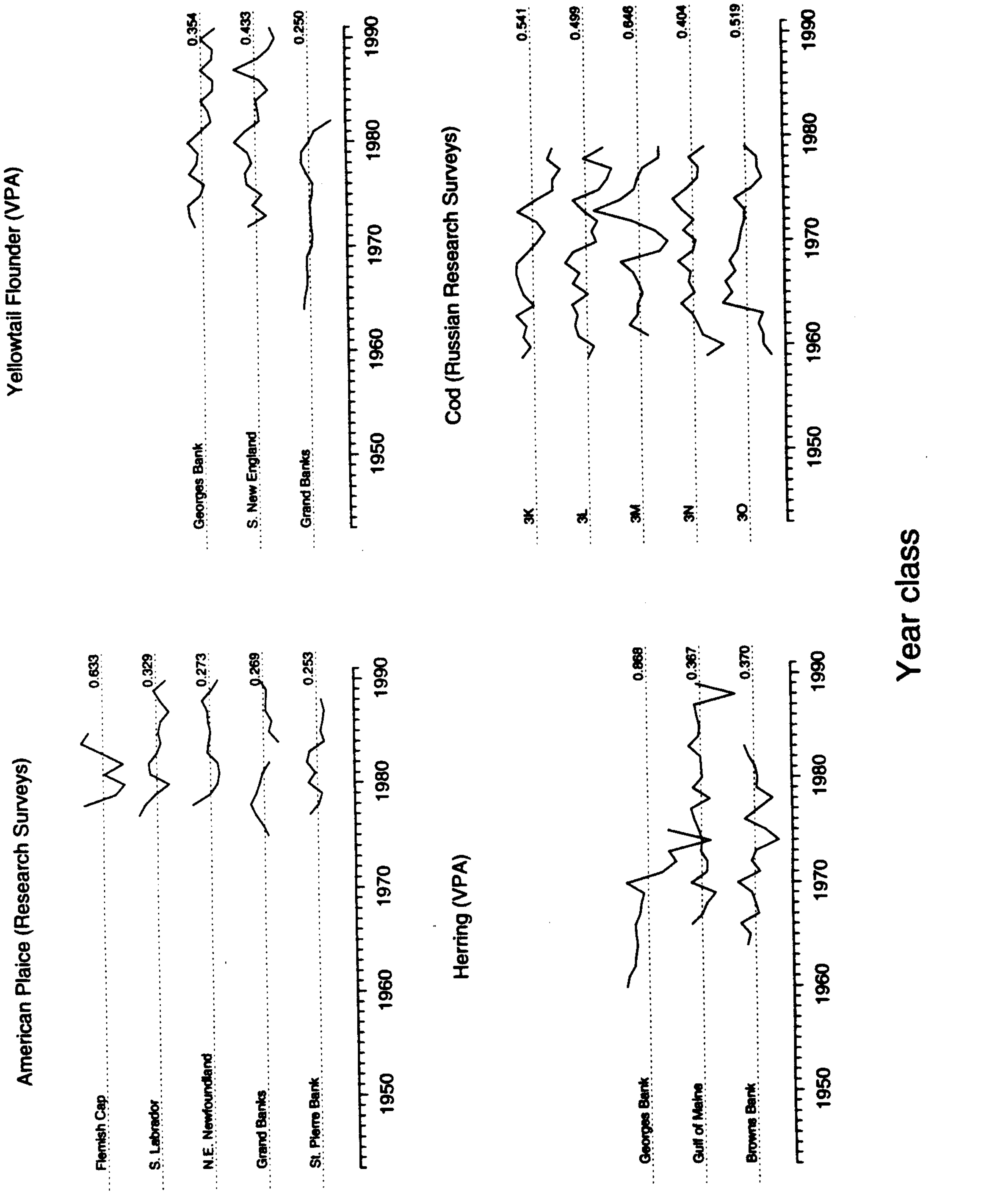
Are our results consistent with oceanographic observations? Loder *et al.* (1988) estimated the residence time from satellite-tracked drifters and from seasonal salinity budgets from data for four banks; the Flemish Cap, the south-east shoal of the Grand Bank, Browns Bank and Georges Bank. They found that residence time of drifters on Georges Bank was longer (mean = 54 days, SD = 26 days, n = 19) than the nearby Browns

Table 1. Recruitment variability for populations on isolated (Flemish Cap and Rockall Bank) banks and a semi-isolated bank (Georges Bank) compared with nearby populations. The variability is estimated as the standard deviation of the logarithmic transform (base 10) of numbers-at-age in a year class. The results for the one-sided *F* test, *P*, that the variance in logarithmically transformed recruitment is larger on the isolated or bank is also given. Each region in the North-west Atlantic is also identified by the NAFO regions depicted in Fig. 1.

	VPA				Research surveys			
Stock	*n*	Age	SD	P	*n*	Ages	SD	P
Cod								
Flemish Cap (3M)	27	3	0.548		8	3	0.957	
S Labrador–N Grand Bank (2J3KL)	31	3	0.324	0.003	14	3	0.267	<0.001
S Grand Bank (3NO)	31	3	0.374	0.023	19	3	0.385	<0.001
St Pierre Bank (3Ps)	29	3	0.143	<0.001	20	3	0.226	<0.001
Cod, Soviet surveys								
Flemish Cap (3M)					15	3	0.646	
N Newfoundland Shelf (3K)					17	3	0.541	0.220
N Grand Bank (3L)					17	3	0.499	0.132
SE Grand Bank (3N)					17	3	0.404	0.022
SW grand Bank (3O)					17	3	0.519	0.171
American plaice								
Flemish Cap (3M)					8	5	0.633	
S Labrador (2J)					14	5	0.329	0.016
NE Newfoundland (3K)					13	5	0.273	0.004
Grand Bank (3LNO)					17	5	0.269	0.002
St Pierre Bank (3Ps)					12	5	0.253	0.003
Cod								
Georges Bank (5Z)	14	1	0.225		27	1	0.429	
Gulf of Maine (5Y)	8	1	0.186	0.315	28	1	0.552	0.903
Browns Bank (4X)	42	1	0.161	0.052	21	1	0.396	0.358
Haddock								
Georges Bank (5Z)	46	1	0.768		23	1	1.18	
Gulf of Maine (5Y)					23	1	0.89	0.092
Browns Bank (4X)	25	1	0.344	<0.001	21	1	0.61	0.002
E Scotian Shelf (4VsW)	39	1	0.383	<0.001				
Yellowtail flounder								
Georges Bank (5Z)	20	1	0.354		27	1	0.677	
S New England	20	1	0.433	0.806	26	1	0.473	0.036
S Grand Bank (3NO)	19	5	0.250	0.07				
Herring								
Georges Bank (5Z)	16	1	0.868					
Gulf of Maine (5Y)	24	1	0.367	<0.001				
Browns Bank region (4X)	20	1	0.370	<0.001				
Haddock								
Rockall Bank	8	1	0.572		8	2	0.724	
North Sea	30	0	0.477	0.222	21	2	0.328	0.002
W of Scotland	23	0	0.486	0.255	12	2	0.605	0.285
Faeroe Plateau	29	1	0.409	0.089	10	2	0.374	0.035
Iceland	28	2	0.263	<0.001				

Figure 2. Recruitment variability for populations on isolated (Flemish Cap and Rockall Bank) banks and a semi-isolated bank (Georges Bank) compared with nearby populations. Estimates of numbers-at-age in a year class are logarithmically transformed (base 10) with the mean removed. The mean of each series is separated by 2 units from the one below. Thus, the distance between the dotted lines gives the vertical scale. The standard deviation of each series is given to the right.




Yellowtail Flounder (VPA)
Georges Bank
0.354
S. New England
0.433
Grand Banks
0.250
1950
1960
1970
1980
1990
Cod (Russian Research Surveys)
3K
0.541
3L
0.499
3M
0.646
3N
0.404
3O
0.519
1950
1960
1970
1980
1990
American Plaice (Research Surveys)
Flemish Cap
0.633
S. Labrador
0.329
N.E. Newfoundland
0.273
Grand Banks
0.269
St. Pierre Bank
0.253
1950
1960
1970
1980
1990
Herring (VPA)
Georges Bank
0.868
Gulf of Maine
0.367
Browns Bank
0.370
1950
1960
1970
1980
1990
Year class

Bank (mean = 14 days, SD = 7 days, n = 10). However, we found recruitment variability to be greater on Georges Bank than Browns Bank for the populations examined. Similarly, Loder *et al.* (1988) found that residence time of drifters on Flemish Cap was longer (mean = 32 days, SD = 17 days, n = 17) than the nearby south-east shoal of the Grand Bank of Newfoundland (mean = 28 days, SD = 10 days, n = 5); we again found recruitment variability to be greater on Flemish Cap than on the Grand Bank. Are the data collected from drifters relevant to the variability seen by fish larvae? Perhaps not. Loder *et al.* (1988) also estimated residence times from salinity budgets. In this case, the south-east shoal of the Grand Bank of Newfoundland has a much longer estimated residence time (>100 days) than Flemish Cap (40 days). It is expected that the residence time calculated from drifters is smaller because they reflect wind-driven variability in the upper layer as well as deeper currents. It appears that more oceanographic research is needed to characterize physical oceanographic effects on recruitment.

The limitations of traditional oceanographic analysis from ships are illustrated by the Flemish Cap study on cod recruitment. Despite intensive oceanographic surveys (Kudla *et al.*, 1984), this study was not able to determine the cause of variation in this population. One of the year classes during the study, the 1979 year class, was the smallest ever observed and yet no unusual oceanographic features can be detected in the circulation charts calculated using geostrophic methods (Kudla *et al.*, 1984). It may be that the physical oceanographic processes important for marine fish recruitment cannot be readily assessed from existing ship surveys. Frequent satellite measurements may be more useful in the study of perturbations in the current field on time scales more relevant to the drift of fish eggs and larvae (Myers and Drinkwater, 1989).

Marine fish populations on isolated banks are more variable than those on nearby shelf regions. These differences are shown for populations of cod and American plaice on Flemish Cap, and for haddock on Rockall Bank when they are compared with nearby shelf populations. The populations on Georges Bank, which is not as isolated as Flemish Cap and Rockall Bank, are not generally more variable than nearby populations. The difference in an isolated bank and a bank on a shelf is probably caused by the fate of larvae that are transported off the bank. We suggest that populations on isolated banks are more variable because of greater interannual variability in water mass replacement than on comparable shelf regions.

It is nearly impossible to infer any species-specific differences in susceptibility to advective losses from banks because of the small number of regions used in our comparison. However, the greater variability of offshelf bank means that these populations will be more dependent upon strong year classes to maintain a fishery. Such populations will be more susceptible to overfishing, and their recovery from overexploitation will be slower and more variable. Thus, it is important that overfishing be avoided for such populations.

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