Journal of Marine Research, *47*, 635–656, 1989

The influence of Gulf Stream warm core rings on recruitment of fish in the northwest Atlantic

by Ransom A. Myers[1] and Ken Drinkwater[2]

ABSTRACT

The *a priori* hypothesis that entrainment of shelf water by warm core rings reduces recruitment of marine fish stocks through offshore transport is tested. Weekly satellite images for 1973 through 1986 are used to generate time-series of the positions and numbers of warm core rings and the locations of the shelf-slope front from the mid-Atlantic Bight to the Grand Banks. These data are combined with estimates of the timing of the spawning and the duration of larval stages to create stock-specific annual indices of ring activity and shelf-slope front variability. There is evidence that increased warm core ring activity reduces recruitment in the 17 groundfish stocks examined, with the exception of cod from Georges Bank. A similar analysis of 7 pelagic stocks and one shellfish stock showed no consistent evidence that warm core rings reduce their recruitment; however, the recruitment data for many of these pelagic species are less reliable than for the groundfish stocks.

1. Introduction

Large eddies generated by unstable meanders from the Gulf Stream can entrain large volumes of water from the northwest Atlantic continental shelf (Morgan and Bishop, 1977; Smith, 1978; Churchill *et al.*, 1986). Such entrainment features are clearly visible from satellite thermal imagery (Smith, 1978) and the offshore currents within these features have been measured directly with satellite-tracked buoys (Trites, 1981; Colton and Anderson, 1983). The eddies are called warm core rings because the central core consists of relatively warm Sargasso Sea water. It has been hypothesized that the shelf water entrained by these warm core rings may transport enough fish eggs and larvae to significantly reduce marine fish recruitment (Colton and Anderson, 1983; Wroblewski and Cheney, 1984; Flierl and Wroblewski, 1985). While larvae have been found off the shelf within entrainment features (Maurer *et al.*, 1979; Friedlander and Smith, 1983; Wroblewski and Cheney, 1984), there has been little empirical evidence that shelf water entrainment affects recruitment.

Our objective is to examine the hypothesis that entrainment of shelf water reduces

1. Department of Fisheries and Oceans, P.O. Box 5667, St. John's, Newfoundland, Canada, A1C 5X1.
2. Department of Fisheries and Oceans, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2.

recruitment, using estimates of entrainment derived from 14 years of satellite thermal imagery and estimates of recruitment for 25 commercially important stocks of fish and shellfish. Regression analysis results are tested by combining each of the one-sided significance tests for a positive regression slope using Fisher's method for combining probabilities from tests of significance (Fisher, 1954, section 21.1).

In most studies relating environmental effects to recruitment, confirmatory statistics have been used for analyses that are essentially exploratory (Sissenwine, 1984; Drinkwater and Myers, 1987). Here, the difficulty of testing significance in an exploratory analysis is overcome by splitting the data into two portions. The first portion is used to choose the hypothesis to be tested and the second portion evaluates its significance. Cox (1975) analyzed this data-splitting method and found it to be quite efficient.

2. Methods

a. Satellite imagery. Sea-surface temperature (SST) data from Florida to the Scotian Shelf have been collected since the early seventies using advanced very high resolution radiometers (AVHRR) on the NOAA TIROS series of satellites. Initially these data were interpreted by the U.S. Naval Oceanographic Office which produced weekly experimental ocean frontal analysis (EOFA) charts. Surface temperature fronts (the shelf-slope front, the Gulf Stream fronts, Gulf Stream eddies) were depicted on the EOFA charts based on the satellite-derived thermal imagery of the thermal gradients for the day closest to the date of issue and augmented by SST data collected from ships of opportunity during the preceding week. A similar product using the same data was published by the U.S. National Oceanic and Atmospheric Administration (NOAA) under the title "Gulf Stream Analysis." The NOAA charts showed cloud positions, whereas in the EOFA charts if clouds prevented good imagery the frontal positions were estimated based on previous data.

Beginning in 1980 these products were replaced by the Oceanographic Analysis charts published by NOAA through the National Weather Service and the National Environmental Satellite Service. At the same time the aerial coverage was expanded to include the Grand Banks and Flemish Cap regions and the frequency of publication increased to three times per week for the area from Cape Hatteras to Newfoundland. In all three products the satellite imagery was augmented by temperature observations from ships. The EOFA chart and copies of their field sheets used in the present study were obtained directly from the Naval Oceanographic Office, while the Gulf Stream Analysis charts and the Oceanographic Analysis charts were obtained from NOAA.

We have used the EOFA charts from 1973 until May 1980 and the Oceanographic Analysis charts after May 1980. From January 1973 until May 1978, the EOFA only covered the region northward to Georges Bank, but in June 1978 the areal coverage was extended to include the Scotian shelf and the Grand Banks. There were, however,

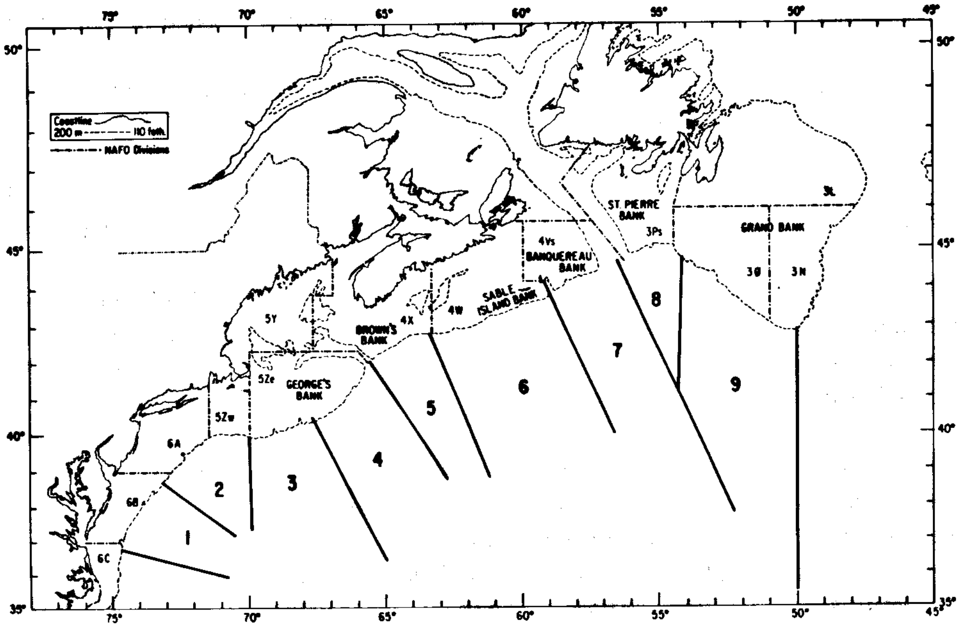

Figure 1. Regions used in the analysis. The boundaries of the fish stocks on the continental shelf are described by divisions and subdivisions designated by the Northwest Atlantic Fisheries Organization (NAFO). These divisions are denoted by a number and a upper case letter; subdivisions are designated by the following lower case letters: w (west), e (east), n (north), and s (south).

initial difficulties in discriminating warm core rings on the Scotian Shelf and the Grand Banks as the EOFA consistently underestimated the number of rings in these regions compared with the Gulf Stream analysis. We thus have not used the ring data from the EOFA charts for these regions. The positions of the shelf-slope front and Gulf Stream were consistent among all three analyses. These satellite-derived frontal positions also agree well with *in situ* measurements (Olson *et al.*, 1983; Vazquez and Watts, 1985; Auer, 1987).

b. Satellite imagery analysis. The northwest Atlantic from the mid-Atlantic Bight to the Grand Banks was divided into nine regions (Fig. 1). These regions were chosen to correspond to the limits of fish stocks and correspond to divisions used by the Northwest Atlantic Fisheries Organization (NAFO) as much as possible. From each satellite chart, the following information was recorded for each region:

A. the shortest distance between the 200 m isobath and the landward edge of the warm core ring (A negative distance was recorded if the ring edge lay shoreward of the 200 m isobath.);

B. the area of shelf water beyond the 200 m isobath (Any slope water within the

200 m isobath was subtracted from this area which sometime resulted in a negative "area.");

C. the area between the 200 m isobath and the northern edge of the Gulf Stream.

B and C provide a measure of the average distance from the shelf break to the shelf-slope front and the Gulf Stream, respectively. The sampling frequency for clear images averaged about once per week. The coverage was less frequent before 1980 and in areas with a higher incidence of fog and cloud; e.g., the Grand Banks (see Auer, 1987).

The following conventions were used in the analysis of the images. (1) If cloud cover obscured a region, then linear interpolation between the closest two observations in time was used to estimate the positions of fronts. (2) If areas were recorded on the original chart as mixed shelf and slope water, then we assigned one-half of the area to shelf water and the other half to slope water. Possible errors due to occasional incorrect assignment of water masses by operational analysts are felt to be minimized by the rigorous error checking we undertook. This quality control included close scrutiny for inconsistencies in the labeling of water masses from chart to chart. (3) Occasionally a warm core ring would entrain shelf water from two regions simultaneously. The surface area was divided by the lines in Figure 1. (4) If shelf water originating from one region was entrained around a ring and into another region the surface area was assigned to the region of origin. (5) When a ring temporarily disappeared from the image analysis because of weak thermal imagery or because it was obscured by clouds, the ring's position during this period was interpolated between clear images.

c. The relationship between warm core rings and recruitment. In order to test our hypothesis, we required an index of shelf water entrainment. We expected ring-induced entrainment to depend upon the number of rings in a region and their distance offshore. The volume of shelf water entrained by a warm core ring per unit time was assumed to be roughly proportional to the azimuthal water velocity which in turn has been observed to decrease approximately exponentially with distance from the edge of the ring (Olson, 1980).

Let $d_i(t)$ be the distance, in kilometers, of the i^{th} ring in the region of interest from the edge of the shelf (200 m isobath) at time t. The index thus constructed assumed that the effect of a ring was

$$f(d_i(t)) = \begin{cases} 1, & \text{if } d_i(t) \leq 0; \\ e^{3\{1-(R+d_i(t))/R\}}, & \text{if } d_i(t) > 0 \end{cases} \tag{1}$$

where the factor 3 was empirically estimated by Olson (1980) and R is the radius of the maximum azimuthal velocity of the ring, which is approximately the edge of the ring. Therefore, the ring has a maximum effect if its landward edge is at or over the shelf break. Although there is variation in both the azimuthal velocity of individual rings and their size, we used a constant value of 40 km for R (Olson, 1980). The ring

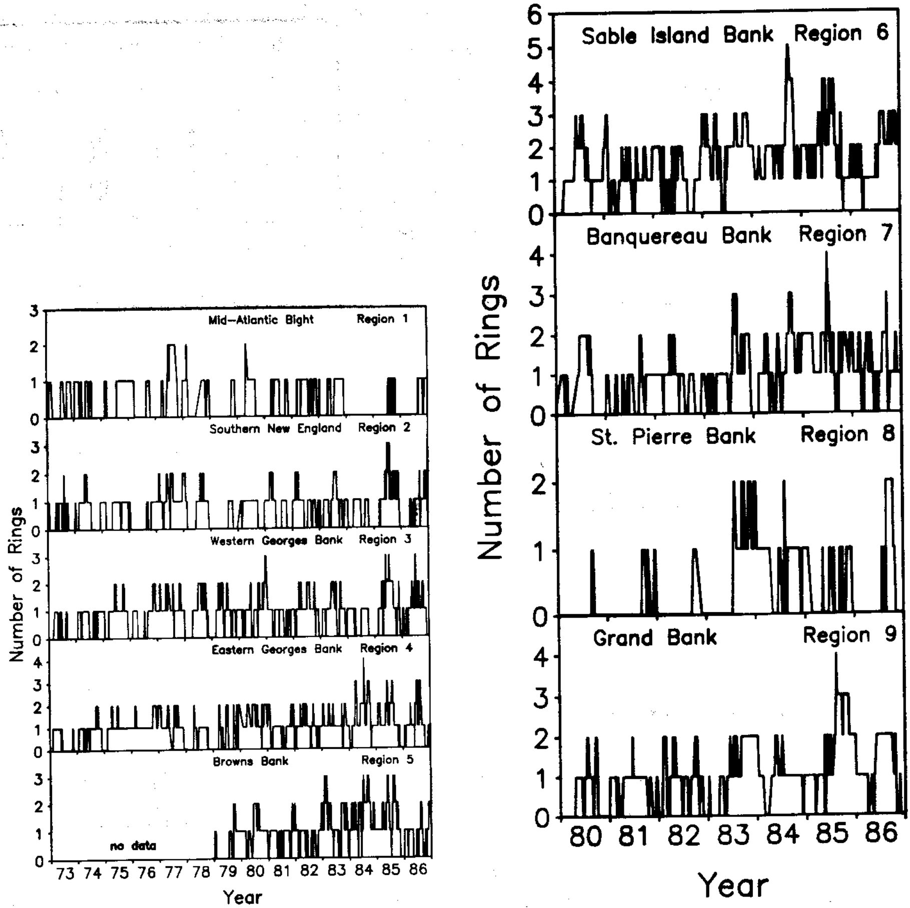

Figure 2. The number of rings in each of the regions.

entrainment index is the sum of $f(d_i(t))$ over the number of rings in the region at time t. The number of rings in each region is shown in Figure 2, and the ring entrainment index is shown in Figure 3.

We also examined the position of the shelf-slope front as an alternative entrainment index (the area of shelf water seaward of the 200 m isobath divided by 10,000 to obtain convenient units). Surprisingly, an increase in ring activity was found to correspond to a decrease in the area of shelf water beyond the 200 m isobath (Fig. 4). We had expected that more rings would result in a general seaward displacement of the shelf-slope front through increased entrainment of shelf water into the slope water region; however, the results suggest that the rings may actually push the front shoreward and the shelf water that is entrained by the rings into the slope water quickly loses (surface thermal) identity through mixing. Therefore, contrary to our initial thinking, we would expect recruitment to be positively related to the frontal index if our hypothesis is correct. However, besides ring activity, the position of the shelf-front

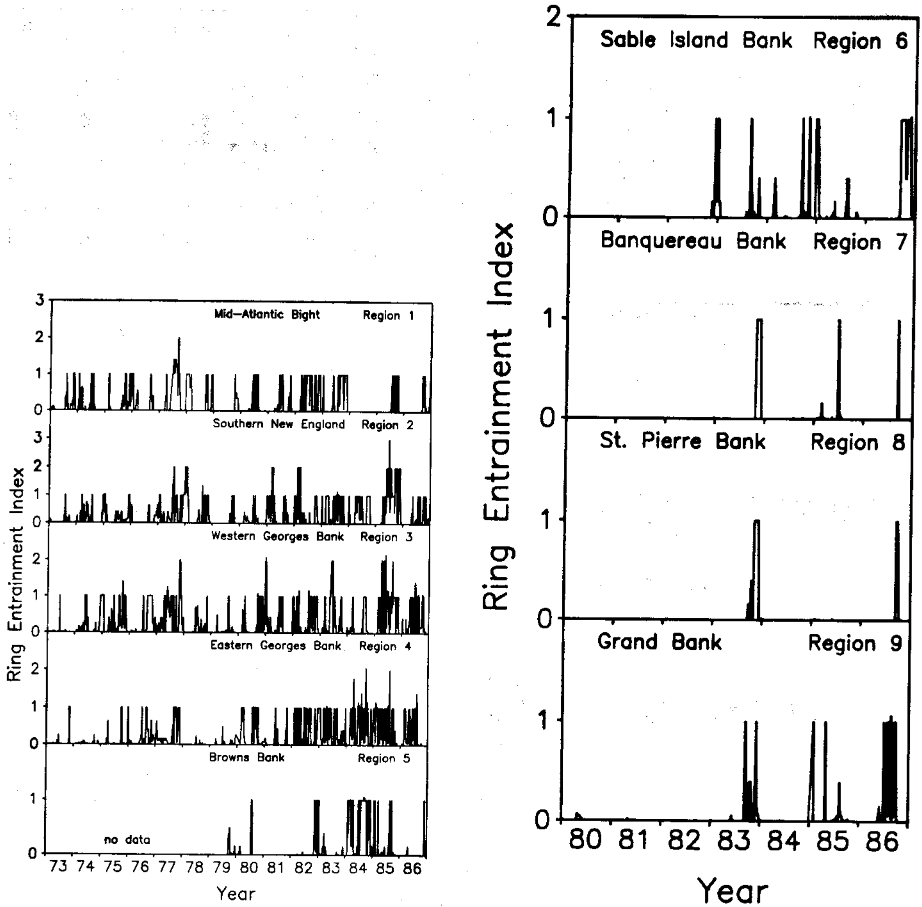

Figure 3. The ring entrainment index for each region as calculated using Eq. 1.

depends upon wind through Ekman transport (Smith and Petrie, 1982) and the position of the Gulf Stream (Halliwell and Mooers, 1979; Myers and Drinkwater, 1986). Owing to the close proximity of the Gulf Stream to the shelf in the mid-Atlantic Bight, meanders in the Gulf Stream may be as important as warm core rings in the entrainment of shelf water. Thus, within the mid-Atlantic Bight and off southern New England, the locations of the shelf-slope front may provide a reasonable measure of transport of larvae by warm core rings and Gulf Stream meanders. Therefore, an index based upon the location of the shelf-slope front tests a more complex hypothesis than an index based upon the position and numbers of warm core rings.

d. Construction of stock specific indices. To test the hypothesis that warm core rings reduce recruitment we constructed an entrainment index specific for each stock (Table 1) based on *a priori* information on the seasonal distributions of its eggs and larvae to

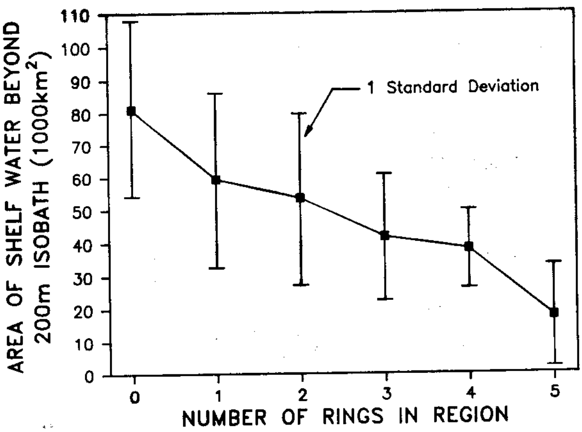

Figure 4. The relationship between the number of rings region 6, the Sable Island Bank, and the area of shelf water beyond the 200 m isobath for the years 1980 through 1986.

entrainment. A flow chart of the data and estimates that we used to construct a stock specific ring entrainment index is shown in Figure 5. We first constructed a seasonal susceptibility function based on when eggs and larvae are found in the shelf waters. Two such functions were calculated, the first based on the egg stage only and the second on the combined egg and larval stages. Three sources of information were available to aid in the construction of these functions:

(1) seasonal ichthyoplankton surveys (Sherman *et al.*, 1984 and Silverman, 1985) were used for the areas off the northeastern USA, O'Boyle *et al.*, (1984) and Markle and Frost (1985) were used for the Scotian shelf, and Bonnyman (1981) was used for the Grand Banks.

(2) seasonal surveys of spawning activity (Leim and Scott, 1966; Colton *et al.*, 1979; Fish and Wildlife Service, U.S. Dept. of Interior, 1978; Fitzpatrick and Miller, 1979; Scott, 1983; Sinclair and Tremblay, 1984), and

(3) laboratory data on the temperature-dependent development times of eggs and larvae (Culliney, 1974; Laurence, 1978; Fish and Wildlife Service, U.S. Dept. of Interior, 1978).

The susceptibility functions were calculated to be proportional to the impact on the population. They were scaled between zero and 100, e.g. if an entire population is born at the beginning of the year and the length of the larval period is six months, then the susceptibility function would be 100 for the first six months, and zero thereafter. Such a formulation implies that ichthyoplankton data must be analyzed with care; at the end of the larval stage there may be few larvae present, but the death of any one of them may be equivalent to the death of 10 younger larvae.

The seasonal susceptibility for the egg stage $S_e(t)$, and the egg-plus-larval stages $S_l(t)$ was calculated for each stock except for those whose egg stage was not planktonic. These functions could only be resolved on a monthly time scale and are

Table 1. Recruitment data used in the analysis. The location of the stock is given by the North Atlantic Fisheries Organization (NAFO) designation, with the exception of Southern New England (S.N.E.) Yellowtail whose distribution does not correspond to the NAFO boundaries. The method used to obtain the recruitment data is from Sequential Population Analysis (SPA) or from research vessel (RV) surveys. For the RV surveys, the ages that were used for the analysis are given in parenthesis. Recruitment data were either transformed by taking the square root (√) or by using residuals from a stock recruitment curve (see text for details). The data sources are: NAFO Scientific Research Council Documents, Canadian Atlantic Scientific Advisory Committee (CAFSAC) Research Documents, the USA National Marine Fisheries Service Woods Hole Library Reference Documents, and the International Council for the Exploration of the Sea (ICES).

NAFO	Years	Method	Transform	Source
Cod (*Gadus morhua*)				
3NO	79-84	RV(2 + 3)	√	Bishop and Baird, NAFO SRC Doc. 87/53
3Ps	79-85	RV(2 + 3)	Residuals	Mabeau *et al.*, ICES 1986 C.M./G:38
4VsW	79-84	SPA	√	Sinclair and Annand, CAFSAC Res. Doc. 86/46
4X	79-85	RV(1 + 2)	√	Campana and Sinclair, CAFSAC 87/30
5Ze	73-84	RV(0 + 1)	√	Hunt, CAFSAC Res. Doc. 87/94
Pollock (*Pollachius virens*)				
4VWX5	79-84	SPA	√	Annand *et al.*, CAFSAC Res. Doc. 87/96
Haddock (*Melanogrammus aeglefinus*)				
3NO	79-85	RV(1 + 2)	√	Bishop, Baird, Hicks, CAFSAC Res. Doc. 87/48
3Ps	79-86	RV(1 + 2)	√	Bishop, Baird, Hicks, CAFSAC Res. Doc. 87/48
4VW	79-86	RV(0 − 2)	Residuals	Zwanenburg *et al.*, CAFSAC Res. Doc. 86/117
4X	79-84	SPA	√	O'Boyle and Wallace, CAFSAC Res. Doc. 86/98
5Ze	73-84	SPA	Residuals	Gavaris and Waiwood, CAFSAC Res. Doc. 86/87
Redfish (*Sebastes* sp.)				
3O	79-84	RV(1 + 2)	√	Atkinson and Power, NAFO SRC Doc. 86/38
3P	79-86	RV(1 + 2)	√	Atkinson and Power, NAFO SRC Doc. 86/38
4VWX	79-85	RV(1 + 2)	√	Zwanenburg and Hurley, CAFSAC Res. Doc. 87/35
5YZ	73-80	SPA	√	Woods Hole Ref. Doc. 86-09
Yellowtail Flounder (*Limanda ferruginea*)				
5Ze	73-84	RV(1 + 2)	√	Woods Hole Ref. Doc. 86-09
S.N.E.	73-84	RV(1 + 2)	√	Woods Hole Ref. Doc. 86-09

Table 1. (Continued)

NAFO	Years	Method	Transform	Source
Silver Hake (*Merluccius bilinearis*)				
4VWX	81-86	RV(0 – 2)	√	Fanning *et al.*, NAFO SCR Doc. 87/56
5ZE	73-84	SPA	Residuals	Almeida, Woods Hole Ref. Doc. 87-03
5Zw6	73-84	SPA	Residuals	Almeida, Woods Hole Ref. Doc. 87-03
Herring (*Clupea harengus*)				
4WX	78-84	SPA	√	Stephenson *et al.*, CAFSAC 86/43
Capelin (*Mallotus villosus*)				
3NO	78-84	RV(1 – 3)	√	Miller and Carscadden, NAFO SRC Doc. 87/69
Argentine (*Argentina silus*)				
4VWX	79-84	RV(2)	√	Dale and Halliday, CAFSAC Res. Doc. 87/19
Butterfish (*Peprilus triacanthus*)				
5 + 6	73-85	RV(0 + 1)	√	Woods Hole Ref. Doc. 86-09
Sea Scallops (*Placopecten magellanicus*)				
5Ze	73-84	SPA	√	Mohn *et al.*, CAFSAC Res. Doc. 87/9

given in Table 2. The egg susceptibilty functions are similar but their duration is reduced.

The susceptibility functions are recognized as crude estimates. The data upon which they were based were sometimes inconsistent. Sources of error include the year to year in the spawning times and changes in water temperature that affect the duration of the

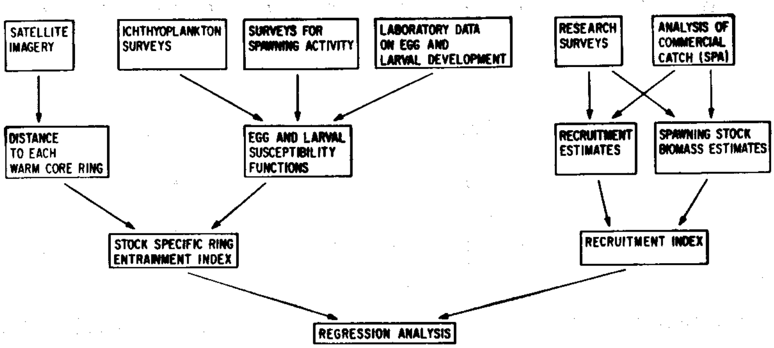

Figure 5. The flow of data and estimates used in the construction of the ring entrainment index. The frontal index was constructed similarly, except that the area between the 200 m isobath and the shelf-slope front was used instead of the distance of the warm core rings to the 200 m isobath.

Table 2. Egg + larval susceptibility functions that were used in the analysis. Note that pollock and cod from NAFO divisions 4VsW and 4X begin to spawn November and December of the year previous to their nominal year class.

NAFO	Nov	Dec	Jan	Feb	Mar	Apl	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Cod														
3NO	0	0	0	0	0	30	100	100	100	90	70	20	0	0
3Ps	0	0	0	0	0	30	100	100	100	90	70	20	0	0
4VsW	20	60	100	100	100	100	90	50	5	0	0	0	0	0
4X	20	30	20	50	80	50	90	100	60	10	5	0	0	0
5Ze	0	0	0	20	100	100	100	70	25	5	0	0	0	0
Pollock														
4VWX5	80	100	100	100	100	100	80	20	0	0	0	0	0	0
Haddock														
3NO	0	0	0	0	0	20	70	100	100	100	80	5	0	0
3Ps	0	0	0	0	10	30	80	100	100	100	80	5	0	0
4VW	0	0	0	0	30	100	100	100	90	15	0	0	0	0
4X	0	0	0	20	95	100	100	90	15	0	0	0	0	0
5Ze	0	0	0	30	100	100	100	90	15	0	0	0	0	0
Redfish														
3O	0	0	0	0	0	50	100	100	100	100	100	50	0	0
3P	0	0	0	0	0	50	100	100	100	100	100	50	0	0
4VWX	0	0	0	0	0	75	100	100	100	100	100	50	0	0
5YZ	0	0	0	0	0	0	15	100	100	100	100	50	0	0
Yellowtail Flounder														
5ZE	0	0	0	0	20	100	100	100	100	90	20	0	0	0
S.N.E.	0	0	0	0	20	100	100	100	100	90	20	0	0	0
Silver Hake														
4VWX	0	0	0	0	0	0	25	50	100	100	100	100	25	0
5ZE	0	0	0	0	0	10	60	100	100	100	100	25	0	0
5Zw6	0	0	0	0	0	10	60	100	100	100	100	25	0	0
Herring														
4WX	0	0	0	0	0	0	0	0	0	100	100	100	100	100
Capelin														
3NO	0	0	0	0	0	0	0	100	100	100	0	0	0	0
Argentine														
4VWX	0	0	0	0	100	100	100	100	100	0	0	0	0	0
Butterfish														
5 + 6	0	0	0	0	0	0	0	100	100	100	100	0	0	0
Sea Scallops														
5Ze	0	0	0	0	0	0	0	0	100	100	100	100	100	50

egg and larval stages; however, there is insufficient information to calculate a different susceptibility function for each year. Also, the length of the larval period at what stage in a pelagic fish's life history and the stage at which the larvae is no longer susceptible to entrainment by warm core rings are not well known. In spite of the potential difficulties with the susceptibility functions, they represent the best estimates given the present state of knowledge.

The susceptibility functions and ring data were then combined to calculate annual stock specific entrainment indices. Denoting January 1, 1980 by T_{1980}, the stock specific entrainment index for the egg stage during 1980 was calculated from

$$\int_{T_{1980}}^{T_{1980+365}} \sum_i S_e(t) f(d_i(T_{1980} + t))\, dt \tag{2}$$

where $d_i(t)$ is the distance of the i^{th} ring in the region of interest to the edge of the shelf and the summation is over each ring in the region at time i. Note that the integration over time, in units of days, is from the start of the year, (time 0), until the end of the year, here denoted by 365 days. For those species whose spawning begins before January 1, the integration would begin prior to the start of the year. The egg-plus-larval specific entrainment index was calculated for each stock as well by replacing the egg susceptibility function, $S_e(t)$, in the above formula with the egg-plus-larval susceptibility function $S_l(t)$.

*e. **Recruitment data.*** Two methods are available to estimate recruitment: research surveys and sequential population analysis (SPA). Sequential population analyses include virtual population analysis (Gulland, 1965), cohort analysis (Pope, 1972), and related techniques which reconstruct populations from catch at age data. Sequential population analysis tends to smear estimates of recruitment year-classes together because of ageing errors. That is, the year-classes before and after a strong year-class will be overestimated, and the strong year-class will be underestimated. This problem also occurs for research vessel data, but to a much lesser extent.

The errors in estimating recruitment from research surveys will generally be less autocorrelated than the SPA, unless there is a change in survey methods or ageing errors are large. With the exception of acoustic surveys for capelin abundance and directed larval surveys for silver hake from 4VWX, all the research survey data came from bottom trawls. Ages of fish from the research vessel surveys were determined by examining otoliths except for agentine and redfish whose ages were estimated from length frequencies.

For several stocks there were reliable estimates of spawning stock biomass (Table 1). For these stocks, we attempted to remove the effect of stock size by using the residuals from a stock recruitment relationship as the index of recruitment in the analysis. The stock recruitment function we examined was

$$R = \alpha S^{\beta} \tag{3}$$

where R is the recruitment estimate, S is the estimate of spawning stock biomass, and α and β are fitted to the parameters. The above stock-recruitment function was fit using a linear regression of the logarithmically transformed data. All the data available were used when these functions were being fit, not just the years when satellite imagery was available.

If a reliable spawning stock biomass was not available, then a square root transformation was applied to the recruitment data before the regression analysis. The square root transformation was used instead of the more commonly used log transformation so that data from years in which recruitment was low would not be given too much weight.

The geographical boundaries of the fish stocks are described using the notation of the Northwest Atlantic Fisheries Organization (NAFO), with the exception of the southern New England yellowtail flounder stock.

f. Statistical methods. The data were split into two parts for the statistical analysis. The first portion was used to choose the hypothesis to be tested (exploratory) and the second portion to evaluate significance (confirmatory, Cox, 1975). In the latter, recruitment estimates were regressed against the entrainment index for that stock. The residuals from this regression were checked for autocorrelation using a Durbin-Watson test. One sided significance tests were used on each regression because we were testing the *a priori* hypothesis that entrainment reduced recruitment.

The assumptions of an ordinary least squares regression could not always be met; therefore, the analysis was repeated using a nonparametric regression which tests whether the dependent variable, recruitment, is a monotonically decreasing function of the independent variable, the ring entrainment index. The test we used was the ordering test, which is equivalent to Kendall's rank correlation coefficient, τ (Sokal and Rohlf, 1981).

Although the significance levels for each regression are reported, we are more concerned with the general hypothesis of entrainment reducing recruitment and thus have combined probabilities from each test of significance (Fisher, 1954, section 21.1). Fisher's method is based upon the fact that the logarithm of the probability of a significance test, P, is distributed as $-\frac{1}{2}\chi^2_{[2]}$, and the reproductive properties of the χ^2 distribution, i.e. if X_j is distributed as $\chi^2_{[\nu_j]}$ $(j = 1, 2)$, then $(X_1 + X_2)$ is distributed as $\chi^2_{[\nu_j+\nu_j]}$. Thus, twice the sum of the logarithm of the P's for n significance tests is distributed as $-\chi^2_{[2n]}$. However, Fisher's method is only applicable to independent tests, and the tests on individual stocks were not independent because recruitment is cross-correlation among stocks of the same species in the northwest Atlantic (Koslow, 1984). The approach used here is to combine the results of the significance tests of the stocks for each species, and then use Fisher's method on the "average" results for the species. If the results for the stocks of a species are to be averaged before they are combined using Fisher's method, then the average value of the logarithm of the P's for each species, which corresponds to the average χ^2 value for the species, should be summed for the combined test of significance.

3. Results and discussion

a. Exploratory analysis. The initial results from the exploratory analysis were reported in Myers and Drinkwater (1986). There we used 6 groundfish stocks (cod and haddock from Georges Bank (5Ze), redfish from the Scotian shelf (4VWX) and St. Pierre Bank (3P), yellowtail flounder from Georges Bank and southern New England), and 2 pelagic stocks (capelin from the southern Grand Bank (3NO), and herring from St. Mary's and Placentia bays in Newfoundland). Only data from 1980 to 1984 were used. There was no evidence of a consistent relationship between ring activity and recruitment in the pelagic stocks. Therefore, the pelagic stocks are not included in the confirmatory portion of this paper; however, the results are reported here for completeness.

In the exploratory analysis, recruitment of the redfish and yellowtail flounder stocks appeared to be related to the number of rings in a region and the position of the shelf-slope front, respectively. Recruitment of the cod and haddock stocks did not appear to be related to the number of rings in a region. Because this result was contrary to the reports of Flierl and Wroblewski (1985) we developed the ring entrainment index previously described. Based upon the results of the exploratory analysis, we decided to combine the results from an examination of the groundfish species in the confirmatory portion of the analysis.

b. The ring entrainment index. The results of the regression analysis (using the ring entrainment index and the egg-plus-larval susceptibility functions given in Table 2) are presented in Table 3 and Figure 6. An examination of the scatterplots (Fig. 6) shows that the assumption of homoscedasticity in the regression residuals is clearly violated for several of the stocks. For these cases the nonparametric results give more reliable results (Table 3). In general, the autocorrelation in the regression residuals does not appear to be a problem (Table 3); the Durbin-Watson test revealed no significant autocorrelations. Sea scallops were not included in the figures because there is no evidence of any relationship and the uncertainty in the length-at-age relationship, i.e. there is a discrepancy in ageing between Canadian and USA researchers.

The groundfish stocks show a general decrease in recruitment associated with the ring entrainment index. Of the 17 groundfish stocks examined, the slope of the ordinary least squares regression of recruitment versus the ring entrainment index was negative for 16 of the stocks. Using the nonparametric measure, Kendall's τ, recruitment in 14 of the stocks was negatively related to the ring entrainment index.

The pelagic stocks (silver hake, herring, capelin, argentine, and butterfish) showed no consistent pattern with ring activity. Argentine recruitment is perhaps related to ring activity. Grand Banks capelin (3NO) recruitment appears to increase with ring activity; however, this relationship relies heavily on a single year-class and may be spurious.

The above analyses were repeated using the egg susceptibility functions. The results were similar to those presented in Table 3 and Figure 6, which imply that our results are robust to minor changes in the susceptibility functions. Also, if the stock recruitment relationship has been removed, we repeated the analysis using the

Table 3. Results for regression analysis of recruitment as a function of two measures of warm core ring activity, the ring entrainment index and the frontal index, and the position of Gulf Stream. The ordinary least squares regression analysis (provided only for the ring entrainment index) is given in terms of the probability that the slope of the regression slope of the recruitment index versus the entrainment index is greater than or equal to zero, $P(\beta > 0)$. The sample autocorrelation coefficient of the regression residuals, $r_{resid.}$, is also given. Kendall's rank correlation coefficient, τ, is a nonparametric measure of a monotone relationship between recruitment and the entrainment index.

	Ring Entrainment Index				Frontal Index		Gulf Stream	
NAFO	$P(\beta \geq 0)$	$r_{resid.}$	τ	$P(\tau \geq 0)$	τ	$P(\tau \leq 0)$	τ	$P(\tau = 0)$
Cod								
3NO	0.15	0.09	−0.20	0.31	0.60	0.04	0.20	0.57
3Ps	0.14	−0.01	−0.77	0.02	0.05	0.44	0.05	0.88
4VsW	0.01	−0.01	−0.40	0.33	0.87	0.007	0.33	0.35
4X	0.30	−0.45	0.05	0.56	0.05	0.44	−0.14	0.65
5Ze	0.71	−0.39	0.27	0.84	0.09	0.34	−0.18	0.41
Pollock								
4VWX5	0.03	−0.43	−0.60	0.07	0.60	0.04	0.33	0.34
Haddock								
3NO	0.13	0.14	−0.33	0.17	0.43	0.09	0.33	0.29
3Ps	0.36	−0.14	−0.17	0.42	0.04	0.45	0.11	0.71
4VW	0.09	0.00	−0.33	0.13	0.43	0.07	0.36	0.22
4X	0.15	−0.50	−0.33	0.17	0.20	0.28	0.33	0.35
5Ze	0.11	−0.17	−0.36	0.05	0.18	0.20	0.12	0.58
Redfish								
3O	0.23	0.13	−0.14	0.35	0.62	0.03	0.31	0.35
3P	0.25	0.29	−0.17	0.32	0.62	0.03	0.71	0.02
4VWX	0.24	−0.32	−0.20	0.29	0.10	0.38	0.29	0.36
5YZ	0.26	−0.04	−0.25	0.19	0.25	0.19	−0.11	0.70
Yellowtail Flounder								
5Ze	0.11	−0.14	−0.30	0.08	0.36	0.05	0.18	0.41
S.N.E.	0.50	0.19	0.03	0.55	0.58	0.004	0.18	0.41
Silver Hake								
4VWX	0.36	−0.47	−0.33	0.17	0.20	0.29	0.47	0.19
5Ze	0.13	0.24	−0.06	0.39	−0.09	0.66	−0.30	0.17
5Zw6	0.80	0.42	0.21	0.82	−0.18	0.80	0.15	0.49
Herring								
4WX	0.64	0.26	0.49	0.94	−0.20	0.73	−0.20	0.54
Capelin								
3NO	0.99	−0.03	0.20	0.68	−0.68	0.98	−0.20	0.54
Argentine								
4VWX	0.32	0.04	−0.32	0.22	0.28	0.22	0.28	0.44
Butterfish								
5 + 6	0.57	−0.03	0.15	0.77	−0.03	0.55	−0.10	0.62
Sea Scallops								
5Ze	0.45	0.12	−0.13	0.29	0.02	0.47	0.13	0.58

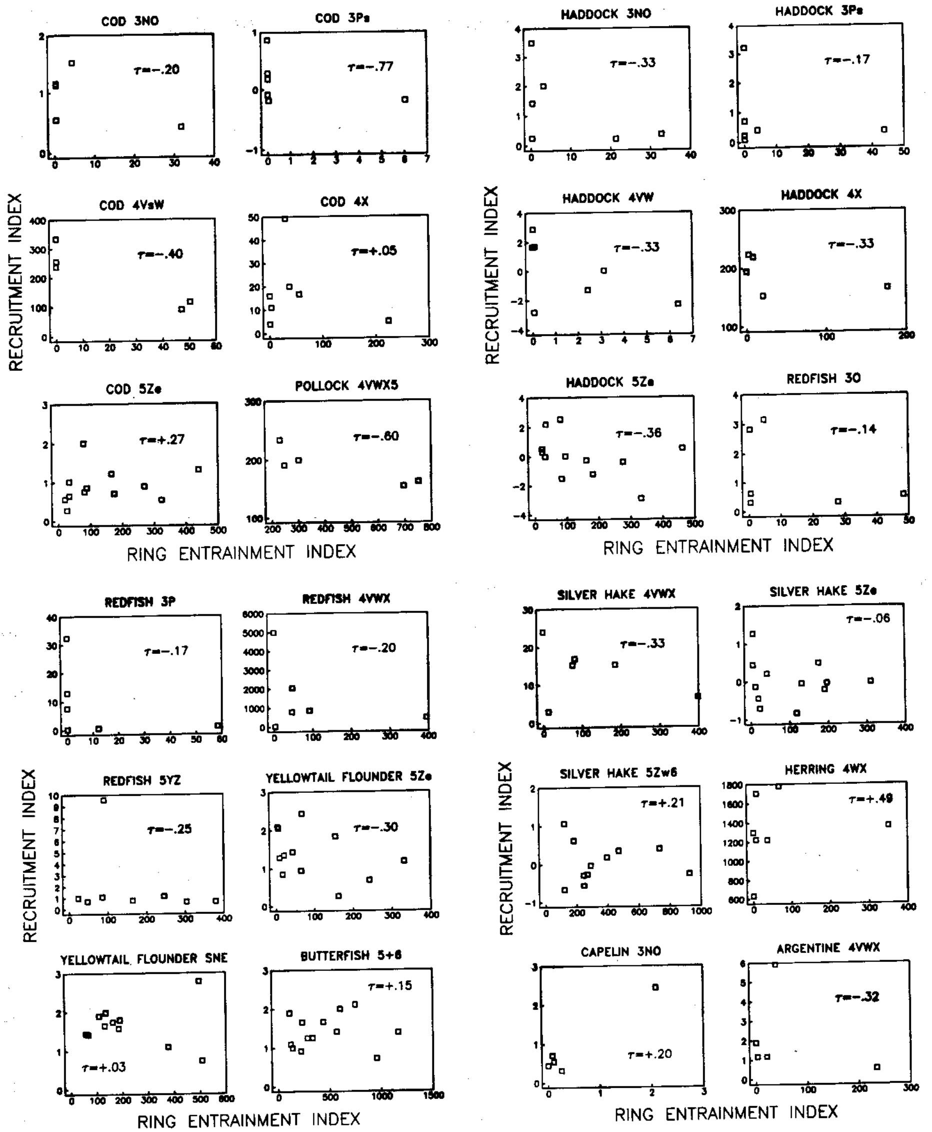

Figure 6. The recruitment index for each stock versus the stock specific entrainment index calculated using Eq. 2. If recruitment was significantly related to spawning stock biomass, the recruitment index is defined as the residuals of the fit to Eq. 3. Otherwise, the recruitment index is defined as the square root of recruitment, which serves to stabilize variance in the regression. Kendall's rank correlation coefficient, τ, is given.

unadjusted recruitment series, but again found that there was no significant change in the results.

Flierl and Wroblewski (1985) examined 5 years (1975-1979) of cod and haddock recruitment data from Georges Bank and found that in years when only a single eddy was observed during the spawning season, the cod and haddock year-classes were "good" to "very good," while in those years of several eddies recruitment was "weak." Our results, based on additional data, confirm the negative relationship between ring activity and haddock recruitment. However, we have found no clear relationship between ring activity and cod recruitment on Georges Bank. Even if we restrict the analysis to the years Flierl and Wroblewski used, we do not find a relationship between ring activity and recruitment of cod. We believe this is because we used a better approximation to the season during which the larvae were susceptible to entrainment, and used a more detailed analysis of ring activity.

c. The shelf-slope front. The position of the shelf-slope front (200 m isobath) is an alternative measure of ring activity (Fig. 4). The results using the area between the shelf-slope front and the 200 m isobath and the egg-plus-larval susceptibility functions are given in Table 2. The sign of the nonparametric regression, i.e. Kendall's τ, is positive for all 17 groundfish stocks (Table 3; Fig. 7), and 7 of these 17 relationships are nominally significant ($P < 0.05$). Although recruitment of yellowtail flounder from southern New England showed little relationship with the ring entrainment index, it appears to be strongly related to the frontal index. Again, the results when using the egg susceptibility functions alone were not significantly different. As before, the pelagic stocks generally show little relationship with the frontal index, with the exception of argentine, and a negative relationship for capelin.

d. The Gulf Stream position. We also examined the possible influence of the position of the Gulf Stream on recruitment; again using the egg-plus-larval susceptibility functions (Table 2). As opposed to the previous two sets of analyses, we consider this an exploratory analysis. The results of two-sided significance tests (Table 3) should not be interpreted in a confirmatory sense. The recruitment in groundfish stocks and argentine was generally positively related to the distance of the Gulf Stream from the shelf break. Several mechanisms could be responsible for these relationships. In particular, warm core rings tend to be closer to the shelf break if the mean distance from the Gulf Stream to the shelf is less (Myers and Drinkwater, 1986). The remaining pelagic stocks and sea scallops again show no consistent pattern with the position of the Gulf Stream.

e. The pelagic species. There was no consistent relationship between recruitment of pelagic stocks and warm-core ring activity. One possible reason is that recruitment data for pelagic species are generally less reliable than those for groundfish species.

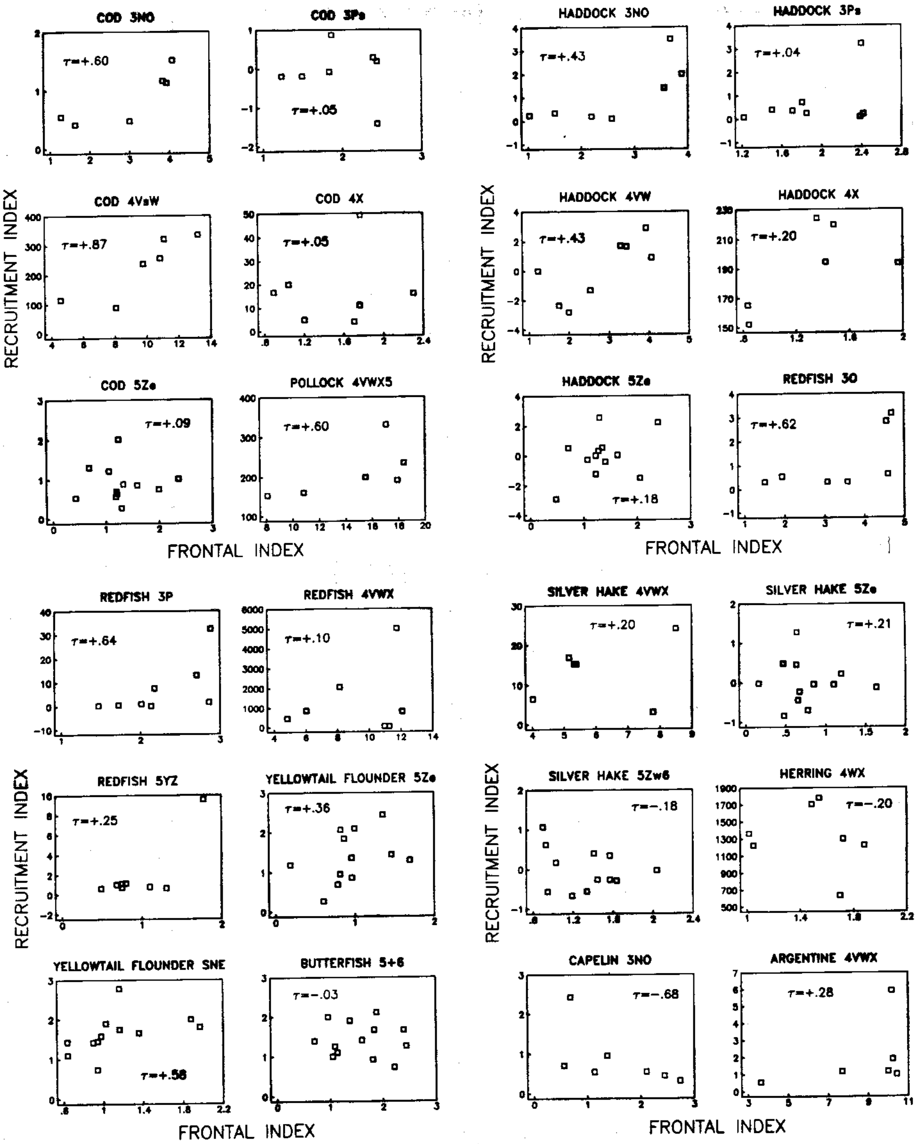

Figure 7. The recruitment index for each stock versus the stock specific frontal index which is calculated using the area between the 200 m isobath and the shelf-slope front. Kendall's rank correlation coefficent, τ, is given.

This is particularly true if the recruitment index were based upon research survey trawl data which are less efficient at capturing pelagic species than groundfish.

Some pelagic species, such as herring, spawn sufficiently far from the edge of the shelf that they may not be as susceptible to the effects of warm core rings, although the entrainment of cold shelf water nearshore off the southern tip of Nova Scotia into the slope water region (Smith, 1978; Trites, 1981) indicates that at times the influence of Gulf Stream rings can penetrate over 100 km inshore of the 200 m isobath. The pelagic species whose recruitment appears to decrease with warm core ring activity, argentine, lives on the outer edge of the continental shelf (Leim and Scott, 1966), and may therefore be influenced to a greater degree by warm core rings; however, silver hake also spawns on the continental shelf (O'Boyle *et al.*, 1984) and its recruitment shows little evidence of being affected by warm core ring activity.

Recruitment of Grand Banks spawning capelin (3NO) was found to increase if the shelf-slope front was close to the edge of the continental shelf or if there was increased ring activity. Although this relationship may be spurious, Frank and Carscaden (1987) have recently suggested a mechanism that may be responsible for this result. Grand Banks spawning capelin deposit their eggs in gravel on the southeast shoal of the Grand Bank, and their emergence appears to be triggered by intrusions of slope water onto the shelf. Our results are consistent with this mechanism because intrusions are more likely to occur when the shelf-slope front and warm core rings are close to the edge of the shelf.

f. Combined tests. How reliable are the results of the analysis? For any individual stock, the number of data points are small, and therefore the relationships between recruitment and the entrainment indices are usually not significant, however, the overall pattern is highly significant in that the ring entrainment index was negatively related to recruitment in 14 out of 17 of the groundfish stocks, and all 17 of the groundfish stocks were positively related to the frontal index. If recruitment was independent among stocks this would be strong evidence indeed, the probabiltiy of obtaining 17 positive regressions from 17 trials from random data is one in 130,000.

To adequately access the true confidence in the results we should remove the part of the data used in the exploratory analysis and take into account that each stock of the same species is not independent, i.e. when recruitment is high in one region it tends to be good in other regions (Templeman, 1972; Koslow, 1984; Thompson and Page, 1989). A conservative approach is to treat each species as being independent, and combine the significance tests for each species.

In order to avoid the problem of nonindependence caused by cross-correlation of recruitment among stocks of a species, we used a single probability from each of the groundfish species using the modification of Fisher's method described previously. Combining these P's for the ordering test, i.e. Kendall's τ, given in Table 3, results in an overall significance result ($P < 0.05$). Statistically significant results were also obtained if the ordinary least squares regression slope was used in the analysis instead of the nonparametric test. This can be repeated using the probability that Kendall's $\tau \leq 0$ from the frontal index; again the combined tests are significant ($P < 0.05$).

g. Is variability in recruitment a function of ring activity? The scatterplots for the recruitment indices of the groundfish stocks versus the ring entrainment indices

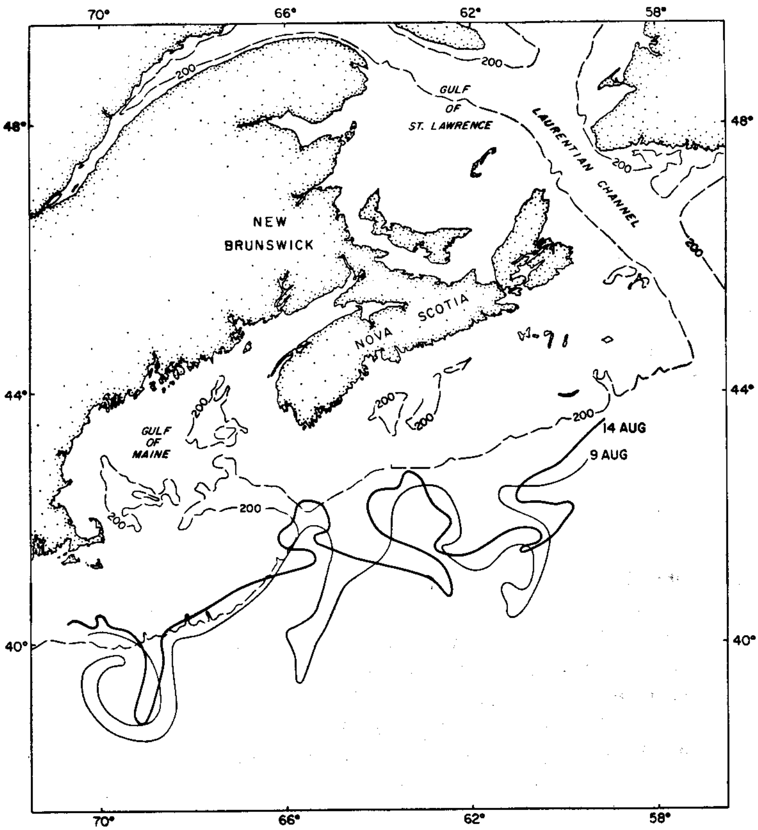

Figure 8. The position of the shelf-slope front on Aug. 9 and 14, 1985 showing the rapid changes in the entrainment features.

(Fig. 6) show a common pattern, i.e. when the ring entrainment index is low, recruitment may be high or low; whereas when the ring entrainment index is high, recruitment is nearly always low. Cod from Georges Bank (NAFO area 5Ze) is the only exception to this pattern. A simple interpretation may be that when the ring activity is low, good recruitment is not assured because many factors affect recruitment; however, when the ring activity is high, recruitment cannot be large. To test this hypothesis we compared the coefficient of variation, the ratio of the standard deviation to the mean, of recruitment below and above the median ring entrainment and frontal index for each stock. For 13 of the 17 groundfish stocks, the coefficient of variation was greater at larger frontal index (fewer rings). This is consistent with our hypothesis, and statistically significant at the 0.02 level on the basis of a nonparametric sign test. However, the coefficient of variation of recruitment was larger at lower levels of the ring entrainment index for only 11 of the 17 groundfish stocks, which is not significant at the 0.05 level ($P = 0.17$). We conclude that variability in recruitment is larger in years in which the frontal index is high, but the similar pattern for the ring entrainment index is not convincing. This may imply that the frontal index is a better measure because it depends upon Gulf Stream meanders and wind as well as warm-core rings.

4. Conclusion

We have found strong evidence that a reduction in recruitment of groundfish in the northwest Atlantic is associated with warm-core ring activity. The consistency of the overall pattern is highly significant, although there is little statistical confidence in the relationship with any individual stock. These results are consistent with our original hypothesis that ring-induced entrainment reduces recruitment in groundfish species, although we recognize the possibility that other mechanisms may in part account for these observed relationships. In view of our results it is at first surprising that more larvae of shelf species are not found in the slope water region. One reason may be related to the rapid mixing of the entrained shelf water with slope water (Fig. 8) which could result in a thermal stress on the larvae causing mortality as is suggested from the observations of Colton (1959).

Acknowledgments. Ron Trites and Peter Smith were responsible for obtaining and archiving the sea surface temperature charts. We thank David Methven for digitizing the sea surface temperature charts and Nick Payton for programming assistance. S. Akenhead, C. Annand, B. Atkinson, J. Baird, C. Bishop, B. O'Boyle, B. Brodie, S. Campana, J. Collie, R. Halliday, J. Hunt, P. Hurley, K. Frank, W. Gabriel, T. Koslow, G. Lilly, J. Loder, R. Mayo, J. McGlade, R. Mohn, R. Mahon, D. Miller, F. Page, P. Pepin, B. Petrie, D. Power, M. Sinclair, R. Stephenson, W. Templeman, K. Thompson, D. Waldron and K. Zwanenburg provided biological advice and/or generously allowed us to use their data.

REFERENCES

Auer, S. J. 1987. Five-year climatological survey of the Gulf Stream system and its associated rings. J. Geophys. Res., *92*, 11709-11726.

Bonnyman, S. 1981. Ichthyoplankton of the Grand Banks of Newfoundland. Section VI of Grand Banks Oceanographic Studies. Mobil Oil Canada Limited.

Churchill, J. H., Cornillon, P. C. and G. W. Milkowski. 1986. A cyclonic eddy and shelf-slope water exchange associated with a Gulf Stream warm-core ring. J. Geophys. Res., *91*, 9615-9623.

Colton, J. B., Jr. 1959. A field observation of mortality of marine fish larvae due to warming. Limnol. Oceanogr., *4*, 219-222

Colton, J. B. Jr. and J. L. Anderson. 1983. Residual drift and residence time of Georges Bank surface waters with reference to the distribution, transport, and survival of larval fishes. U.S. Department of Commerce, National Oceanic and Atmospheric Administration Technical Memorandum NMFS-F/NEC-24.

Colton, J. B., Jr., W. G. Smith, A. W. Kendall, Jr., P. L. Berrien and M. P. Fahay. 1979. Principal spawning areas and times of marine fishes, Cape Sable to Cape Hatteras. Fish. Bull., *76*, 911-915.

Cox, D. R. 1975. A note on data-splitting for the evaluation of significance levels. Biometrika, *62*, 441-444.

Cullliney, J. L. 1974. Larval development of the giant scallop, *Placopecten magellanicus* (Gmelin). Biol. Bull., *147*, 321-332.

Drinkwater, K. F. and R. A. Myers. 1987. Testing predictions of marine fish and shellfish landings from environmental variables. Can. J. Fish. Aquat. Sci., *44*, 1569-1573.

Fish and Wildlife Service, U.S. Department of the Interior. 1978. Development of fishes of the mid-Atlantic Bight, An atlas of egg larval and juvenile stages. 6 volumes.

Fisher, R. A. 1954. Statistical Methods for Research Workers, 12th ed., Oliver and Boyd, Edingburgh. 356 pp.

Fitzpatrick, C. and R. J. Miller. 1979. Review of spawning times and locations for some commercial finfish on the Newfoundland and Labrador coasts. Fish. Mar. Serv. Tech. Rep., *905*.

Flierl, G. R. and J. S. Wroblewski. 1985. The possible influence of warm core Gulf Stream rings upon shelf water larval fish distribution. Fish Bull., *83*, 313-330.

Frank, K. T. and J. E. Carscadden. 1987. Factors affecting recruitment variability of capelin (*Mallotus villosus*) in the Northwest Atlantic ICES C.M. 1987/Mini Symposium No. 1, 30 pp.

Friedlander, A. and D. Smith. 1983. Sand lance larvae found in entrainment feature associated with warm core ring off Hudson Canyon. Coastal Oceanogr. Climatol. News, *5*, 13-14.

Gulland, J. A. 1965. Estimation of mortality rates. Annex to Rep. Arctic Fish. Working Group, ICES C.M. 1965(3), 9 pp.

Halliwell, G. R. and C. N. K. Mooers. 1979. The space-time structure and variability of the shelf water-slope water and Gulf Stream surface temperature fronts and associated warm-core eddies. J. Geophys. Res., *84*, 7707-7725.

Koslow, J. A. 1984. Recruitment patterns in northwest Atlantic fish stocks. Can. J. Fish. Aquat. Sci., *41*, 1722-1729.

Laurence, G. C. 1978. Comparative growth, respiration and delayed feeding abilities of larval cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) as influenced by temperature during laboratory studies. Mar., Biol., *50*, 1-7.

Leim, A. H. and W. B. Scott. 1966. Fishes of the Atlantic Coast of Canada. Fish. Res. Board Can. Bull., *155*, 1-485.

Markle, D. F. and L. A. Frost. 1985. Comparative morphology seasonality, and a key to planktonic fish eggs from the Nova Scotian shelf. Can. J. Zool., *63*, 246-257.

Maurer, R., D. Busch and J. Green. 1979. Observations on the slope/shelf front in the immediate vicinity of a warm eddy. Coastal Oceanogr. Climatol. News, *2*, 3-4. (Available from Center for Ocean Management Studies, University of Rhode Island, Kingston, RI 02881).

Morgan, C. W. and J. M. Bishop. 1977. An example of Gulf Stream eddy-induced water exchange in the mid-Atlantic Bight. J. Phys. Oceanogr., *7*, 472-479.

Myers, R. A. and K. Drinkwater. 1986. The effects of entrainment of shelf water by warm core rings on Northwest Atlantic fish recruitment. ICES C.M.1986/C:13, 18 pp.

Mysak, L. A. 1986. El Niño, interannual variability and fisheries in the northeast Pacific Ocean. Can. J. Fish. Aquat. Sci., *43*, 464-497.

O'Boyle, R. N., M. Sinclair, R. J. Conover, K. H. Mann and A. C. Kohler. 1984. Temporal and spatial distribution of ichthyoplankton communities of the Scotian Shelf in relation to biological, hydrological, and physiographic features. Rapp. P.-V. Réun. Cons. Int. Explor. Mer, *183*, 27-40.

Olson, D. B. 1980. The physical oceanography of two rings observed by the Cyclonic Ring Experiment. J. Phys. Oceanogr., *10*, 514-528.

Olson, D. B., O. B. Brown and S. R. Emmerson. 1983. Gulf Stream frontal statistics from Florida Straits to Cape Hatteras derived from satellite and historical data. J. Geophys. Res., *88*, 4569-4577.

Pope, J. G. 1972. An investigation of the accuracy of virtual population analysis using cohort analysis. ICNAF Res. Bull. *9*, 65-74.

Scott, J. S. 1983. Inferred spawning areas and seasons of groundfishes on the Scotial Shelf. Can. Tech. Rep. Fish. Aquat. Sci., *1219*, iii + 14 pp.

Sherman, K., W. Smith, W. Morse, M. Berman, J. Green and L. Ejsymont. 1984. Spawning strategies of fishes in relation to circulation, phytoplankton production, and pulses in zooplankton off the northeastern United States. Mar. Ecol. Prog. Ser., *18*, 1-19.

Silverman, M. J. 1985. Distribution, abundance, and production estimates of Yellowtail Flounder, *Limanda ferruginea,* larvae off northeastern United States, 1982-1984. ICES C.M.1985/L:18.

Sinclair, M. and M. J. Tremblay. 1984. Timing of spawning of Atlantic herring (*Clupea harengus harengus*) populations and the match-mismatch theory. Can. J. Fish. Aquat. Sci., *41*, 1055-1065.

Sissenwine, M. P. 1984. Why do fish populations vary?, *in* Exploitation of Marine Communities, R. M. May, ed., Dahlem Konferenzen. Springer-Verlag, Berlin, 59-94.

Smith, P. C. 1983. The mean and seasonal circulation off southwestern Nova Scotia. J. Phys. Oceanogr., *13*, 1034-1054.

—— 1978. Low-frequency fluxes of momentum, heat, salt, and nutrients at the edge of the Scotian Shelf. J. Geophys. Res., *83*, 4079-4096.

Smith, P. C. and B. D. Petrie. 1982. Low-frequency circulation at the edge of the Scotian Shelf. J. Phys. Oceanogr., *12*, 28-46.

Sokal, R. R. and F. J. Rohlf. 1981. Biometry, W. H. Freeman, San Francisco, 859 pp.

Templeman, W. 1972. Year-class success in some North Atlantic stocks of cod and haddock. ICNAF Spec. Publ. *8*, 223-239.

Thompson, K. R. and F. H. Page. 1989. Detecting synchrony of recruitment using short autocorrelated time series. Can. J. Fish. Aquat. Sci. (in press).

Trites, R. W. 1981. Application of satellites and remote sensing to studies of surface circulation off the Nova Scotian coast, *in* Oceanography from Space, Proceeding of a COSPAR/SCOR/IUCRM Symposium held May 26-30, 1980 in Venice, Italy, J.F.R. Gower, ed. Marine Science, *13*, Plenum Press, New York.

Vazquez, J. and D. R. Watts. 1985. Observations on the propagation and growth, and predictability of Gulf Stream meanders. J. Geophys. Res., *90*, 7143-7151.

Wroblewski, J. S. and J. Cheney. 1984. Ichthyoplankton associated with a warm core ring off the Scotian Shelf. Can. J. Fish. Aquat. Sci., *41*, 294-303.

Received 9 *October, 1987;* revised: *18 April, 1989.*