

An age-structured index of cod larval drift and retention in the waters off southwest Nova Scotia

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Campana, Steven E., Smith, Stephen J., and Hurley, Peter C. F. 1989. An age-structured index of cod larval drift and retention in the waters off southwest Nova Scotia. - Rapp. P.-v. Réun. Cons. int. Explor. Mer, 191: 50-62.

This study was designed to test between alternative hypotheses concerning the retention and/or drift of cod larvae from their spawning location on Browns Bank. The study was based upon comprehensive larval surveys off southwestern Nova Scotia conducted at monthly intervals through the winter-spring of 1985. Otolith microstructure examination was used to determine the ages of over 500 cod larvae. Trend surface analysis of the age-structured spatial distribution of the larvae indicated net shoreward movement of larvae greater than 20 d old, but at a rate significantly less than that of the associated water masses. Components of both drift and retention apparently influenced the distribution of larvae subsequent to hatching. Given the stochasticity of gyre activity on Browns Bank and the observed distribution of larvae, it appears that the latter was the product of a sequential and three-stage process, consisting of retention on Browns Bank, probabilistic extrusion to, and retention in, a shear zone just north of Browns Bank, and probabilistic entrainment in a coastal current. This proposed mechanism would result in a retention/drift dichotomy for individual larvae, but would appear as a net larval displacement towards shore at a low mean rate for the population as a whole.

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Introduction

Passive advection (drift) of ichthyoplankton away from the spawning site has been observed in both freshwater (Fortier and Leggett, 1983; Muth and Schmulbach, 1984; Ouellet and Dodson, 1985) and marine systems (Lear and Green, 1982; Ellertsen *et al.*, 1984; Lockwood and Lucassen, 1984; Smith and Morse, 1985; Cushing, 1986; Jahn and Lavenberg, 1986; Power, 1986; Kendall *et al.*, 1987). In instances where the spawning site and the subsequent centre of juvenile abundance were widely separated, and particularly where discrete larval cohorts were monitored along their drift path, interpretations other than that of drift (advection) are difficult to support. Larval drift to a juvenile "nursery area", with a subsequent return migration of adults to spawn, describes the well-known "migration triangle" of Harden-Jones (1968), and provides the basis for a widely-accepted hypothesis concerning variability in marine fish production (Cushing, 1972). However, there are a number of marine systems in which the advective drift of ichthyoplankton, particularly larvae, is restricted

or absent, even in the presence of directed residual currents (Iles and Sinclair, 1982). The "larval retention" hypothesis of Iles and Sinclair (1982) is based upon observations of retention of early life history stages in well-defined geographic regions. Retention is reported to have been associated most often with physical, particularly tidal, features of the circulation, but vertical movements of larvae have also been implicated (Fortier and Leggett, 1983; McCleave *et al.*, 1987; Sinclair and Iles, 1988). Despite reports of supporting evidence among other species (Gagné and O'Boyle, 1984; O'Boyle *et al.*, 1984; Smith and Morse, 1985; Sinclair and Iles, 1988), the retention hypothesis has yet to be rigorously tested in species other than herring (*Clupea harengus*).

The spatial coincidence of cod (*Gadus morhua*) eggs and larvae on several banks on the Scotian Shelf has been interpreted as the first demonstration of retention in this species (Gagné and O'Boyle, 1984; O'Boyle *et al.*, 1984). Unfortunately, interpretation of the above studies was confounded by the broad temporal and spatial scale of the sampling, the inability to follow

discrete larval cohorts, and the aggregation of larvae of all sizes and ages into a single class. As noted by Cushing (1986), coincidence of eggs and young larvae may occur even in the presence of drift; any displacement of the older larvae would almost certainly be masked by the numerically-dominant younger larvae, which by definition would be in closer proximity to the spawning site. Accordingly, a proper test of the retention hypothesis in this system requires an age-structured analysis of the larval distribution data.

Browns Bank, on the southern Scotian Shelf, has been identified as a circumscribed spawning site for cod (Gagné and O'Boyle, 1984; Hurley and Campana, in press). In this paper, we use the results of five surveys of the region to examine the age-structured spatial distribution of cod larvae in and around the spawning site. The objective is to quantify the change in larval distribution as a function of age, and to compare this with estimates based on properties of the circulation. The findings will then be discussed in the context of the drift-retention controversy: if drift is present, larval displacement from the spawning site should increase with age in a direction and at a rate consistent with the residual currents.

Materials and methods

Cod larvae were collected in five different cruises over a fixed survey grid as part of the Fisheries Ecology Program ichthyoplankton survey. The survey encompassed 97 stations off southwestern Nova Scotia, down to and including portions of Georges Bank (Fig. 1). Collections were made monthly between February and June of 1985, although weather restricted grid coverage on some cruises (Table 1). Each station was sampled with paired bongo nets fitted with 61 cm frames, 333 μ m Nitex mesh, and mouth-mounted flowmeters. Tows were made obliquely to within 5 m of the bottom (to a maximum of 200 m) and immediately replicated. Full sampling details and cruise-by-cruise station locations are documented elsewhere (Hurley and Campana, in press).

Otolith microstructure examination is the most effective and precise age determination tool available for

young fish (Pannella, 1971; Brothers *et al.*, 1976; reviewed by Campana and Neilson, 1985) and thus was adopted for this study. Ichthyoplankton samples were preserved and processed as described elsewhere (Campana and Hurley, 1989). All larvae, except those damaged by preservation, were aged. Both pairs of sagittal and lapillar otoliths were removed, mounted individually, and prepared according to standard techniques (Campana and Neilson, 1985). Microstructural interpretations were independently validated with known-age cod larvae (Campana and Hurley, 1989), indicating that daily growth increment counts of the lapillus (plus one, corresponding to the age at hatch check formation (Campana, 1989)) accurately represented the age of the larvae. Ages were probably underestimated by 2–3 d due to the presence of daily increments too narrow to resolve with a light microscope (Campana, 1989), but this level of bias was considered both acceptable and unavoidable. The accuracy of the age estimates cannot be stated unequivocally, but appears to be in the order of ± 3 d for 10 d old larvae, and ± 5 d for larvae 100 d old.

All spatial analyses of the larvae were based upon the age-structured mean number of larvae per m^2 of ocean surface. Larval ages were subsequently categorized by 10 d intervals, with the oldest larvae categorized as a plus group (51+ d). Sample size requirements for the trend surface model necessitated fewer age categories (0–10, 11–20, 21–30, and 31+ d) and the removal of Cruise H130. For the purpose of presentation (only), larval age structure was also aggregated by region; regional boundaries were assigned on the basis of bathymetry, proximity to land, and apparent homogeneity of age structure among stations. The age-proportion histograms for each region represent the percent contribution of a given age category within that region to the total abundance of that age category within the cruise.

Age-structured centres of abundance (centroids) were calculated as the weighted mean latitude and longitude in decimal degrees for larvae in each age category. Larvae collected on Georges Bank were not included in this or the other spatial analyses, since Georges Bank ichthyoplankton are effectively isolated from those on Browns Bank (O'Boyle *et al.*, 1984; Perry and Hurley, 1986).

Table 1. Summary of cruises represented in this study.

Year	Cruise	Date	No. of stations sampled	No. of stations with larvae	No. of larvae	No. of larvae aged
1985	H130	Feb 4–22	93	8	17	15
	H132	Mar 11–29	49	18	62	47
	H133	Apr 6–17	90	34	236	225
	H135	May 6–16	57	43	201	113
	H137	Jun 3–14	59	22	49	34

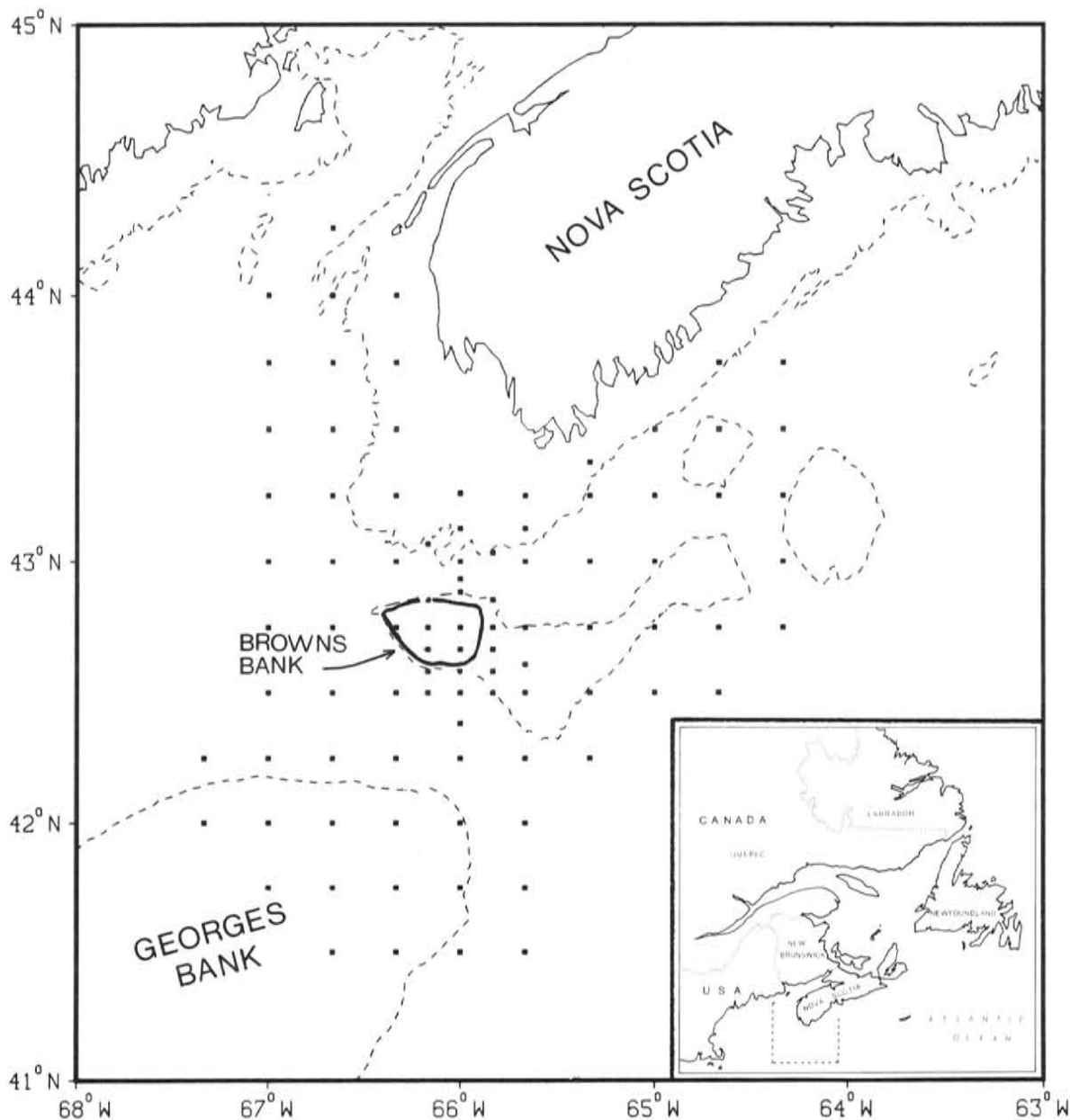


Figure 1. Map of study area showing collection stations. The 100-m contours have been included. Browns Bank has been delimited by a solid line.

Trend surface analysis

Trend surface analysis is a form of polynomial regression suited to modelling broad trends in spatial data (Cliff and Ord, 1981; Ripley, 1982). In the formulation used here the spatial coordinates of latitude (x_{1i}) and longitude (x_{2i}) for the i th sample site were defined as co-variables in the following polynomial:

$$\mu_i = \sum_{s=0}^p \sum_{r=0}^q \beta_{rs} x_{1i}^r x_{2i}^s \quad (1)$$

where $p + q \leq k$ denotes the highest order polynomial terms. Conceptually, trend surface analysis can be envisioned as the planar version of a simple, least squares regression. Continuing the analogy, the β parameter in equation (1) is the slope of the regression, and the two x variables correspond to the two dimensions of the plane. The dependent variable is, of course, larval abundance. The most difficult components to conceptualize are the higher order polynomial terms. These introduce curvature into the trends in larval abundance. For example, while a first order model would allow a linear

gradient in abundance to be modelled (e.g. high abundance in the South to low in the North), a second order (quadratic) model could be used to detect a localized centre of abundance (a dome-shaped abundance pattern), and a cubic model two centres. Again, the analogy to regression analysis applies, where a simple regression model would be used to fit a straight line, a quadratic model for a parabola, etc. The same advantages of regression analysis also apply, in that an increase in the number of stations increases the potential precision of the model fit. Thus, there is no danger in fitting a model to cruises with differing station coverage. For further clarification and examples of use, the reader is referred to Campana *et al.* (1989).

While Gaussian errors are generally assumed for trend surface models, the variances were proportional to the means in this study. Therefore the densities of the cod larvae were modelled assuming a generalized Poisson distribution for the response variable with $E\{y_i\} = \exp\{\mu_i\}$. The exponential was used to ensure that the predicted values were ≥ 0 as expected for the Poisson distribution. Parameter estimates were obtained using iteratively re-weighted least squares with the computer package GLIM (Payne, 1986). Models were selected using the analysis of deviance approach discussed in McCullagh and Nelder (1983).

The focus for a trend surface approach is a reactive process where the spatial distribution of the response variable is due to location of the sites rather than inter-site interactions. Therefore the spatial process is assumed to be non-stationary in the mean but trivially stationary in the covariance structure. In other words,

this type of model is most appropriate when external forces (i.e. currents), rather than inter-site biological interactions, dominate the data. This type of structure limits these models to describing broad trends, in contrast to autoregressive and regionalized variable methods which are used to model more localized variations.

Results

A total of 565 cod larvae were collected during the five cruises (Table 1), with catches at individual stations ranging from 0 to 26. Sixty-four per cent of the stations produced no cod larvae. The range of larval ages spanned 4–154 d, with larvae less than 40 d old making up 84% of the collection (Fig. 2). The February (H130) and June (H137) cruises were characterized by catches of older larvae, while the other surveys were dominated by larvae less than 20 d old. The mean age of all larvae sampled was 23.1 d (the median age was 13 d).

The relative abundance and spatial distribution of each age category is presented in Figure 3. All cruises except that of February (H130) showed the same general pattern of distribution, with centres of abundance on and to the NNW of Browns Bank. Larvae were consistently found on Georges Bank as well, but in smaller numbers. Few larvae were found to the east or west of Browns Bank, or in the waters between Browns and Georges banks. Most of the larvae captured in February (H130) were found at the stations nearest shore, particularly to the northeast of Browns Bank.

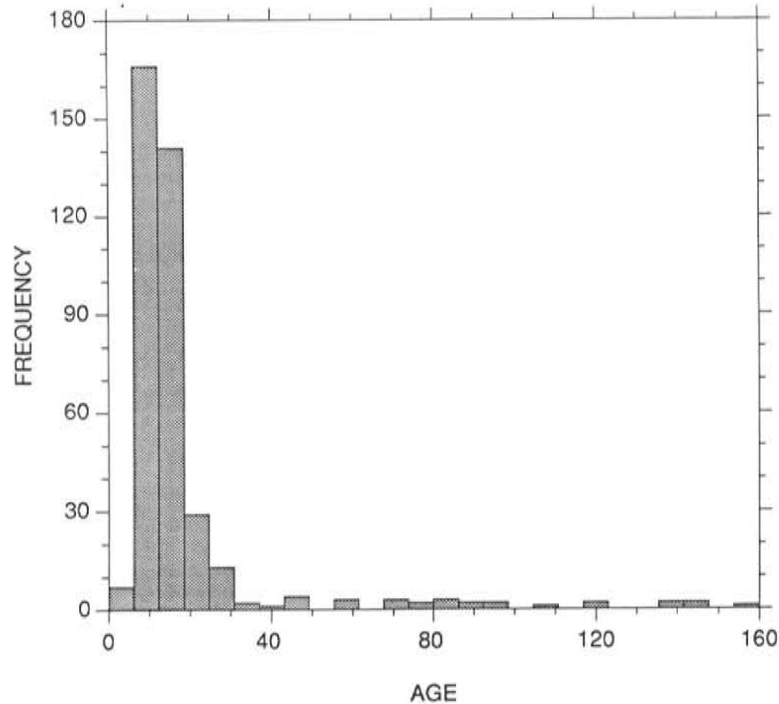


Figure 2. Frequency of observed ages (days) among cod larvae collected on five cruises in 1985.

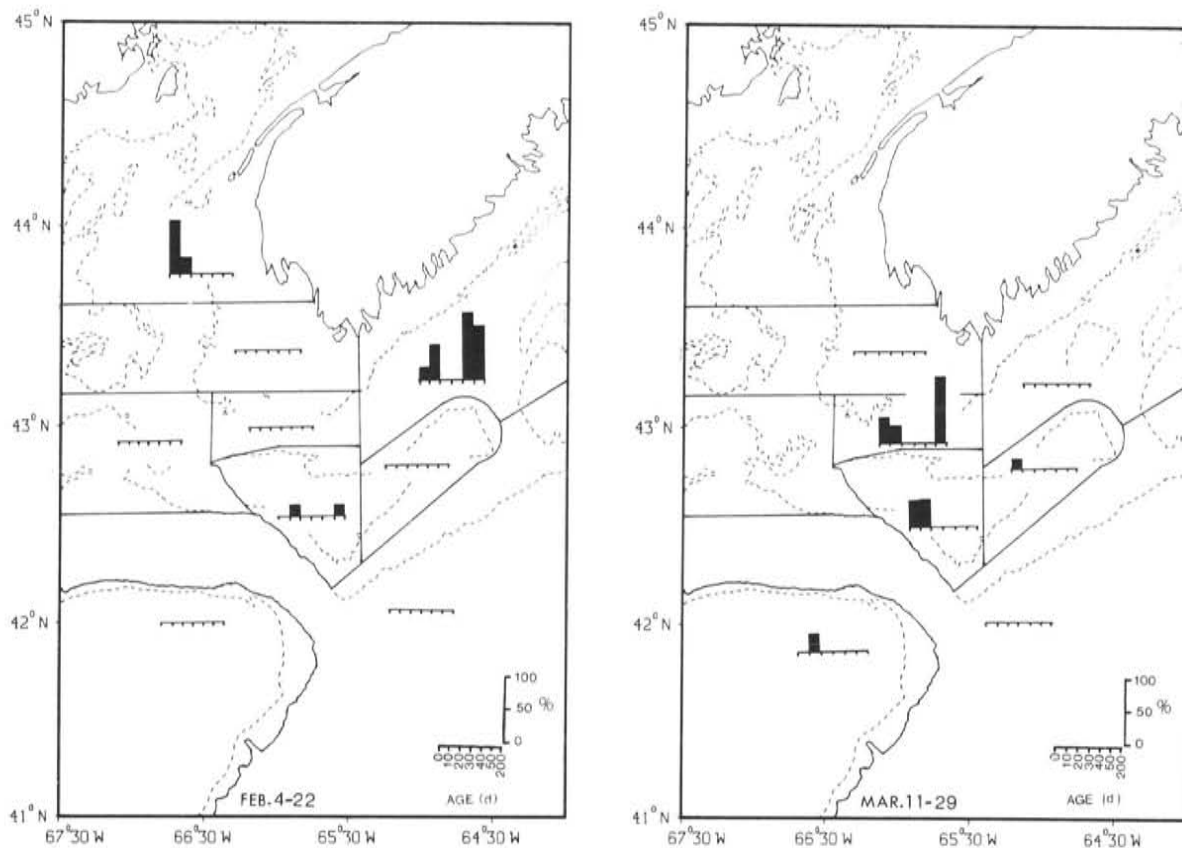


Figure 3a. Spatial distribution by age (days) of cod larvae collected on each of five cruises in 1985. Histograms represent proportion of each age category found within each region (regions shown by heavy lines) relative to the total abundance of that age category within the cruise. Regions without a histogram axis were not sampled.

The age composition of the samples differed significantly both among cruises and among stations (Kruskal-Wallis, $p < 0.01$). On the basis of Figure 3, the larval age composition in each region appeared to be roughly comparable among all cruises, with the exception of that of February (H130). Browns Bank and the region immediately north of it (along the 100 m contour) was consistently characterized by a large proportion of larvae less than 30 d old, and lesser proportions of older larvae. The age compositions of regions to the northwest of Browns Bank were generally skewed to the right, indicating an older age distribution, but were seldom associated with larvae greater than 40 d old. The regions east of Browns Bank contained relatively few larvae, but those were either very young (<10 d) or very old (>40 d).

Calculations of the Julian hatch dates of the larvae, based upon their age and date of sampling, were used to identify and track discrete cohorts across cruises. However, high larval mortality rates reduced the number of cohort survivors to levels unsuited for statistical analysis. As a proxy for this type of analysis, the following analyses assume that the spatial distribution by

age within a cruise resembles that of a single cohort through time; the similarity in the age-structured distribution of larvae among five different cruises supports this assumption.

As a corollary of the larval drift hypothesis, distance from the spawning site was tested for a relationship with larval age. When aggregated across cruises, the centres of abundance (centroid) for each age category (excluding Georges Bank larvae) were tightly clustered and showed relatively little displacement from Browns Bank (Fig. 4). Larvae less than 20 d old were centred directly on the bank, while all four of the older age categories were just to the north, near the 100 m contour. Cruise-by-cruise plots of the age-structured centroids were consistent with this pattern. In a more sensitive test of the same corollary, the relationship between larval age and distance from Browns Bank was again examined, under the explicit assumption that the centre of Browns Bank was the spawning site. No relationship was evident, either in terms of correlation or variance (Fig. 5). However, there was a suggestion of spatial clustering at ages greater than 40 d.

The results of the trend surface analysis demonstrated

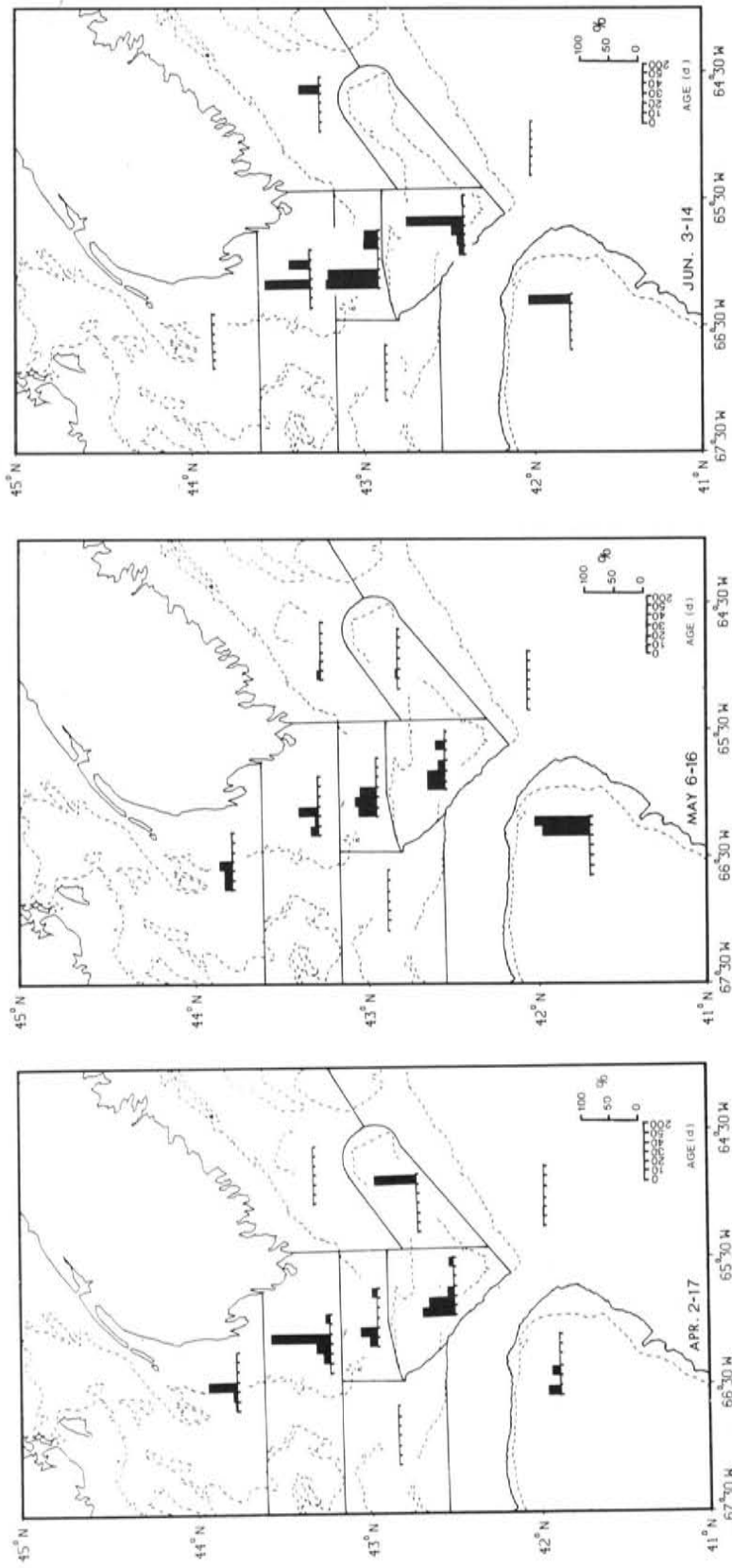


Figure 3b. Spatial distribution by age (days) of cod larvae collected on each of five cruises in 1985. Histograms represent proportion of each age category found within each region (regions shown by heavy lines) relative to the total abundance of that age category within the cruise. Regions without a histogram axis were not sampled.

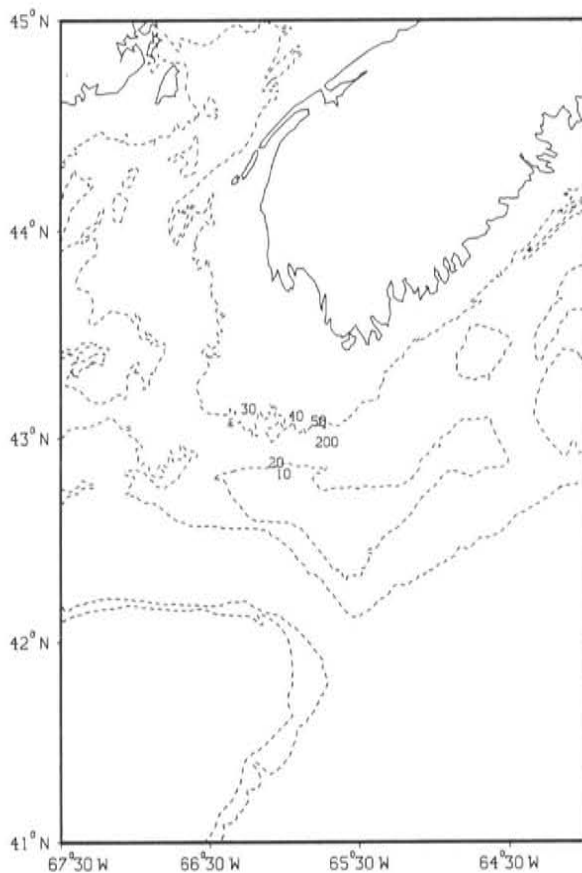


Figure 4. Centres of abundance (centroids) for each of six age categories of larval cod. Age labels represent 0–10(10), 11–20(20), 21–30(30), 31–40(40), 41–50(50), and 51–200(200) days. Data have been aggregated across cruises.

the presence of differing spatial distributions between the larval age categories. In fitting the model, spatial coordinate terms were nested within age, since similarity in the distribution of larvae among ages could not be assumed. This model structure allowed both linear and quadratic surfaces to be fit, although the latter proved to be more informative (Table 2). A model where age and position were nested within cruise indicated that within-cruise nesting was unnecessary, and that differences in larval abundance among cruises were adequately described by cruise-specific factors. Of the four cruises entered into the model, all provided comparable station coverage of the area important to the analysis. The one exception, H132, lacked coverage of the northernmost stations (Hurley and Campana, in press). However, there is no reason to believe that this affected the results of the model. The final model demonstrated that larval abundance differed significantly among cruises, as did abundance within each age category (Table 2). Parameters associated with larval location were not significantly different between ages 0–10 and 11–20, but the latter were significantly different

from those of the older larvae. While no strong patterns were evident in the residuals, some of the residual plots suggested that other model formulations might improve upon the fit. However, we would not expect the parameter estimates to change appreciably.

Contour plots of the fitted values from the trend surface model (with the cruise factor, or mean abundance, removed) were used to examine the relative locations of each age category (Fig. 6). Consistent with the parameter estimates in Table 2, larvae of ages 0–10 and 11–20 demonstrated nearly identical spatial distributions. Both were centred near and slightly to the north of Browns Bank, although the latter appeared to be slightly more dispersed. Larvae between the ages of 21 and 30 d were centred 80 km to the NNW of Browns Bank, while larvae older than 30 d were broadly distributed, both around Browns Bank and to the NNW.

Discussion

As a corollary of the larval drift hypothesis, larval age should increase with net displacement from the spawning site. The trend surface analysis confirmed the presence of larval advection from Browns Bank. However, the transport process was so weakly defined that it could not be detected with more conventional tests (Figs. 4, 5), and was certainly not evident on the basis of simple length-structured larval distributions (Campana, unpublished). Therefore it is not at all surprising that earlier studies of the region, which compared aggregate distributions of eggs versus larvae, failed to detect evidence of larval drift (Gagné and O'Boyle, 1984; O'Boyle *et al.*, 1984). Indeed, the transport of Browns Bank cod larvae appears to be more

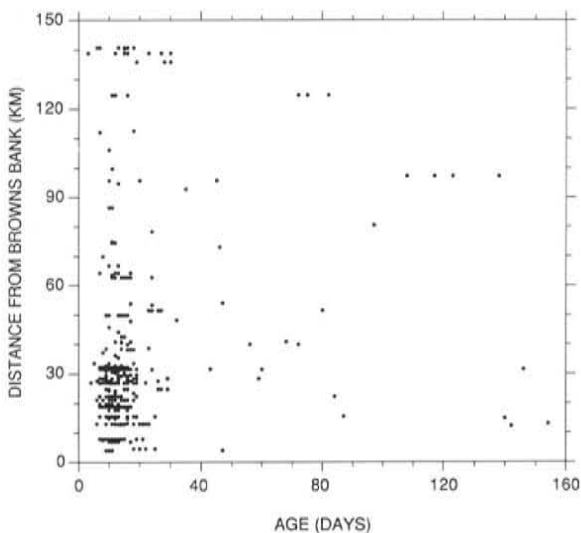


Figure 5. Relationship between the age of larval cod and their distance from the Browns Bank spawning site at the time of collection.

Table 2. Fit of the trend surface model relating the abundance of cod larvae (number/0.047 per m²) to their age category, date (cruise), and location of capture. Cruises 1-4 represent H132, H133, H135, and H137, respectively. Ages 1-4 represent 0-10 d, 11-20 d, 21-30 d, and 31+ d, respectively.

Model	Reduction in deviance	D.F.	χ^2 statistic	p-level
μ				
+ cruise	159.0	3	56.61	<0.0001
+ age	915.6	3	439.25	<0.0001
+ age.linear	108.8	8	54.12	<0.0001
+ age.quadratic	624.10	20	387.16	<0.0001

	Parameter	Estimate	Standard error
	μ	0.1381	0.1862
	Cruise(2)-Cruise(1)	1.0770	0.1595
	Cruise(3)-Cruise(1)	0.4404	0.1718
	Cruise(4)-Cruise(1)	-0.3873	0.2028
	Age(2)-Age(1)	0.6257	0.1612
	Age(3)-Age(1)	-2.914	0.5820
	Age(4)-Age(1)	-1.270	0.2801
Age 1 terms:	Latitude	-0.4474	0.5131
	Longitude	2.145	0.5879
	Latitude ²	-3.855	1.099
	Longitude ²	-5.156	1.094
	Latitude \times Longitude	2.775	1.701
Age 2 terms:	Latitude	0.2011	0.3036
	Longitude	2.039	0.3315
	Latitude ²	-3.228	0.5667
	Longitude ²	-3.300	0.4808
	Latitude \times Longitude	2.259	0.8412
Age 3 terms:	Latitude	-1.533	1.402
	Longitude	13.66	3.370
	Latitude ²	-3.802	1.341
	Longitude ²	-19.21	5.097
	Latitude \times Longitude	11.03	4.551
Age 4 terms:	Latitude	1.757	0.8471
	Longitude	-0.7187	0.5273
	Latitude ²	-6.847	2.356
	Longitude ²	-1.468	0.7265
	Latitude \times Longitude	4.063	1.988

limited than that of any other larval drift system yet described; drift paths of >300 km are common elsewhere, and are usually so well-defined that unstructured larval collections are sufficient to track the movement of a cohort (Lear and Green, 1982; Ellertsen *et al.*, 1984; Ouellet and Dodson, 1985; Warlen and Chester, 1985; Smith and Morse, 1985; Cushing, 1986; Jahn and Lavenberg, 1986; Power, 1986; Kendall *et al.*, 1987). In this study, drift from Browns Bank to the southwestern tip of Nova Scotia would result in a maximum displacement of 100 km. The observed mean displacement (based upon the trend surface contour) was closer to 80 km. While this distance is relatively short, use of age-structured distributions has proven to be a powerful discriminator of drift/retention in other systems (Beckman and Dean, 1984; Warlen and Chester, 1985); the

fact that a full spatial model was required for the detection of drift in this study suggests that net advection was minimal and that larvae were largely retained offshore.

A comparison of the relative transport rates of the water and ichthyoplankton from Browns Bank indicated that there may have been a behavioural component to the larval retention on and around the bank. Estimates of larval transport rate were made through use of the trend surface contours. The distances between the contoured centres of abundance for the first three age categories suggested net rates of movement of 2.5 km/d (0-10 to 11-20 d old larvae) and 6.5 km/d (11-20 to 21-30 d old larvae); the contoured distribution of the 31+ d old larvae was too broad to consider. A more complete calculation would include the duration of the egg state (14-21 d; Laurence and Rogers, 1976), result-

ing in net movement of 2.0 km/d from the time of spawning to age 21–30 d. This rate is considerably less than that of the associated water masses. Surface waters would be expected to reach the Nova Scotia coastline in less than 20 d (an approximate rate of 5 km/d) (Lawrence and Trites, 1983), but are probably not representative of the depth profile of the larvae. In a more relevant study, Smith (1983, 1989) used satellite-tracked drogues (centred at a depth of 10 m) and year-long current meter measurements in a study of water circulation patterns on and around Browns Bank, and concluded that a temporally variable but persistent gyre was present. After a mean residence time of 14 d on the bank, drogues tended to exit to the northwest and become entrained in a current following the 100 m bathymetric contour; mean winter current speed along this contour at a depth of 15 m was 8.6 km/d. The presence of the “leaky” gyre and the direction of displacement of the drogues was completely consistent with the observed age-structured distribution of the cod larvae. However, based upon Smith’s (1989) data, the mean displacement rate of all drogues that remained at large more than 4 d was calculated as 7.0 km/d ($s = 3.8$, $N = 18$); this value is significantly greater ($p < 0.01$) than the estimated egg and larval drift rate of 2.0 km/d. The association of a gyre with the Browns Bank cod spawning area suggests that physical retention of ichthyoplankton would be likely in any case. Given the assumption that drogue displacement adequately represented water displacement in the spawning area, the discrepancy between the water mass and ichthyoplankton transport rates suggests the presence of a behavioural component to the retention process.

Inadequacies in the survey design and/or sampling methodology would not have resulted in the concurrent drift and retention patterns reported here. The five cruises spanned virtually all of the spring spawning activity on Browns Bank (Hurley and Campana, in press) and appeared to circumscribe the larval distribution to the west, east, and south of Browns Bank. While the area inshore of approximately the 60 m contour was not sampled, an independent larval survey reported no significant larval numbers in this inshore region in 1985 (Suthers and Frank, 1989). Even if present, unsurveyed larvae would artifactually lower the apparent drift rate, but would not invalidate observations of retained older larvae on and around Browns Bank. A similar effect would be expected given immigration of eggs and/or larvae from alternate spawning sites. There is no evidence of drift from Georges Bank, either in this study or elsewhere (O’Boyle *et al.*, 1984; Perry and Hurley, 1986). Longshore drift from a different spawning site on the eastern shore of Nova Scotia was clearly evident in the February (H130) cruise, and was expected on the basis of previous observations of inshore fall spawning (Gagné and O’Boyle, 1984). However, the influx of fall-spawned larvae was easily

separated from that originating on Browns Bank, and was one of the bases for the exclusion of the February cruise from the trend surface analysis. With respect to sampling methodology, there is little doubt that the use of bongo gear is inappropriate for abundance estimation of older larvae and juveniles (Cushing, 1986; Frank, 1988; Suthers and Frank, 1989). However, since this study analysed the relative spatial distribution within an age category, it was insensitive to any size-related gear avoidance that may have occurred.

This study has demonstrated that there was a net displacement of cod larvae inshore from the spawning site, but that the larvae as a whole were retained offshore longer than would be expected on the basis of water residence times. While the analysis suggested a steady, net transport inshore, the displacement was probably all-or-none for individual larvae. The stability of the Browns Bank gyre is highly variable, to the point of being stochastic (Smith, 1989; Loder *et al.*, 1988). Individual particles contained therein, such as drogues and ichthyoplankton, may exit the gyre very quickly or be retained for extended periods. In other words, their retention is a probabilistic dichotomy. Of those larvae extruded from the gyre, many appeared to become entrained in the shear zone between the bank and the 100 m contour, formed by the near-confluence of the Nova Scotia coastal current and the oppositely-directed Browns Bank gyre. There is, as yet, no physical basis for retention in this shear zone, but high concentrations of larvae were consistently observed there. If physically based, retention within this zone would presumably be stochastic and dichotomous. Displacement from this second region would almost certainly result in entrainment in the rapid flow of the coastal current, which proceeds in the same direction as that of the net movement of the larvae. The result of this three-stage process would be retention of some larvae on Browns Bank, retention of others in the shear zone north of the bank, and transport of others towards the inshore and/or mouth of the Bay of Fundy. This proposed mechanism is fully consistent with the observed aggregations of older larvae on and around the bank and near shore, and would result in a net larval displacement towards shore at a low mean rate. Biological mechanisms for retention are easily added to this physically-based scenario.

Until recently, there has been no precedent for our findings which report the concurrent action of both drift and retention processes on a single cohort of ichthyoplankton (Iles and Sinclair, 1982; Cushing, 1986). Yet there is no apparent reason why the two processes should be mutually exclusive. In an elaboration of the retention hypothesis (termed the member-vagrant hypothesis), the potential for drift within a retention area was acknowledged through emphasis on population discreteness during the early life history stage, rather than larval fidelity to the spawning site (Sinclair, 1988;

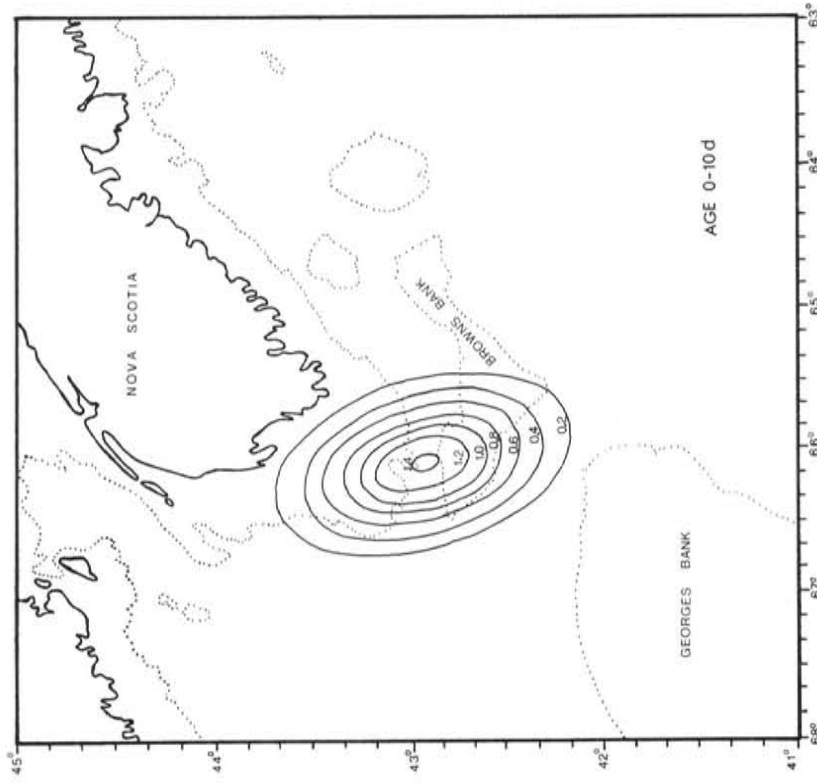
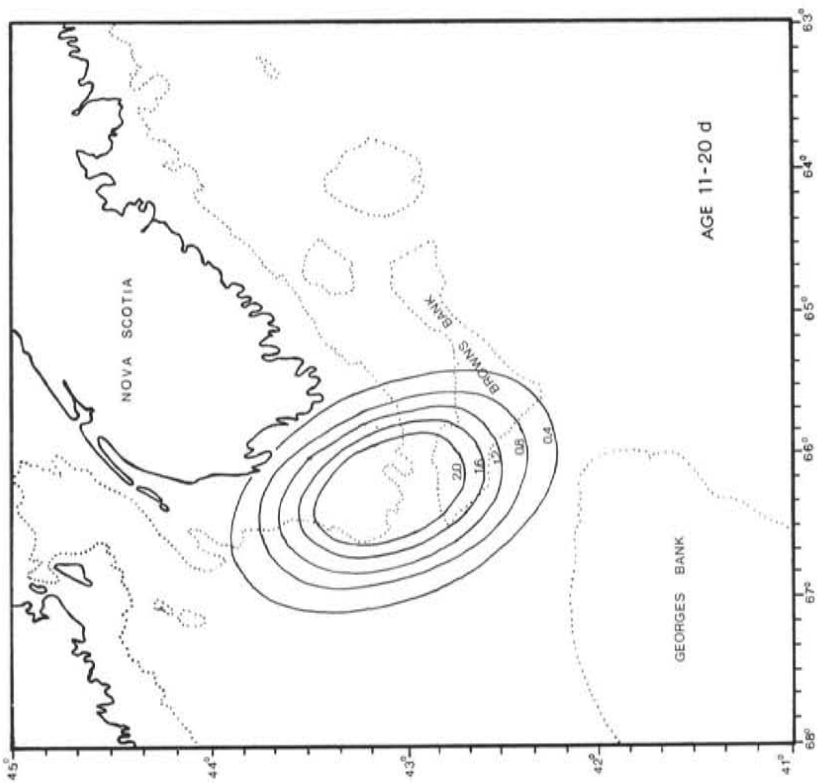


Figure 6a. Contours of cod larval abundance (number/0.047 per m²) for each of four daily age categories. Contours represent results of fitted trend surface model, with the cruise factor removed.

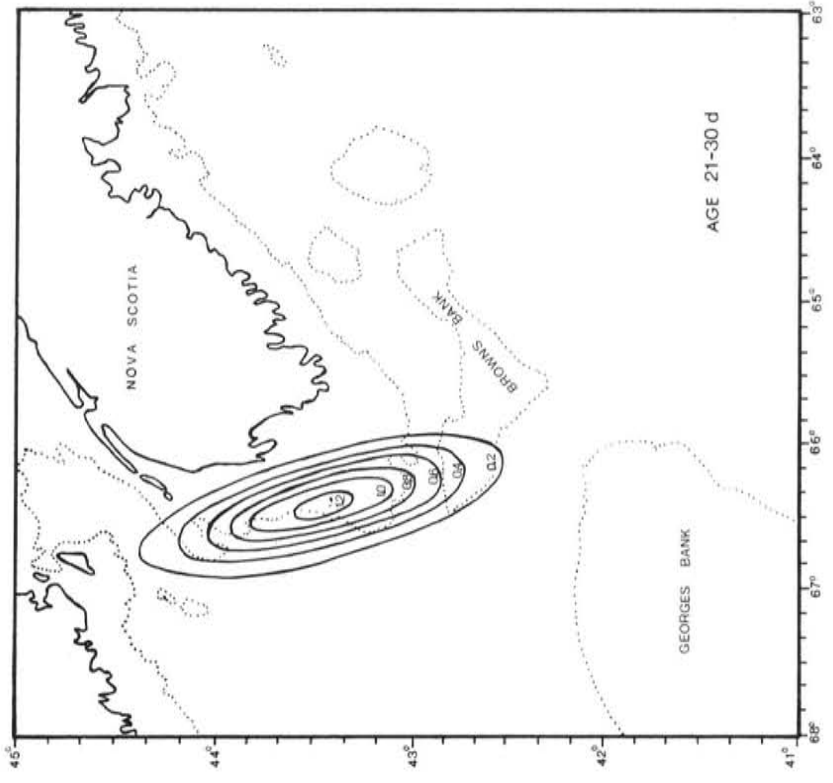
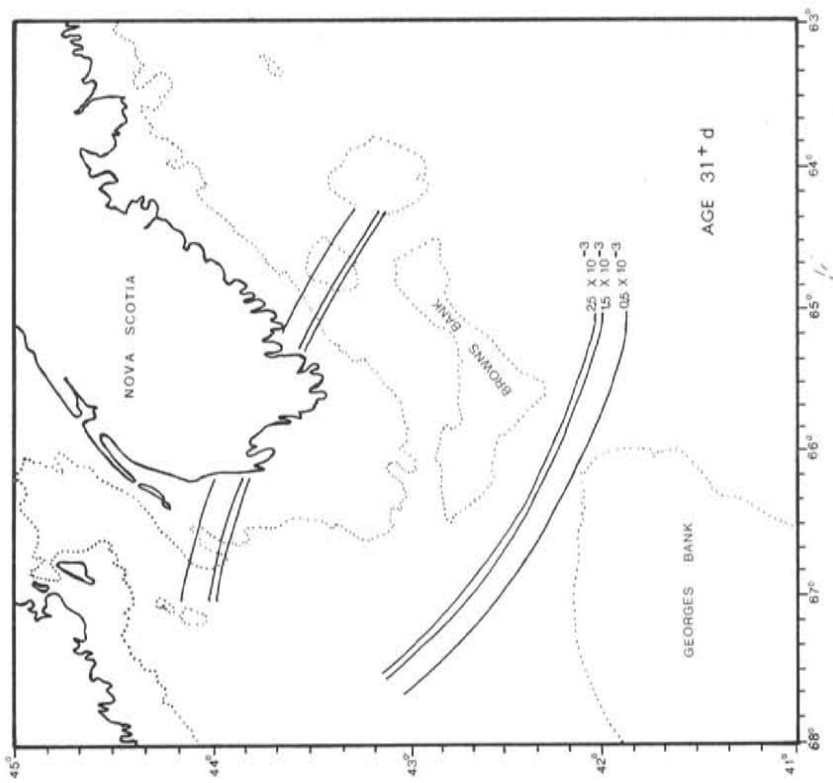


Figure 6b. Contours of cod larval abundance (number/0.047 per m²) for each of four daily age categories. Contours represent results of fitted trend surface model, with the cruise factor removed.

Sinclair and Iles, 1988). If such were true in the case of Browns Bank cod, the entire region between Browns Bank and the inshore region would have to be considered a single retention zone. Within the context of the member-vagrant hypothesis, the alternative interpretation would be that all larvae that drift inshore are "vagrants", and thus lost to the population gene pool. Given the numbers of juvenile cod that are later found inshore (Campana, unpublished), the latter appears unlikely. Whether consistent with the member-vagrant hypothesis or not, it appears that Browns Bank cod have evolved an excellent dispersal and survival strategy. Through segregation of the larval population into both inshore and offshore components, environmental differences between the two regions almost certainly enhance the probability of overall population survival in the face of interannual variations in the environment.

Acknowledgements

We sincerely thank the many individuals involved in the collection of these larvae, particularly Jim Reid and Jim Simon. Lou Van Guelpen and the Huntsman Marine Laboratory confirmed the larval identifications. Chris Hodgkinson and Estelle Laberge provided the expertise for otolith removal and otolith examination, respectively. Thanks also to Mark Fowler and Joanne Hamel for technical assistance. An anonymous reviewer made many helpful comments on an earlier version of the manuscript.

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