

# A Drift–Retention Dichotomy for Larval Haddock (*Melanogrammus aeglefinus*) Spawned on Browns Bank<sup>1</sup>

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This study was designed to assess the dispersal of haddock (*Melanogrammus aeglefinus*) larvae from their Browns Bank spawning site in terms of either drift or retention mechanisms. Larvae were collected in comprehensive surveys of southwestern Nova Scotia conducted at monthly intervals through the winter–spring of 1985. To avoid any confounding of larval displacement patterns by the numerically dominant young larvae, all spatial analyses were structured by age through otolith microstructure techniques. The results of a trend surface analysis indicated that both drift and retention processes operated in concert to split and disperse the larval population. Retention was probably physically based, through the action of a “leaky” gyre around Browns Bank. Although similar processes are believed to have influenced the distribution of Browns Bank cod (*Gadus morhua*) larvae, the interspecific difference in spawning time, coupled with the apparent instability of the gyre, produced a different balance between transported and retained larvae. A drift–retention dichotomy for Browns Bank ichthyoplankton has implications for both recruitment and stock structure studies.

Cette étude visait à évaluer la dispersion des larves d'aiglefin (*Melanogrammus aeglefinus*) depuis leur aire de fraye du banc Browns en fonction soit de la dérivation ou des mécanismes de rétention. Des larves ont été recueillies au cours de levés exhaustifs mensuels effectués dans le sud-ouest de la Nouvelle-Écosse au cours du printemps et de l'hiver 1985. Afin de ne pas confondre les modes de déplacement des larves à cause du nombre dominant de jeunes larves, toutes les analyses spatiales ont été structurées par âge au moyen de techniques d'évaluation de la microstructure de l'otolithe. Les résultats d'une analyse superficielle de tendances révèlent que les deux processus de dérivation et de rétention entrent en jeu de concert pour séparer et disperser les populations larvaires. La rétention est probablement d'origine physique, causée par l'action du tourbillon « irrégulier » dans le banc Browns. Bien que des processus semblables pourraient avoir influencé la répartition des larves de morue (*Gadus morhua*) dans le banc Browns, la différence entre les espèces pendant le temps de la fraye, couplée à l'instabilité apparente du tourbillon, a produit un équilibre différent entre les larves transportées et les larves retenues. Une dichotomie dérivation–rétention pour l'ichthyoplancton du banc Browns a des implications tant pour les études sur le recrutement que pour celles sur la structure des stocks.

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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). 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 advective drift are difficult to support (e.g. Lear and Green 1982; Fortier and Leggett 1983; Ellertsen et al. 1984; Lockwood and Lucassen 1984; Ouellet and Dodson 1985; Smith and Morse 1985; Cushing 1986; Jahn and Lavenberg 1986; Power 1986; Kendall et al. 1987). However, there are a number of systems in which the advection of ichthyoplankton, particularly larvae, is restricted or absent, even in the presence of directed residual currents (Iles and Sinclair 1982). 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 several 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 Atlantic herring (*Clupea harengus*).

Browns Bank is an appropriate test site for the retention hypothesis, since controversy concerning the importance of retention to the progeny of the resident haddock (*Melanogrammus aeglefinus*) stock already exists. Grosslein and Hennemuth (1973) interpreted captures of settled young-of-the-year haddock, stretching from Browns Bank to the mouth of the Bay of Fundy, as evidence of advective drift. In contrast, O'Boyle et al. (1984) interpreted the spatial coincidence of haddock eggs and larvae on the bank as the first demonstration of retention in this species. Unfortunately, both of these interpretations were confounded by the broad temporal and spatial scales of sampling, the inability to follow discrete larval cohorts, and the aggregation of larvae of all sizes and ages into a single class.

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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.

In this paper, we use the results of five synoptic surveys to assess the age-structured spatial distribution of haddock larvae in and around the Browns Bank spawning site. The objective is to quantify the change in larval distribution as a function of larval age and to discuss the findings in the context of the drift-retention controversy: if passive 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

Haddock larvae were collected in five different cruises over a fixed survey grid as part of the Fisheries Ecology Program (FEP) ichthyoplankton survey. The survey encompassed 97 stations to the south, east, and west of Nova Scotia, down to and including portions of Georges Bank (Fig. 1). Collections were

made monthly between February and June 1985, although weather restricted grid coverage on some cruises (Table 1). Each station was sampled with paired, 61-cm bongo nets fitted with 333- $\mu$ m Nitex mesh and mouth-mounted flowmeters. Tows were made obliquely to within 5 m of the bottom (to a maximum depth of 200 m) and immediately replicated. Full sampling details and cruise-by-cruise station locations are documented elsewhere (Hurley and Campana 1989).

Ichthyoplankton samples were preserved and processed as described elsewhere (Campana and Hurley 1989). Since 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), its use was appropriate in this study. Both pairs of sagittal and lapillar otoliths were removed, mounted individually, and prepared according to standard techniques (Campana and Neilson 1985). All larvae, except those damaged by preservation, were aged. Microstructural interpretations were not independently validated with known-age larvae, but were assumed to be comparable with the morphologically similar (and validated) cod (*Gadus morhua*) otolith (Campana 1989). Thus, daily growth increment counts of the lapillus (plus 1, corresponding to the presumed age at hatch check formation) were taken to accu-

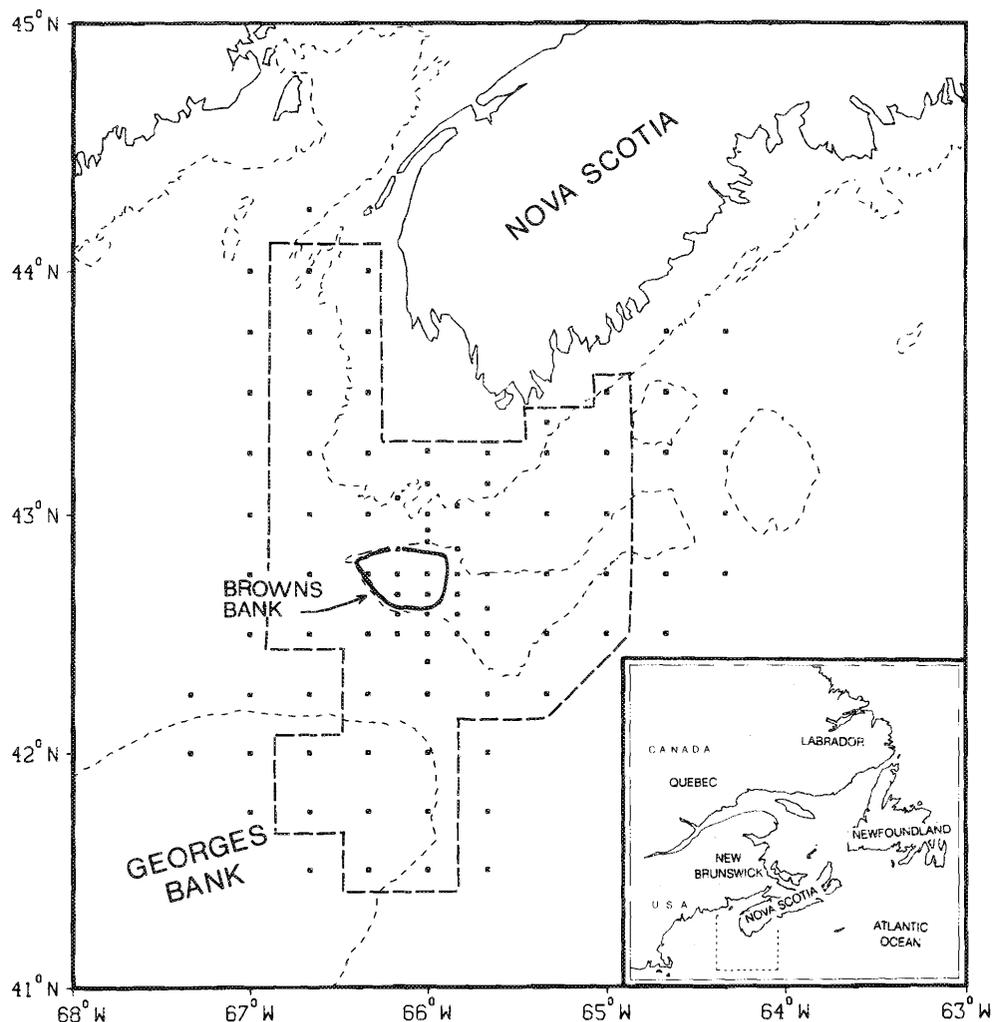


FIG. 1. Study area showing collection stations in reference to the 100-m contour. Browns Bank has been delimited by a solid line. The stations sampled in the May and June cruises are delimited by the broken line.

TABLE 1. Summary of cruises represented in this study.

Cruise	Date (1985)	No. of stations sampled	No. of stations with larvae	No. of larvae	No. of larvae aged
H130	February 4-22	93	0	0	0
H132	March 11-29	49	9	13	7
H133	April 6-17	90	29	53	43
H135	May 6-16	57	31	436	246
H137	June 3-14	59	44	974	881

rately represent the age of the larvae. Ages were probably underestimated by 2-3 d due to the presence of daily increments too narrow to resolve by light microscopy (Campana 1989), but this level of bias was considered both acceptable and unavoidable.

All spatial analyses of the larvae were based upon the age-structured mean number of larvae per square metre of ocean surface. Larval ages were subsequently categorized by 10-d intervals, with the oldest larvae categorized as a plus group (51 + d). The oldest larvae were categorized as 31 + d for the trend surface model. Subsequent stages of data preparation are described elsewhere (Campana et al. 1989).

#### Trend Surface Analysis

Trend surface analysis is a form of polynomial regression suited to modelling spatial gradients in distributional data (Cliff and Ord 1981; Ripley 1982). In this study, its use simplified the interpretation of the complex, multidimensional age-structured larval distribution data. Several formulations are possible; this study defined the spatial coordinates of latitude ( $x_{1i}$ ) and longitude ( $x_{2i}$ ) for the  $i$ th sample site as covariates in the following polynomial:

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

where  $p + q \leq k$  denotes the highest order polynomial terms. Conceptually, trend surface analysis can be envisioned as the topological, or planar, version of a simple, least squares regression. Continuing the analogy, the  $\beta$  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 curvilinear gradients 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 simple regressions applies, where a simple regression model would be used to fit a straight line, a quadratic model for a parabola, etc. An example of first-, second-, and third-order trend surface models fitted to simulated data is presented in Fig. 2. Trend surface models do not incorporate a spatially dependent covariance structure and therefore are most appropriate for use when external forces (i.e. currents), rather than interindividual interactions, dominate the data. In this study, correlogram tests (Cliff and Ord 1981) indicated that there was no evidence for spatial autocorrelation, either among the observed larval numbers at age or in the model residuals.

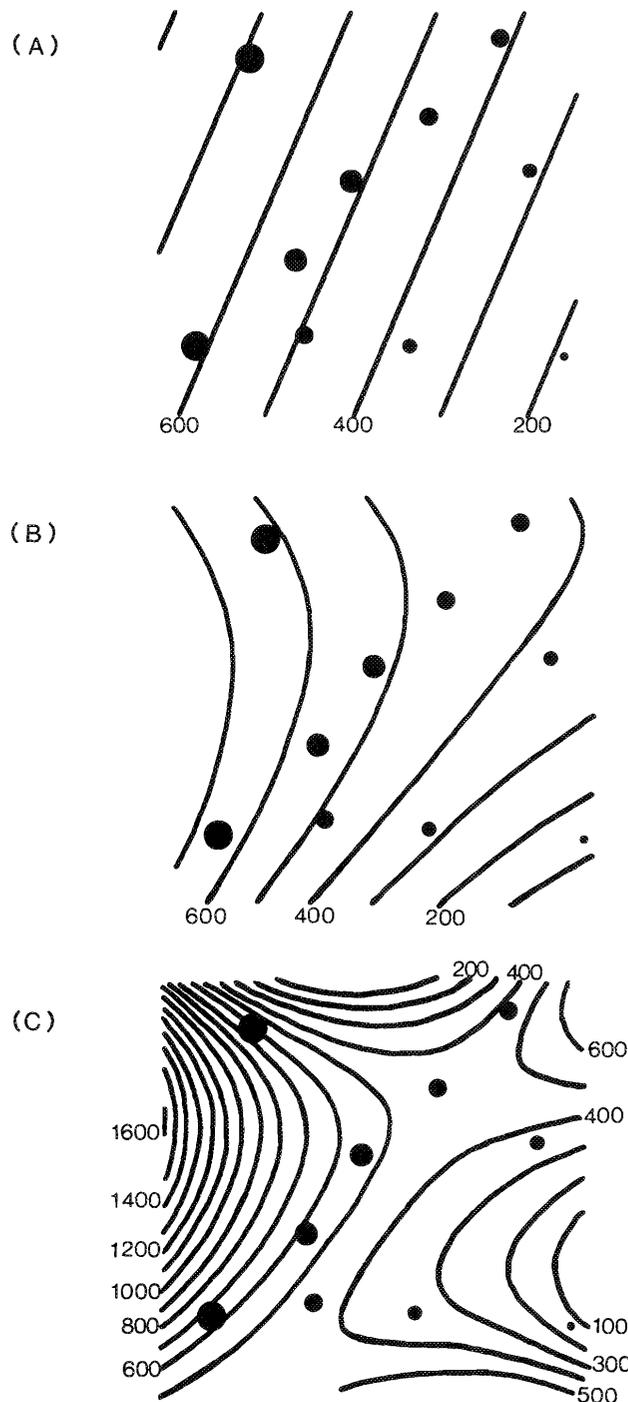


FIG. 2. Example of the abundance contours that would result from the fit of three different trend surface models to a single set of simulated data (modified from Ripley (1982, p. 31-33) with permission of the publisher). (A) First-order model; (B) second-order (quadratic) model; (C) third-order (cubic) model.

In this study, second- and third-order trend surface models were used to allow broad, curvilinear trends in haddock larval abundance to be described. Since station coordinates differed slightly among cruises (despite the fixed survey grid), a standard location was used for each station across cruises. Station coordinates were centred prior to entry into the model. Similarities among age categories and cruises were not assumed: spatial terms were nested within each age category, and ages were nested within cruise. Since the variances were propor-

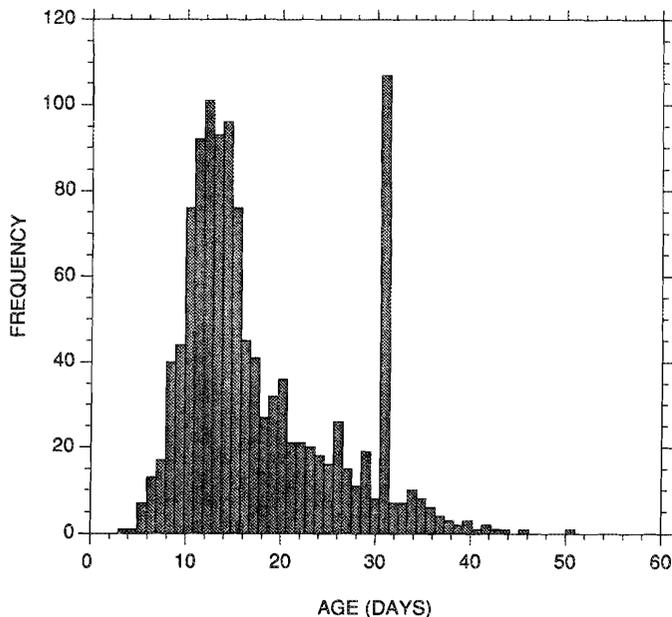


FIG. 3. Frequency of observed ages among haddock larvae collected on five cruises in 1985. The peak at 31 d is largely due to the catch at a single station in the June (H137) cruise.

tional to the means, a generalized Poisson distribution for the response variable was also assumed, with  $E[y_i] = \exp(\mu_i)$ . The exponential was used to insure that the predicted values were  $\geq 0$  as expected for the Poisson distribution. Parameter estimates were obtained using iteratively reweighted least squares with the computer package GLIM (Payne 1986). Models were selected using the analysis of deviance approach discussed in McCullagh and Nelder (1983).

## Results

A total of 1476 haddock larvae were collected during the five cruises (Table 1), with catches at individual stations ranging from 0 to 171. No larvae were captured in February. Over the remaining cruises, 44% of the stations produced larvae. The age composition of the samples differed both among cruises and among samples (Kruskal-Wallis,  $P < 0.01$ ), with the June cruise (H137) contributing significantly more of the older larvae. Overall, the range of ages spanned 3–51 d, with larvae less than 29 d old making up 86% of the collection (Fig. 3). The mean age of all larvae sampled was 17.5 d (the median age was 15 d).

The relative abundance and spatial distribution of each age category are presented in Fig. 4 although the catches in the March cruise (H132) were too few to present. Both the April (H133) and the May (H135) cruises showed the same general pattern of distribution, with centres of abundance on and to the north-northwest of Browns Bank. Few larvae were found to the east or west of the bank, or in the waters between Browns and Georges banks. In contrast, substantial concentrations of larvae were captured in these latter areas in the June cruise (H137), particularly to the east on Baccaro Bank. Larvae were occasionally found on Georges Bank as well, but in much smaller numbers.

The larval age composition in each region differed slightly among cruises (Fig. 4). Browns Bank and the region immediately north of it (along the 100-m contour) were consistently characterized by a large proportion of larvae less than 20 d old,

with significant but 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. The regions east of Browns Bank were virtually devoid of larvae in all cruises but that of June, but in the latter, a high proportion of both young (<30 d) and old (31–40 d) larvae was observed. Note that the high proportion of 31- to 40-d-old larvae present in the southeasternmost region was actually captured just to the east of Browns Bank.

Calculations of the hatch dates of the larvae, based on their age and date of sampling, were used to identify and track discrete cohorts across cruises. However, high rates of apparent mortality reduced the number of cohort survivors to levels unsuited for monitoring the location of an individual cohort through time. As a proxy for true cohort tracking, the following analyses assume that the spatial distribution by age within a cruise resembles that of a single cohort through time.

Larval age should increase with distance from the spawning site if the larval drift hypothesis holds. The centre of abundance (centroid) for all but the oldest age category (excluding Georges Bank larvae) differed little among ages and cruises and showed relatively little displacement from Browns Bank. Centroid locations for the April (H133) and May (H135) cruises were closer to the northern cap of the bank than those depicted for the June (H137) cruise (Fig. 5). The position of the centroid corresponding to the oldest age category (age 65 d) in Fig. 5 is somewhat misleading in that it was based on a single capture. In a more sensitive test of the same larval drift corollary, the relationship between larval age and distance from Browns Bank was examined under the explicit assumption that the centre of Browns Bank was the spawning site. No relationship between distance and age was evident, either in terms of correlation or variance (Fig. 6). However, there was a suggestion of spatial clustering at all ages.

The results of the trend surface analysis were consistent with those above in demonstrating the presence of broadly dispersed spatial distributions within each age category. In fitting the model, spatial coordinate terms were nested within age for each cruise individually, since similarities in the distribution of larvae among ages and cruises could not be assumed. This model structure allowed linear, quadratic, and, in one case, cubic surfaces to be fit, although the higher order surfaces proved to be most informative (Table 2). The resulting model demonstrated that larval abundance differed significantly among most age categories (Table 3). Insufficient data were available for a significant fit to the April (H133) cruise data, while only one age category proved to be significant in the May (H135) cruise. In the June (H137) cruise, where larvae were most abundant, almost all model parameters were significant. Parameter significance in this context implies that spatial patterns in larval abundance were present. Note that the varying levels of station coverage among cruises (Table 1) only affect the precision of the parameter estimates and do not impair intercruise comparisons.

Contour plots of the fitted values from the trend surface models were used to examine the relative locations of each age category (Fig. 7). The spatial distributions of all age categories were centred on or around Browns Bank, although the centres appeared to shift to the northwest with age. A net northward movement of the larvae was also indicated by the orientation of the contour ellipses (with the exception of the 0- to 10-d-old larvae in June), while the flattening of the contour surface with age demonstrates increased dispersion with age.

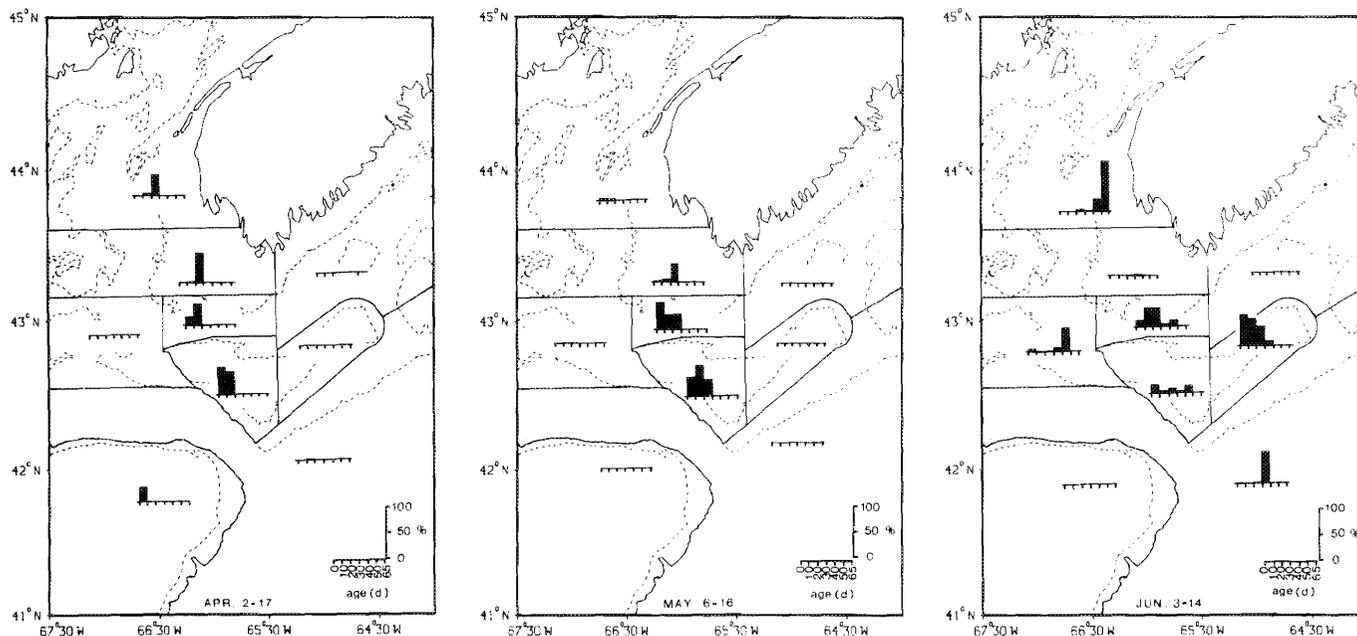


FIG. 4. Spatial distribution by age (days) of haddock larvae collected on each of three cruises in 1985. Histograms represent the proportion of each age category found within each region (regions delineated by heavy lines) relative to the total abundance of that age category within the cruise.

In the only age category successfully fitted with a cubic surface (age 11–20 d), an inshore–offshore bimodality in abundance was evident. The bimodality was not evident when a quadratic model was fitted to the same age–cruise data (Fig. 7). A comparison of the distributions of the 0- to 10-d-old larvae in May and June indicates a more easterly centre in the latter.

## Discussion

This study clearly demonstrated that a significant proportion of the larval haddock were retained on or around Browns Bank. Larvae of all ages were consistently found in the vicinity of the bank. In addition, there was no significant shift in the centre of mass of the larvae with age, nor was there a significant relationship between age and distance from the Browns Bank spawning site. Since haddock do not spawn in southwestern Nova Scotia waters other than on Browns Bank (O'Boyle et al. 1984; Hurley and Campana 1989), the necessary corollaries of the retention hypothesis have been met. The presence of a tidally dominated circulation, resulting in a permanent gyre around the bank (Smith 1983, 1989; Loder et al. 1988), provides a physically based mechanism for the retention of the larvae. Yet with an egg stage duration of 12–19 d at ambient temperatures (Laurence and Rogers 1976), a mean water residence time of 14 d (Smith 1983, 1989), and a mean water displacement rate from the bank of 7.0 km/d (Campana et al. 1989), few of the older larvae should have been found anywhere near the bank. Indeed, both the trend surface analysis and the age-structured spatial distributions (Fig. 4) indicated that a significant proportion of the larvae were transported away from Browns Bank in a direction consistent both with the residual circulation and a previously postulated haddock drift model (Grosslein and Hennemuth 1973). While individual larvae cannot be both transported and retained, it appears that one part of the larval population was transported inshore from the spawning site,

while the remainder was retained offshore longer than would be expected on the basis of water residence times.

In a parallel study of Browns Bank cod (Campana et al. 1989), a mechanism was suggested by which drift and retention processes might act in concert to split and disperse a larval population. The mechanism was based on the highly dispersive nature of the Browns Bank gyre. Individual particles in the gyre, such as drogues or ichthyoplankton, have the potential to exit the gyre very quickly or be retained for extended periods of time (Smith 1983, 1989; Loder et al. 1988). Of those larvae extruded from the gyre, many appeared to reside in what may be a region of reduced current flow between the bank and the 100-m contour (Campana et al. 1989; Hurley and Campana 1989). This area appears to be a shear zone between the Nova Scotia coastal current and the oppositely directed Browns Bank gyre. While there is, as yet, no physical basis for retention in this shear zone (Page and Smith 1989), high concentrations of larvae were consistently observed there. Irrespective of mechanism, 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 region just north of the bank, and transport of others towards the inshore and/or mouth of the Bay of Fundy.

The results of the trend surface model provide strong support for the concept of a drift–retention dichotomy for individual haddock larvae. A dichotomy is clearly evident in the one age category successfully fitted with a cubic surface (Fig. 7: age 11–20 d); there, larvae are concentrated both on eastern Browns Bank and inshore along the 100-m bathymetric contour, but not in between. While a similar pattern would also be expected of the older larvae, such cannot be demonstrated with a quadratic surface. The quadratic representation of the cubic surface for age 11–20 d (Fig. 7) clearly shows the limitation of the quadratic model in highlighting a bimodal abundance contour. How-

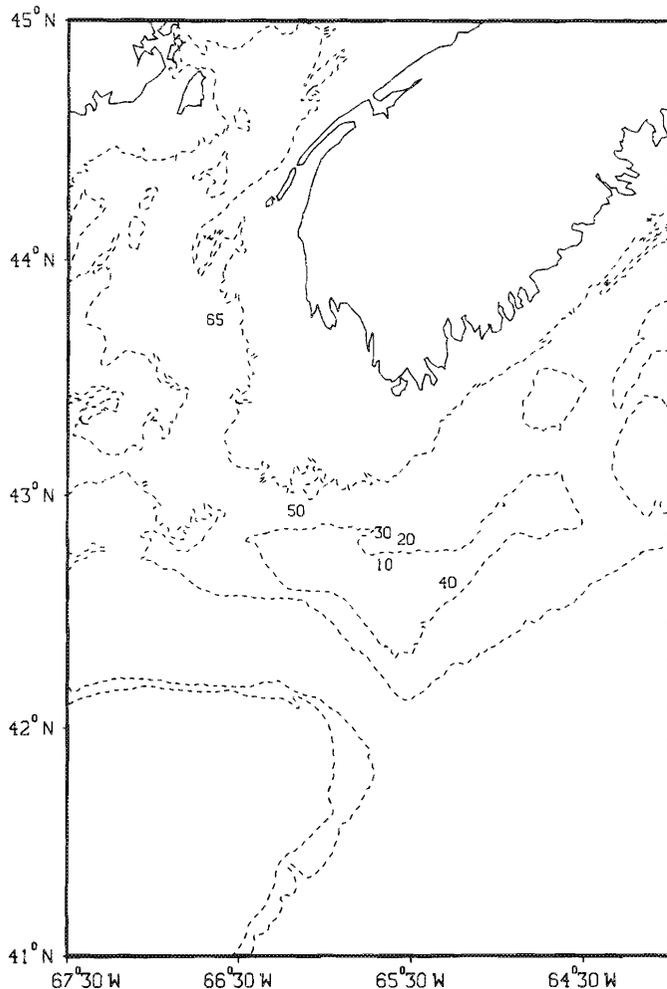


FIG. 5. Centres of abundance (centroids) for each of six age categories of larval haddock collected in June 1985. Age labels represent 0–10 (10), 11–20 (20), 21–30 (30), 31–40 (40), 41–50 (50), and 51–65 (65) d.

ever, in the same way that examination of residuals can be used to assess curvilinearity in a simple linear regression, maps of the residuals of the trend surface model can be used to reveal possible bimodal abundance patterns. On the basis of the residuals, the flat surfaces apparent in Fig. 7 for the older larvae appear to be the best quadratic approximation of a bimodal abundance contour, where larvae were concentrated both on eastern Browns Bank and inshore towards the mouth of the Bay of Fundy. Whether bimodality was present or not, the flat surfaces demonstrate that there was no spatial gradient in abundance within an age category; in other words, the older larvae were broadly distributed between the offshore and the inshore. This observation is most consistent with a dispersal process comprising both drift and retention components.

The drift–retention hypothesis appears to be robust to the assumptions and methodologies used in this study. The age determinations were probably accurate to within several days (Campana 1989), and the resulting larval age compositions were consistent both with expected mortality rates and observed spawning times (Hurley and Campana 1989). The five cruises spanned virtually all of the haddock spawning activity on Browns Bank (Hurley and Campana 1989) and appeared to circumscribe the larval distributions on all sides, although it is

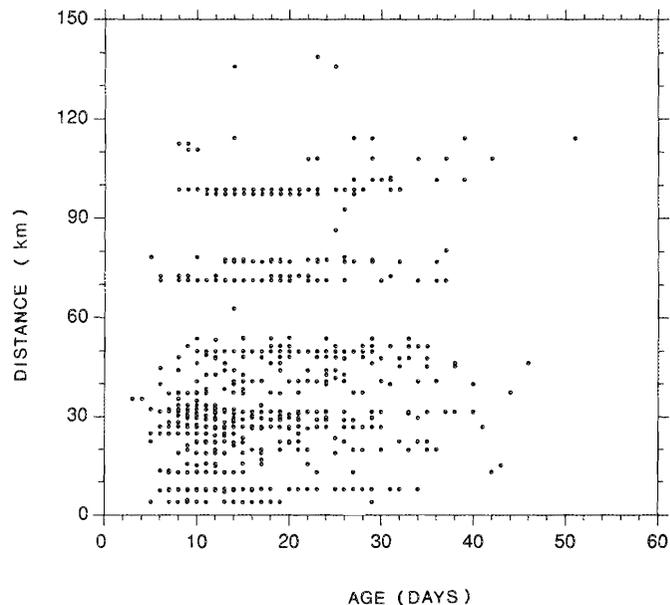


FIG. 6. Relationship between the age of larval haddock and their distance from the Browns Bank spawning site at the time of collection in June 1985.

TABLE 2. Analysis of deviance after fitting the trend surface model to the abundance of haddock larvae ((number/0.047)/m<sup>2</sup>) according to age category and position of capture. *P* level refers to the  $\chi^2$  statistic.

Model	First difference in deviance	df	<i>P</i> level
<i>Cruise H135</i>			
Mean + age	15.37	2	0.0000
Mean + age.linear	7.02	6	0.5355
Mean + age.quadratic	36.89	15	0.0000
<i>Cruise H137</i>			
Mean + age	71.05	3	0.0000
Mean + age.linear	74.90	8	0.0000
Mean + age.quadratic	216.04	20	0.0000
Mean + age.cubic	247.56	36	0.0000

possible that the southeastern- and northern-most ranges of the older larvae were not surveyed. However, the presence of unsurveyed larvae in these regions would serve only to strengthen our conclusions. There was no evidence of drift from Georges Bank, either in this study or elsewhere (O'Boyle et al. 1984; Perry and Hurley 1986). While the use of bongo gear is known to be inappropriate for abundance estimation of older larvae and juveniles (Cushing 1986; Frank 1988; Suthers and Frank 1989), this study analyzed the relative spatial distribution within an age category, and thus was insensitive to any age-related gear avoidance that may have occurred.

Since trend surface models are new to fisheries applications, it is natural to question their value relative to more conventional approaches, such as the centroid and distance–age models used in Fig. 5 and 6. Trend surface models have been applied for years in geological, hydrological, and botanical contexts (Cliff and Ord 1981), where their utility for the interpretation of spatially structured data is now accepted. They are particularly valuable in the synthesis of multidimensional data; in the pre-

TABLE 3. Parameter estimates from Poisson trend surface models of haddock larval abundance ((number/0.047)/m<sup>2</sup>). Ages 1–4 represent 0–10, 11–20, 21–30, and 31+ d, respectively.

Parameter	Estimate	Standard error
<i>Cruise H135 (quadratic model)</i>		
Mean	-1.97	0.93
Age 2 – Age 1	0.76	1.15
Age 3 – Age 1	-6.53	7.10
Age 1 terms		
Latitude	-12.98	6.04
Longitude	-15.63	6.44
Latitude <sup>2</sup>	-26.78	11.01
Longitude <sup>2</sup>	-24.54	11.04
Latitude × longitude	-44.31	19.90
Age 2 terms		
Latitude	-6.55	4.62
Longitude	-8.42	5.05
Latitude <sup>2</sup>	-17.26	9.81
Longitude <sup>2</sup>	-15.86	9.94
Latitude × longitude	-23.24	16.30
Age 3 terms		
Latitude	-5.55	18.75
Longitude	-34.96	43.83
Latitude <sup>2</sup>	-6.25	14.73
Longitude <sup>2</sup>	-51.79	69.38
Latitude × longitude	-21.00	57.37
<i>Cruise H137 (quadratic model)</i>		
Mean	-1.93	0.77
Age 2 – Age 1	3.10	0.80
Age 3 – Age 1	1.80	0.83
Age 4 – Age 1	0.31	0.96
Age 1 terms		
Latitude	-4.77	4.25
Longitude	1.36	1.77
Latitude <sup>2</sup>	-12.45	9.69
Longitude <sup>2</sup>	-0.42	2.24
Latitude × longitude	0.30	5.58
Age 2 terms		
Latitude	0.72	1.04
Longitude	2.58	0.69
Latitude <sup>2</sup>	-16.46	3.66
Longitude <sup>2</sup>	-2.55	1.02
Latitude × longitude	-7.89	2.37
Age 3 terms		
Latitude	1.84	1.15
Longitude	2.18	0.99
Latitude <sup>2</sup>	-7.86	3.09
Longitude <sup>2</sup>	-2.98	1.62
Latitude × longitude	-8.50	3.37
Age 4 terms		
Latitude	-0.64	1.56
Longitude	0.54	1.03
Latitude <sup>2</sup>	-10.55	4.68
Longitude <sup>2</sup>	-0.72	2.11
Latitude × longitude	-14.56	5.76
<i>Cruise H137 (cubic model age 2 only)</i>		
Mean	-1.74	0.88
Age 2 – Age 1	2.99	0.91
Age 2 terms		
Latitude	4.78	1.32
Longitude	3.92	0.77
Latitude <sup>2</sup>	-23.19	6.05
Longitude <sup>2</sup>	-2.05	1.33
Latitude × longitude	-8.27	3.63
Latitude <sup>2</sup> × longitude	-33.41	8.68
Latitude × longitude <sup>2</sup>	-14.62	5.56
Latitude <sup>3</sup>	-38.46	10.77
Longitude <sup>3</sup>	-2.43	1.76

sent study, where larval abundance was a function of latitude, longitude, cruise, and age, conventional interpretation would have required the visual assimilation of 12 maps containing rather complex patterns of age-structured larval distribution and abundance. Further, interpretation would have been confounded by intercruise differences in survey coverage and station spacing. The trend surface approach was not subject to these constraints. The statistical structure of the trend surface model provided an objective basis for the resulting inferences about the spatial patterns. Deficiencies of the simpler centroid/distance-age models, such as the absence of directional information and confidence limits, and the inability to aggregate cruises, were not a factor in the trend surface model, making the latter not only more informative, but more reliable.

The trend surfaces associated with an analysis of Browns Bank cod (Campana et al. 1989) were not nearly as flat as those of haddock, indicating a more substantial drift component in the former. Since the two species of larvae were collected during the same cruises, a species-specific response to a single oceanographic system initially appears unlikely. There are three possible physical explanations. Firstly, the model formulation applied to cod differed from that applied to haddock: models were fitted on a cruise-by-cruise basis for haddock whereas cruises were treated as factors within a single model for cod. The latter formulation effectively smoothed out any cruise-to-cruise spatial pattern differences that might have existed for cod. Secondly, the cod and haddock may have had slightly different spawning locations on Browns Bank, and thus were affected to differing degrees by the retentive mechanism of the gyre. For instance, current speeds appear to be lower on the eastern half of the bank than on the western half (Loder and Greenberg 1986). However, if differences in spawning location did exist, they were on a scale that could not be resolved (Hurley and Campana 1989). Finally, and we consider this to be the most likely explanation, the balance between drift and retention for cod and haddock may have differed because of differences in spawning dates in conjunction with short-term changes in gyre stability. Changes in gyre stability may occur over a much shorter time scale (Smith 1989) than the interval between peak larval abundances of cod (April–May) and haddock (June) and thus result in an apparently species-specific response. Support for the concept of timing effects comes from the nearly identical trend surfaces for cod and haddock of ages 0–10 d in the May cruise, the only cruise and age where both species were adequately represented. The influence of short-term changes in gyre stability is best demonstrated by a comparison of the distribution of the youngest haddock larvae between the May and June cruises; a substantial shift in distribution is apparent between the two cruises. All of the above suggests that seasonal timing, more than interspecific differences, is influential in affecting the relative balance between drifted and retained larvae.

There is no evidence to suggest that behaviour aided in the retention of larval haddock around Browns Bank. While larval retention has often been linked to vertical migration patterns (Fortier and Leggett 1983; Sinclair and Iles 1988), the latter was not evident in a study of Browns Bank haddock larvae (unpublished observations). Physically based drift and retention mechanisms must clearly be invoked to explain the observed distribution of nonmotile eggs and young larvae, but similar arguments may not apply to the older larvae. Since few larvae greater than 40 d old (corresponding to a length of approximately 7 mm (Campana and Hurley 1989) were captured, sev-

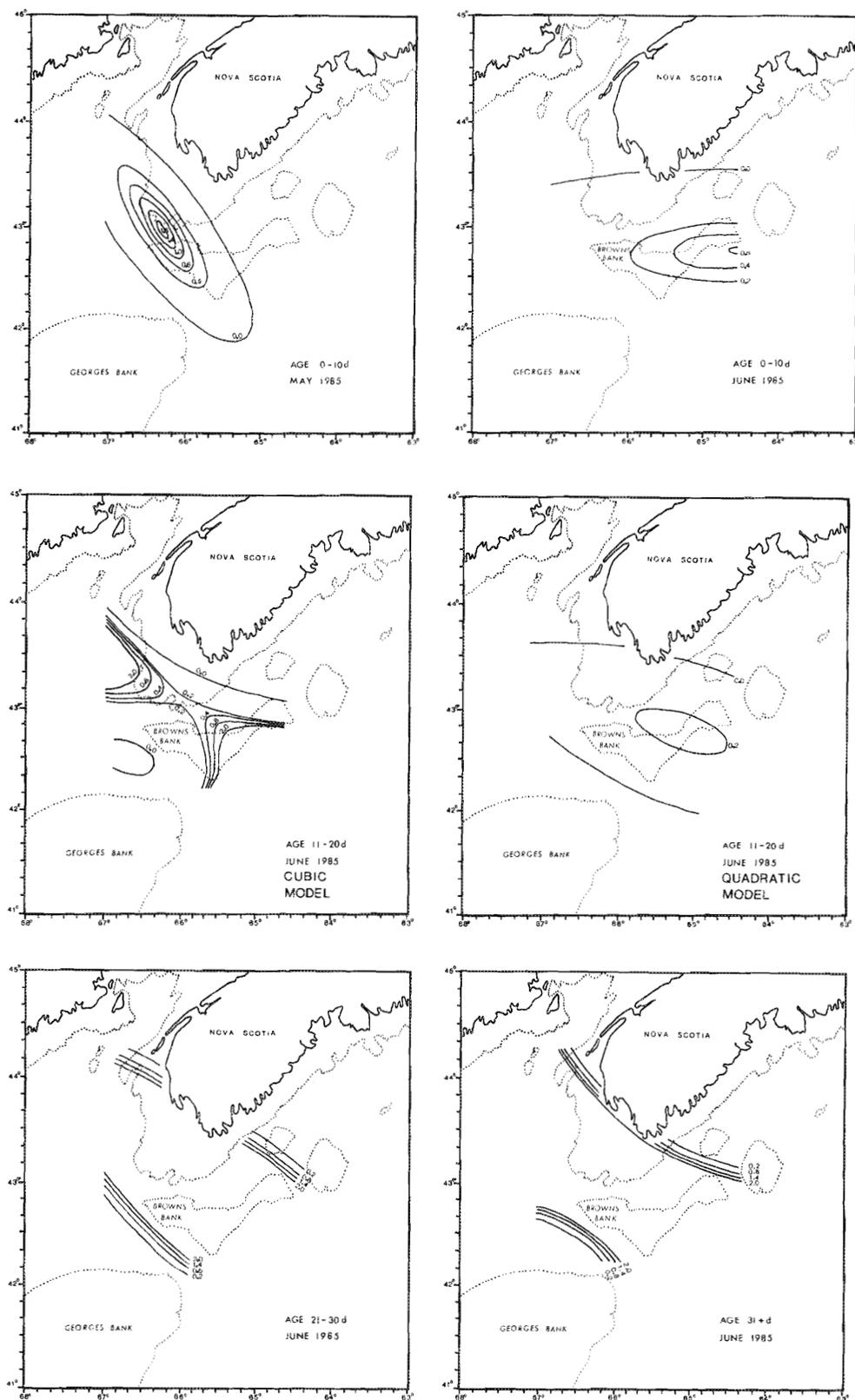


FIG. 7. Contours of haddock larval abundance ((numbers/0.047)/m<sup>2</sup>) in May and June of 1985 for each of four daily age categories. Contours represent results of fitted quadratic trend surface models, with the exception of ages 11–20 d which were also fitted with a cubic surface. Abundances are in units of 10<sup>-3</sup> for ages 21–30 and 31 + d.

eral months of life history were unsampled prior to settling (Koeller et al. 1986). A distribution of settled juveniles (Grosslein and Hennemuth 1973) similar to that of larvae greater than 20 d old is consistent with the concept of enhanced retention in older larvae.

Proponents of both the larval drift (Cushing 1986) and retention (Sinclair 1988) hypotheses now agree that the two concepts are not necessarily mutually exclusive. While the possibility of drift within a retention zone has been acknowledged, the segregation of a single population by both drift and retention processes is, to our knowledge, unique. In an elaboration of the retention hypothesis (the member-vagrant hypothesis), emphasis was placed upon population discreteness during the early life history stage rather than larval fidelity to the spawning site (Sinclair 1988; Sinclair and Iles 1988). Under these conditions, the entire region between Browns Bank and the inshore would have to be considered a single retention zone. The alternative interpretation would be that all larvae that exit the bank are "vagrants" and thus lost to the population gene pool. Given the continuous band of settled young-of-the-year stretching from Browns Bank to the mouth of the Bay of Fundy (Grosslein and Hennemuth 1973) and the significant portion of the stock found off-bank (Bowen 1987), the vagrancy interpretation appears unlikely.

Whether placed in the context of the member-vagrant hypothesis or not, a drift-retention dichotomy has significant implications for both recruitment and stock structure studies of Browns Bank haddock. Segregation of the population into inshore and offshore components would appear to maximize the probability of population survival in the face of adverse (and spatially variable) conditions. A prerequisite of this adaptive strategy would be that survival/environmental conditions differ between the inshore and offshore. Since the relative contribution of the drifted/retained larvae to a given cohort would depend on the "leakiness" of the Browns Bank gyre, overall cohort survival may vary with gyre activity. As noted previously, changes in gyre stability may occur on a very short time scale. While the cod-haddock comparison assumed interspecific similarities in behaviour and vertical distribution, it supported the idea that intraannual variations in gyre stability may be important in determining the balance between drift and retention. Such variations, integrated over a spawning season, might then help explain year-to-year variations in year-class strength. A test of this hypothesis would require a quantitative index of gyre leakiness that could then be related to independent indices of year-class strength. Intraannual gyre variations, in conjunction with species-specific spawning times, may also explain apparent asynchronies in year-class strengths between Browns Bank cod and haddock. Speculations aside, the drift-retention dichotomy on Browns Bank highlights the potential flexibility in larval dispersal strategies and suggests that undescribed permutations of the drift-retention continuum may yet exist in other systems.

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