

Inter-Annual Distributions of Larval and Pelagic Juvenile Cod (*Gadus morhua*) in Southwestern Nova Scotia determined with two Different Gear Types¹

Iain M. Suthers

Department of Biology, Dalhousie University, Halifax, N.S. B3H 4J1

and Kenneth T. Frank

Marine Fish Division, Department of Fisheries and Oceans, Bedford Institute of Oceanography, Dartmouth, N.S. B2Y 4A2

Suthers, I. M., and K. T. Frank. 1989. Inter-annual distributions of larval and pelagic juvenile cod (*Gadus morhua*) in Southwestern Nova Scotia determined with two different gear types. *Can. J. Fish. Aquat. Sci.* 46: 591–602.

Ichthyoplankton surveys conducted during 1979 on the Scotian Shelf have shown coincident egg and larval distributions for cod (*Gadus morhua*) and other related groundfish species. These data have been used by other investigators to support the larval retention hypothesis, in spite of three limitations: the exclusive use of a single type of small sampling gear, limited sampling landward of the 50-m isobath, and analysis of data collected in a single year. During May of 1985, 1986, and 1987 two gear types were used, from the shelf to coastal waters in southwestern Nova Scotia to assess the horizontal distributions of larval and pelagic juvenile cod. Tucker trawl collections made in each year revealed a cohort of cod ≥ 10 mm that was not evident in the smaller gear, which effectively sampled cod larvae < 10 mm. During 1985 and 1986, when both larvae and juveniles were abundant, their distributions coincided. The mixture of sizes of cod from 3–45 mm reduced the importance of using multiple gear types. The interannual location of young cod shifted markedly between the nearshore and offshore demonstrating that a single year of sampling effort is inadequate to assess their distribution. Nearshore sampling revealed high densities of young cod as much as three-fold greater than offshore. The inshore waters may serve as a nursery area for young cod originating from offshore spawning sites. Our results confirm the existence of two important sampling limitations of previous cod ichthyoplankton surveys that reduce their utility as empirical support for the retention hypothesis.

Des levés d'ichthyoplancton, effectués en 1979 sur le plateau Scotian, ont montré des distributions concordantes d'oeufs et de larves pour la morue (*Gadus morhua*) et autres espèces apparentées de poissons de fond. Ces données ont été utilisées par d'autres chercheurs pour étayer l'hypothèse de rétention des larves, malgré trois limites : 1) l'utilisation exclusive d'un seul type de petit engin d'échantillonnage, 2) un échantillonnage limité du côté terre de l'isobathe de 50 m et 3) l'analyse des données prélevées au cours d'une seule année. En mai 1985, 1986, et 1987, deux types d'engins ont servi à évaluer les distributions horizontales des larves et des jeunes morues pélagiques entre le plateau et les eaux côtières du sud-ouest de la Nouvelle-Écosse. Les échantillons récoltés par le chalut Tucker chaque année ont montré qu'il existait une cohorte de morues de taille supérieure ou égale à 10 mm, dont la présence n'était pas évidente lors des collectes à l'aide du plus petit engin, qui n'a prélevé que des larves de morues inférieures à 10 mm. En 1985 et 1986, lorsque les larves et les jeunes étaient abondants, les distributions ont coïncidé. Étant donné que la taille des morues variait de 3–45 mm, il était moins important d'utiliser plusieurs types d'engins. L'aire des jeunes morues a varié de façon marquée entre la région pré-côtière et la région hauturière d'une année à l'autre, montrant qu'un échantillonnage réalisé sur une seule année ne permet pas d'évaluer la distribution. L'échantillonnage réalisé près des côtes a montré la présence de densités élevées de jeunes morues, qui atteignaient trois fois celles des régions plus au large. Les eaux côtières peuvent servir de nourricerie pour les jeunes morues provenant des aires de frai plus au large. Nos résultats montrent bien que l'échantillonnage de larves planctoniques de morues présente deux limites majeures qui en diminuent l'utilité comme résultats empiriques permettant d'étayer l'hypothèse de la rétention.

Received July 11, 1988

Accepted December 2, 1988
(J9806)

Reçu le 11 juillet 1988

Accepté le 2 décembre 1988

The conceptual model of fish migration of Harden Jones (1968) assumes that fish eggs and larvae drift passively from a spawning area to a separate nursery area. However, large-scale ichthyoplankton surveys conducted during the past

decade have indicated that several species spawning on either offshore banks or coastal locations produce eggs and larvae which appear to remain within the confines of the spawning area (Gagne and O'Boyle 1984; O'Boyle et al. 1984; Sherman et al. 1984; Koslow et al. 1985; Sinclair and Iles 1988), consistent with the hypothesis of larval retention (Iles and Sinclair

¹Fisheries Ecology Program Contribution Number: 4

1982). O'Boyle et al. (1984) showed that distributions of eggs and larvae overlapped for a guild of fishes spawning on the Scotian Shelf, including commercially important gadoids such as cod, haddock (*Melanogrammus aeglefinus*) and pollock (*Pollachius virens*). They argued that these data were indicative of larval retention. Gagne and O'Boyle (1984) concluded that "...over most areas of the Scotian Shelf, cod larvae do not drift from spawning grounds to nursery grounds...instead...are retained in large areas where both types of grounds are located" (p. 514). They suggested that tidally generated gyres occurring over some of the offshore banks may provide a means for retaining eggs and larvae. The limited distribution of cod and haddock larvae within the gyre on Georges Bank also supports the hypothesis of larval retention (Sherman et al. 1984; Smith and Morse 1985).

The conclusions of these recent studies (Gagne and O'Boyle 1984; Koslow et al. 1985; O'Boyle et al. 1984; Sherman et al. 1984; Smith and Morse 1985) should, however, be viewed with caution because of possible biases in the survey design (Cushing 1986; Frank 1988). The foremost limitations are believed to be the exclusive use of a single type of small sampling gear, limited sampling landward of the 50-m isobath, and analysis of data collected in a single year.

The primary sampling gear used in the previous studies was a 61-cm diameter bongo net (333- μ m mesh), which cannot provide reliable abundance estimates of the larger, more evasive older larvae and pelagic juveniles (Murphy and Clutter 1972). Cushing (1986) criticized the sampling design of O'Boyle et al. (1984), on the grounds that a spatial separation of eggs, larvae, and pelagic juveniles would have been observed had a larger net been used to sample the larger individuals. For example, haddock eggs and larvae appear to drift from Georges and Browns Banks in a direction consistent with the residual circulation (Colton 1965; Grosslein and Hennemuth 1973), as do lobster larvae originating from Browns Bank (Harding and Trites 1988). The distinguishing feature of the former study was the use of one gear type to sample the egg and larval stages and another to sample the juveniles. An exact analysis of the stage specific distributional patterns during the early life history can only be achieved by sampling the full size (stage) range of the pelagic phase, using both small and large sampling gear. No single sampling device can satisfactorily overcome the dual problems of net avoidance and extrusion (Clutter and Anraku 1968; Green 1979; Cushing 1986; Frank 1988).

The coastal and estuarine environments are often nursery grounds for a variety of 0-group fish, including juvenile cod (Daan 1978; Pihl 1982; Godo and Sunnana 1984; Lear and Wells 1984; Riley and Parnell 1984; MacDonald et al. 1984;

Tremblay and Sinclair 1985). Yet many studies of the early life history of gadoids are conducted offshore, with little or no sampling in the coastal (<50 m depth) locations (O'Boyle et al. 1984; Scott 1984; Sherman et al. 1984; Smith and Morse 1985).

The geographic distribution of larvae may vary considerably between years which can have a profound effect on recruitment (e.g. Hjort 1914; Beverton and Lee 1965; Bailey 1981; Cushing 1982). Any conclusions drawn from a single year's survey would be, at best, preliminary (Wiens 1981). The practice of condensing observations from a number of years or even surveys within a year into a single analysis (e.g. Koslow et al. 1985; Sinclair and Iles 1985; Smith and Morse 1985) will also obscure meaningful variability in ichthyoplankton distributions.

We report here on the results of a multi-year survey designed to assess the distribution of larval and pelagic juvenile cod off southwestern Nova Scotia. Two different sized sampling gears were used to sample the early life stages of cod over a sampling grid extending from the offshore spawning area (Browns Bank) to the nearshore zone. The geographic extent of the sampling grid was based on previous biological and physical oceanographic studies conducted in the region (Grosslein and Hennemuth 1973; Smith 1983). We tested the hypothesis that the size and spatial distribution of cod derived from the two types of sampling gear were not significantly different. We also compared the distribution of larvae and early pelagic juveniles between years over the main survey grid. Whether or not significant concentrations of young cod occurred in the shallow (<50 m depth) coastal environment relative to the offshore was assessed from collections made over the main sampling grid and from an additional set of exploratory collections. Finally, we comment on the extent to which each of the suspected sampling limitations has influenced the conclusions of previous studies on the distribution of the early life stages of cod on the Scotian Shelf.

Methods

Study Area

Four young cod surveys were conducted in the spring and early summer of 1985, 1986, and 1987 in the coastal and shelf waters of southwestern Nova Scotia (Table 1). The study area overlapped the southwestern portion of the Scotian Shelf Ichthyoplankton Program sampling grid (O'Boyle et al. 1984), but had approximately twice the station density, and extended farther north from Browns Bank in the direction of the residual current, to include coastal stations at depths <50 m (Fig. 1).

The southwestern Scotian Shelf circulation is dominated by strong semidiurnal tides, particularly over the offshore banks

TABLE 1. Sampling information pertaining to young cod surveys conducted during May of 1985, 1986, and 1987. Range of station distances (from southeastern Browns Bank) and depths are shown. Key to gear deployed: BN, BIONESS; HM, 0.5-m ring; Tt, Tucker trawl.

Cruise	Region	Year	Date	Gear Deployed	Maximum Sampling Depth (m)	No. Stations	Station depth (m)	Distance from Browns Bank (km)
85-1	Browns Bank, and shelf	1985	9-21 May	BN	65	33	40-180	0-167
				Tt	65	29		
86-1	Browns Bank, and shelf	1986	10-18 May	BN	55	34	40-192	9-144
				Tt	55	34		
86-2	Coastal and shelf	1986	14-23 May	HM	15	20	10-110	83-203
				Tt	25	20		
87-1	Browns Bank, and shelf	1987	28 May-4 June	BN	55	56	35-194	9-203
				Tt	40	56		

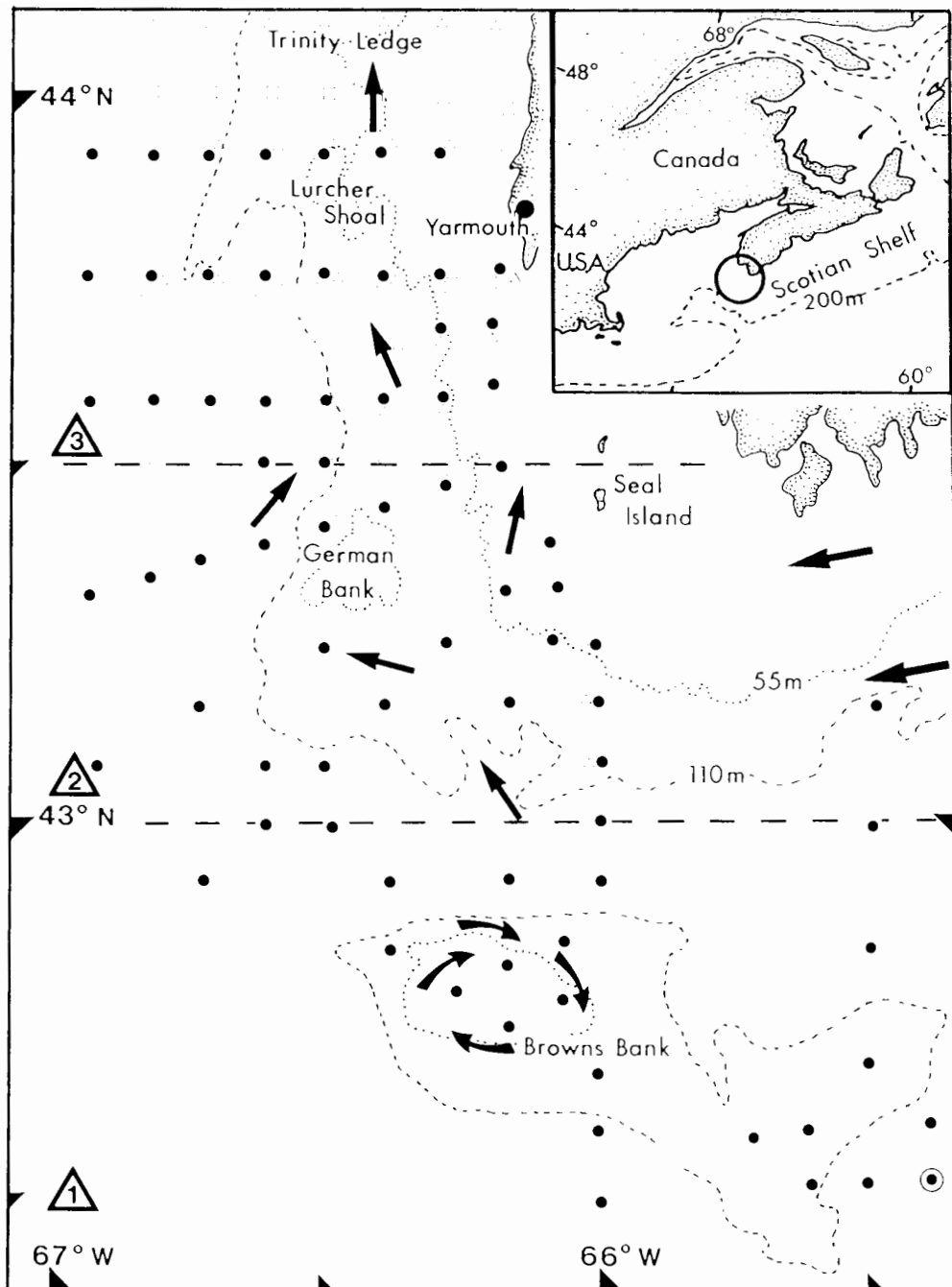


FIG. 1. Stations (closed circles, ●) sampled with small and large gear off southwestern Nova Scotia during May of 1985, 1986, and 1987. Exploratory coastal stations are indicated by open symbols: ○ = 1985, Δ = 1986, □ = 1987. The mean circulation (depicted by arrows) is dominated by an alongshore current of 1–8 km·d⁻¹ and a permanent clockwise gyre on Browns Bank (Greenberg 1983; Smith 1983). All catch versus distance relationships examined used the most southeastern station in the grid (circled station) as the origin. Numbered triangles refer to three geographic regions used to further assess the spatial distributions of cod larvae.

where topographic gradients induce eddy formation. The interested reader should consult Smith (1983, 1989) for a detailed description of the hydrographic properties and features of the southwestern Scotian Shelf and Browns Bank region.

Sampling Gear

A 0.25-m², 333-μm-mesh mini-BIONESS was used during cruises 85-1, 86-1, and 87-1 (see Frank (1986) for details) and was replaced with a standard 0.5-m diameter, 405-μm mesh

ring net on cruise 86-2 (Table 2). The mini-BIONESS recorded temperature, conductivity, depth, pitch, roll, and volume filtered. Temperature and depth were recorded during the 0.5-m ring tows via a conducting cable and towed body that contained the electronic sensors, and volume filtered was recorded with a TSK (Tsurumi-Seiki Co. Ltd.) flow meter.

The two small gear types used during the study were essentially the same with respect to their sampling characteristics. Seven stations sampled with the BIONESS (15–16 May, 158

TABLE 2. Dimensions of the sampling gear used in this study relative to the standard bongo used in previous studies of ichthyoplankton distribution on the Scotian Shelf.

	Mini-BIONESS	0.5-m Ring	Tucker trawl	Bongo
Mouth size (m)	0.5 × 0.5 m	0.5 m diameter	2.5 × 2m	0.61 m diameter
Mouth area (m ²)	0.250	0.196	2.5 ^a	0.292
Sample volume (m ³) ^b	1200 ^c	250	10 000	350
Mesh size (μm)	333	405	1600	333

^aEffective mouth opening at 1.5 m·s⁻¹ towing speed.

^bTypical.

^cCumulative volume of the seven nets.

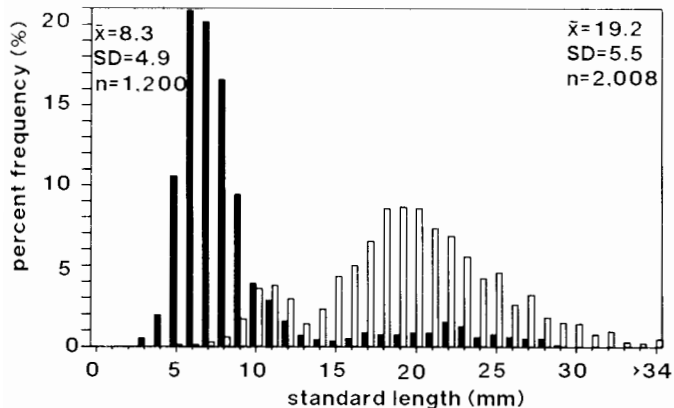


FIG. 2. Composite length frequency distributions of larval and pelagic juvenile cod sampled with the small (shaded bars) and large (Tucker trawl) gear (open bars), respectively during 1985–87.

TABLE 3. Abundance (No.·1000 m⁻³) and size composition of cod from the small and large gear (Tucker trawl) collections during each cruise period. SL refers to average standard length (in mm).

Cruise	No.	SL	Range	(n)	%	
					<10 mm	≥10 mm
<i>Small gear</i>						
85-1	2.10	7.9	2.3–26.5	(104)	83	17
86-1,2	22.02	7.7	3.2–28.0	(1001)	82	18
87-1	0.95	18.2	4.1–29.0	(66)	32	68
<i>Tucker trawl</i>						
85-1	0.64	20.5	4.1–31.9	(152)	3	97
86-1,2	1.39	17.0	7.5–45.4	(1204)	4	96
87-1	1.28	23.7	15.0–44.0	(577)	0	100

TABLE 4. Spearman rank correlation coefficients between larvae, juveniles, and distance from southeastern Browns Bank for each cruise. All correlations are significant ($p < 0.05$).

	Cruise		
	85-1 (n)	86-1,2 (n)	87-1 (n)
Larvae/juveniles	0.56 (25)	0.34 (54)	—
Larvae/distance	0.69 (33)	0.44 (54)	—
Juveniles/distance	0.85 (31)	0.56 (54)	-0.33 (56)

larvae) were at the same time and area as 10 0.5-m ring samples (17–18 May, 73 larvae) during cruises 86-1 and 86-2. The size distribution of cod larvae from these collections was not significantly different (Kolmogorov Smirnov test, $p > 0.50$; BIONESS: average standard length = 6.9 mm, 0.5-m ring net;

average standard length = 7.2 mm). The results of the synoptic cruises 86-1 and 86-2 were therefore combined and hereafter designated as 86-1,2.

A 4.5 m²-mouth area, 1600-μm mesh Tucker trawl was used to sample larger larvae and pelagic juvenile fishes (Table 2; also see Harding et al. (1987) for details). During cruises 85-1, 86-1, and 87-1 the Tucker trawl was equipped with an electronics package similar to the one on the BIONESS. During cruise 86-2 the Tucker trawl was not electronically equipped, so trawl depth was determined by the length and angle of wire out and subsequently verified with an in situ time-depth recorder. Flow through the net was recorded with a TSK flow meter.

Gear Deployment

The BIONESS sampled seven depth intervals: 5, 10, 20, 30, 35, and where depth permitted, 45 and 55 m (or 65 m), while the 0.5-m ring was towed obliquely from 15 m to the surface. The Tucker trawl sampled two depth intervals in cruise 85-1, 35–5 m and, where possible, 65–35 m. During cruises 86-1 and 87-1 the Tucker trawl was towed between 55 and 5 m, and 45 and 5 m, respectively. During cruise 86-2 the Tucker trawl was simply towed obliquely from 25 m to the surface. Net towing speed for all gear types was approximately 1.5 m·s⁻¹.

During cruise 85-1 the entire grid was first sampled with the BIONESS then, starting at the last station, the Tucker trawl sampling commenced and the stations were occupied in reverse order. During cruises 86-1 and 87-1 the large and small gear types were towed consecutively at each station before proceeding to the next station, and during cruise 86-2 the two nets were towed simultaneously at each station.

On deck, immediately following each tow, samples were first passed through a 4- and 10-mm mesh sieve to exclude macrozooplankton (jellies, shrimps, debris), then rinsed into separate containers with freshwater and preserved in 5% formalin, buffered with sodium borate. Most pelagic juvenile cod in the Tucker trawl were transferred to 95% alcohol within 3–10 d of collection to preserve their otoliths.

Exploratory Coastal Surveys

The abundance of larval and pelagic juvenile cod landward of the main sampling grid (Fig. 1) was evaluated during three exploratory cruises: 8–29 May 1985 (30 stations), 5–12 June 1986 (36 stations) and 9–18 May 1987 (18 stations). A 0.5-m (405-μm mesh) and 1.0-m diameter (1000-μm mesh) ring net were used to make the collections. A Tucker trawl was used in addition to the 0.5-m ring net during June 1986. The gear was deployed in a manner identical to that previously described.

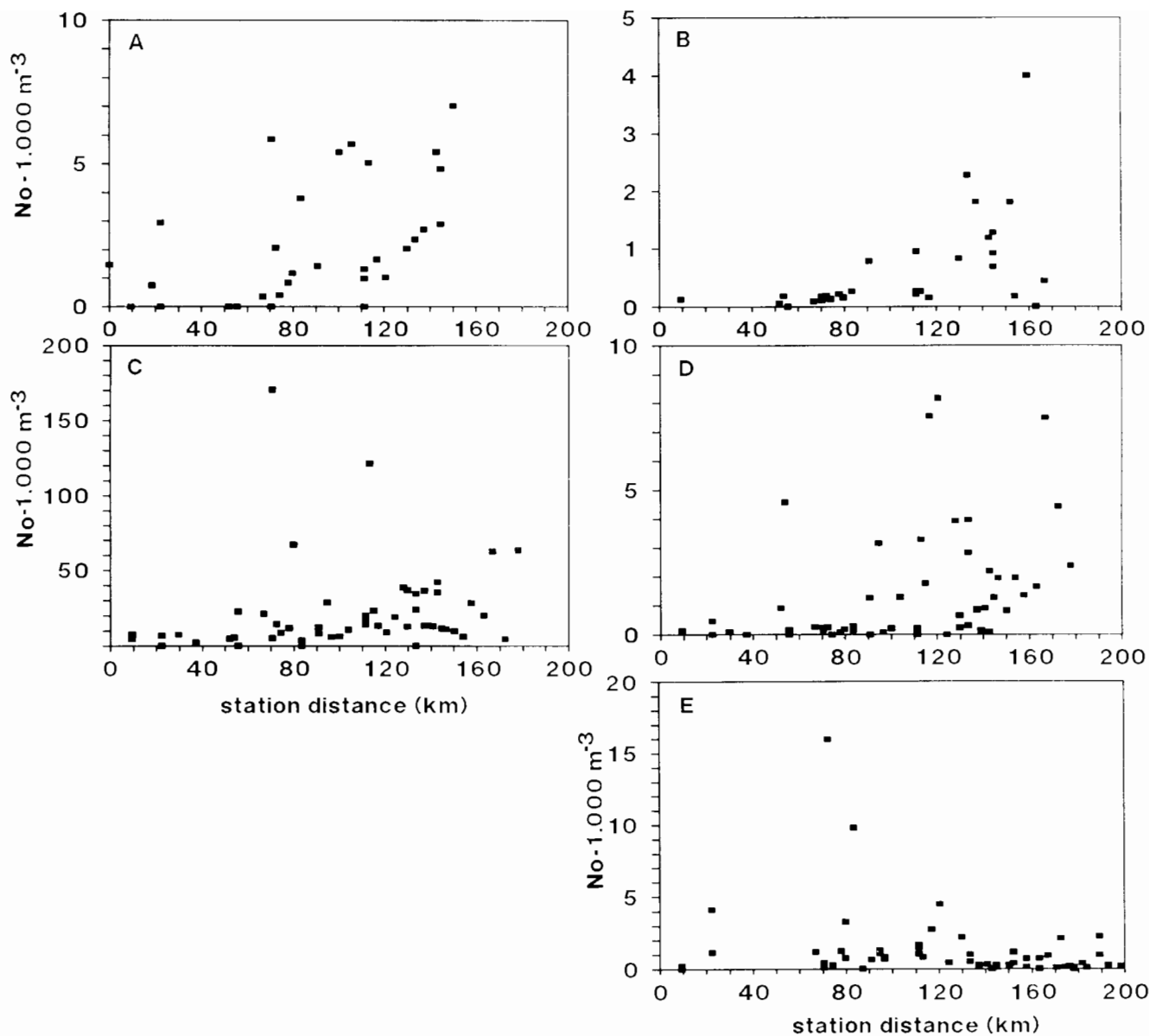


FIG. 3. Relationship between concentration of larvae and juveniles and distance from southeastern Browns Bank during cruise 85-1 for (A) larvae and (B) juveniles, 86-1.2 for (C) larvae and (D) juveniles and 87-1 for (E) juveniles. Spearman rank correlation coefficients in Table 4.

Analysis

All cod were counted and standard lengths of larvae measured to the nearest 0.1 mm using an ocular micrometer. Standard lengths of juveniles were measured to the nearest 0.5 mm using a ruler. No length corrections were made for preservation shrinkage. Cod densities were expressed as individuals $\cdot 1000 \text{ m}^{-3}$. Abundance of cod larvae at each station estimated from the BIONESS was calculated as a weighted average concentration (i.e. the total number collected at each station was divided by the total volume filtered over the seven depth strata). The Tucker trawl collections were treated similarly when more than one depth stratum was sampled per station.

The distribution of cod larvae and juveniles was assessed during each survey by rank correlation analysis. The relationship between larval and juvenile cod density and distance from the most southeastern station sampled (Fig. 1) was also assessed using rank correlation methods. This location is within the vicinity of major offshore spawning concentrations of cod (Scott

1983; O'Boyle et al. 1984), it was assumed to represent the origin of cod eggs in our study, and distance-density relationships were deemed useful for interpreting inter-annual variability in distribution.

The sampling grid was broken down into three transverse regions (Fig. 1) in order to assess inter-regional differences in the abundance and size composition of cod collected from the two gear types. Region 1 included Browns Bank (the principal late winter-early spring cod spawning grounds in the area). Both regions 2 and 3 contained several nearshore stations at depths less than 50 m (Fig. 1). Mann-Whitney U tests were used to make multiple comparisons of cod densities between regions (1-2, 2-3, 3-1). A similar set of comparisons were made on the length frequency distributions using the Kolmogorov-Smirnov test. Significance levels for these tests were adjusted to comply for multiple comparisons (Steele and Torrie 1980). All statistical analyses were performed using SYSTAT 3.0 (Systat Inc. 1984, Evanston, Illinois).

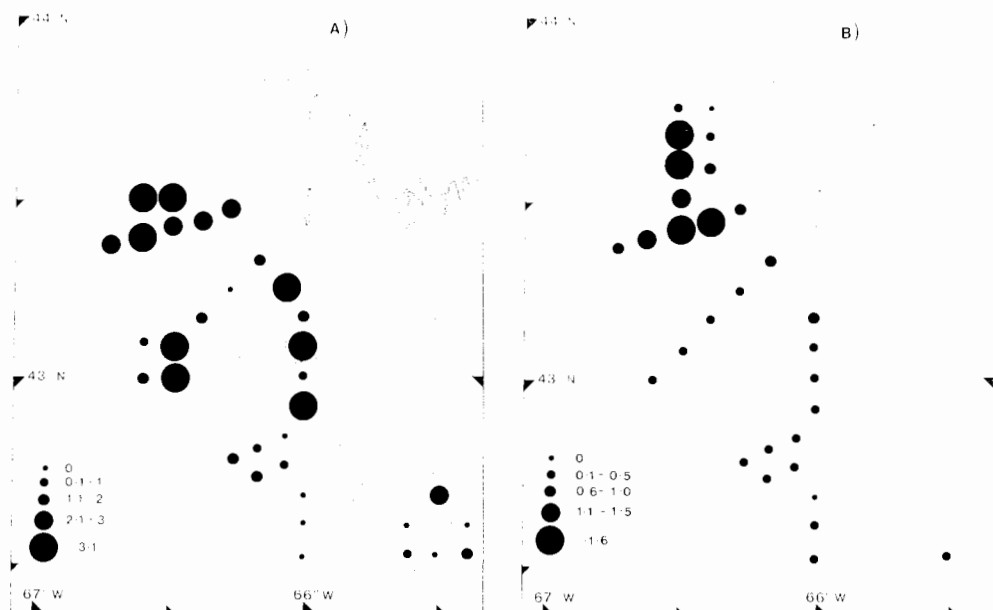


FIG. 4. Expanding symbol plot of cod concentration (No. · 1000 m⁻³) during cruise 85-1. (A) cod larvae sampled with small gear and (B) pelagic juveniles sampled with the Tucker trawl. Note five extra stations were sampled on Browns Bank with the BIONEISS, and seven extra stations were sampled at the northern boundary of the grid with the Tucker trawl.

TABLE 5. (a) Regional summary of average cod densities (No. · 1000 m⁻³) from the small and large (Tucker trawl) gear types for each cruise. *n* refers to number of stations sampled and percentage shows regional breakdown of mean catch. (b) Probability values of Mann-Whitney U test comparing cod concentrations between regions sampled by the small gear (SG) and the Tucker trawl (Tt). Insufficient data for analysis (I).

Cruise	Region	Small gear			Tucker trawl		
		No.	<i>n</i>	%	No.	<i>n</i>	%
(a) 85-1	3	5.90	(2)	62	1.23	(7)	59
	2	2.66	(16)	28	0.76	(13)	36
	1	0.99	(15)	10	0.11	(11)	5
86-1,2	3	24.61	(11)	36	2.45	(11)	53
	2	20.37	(28)	30	1.17	(28)	25
87-1	1	23.21	(15)	34	1.04	(15)	22
	3	I			0.53	(21)	13
	2	I			1.31	(21)	31
	1	I			2.35	(14)	56

Cruise	Gear	Region 1-2	Region 2-3	Region 3-1
(b) 85-1	SG	0.01 ^a	I	I
	Tt	<0.01 ^a	0.66	0.02 ^a
86-1,2	SG	0.17	0.55	0.14
	Tt	0.44	0.02 ^a	0.01 ^a
87-1	Tt	0.95	0.02 ^a	0.13

^aStatistically significant difference.

Results

1. Gear Comparison

More than 80% of the catch with the small gear during 1985, 1986, and 1987 was less than 10 mm (Fig. 2). The grand mean

and range of the size distribution was 8.3 mm and 3–29 mm, respectively. The range in sizes was quite broad during each of the surveys in all 3 yr (Table 3). Standard lengths averaged 7.9 and 7.7 mm for cruises 85-1 and 86-1,2, respectively, in spite of a nearly 10-fold greater density of young cod witnessed during cruise 86-1,2 (Table 3). During cruise 87-1 (conducted later than the other cruises by 3 wk) there were very few cod larvae and relatively more cod >10 mm collected. This resulted in a greater average length (18.2 mm) and a lower percentage of larvae <10 mm (32%).

The Tucker trawl consistently caught large cod larvae and pelagic juveniles that were evident only infrequently in the small gear samples. Greater than 95% of the Tucker trawl catch was composed of cod ≥10 mm (Fig. 2). The grand mean and range of the size distribution was 19.2 mm and 4–41 mm, respectively. The average length of cod collected during the 1985 and 1986 cruises was quite similar (85-1: 19.0 mm, 86-1,2: 17.7 mm) whereas during cruise 87-1 the mean was 23.7 mm. Cod larvae <10 mm made up less than 4% of the catch during each of the cruises over the 3-yr period.

Overall, there were at least two cohorts of cod in the study area, one comprising larvae between 4 and 10 mm and the other composed of late larval and early pelagic juveniles >10 mm (Fig. 2). In all cruises, the small sampling gear occasionally caught large larvae while the Tucker trawl occasionally caught small larvae. In the following analyses we define "larvae" as those cod sampled by the BIONEISS and 0.5-m ring net, of which >80% were <10 mm. "Juveniles" are defined as those individuals, both large larvae and pelagic juveniles (after the definitions of Hardy (1978), Fahay (1983), and Kendall et al. (1984)), sampled by the Tucker trawl, greater than 95% of which were ≥10 mm.

The abundance of cod larvae <10 mm collected in the small gear always exceeded the large gear catch, on average, by one to two orders of magnitude ($p < 0.001$). This difference can be attributed to the extrusion of small larvae (<8 mm) through

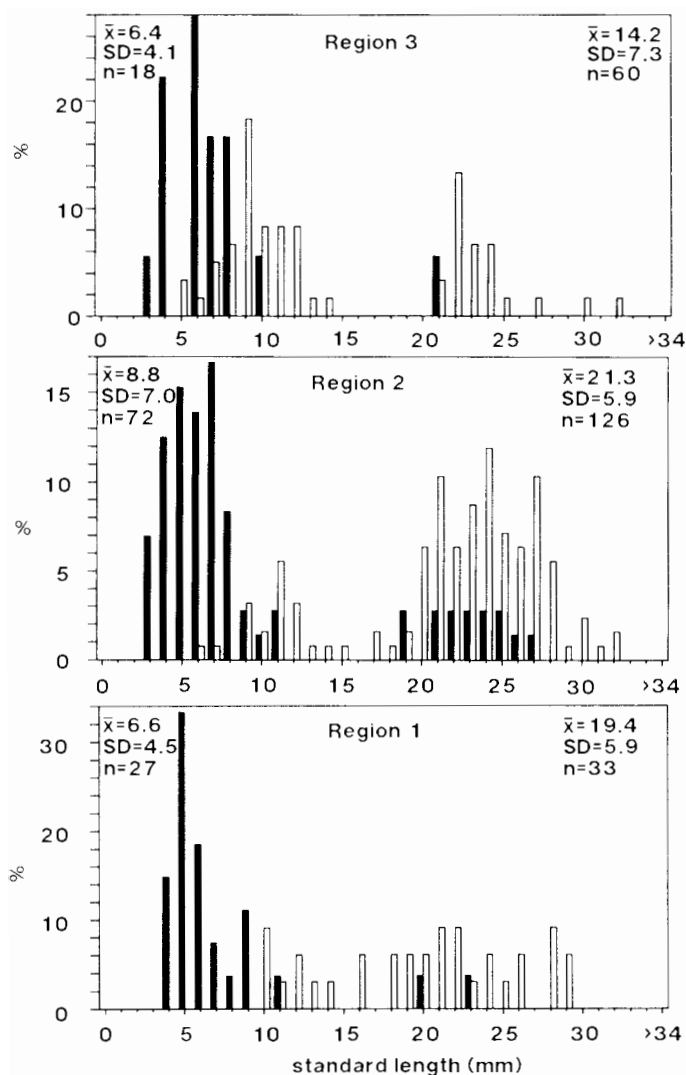


FIG. 5. Regional size frequency distributions of larvae in the small gear (shaded bars) and pelagic juveniles in the Tucker trawl (open bars) during May 1985 (cruise 85-1). Probability values associated with Kolmogorov Smirnov comparisons of length frequency distributions between regions for small gear: region 1,2; 0.99. Tucker trawl; region 1,2; 0.91, region 2,3; 0.01*, region 3,1; 0.08. * - refers to occurrence of statistically significant differences.

the 1600- μ m mesh of the Tucker trawl. Conversely, the density of young cod >10 mm was significantly greater in the Tucker trawl ($p = 0.025$, Mann-Whitney test). The frequency of zero catches of cod ≥ 10 mm exceeded 50% among those stations sampled with the small gear compared with only 17% with the Tucker trawl.

II. Intra- and Inter-Annual Distribution

The horizontal distribution of larval and juvenile cod coincided during cruises 85-1 and 86-1,2, as indicated by the significant ($p < 0.05$) positive correlations between their relative abundances at each station and similar positive correlations with distance (Fig. 3, Table 4). During cruise 87-1, too few larvae were collected for statistical analysis although juveniles were abundant. In contrast to the results obtained in the May cruises of 1985 and 1986, pelagic juveniles were negatively correlated with distance from Browns Bank (Fig. 3).

Cruise 85-1

Cod larvae and juveniles were distributed to the northwest of Browns Bank during May 1985 (Fig. 4). Only 10% of the total mean catch of larvae and 5% of the total mean catch of juveniles were collected in the vicinity of the bank (region 1). The density of cod larvae and juveniles increased from region 1-3 such that 62% of the larvae and 59% of the juveniles occurred in region 3 (Table 5) (i.e. at stations in excess of 145 km from the bank). Mann-Whitney U comparisons of larval cod densities revealed significant differences between region 1 and region 2 (Table 5). Only two stations were sampled in region 3 therefore no density comparisons were made with the other regions. Juvenile densities in regions 2 and 3 were not significantly different, but both were different from region 1 (Table 5).

There was no simple trend in the average length of cod larvae and juveniles across the three regions (Fig. 5). Significant differences in the juvenile size frequency distributions existed between regions 2 and 3. The difference in average size of larvae between regions was less than 3 mm and for juveniles it was 7 mm (Fig. 5). The high proportion of small cod (5-15 mm) in the large gear collections in region 3 was peculiar, given the great distance from Browns Bank. The exploratory coastal survey conducted in region 3 did, however, reveal large pelagic juveniles in the 20-30 mm size range (I. M. Suthers, unpubl. data).

Cruise 86-1,2

The larvae were uniformly distributed across the three regions during May 1986 (Fig. 6), and no significant differences in the abundance of larvae was observed between regions (Table 5). The size frequency distributions of larvae were also similar between regions (Fig. 7) with a regional difference in average length of 1.2 mm.

The abundance of juveniles increased from region 1-3 (Fig. 6), an observation consistent with the results from cruise 85-1 (Table 5). Region 3 yielded 53% of the total mean catch and the abundance of juveniles in this region differed significantly from the other two (Table 5). The differences in the average size of juveniles between regions was less than 0.5 mm, and no length frequency distributions were significantly different (Fig. 7).

Cruise 87-1

Too few larvae were collected in 1987 for any meaningful analysis. Juveniles were abundant however, especially in region 1 where 56% of the total mean catch occurred. Abundance decreased from regions 1-3 (Table 5). This trend was opposite to that seen in the previous surveys. Only regions 2 and 3 showed significant differences in abundance which is a surprising result given the regional catch distribution (Fig. 8). Equal ranking of a few high catches in region 1 with those in region 3 explains this result. The juvenile size frequency distributions between region 1 and the other two regions were significantly different (Fig. 9). The difference in average length between regions 1 and 3 was less than 3 mm.

III. Coastal Distribution

Several coastal stations were occupied during the main grid sampling. In addition, exploratory coastal surveys were conducted in May 1985, June 1986, and May 1987. Collectively,

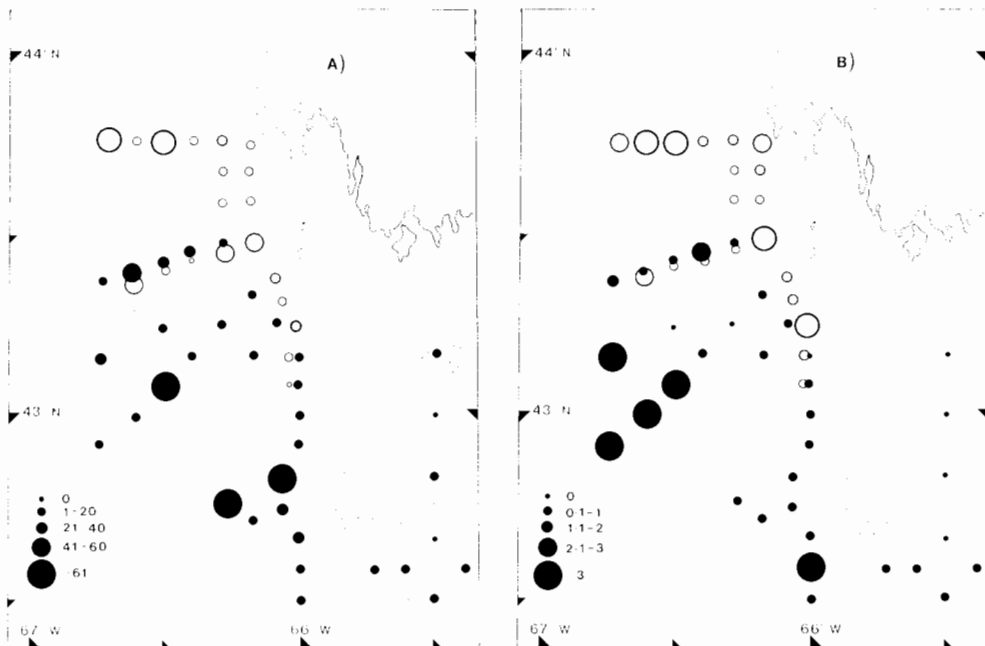


FIG. 6. Expanding symbol plot of cod concentration (No. · 1000 m⁻³) during cruise 86-1 (closed symbol) and cruise 86-2 (open symbol) for (A) cod larvae and (B) pelagic juveniles.

these surveys revealed significant concentrations of larval and pelagic juvenile cod that in some years were greater than in adjacent deeper water (Fig. 10). During May 1985 the coastal abundance of larval and pelagic juvenile cod was three-fold greater than in offshore areas.

Discussion

Any interpretation of larval fish distributions, and inferences regarding the processes underlying larval drift and retention require unbiased estimates of size and abundance. We addressed these requirements by (1) using multiple gear types, (2) examining inter-annual variability over a 3-yr period, and (3) sampling a grid of stations that encompassed the spawning areas and the most probable drift trajectory.

One important result of our study was that each gear effectively sampled only one of two size categories of cod with no one gear being adequate over the full size range. Reliable abundance estimates of cod <10 mm and ≥10 mm were obtained by the small and large gear, respectively. Another important finding was the annual occurrence of significant concentrations of cod larvae and juveniles in the nearshore (<50 m) waters off southwestern Nova Scotia suggesting that the coastal region may serve as an important nursery area for cod. The restricted size range of cod available to the small gear, coupled with limited sampling in the coastal regions, suggests that previous data generated in this way used to analyse the dispersal of the early life stages of cod (Gagne and O'Boyle 1984; O'Boyle et al. 1984) was not representative of the true distribution.

Our null hypothesis that the spatial distributions of cod from the large and small sampling gear would be similar could not be rejected. Although the large and small gear captured different sizes of fish, the positive correlations between cod larvae and juveniles witnessed during 1985 and 1986 supports the null hypothesis. Apparently this is due to the lack of any gradient in size from offshore to nearshore (Fig. 5, 7, and 9). Instead we observed a mixture of sizes during each survey. The length

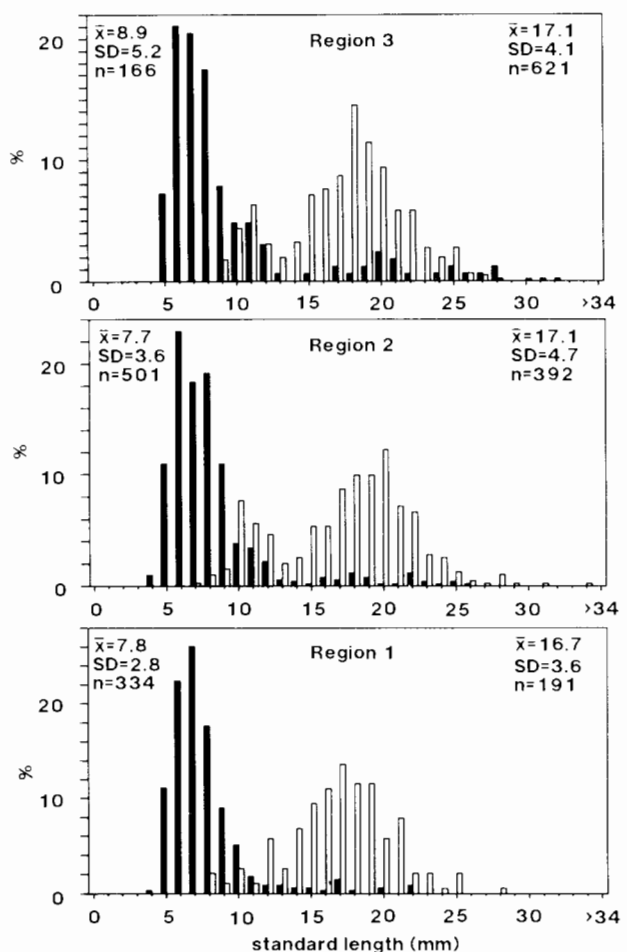


FIG. 7. Regional size frequency distributions of larvae (shaded bars) and pelagic juveniles (open bars) sampled during May 1986 (cruise 86-1,2). Probability values for K.S. comparisons for small gear: region 1,2; 0.99, region 2,3; 0.44, region 3,1; 0.99. Tucker trawl: region 1,2; 0.23, region 2,3; 0.99; region 3,1; 0.39.

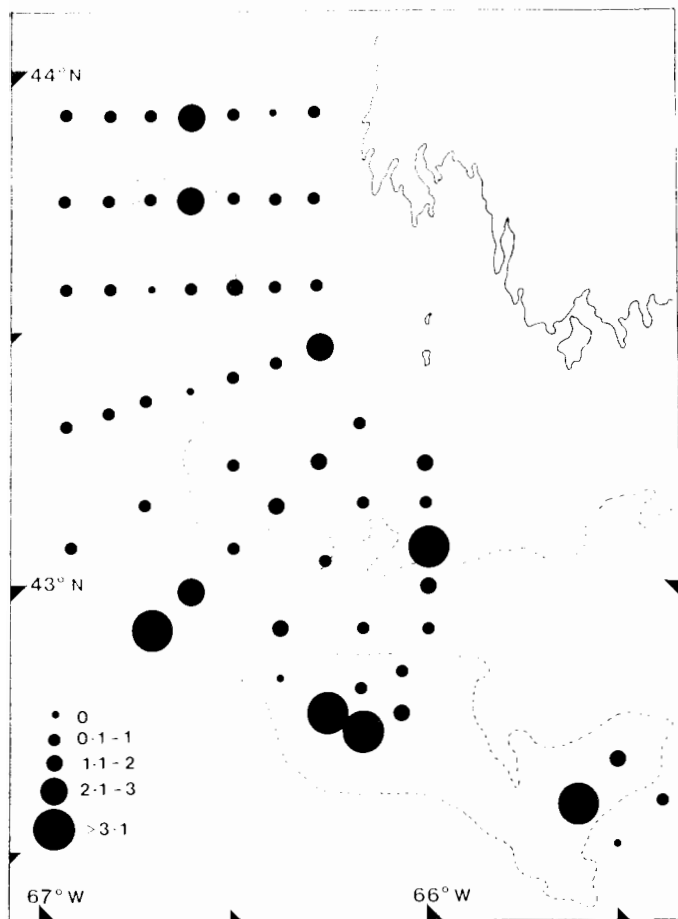


FIG. 8. Expanding symbol plot of pelagic juvenile cod density (No. ·1000 m⁻³) sampled during cruise 87-1.

frequency distributions of the larvae and juveniles across the three regions were significantly different in some cases, but in all but one comparison the size differences were less than 3 mm. Thus, Cushing's (1986) criticism of O'Boyle et al. (1984), that a spatial separation of eggs, larvae, and juveniles would have been observed had a larger net been used to sample the larger individuals, is probably not valid for southwestern Nova Scotia. It is evident that had there been a spatial gradient in size, the effect of sampling gear on our perception of the distribution would have been considerable.

The distribution of larval and pelagic juvenile cod, although similar to one another within years, varied dramatically between years. The percentage of larvae and juveniles in the offshore was the least in 1985 and greatest in 1987. This is corroborated by both positive and negative correlations of juvenile cod with distance from Browns Bank from 1985 to 1987 (Fig. 3). The inter-annual comparisons support our claim that meaningful conclusions about distributional patterns during the early life history cannot be made from single year surveys.

The range in size of cod larvae was similar between the three regions which could imply broad-scale, protracted spawning by cod. However, this interpretation was found wanting in light of the following evidence. Most cod that spawn during March and April in southwestern Nova Scotia do so on Browns Bank. Seasonal groundfish surveys conducted in NAFO Division 4X show that ripe female cod are concentrated on Browns Bank during March (Scott 1983). The results of past Scotian Shelf ichth-

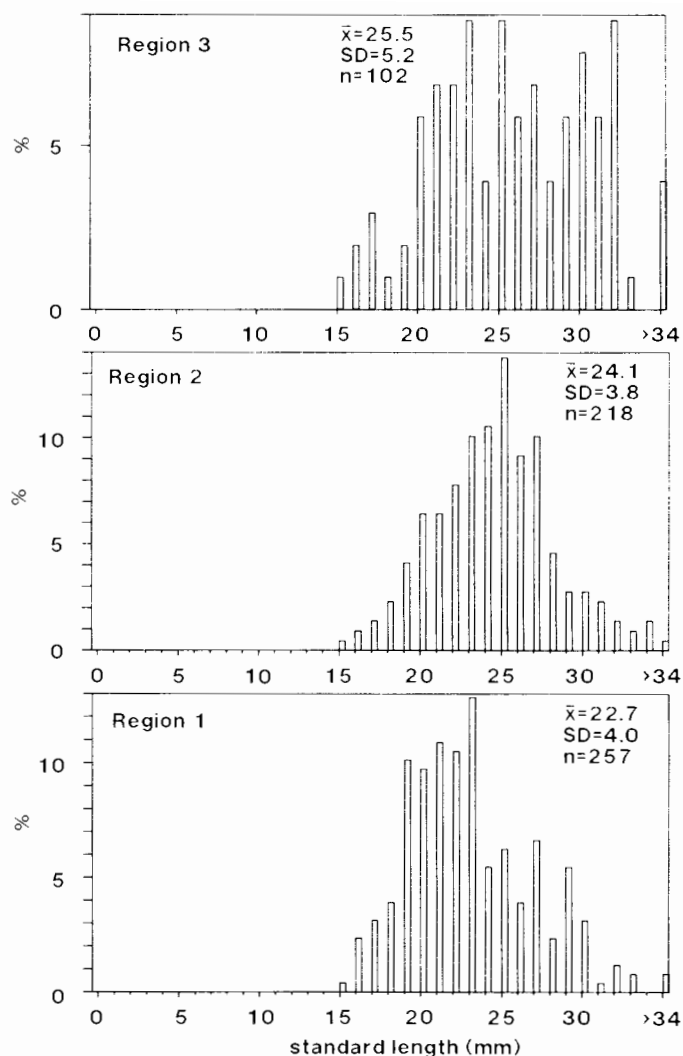


FIG. 9. Regional size frequency distributions of pelagic juvenile cod sampled during cruise 87-1 across the three regions. Probability values for K.S. comparisons for Tucker trawl: region 1,2: 0.01*, region 2,3: 0.17, region 3,1: 0.01. * refers to statistically significant differences.

yoplankton surveys have shown that peak concentrations of cod eggs were centred on Browns Bank during March and April (Gagne and O'Boyle 1984; O'Boyle et al. 1984). Five ichthyoplankton cruises, conducted independently of our study, from February to June 1985 in southwestern Nova Scotia showed cod egg abundance peaked in April with 95% of the eggs in region 1, with the majority occurring inside the 100-m isobath of Browns Bank (P.C. Hurley, Marine Fish Division, Bedford Institute of Oceanography, N.S. B2Y 4A2, pers. comm.). Coastal spring spawning may occur along the southern shore of Nova Scotia, but its magnitude relative to the offshore appears slight (Gagne and O'Boyle 1984).

The circulation features characteristic of Browns Bank may explain the variable inter-annual distributions of cod larvae and juveniles. A permanent clockwise gyre is situated over the western cap of Browns Bank, with an average residence time of 14 d (5-25 d range), episodically disrupted by winds persisting over a few days (Greenberg 1983; Smith 1983, 1989). North of Browns Bank a residual current flows westward and then northward towards the Bay of Fundy at 1-8 km·d⁻¹ (seasonal average). Depending upon wind stress reversals in flow can

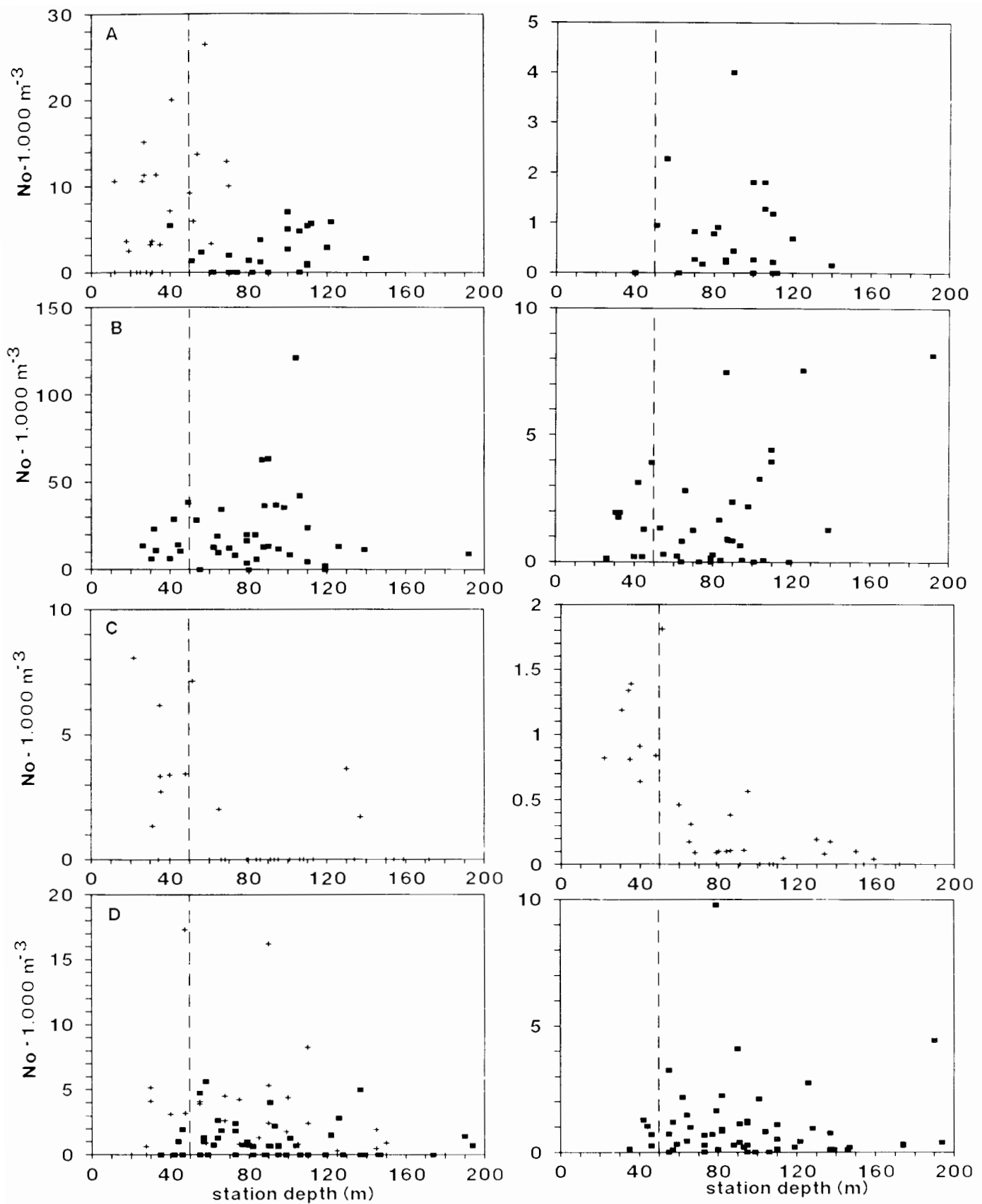


FIG. 10. Relationship between cod density and depth estimated by small (left-hand column) and large (right-hand column) gear types. Stations from Browns Bank were excluded. Broken line shows 50-m depth which is the limit of past offshore ichthyoplankton surveys conducted in southwestern Nova Scotia. Stations sampled on exploratory cruises are designated by +. (A) cruise 85-1 (B) cruise 86-1,2, (C) 5-12 June 1986, (D) cruise 87-1.

occur at daily intervals (Smith 1989). Smith (1989) concludes that 60–80% of the total variance in current variability is due to high frequency wind events in the 2–10 d band, a phenomenon confirmed by the variable drogue tracks.

The occurrence of young cod on Browns Bank, particularly in 1987 (Fig. 8), is consistent with the observation of O'Boyle et al. (1984) that the gyre acts to retain larvae. Obviously, this situation was not true in other years of our study (Fig. 4, 6). The location of juvenile cod should, in part, be determined by the magnitude of displacement of eggs and larvae from the spawning site. In our study pelagic juveniles were, on average, 30 d older than the larvae during 1985 and 1986 (I. M. Suthers, unpubl. data), yet the spatial distributions did not reflect the additional period of drift. This supports the notion of pelagic juveniles limiting further horizontal displacement (e.g. through behavioural means), and is one explanation for the mixture of sizes observed during all of the surveys. We use the term "retention" to describe the apparent persistence of young cod in time and space; whether the fraction of pelagic juveniles remaining near Browns Bank are members or vagrants of that population (Sinclair 1988) remains to be determined.

Acknowledgements

We gratefully acknowledge the ideas and assistance of Jeff McRuer, Dwight Reimer, and Peter Vass. The technical efforts of R. Stone, B. Meredith, W. Hingley, K. Lind, H. Budgey, A. D'Eon, C. Parsons, C. Jarvis, C. Barr, and P. Bidgood are greatly appreciated. We thank Drs. S. Kerr, C. Taggart, S. Campana, Mr. T. Lambert, and one anonymous reviewer for critical reviews of an earlier version of the manuscript. The captain and crew of the *C.S.S. Dawson* and *R.V. Navicula* are to be thanked for their assistance at sea. This study was supported in part by a Killam predoctoral award, the Natural Sciences and Engineering Research Council of Canada, and the Department of Fisheries and Oceans.

References

- BAILEY, K. M. 1981. Larval transport and recruitment of Pacific hake *Merluccius productus*. Mar. Ecol. Prog. Ser. 6: 1–9.
- BEVERTON, R. J. H., AND A. J. LEE. 1965. Hydrographic fluctuations in the North Atlantic Ocean and some biological consequences, p. 79–107. In C. C. Johnson, and L. P. Smith [ed.] The biological significance of climatic changes in Britain. Academic Press, Symposium of the Inst. of Biology (14): 222 p.
- CLUTTER, R. I., AND M. ANRAKU. 1968. Avoidance of samplers, p. 57–76. In D. J. Tranter and A. J. Fraser [ed.] UNESCO monographs on oceanographic methodology 2. Zooplankton sampling.
- COLTON, J. B. 1965. The distribution and behaviour of pelagic and early stages of haddock in relation to sampling techniques. ICNAF Spec. Publ. 6: 318–333.
- CUSHING, D. H. 1982. Climate and fisheries. Academic Press, London. 373 p.
1986. The migration of larval and juvenile fish from spawning ground to nursery ground. J. Cons. Int. Explor. Mer. 43: 43–49.
- DAAN, N. 1978. Changes in cod stock and cod fisheries in the North Sea. Rapp. P.-V. Reun. Cons. Int. Explor. Mer. 172: 39–57.
- FAHAY, M. P. 1983. Guide to the early stages of marine fishes occurring in the western North Atlantic Ocean, Cape Hatteras to the Southern Scotian Shelf. J. Northw. Atl. Fish. Sci. 4: 423 p.
- FRANK, K. T. 1986. Ecological significance of the ctenophore *Pleurobrachia pileus* off southwestern Nova Scotia. Can. J. Fish. Aquat. Sci. 43: 211–222.
1988. Independent distributions of fish larvae and their prey: natural paradox or sampling artifact? Can. J. Fish. Aquat. Sci. 45: 48–59.
- GAGNE, J. A., AND R. M. O'BOYLE. 1984. The timing of cod spawning on the Scotian Shelf, p. 501–517. In E. Dahl, D. S. Danielssen, E. Moksness, and P. Solemdal [ed.] The propagation of cod *Gadus morhua* L. Flødevigen rapportser 1.
- GODO, O. R., AND K. SUNNANA. 1984. Spawning area and distribution of 0-group cod *Gadus morhua* L., on the More coast. In E. Dahl, D. S. Danielssen, E. Moksness, and P. Solemdal [ed.] The propagation of cod *Gadus morhua* L. Flødevigen rapportser 1.
- GREEN, R. H. 1979. Sampling design and statistical methods for environmental biologists. Wiley-Interscience. 257 p.
- GREENBERG, D. A. 1983. Modelling the mean barotropic circulation in the Bay of Fundy and Gulf of Maine. J. Phys. Oceanogr. 13: 886–904.
- GROSSEIN, M. D., AND R. C. HENNEMUTH. 1973. Spawning stock and other factors related to recruitment of haddock on Georges Bank. Rapp. P.-V. Reun. Cons. Int. Explor. Mer. 164: 77–88.
- HARDEN JONES, J. R. 1968. Fish migration. Arnold, London. 325 p.
- HARDY, J. D. 1978. Development of fishes of the mid-Atlantic Bight. An atlas of egg, larval and juvenile stages. Volume II. Anguillidae through Syngnathidae. Center for environmental and estuarine studies of the University of Maryland. Contribution number 784. U.S. Fish Wildl. Serv. 458 p.
- HARDING, G. C., J. D. PRINGLE, W. P. VASS, S. PEARRE, AND S. J. SMITH. 1987. Vertical distribution and daily movements of larval lobsters *Homarus americanus* over Browns Bank, Nova Scotia. Mar. Ecol. Prog. Ser. 41: 29–41.
- HARDING, G. C., AND R. W. TRITES. 1988. Dispersal of *Homarus americanus* larvae from Browns Bank in the Gulf of Maine. Can. J. Fish. Aquat. Sci. 45: 416–425.
- HJORT, J. 1914. Fluctuations in the great fisheries of southern Europe in the light of biological research. Rapp. P.-V. Reun. Cons. Int. Explor. Mer. 20: 1–228.
- ILES, T. D., AND M. SINCLAIR. 1982. Atlantic herring: stock discreteness and abundance. Science (Wash., DC) 215: 627–633.
- KENDALL, A. W., W. H. AHLSTROM, AND H. G. MOSER. 1984. Early life history stages of fishes and their characters, p. 11–22. In H. G. Moser [ed.] Ontogeny and systematics of fishes. Am. Soc. Ichth. Herp. Spec. Publ. 1.
- KOSLOW, J. A., S. BRAULT, J. DUGAS, R. O. FOURNIER, AND P. HUGHES. 1985. Condition of larval cod (*Gadus morhua*) off southwest Nova Scotia in 1983 in relation to plankton abundance and temperature. Mar. Biol. 86: 113–121.
- LEAR, W. H., AND R. WELLS. 1984. Vertebral averages of juvenile cod, *Gadus morhua*, from coastal waters of eastern Newfoundland and Labrador as indicators of stock origin. J. Northw. Atl. Fish. Sci. 5: 23–31.
- MACDONALD, J. S., M. J. DADSWELL, R. G. APPY, G. D. MELVIN, AND D. A. METHVEN. 1984. Fishes, fish assemblages, and their seasonal movements in the lower Bay of Fundy and Passamaquoddy Bay, Canada. Fish. Bull. 82: 121–139.
- MURPHY, G. I., AND R. I. CLUTTER. 1972. Sampling anchovy larvae with a plankton purse seine. Fish. Bull. 70: 789–798.
- O'BOYLE, R. M., 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. Reun. Cons. Int. Explor. Mer. 183: 27–40.
- PIHL, L. 1982. Food intake of young cod and flounder in a shallow bay on the Swedish west coast. Neth. J. Sea Res. 15: 419–432.
- RILEY, J. D., AND W. G. PARNELL. 1984. The distribution of young cod, p. 563–580. In E. Dahl, D. S. Danielssen, E. Moksness, and P. Solemdal [ed.] The propagation of cod *Gadus morhua* L. Flødevigen rapportser 1.
- SCOTT, J. S. 1983. Inferred spawning areas and seasons of groundfishes on the Scotian Shelf. Can. Tech. Rep. Fish. Aquat. Sci. 1219: iii + 14 p.
1984. Juvenile haddock abundance and water temperature on the Scotian shelf in 1983. NAFO SCR Doc. 84/VI/64. Ser. No. N853.
- SHERMAN, K., W. SMITH, W. MORSE, M. BERMAN, J. GREEN, AND L. EJSY-MONT. 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.
- SINCLAIR, M. 1988. Marine populations. An essay on population regulation and speciation. University of Washington Press, Seattle. 252 p.
- SINCLAIR, M., AND T. D. ILES. 1985. Atlantic herring (*Clupea harengus*) distributions in the Gulf of Maine — Scotian Shelf area in relation to oceanographic features. Can. J. Fish. Aquat. Sci. 42: 880–887.
1988. Population richness of marine fish species. Aquat. Living Resour. 1: 71–83.

- SMITH, P. C. 1983. The mean and seasonal circulation off southwest Nova Scotia. *J. Phys. Ocean.* 13: 1034–1054.
1989. Circulation and dispersion on Browns Bank. *Can. J. Fish. Aquat. Sci.* 46: (This issue)
- SMITH, W. G., AND W. W. MORSE. 1985. Retention of larval haddock *Melanogrammus aeglefinus* in the Georges Bank region, a gyre-influenced spawning area. *Mar. Ecol. Prog. Ser.* 24: 1–13.
- STEELE, R. G. D., AND J. H. TORRIE. 1980. Principles of statistics. A biometrical approach. 2nd ed. McGraw-Hill, N.Y. 639 p.
- TREMBLAY, M. J., AND M. SINCLAIR. 1985. Gulf of St. Lawrence cod: age-specific geographic distributions and environmental occurrences from 1971 to 1981. *Can. Tech. Rep. Fish. Aquat. Sci.* 1387: iv + 43 p.
- WIENS, J. A. 1981. Single-sample surveys of communities: are the revealed patterns real? *Am. Nat.* 117: 90–98.