

# Geographic Variation in the Spawning of Atlantic Cod, *Gadus morhua*, in the Northwest Atlantic

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We analyzed 47 yr (1946–92) of research trawl data and 5 yr (1964–68) of research gillnet data to identify spawning locations of Atlantic cod, *Gadus morhua*, in the Newfoundland–Labrador region. Offshore, spawners are common on the continental shelf but generally rare on the slope. Relative abundance of spawning individuals on the shelf is comparably high off northeast Newfoundland, within 100 km of the Newfoundland coast from Cape Freels to Cape Race, on central Grand Bank, and on St. Pierre Bank. Slope spawning is largely restricted to the eastern slope of Hamilton Bank, a small section of northern Grand Bank, and Flemish Cap. Inshore spawning is evident in southeastern Labrador and southeastern Newfoundland, particularly in St. Mary's, Placentia, Trinity, and Bonavista bays. Trajectories of satellite-tracked drifter buoys indicate that it is highly improbable that eggs spawned on the slope of Grand Bank and much of the northeastern Newfoundland slope will be transported into shelf and coastal waters. We conclude that cod spawn in areas in which their eggs and larvae are likely to be retained and that inshore spawning populations may provide a considerably larger contribution to cod recruitment in coastal Newfoundland than has previously been believed.

Nous avons analysé les données de recherche recueillies pendant 47 a (1946–1992) à l'aide de chaluts et celles obtenues sur 5 a (1964–1968) avec des filets maillants dans le but de déterminer l'emplacement des frayères de la morue franche, *Gadus morhua*, dans la région de Terre-Neuve et du Labrador. Au large, on trouve beaucoup de géniteurs sur le plateau continental mais généralement peu sur la pente. On observe à peu près la même abondance relative de géniteurs au large du nord-est de Terre-Neuve, à moins de 100 km de la côte de Terre-Neuve entre Cape Freels et Cape Race, au centre du Grand Banc et sur le Banc de Saint-Pierre. Le frai sur le talus continental se limite en gros à la pente est du Banc Hamilton, une petite zone de la partie nord du Grand Banc, et au Bonnet Flamand. La reproduction côtière se fait au sud-est du Labrador et de Terre-Neuve, notamment dans les baies Sainte-Marie, de Plaisance, de la Trinité et de Bonavista. D'après les trajectoires des balises itinérantes suivies par satellite, il est très peu probable que les oeufs pondus sur la pente du Grand Banc et sur la majeure partie de la pente du nord-est de Terre-Neuve soient transportés jusque dans les eaux du plateau et de la côte. On en conclut que la morue fraie dans des zones où les oeufs et les larves ont des chances de rester et que les populations qui fraient dans les eaux côtières contribuent sans doute beaucoup plus qu'on ne le pensait au recrutement de la morue aux abords de Terre-Neuve.

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The successful management of an exploited species or population requires reliable knowledge of the environment in which individuals reproduce. In the absence of such basic information, the relative importance of biological and physical environmental factors on variability in reproductive success and survival cannot be fully assessed. In the Northwest Atlantic off Newfoundland and Labrador, the Atlantic cod, *Gadus morhua*, is a species of great commercial importance for which few data on spawning location exist. Based largely upon the ichthyoplankton surveys described by Serebryakov (1965, 1967) and two research cruises conducted in the early 1960s by Templeman (1965), cod have typically been described as spawning primarily over the continental slope with the greatest concentration of spawning individuals located off southeastern Labrador (Serebryakov 1965, 1967; Templeman and May 1965; Fitzpatrick and Miller 1979; Templeman 1981). The spawning locations identified by Fitzpatrick and Miller (1979) (Fig. 1), based almost entirely upon the aforementioned work, are cur-

rently accepted as the major spawning locations of cod in the Newfoundland–Labrador region (e.g., Templeman 1981; Helbig et al. 1992; de Young and Rose 1993). However, as noted by Helbig et al. (1992), eggs and larvae produced over most of the purported spawning areas would be transported away from the continental shelf and coastal bays and would likely be lost to the population(s).

Our first objective is to address the inconsistency that underlies the reported spawning areas and the predicted trajectories of egg and larval transport. We combine offshore research data from 1946 to 1992 to determine the geographical distribution of spawning individuals throughout the continental shelf and slope waters. Secondly, by incorporating variability in sampling effort, we calculate indices that describe the relative abundance of spawning individuals in the Newfoundland–Labrador region. Our third objective is to collate all data on spawning cod in coastal areas in order to assess the prevalence of inshore spawning. Finally, we include a review of extant research spawning

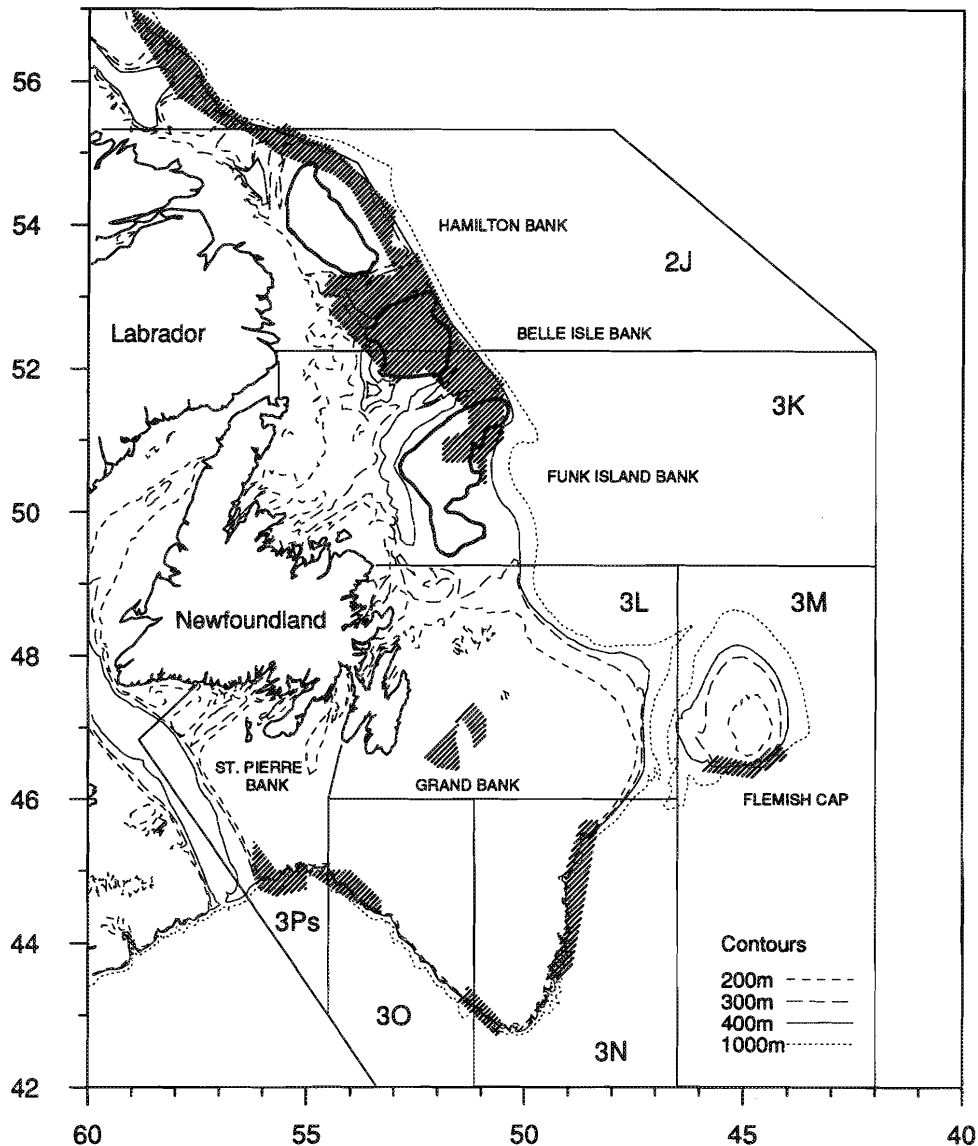


FIG. 1. Spawning locations (hatched areas) of Atlantic cod identified by Fitzpatrick and Miller (1979) off Newfoundland and Labrador. Hamilton, Belle Isle, and Funk Island banks are delineated along their respective 200-m (Hamilton Bank) and 300-m depth contours. Number and letter codes indicate NAFO Divisions.

records of cod off Newfoundland and Labrador in order to evaluate our results within a historical and biological context.

## Materials and Methods

### Offshore Region

Offshore spawning locations were determined from research trawl data collected from 1946 to 1992 over the continental shelf and slope off Newfoundland and Labrador. The geographical area extended from Hamilton, Belle Isle, and Funk Island banks (NAFO Divisions 2J and 3K) in the north to Grand Bank (3LN), Flemish Cap (3M), and St. Pierre Bank (3Ps) in the south (Fig. 1). Our definitions of the continental shelf and slope in the Newfoundland–Labrador region conform to those used by physical oceanographers (e.g., Helbig et al. 1992). The northeast Newfoundland shelf (NAFO Divisions 2J and 3K) is defined by the shelf break between 300–400 and 1000 m although it in-

cludes deep (>200 m) bays and a deeper (up to 500 m) basin. Eastward and southward, the shelf broadens somewhat to form Grand Bank and St. Pierre Bank and the slope begins at the 200-m isobath. Trawl data were available for most years from 1962 to 1992 in all regions except Flemish Cap where annual data were limited largely to 1977–85 (Table 1). From 1946 to 1961, data were available for most years for the Grand and St. Pierre banks only (prior to 1962, 2J was sampled only once during the spawning period, while 3K was not sampled).

Reproductive status of female and male cod was assessed following the criteria defined by Templeman et al. (1978). Females were deemed to be in spawning condition if clear eggs were present in the ovary (clarity being indicative of hydration). Given that eggs will normally be released within 3 d of hydration (Kjesbu et al. 1990), the collection locations of females containing hydrated eggs should closely approximate spawning locations. Females were deemed to be spent if their ovaries were

TABLE 1. Research vessels and years in which otter trawls were used, by NAFO Region, during the spawning periods (see text for months) of Atlantic cod off Newfoundland and Labrador:

NAFO Region	Years sampled	Research vessel
2J (Hamilton Bank)	1958	<i>Investigator II</i>
	1962–64, 1966, 1969–71, 1973–74	<i>A.T. Cameron</i>
	1978–79, 1981–83, 1986–92	<i>Gadus Atlantica</i>
	1991	<i>Alfred Needler</i>
	1992	<i>Northern Kingfisher</i>
3K (northeastern Newfoundland)	1963–64, 1969–71, 1974	<i>A.T. Cameron</i>
	1978–83, 1985–91	<i>Gadus Atlantica</i>
	1992	<i>Northern Kingfisher</i>
3L (including northern Grand Bank)	1946–48, 1950–51, 1953	<i>Investigator II</i>
	1959, 1961, 1963–78, 1980–82	<i>A.T. Cameron</i>
	1979–80, 1984–90	<i>Gadus Atlantica</i>
	1983–92	<i>Wilfred Templeman</i>
	1984	<i>Alfred Needler</i>
3M (Flemish Cap)	1961, 1964, 1968, 1977	<i>A.T. Cameron</i>
	1978–85	<i>Gadus Atlantica</i>
3N (southeastern Grand Bank)	1946–48, 1950–53, 1956–59	<i>Investigator II</i>
	1959–62, 1964–82	<i>A.T. Cameron</i>
	1984–85	<i>Alfred Needler</i>
	1985–92	<i>Gadus Atlantica</i>
3O (southwestern Grand Bank)	1946–48, 1951–52, 1955–59	<i>Investigator II</i>
	1959–62, 1964–66, 1968, 1971, 1973, 1975–82	<i>A.T. Cameron</i>
	1984–85	<i>Alfred Needler</i>
	1985–91	<i>Gadus Atlantica</i>
3Ps (St. Pierre Bank)	1947–48, 1950–51, 1953–54, 1956–60, 1963, 1965	<i>Investigator II</i>
	1960, 1962, 1964, 1967–70, 1972–82	<i>A.T. Cameron</i>
	1984–85	<i>Alfred Needler</i>
	1985–87	<i>Wilfred Templeman</i>
	1986	<i>Gadus Atlantica</i>

whitish grey or bluish grey, slack, and often wrinkled; residual eggs may have been present. Males were defined as spawning individuals if their testes and vasa deferentia were white and not depleted of milt. Males were deemed to be spent if their testes were grey or pink and if milt was not evident in the outer edges at the time when all females were spent.

To identify spawning locations of cod, we initially plotted the locations in which research gear had sampled at least one spawning female or male. We then restricted our analysis to research trawl data to quantify the relative abundance of spawning individuals offshore. This analysis incorporated the geographical bias in spawning concentrations induced by variation in sampling effort. Effort was defined as the number of research trawls (each of approximately 30-min duration) conducted in a given unit area during the 4 months in which most spawning occurs. These regional time periods, as determined from Myers et al. (1993), were February–May for 3M, March–June for 2J, 3K, 3N, 3O, and 3Ps, and April–July for 3L. Generally, a subset of all cod captured in a given trawl were sampled for state of maturity. For each of these subsamples, we calculated the proportion of fish greater than the mean length of maturity (calculated separately for each NAFO Division) that were in a spawning state. We then calculated the number of spawning fish per trawl by multiplying the actual number of fish greater than the mean length at maturity by the incidence of the spawning state among fish of the same size in the subsample. If fewer than five individuals greater than the mean length at maturity were

examined for spawning condition, the trawl was excluded from the analysis. We report the median number of spawning fish per trawl to reduce the effect of rare trawls in which very large numbers of cod were caught. The number of spawning fish per trawl will be related to population density (e.g., if population density is low in one region, the maximum number of spawners per trawl will be less than observed elsewhere). Trawls that were damaged during operation (i.e., deemed to have adversely affected the catch in some manner) or fished at depths below which cod are generally not found (>500 m; e.g., Baird et al. 1992) were excluded from the analysis. A total of 3181 trawls met our criteria and were included in the analysis. The size of the unit areas depended upon the region and was designed to maximize the number of trawls per unit area but minimize the size of each area. Sampling effort was higher in the south primarily because of the difficulty that ice conditions impose on sampling of spawning cod in the north. Thus, unit areas were relatively small but numerous in the south, being 0.5° latitude × 0.5° longitude on Grand Bank ( $n = 77, 34,$  and  $32$  unit areas in 3L, 3N, and 3O, respectively), St. Pierre Bank ( $n = 30$  in 3Ps), and Flemish Cap ( $n = 18$  in 3M) (Fig. 2). Unit areas were larger in the north (1° latitude × 1° longitude) and fewer in number ( $n = 14$  and  $13$  in 3K and 2J, respectively). Unit areas in which only one or two trawls were sampled were excluded from the analysis (Fig. 2). This criterion removed 6% ( $n = 13$ ) of the unit areas.

Trawl data were obtained from six research vessels. Of these,

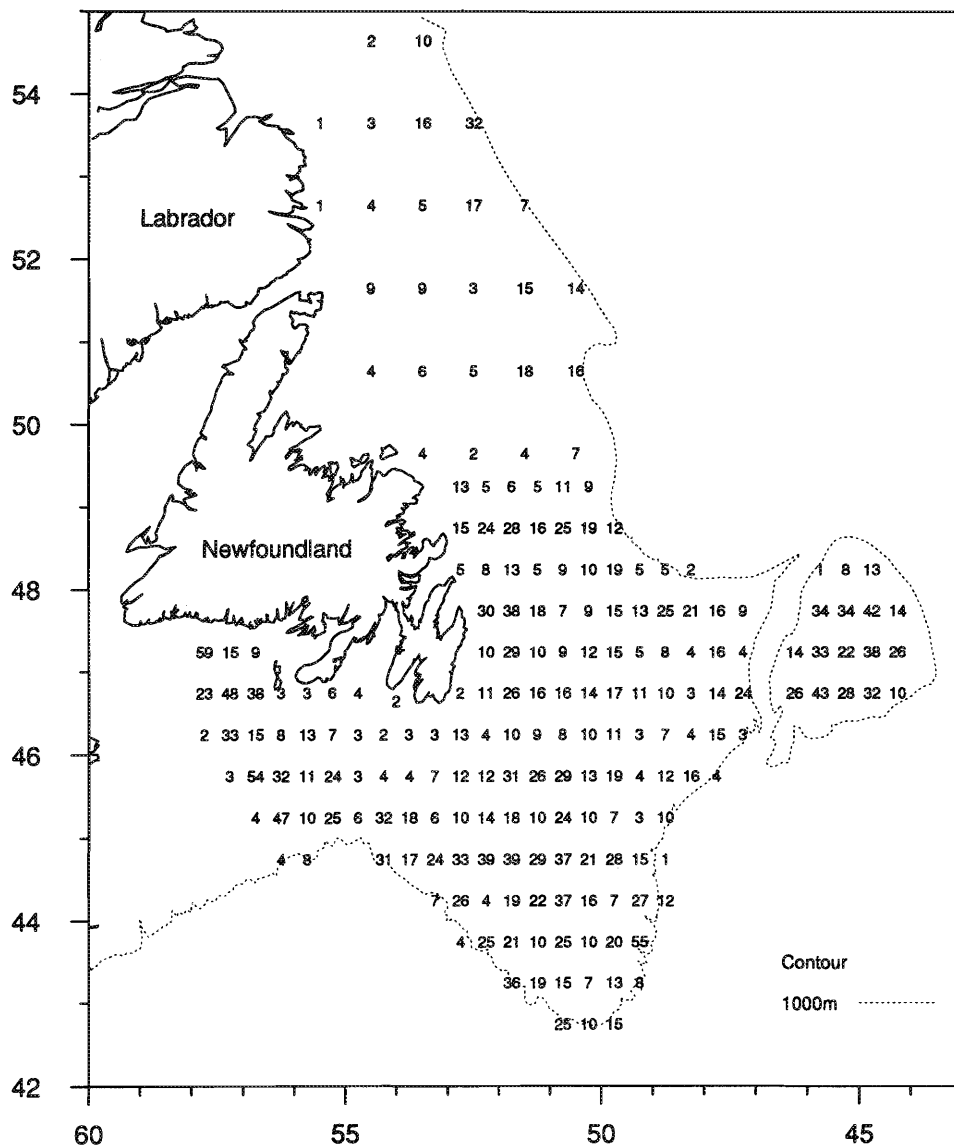


FIG. 2. Number of research otter trawls conducted from 1946 to 1992 during potential Atlantic cod spawning periods within unit areas of the continental shelf and slope off Newfoundland and Labrador (the sizes of the unit areas and the potential spawning periods specific to different regions are described in the text). Only those trawls in which cod were sampled for state of maturity are included here.

the *A.T. Cameron* and *Wilfred Templeman* have been shown to be equally efficient in catching cod (Gavaris and Brodie 1984). The *Alfred Needler* can be included with these, as it is the sister ship of the *Wilfred Templeman*. The trawls fished by the *Gadus Atlantica* are the same as those fished by the *Wilfred Templeman* and the *Alfred Needler*. The remaining ships, the *Investigator II* and *Northern Kingfisher*, contributed 212 and 46 trawls, respectively; their total contribution represents only 3% of the total number of trawls in the analysis. We therefore assumed that sampling efficiency was similar among research vessels. We pooled all data because our intent was to identify spawning sites that either have been or are presently being utilized by cod. In addition, there is no evidence that either the months in which trawls were conducted or the average number of spawning females per trawl has changed significantly through time. Thus, it is reasonable to assume that our descriptions represent "average" depictions of spatial variation in cod spawning for the

time period examined.

The relative abundance of spawning cod on the shelf versus the slope was compared with a one-way ANOVA. The probability of obtaining the observed *F*-statistic in each analysis was assessed from 1000 data randomizations (cf. Manly 1991).

#### Inshore Region

Data on inshore spawning were obtained primarily from research trawl and gillnet surveys. From 1964 to 1966, the Fisheries Research Board of Canada conducted experimental gillnet surveys at two stations in St. Mary's Bay (Colinet Island and Broad Cove) and two in Placentia Bay (Merashen and Woody Point). Additional gillnet sampling was conducted in 1967 and 1968 in Trinity Bay (Horse Chops and Tickle Harbour Point) and Bonavista Bay (Cabot Island and Little Denier). The details of these surveys are available in cruise reports of the *M.V. Marinus* (reports 1964(1), 1965(1), 1966(1), 1967(1), and

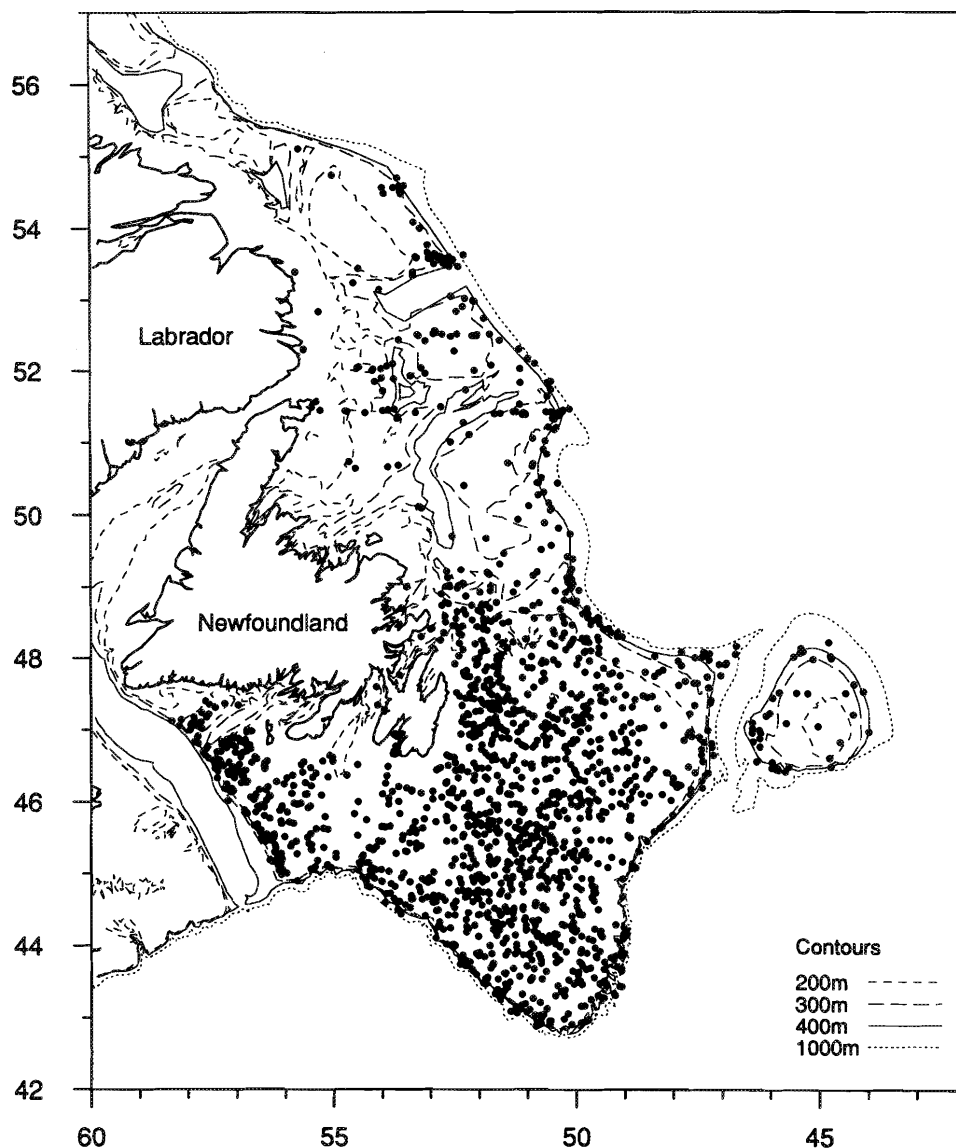


FIG. 3. Locations of Atlantic cod (male and female) in spawning condition sampled by research trawls, gill nets, and jiggers from 1946 to 1992 off Newfoundland and Labrador.

1968(1 and 2)). The gill nets measured 91.4 m in length and contained mesh sizes of 6 in. (Trinity and Bonavista bays), 6.5 in. (St. Mary's and Placentia bays), or 7 in. (all bays). An index of abundance was calculated for each station by dividing the total number of spawning males and females caught by the total number of gill nets fished. The relative abundance of spawning cod among bays was compared with a one-way ANOVA. Statistical significance was evaluated by the randomization method, using 1000 data randomizations (Manly 1991). Maturity data on inshore cod were also obtained from samples collected by commercial gill nets off Cape Bonavista in 1983 and 1984 and by research jiggers off Labrador.

## Results

### Offshore Spawning

Spawning cod have been captured throughout the continental shelf and slope of Newfoundland and Labrador (Fig. 3). Shelf

spawning was evident on all banks and on Flemish Cap. The lower frequency of collections at shelf locations in 2J and 3K is a reflection of the difficulty that ice cover imposes on sampling during the spawning period. Spawning individuals were captured on the slopes of all banks, including Flemish Cap.

Spawning was concentrated primarily in shelf areas (Fig. 4). Labrador shelf spawning was evident on southeastern Hamilton Bank and Belle Isle Bank, while spawning occurred throughout the northeastern Newfoundland shelf. Off southeastern Newfoundland, spawner abundance was highest within 100 km of the coast and on central Grand Bank. Throughout Grand and St. Pierre banks, spawning fish were encountered more frequently on the shelf than on the slope. Only off Hamilton Bank (2J) were reproductive individuals more abundant on the slope than they were further inshore (although this may reflect spatial bias in sampling). The relative abundance of spawning cod in unit areas located on the shelf (mean  $\pm$  SD:  $5.16 \pm 5.91$ ,  $n = 135$ ) was more than double that for unit areas located on the slope

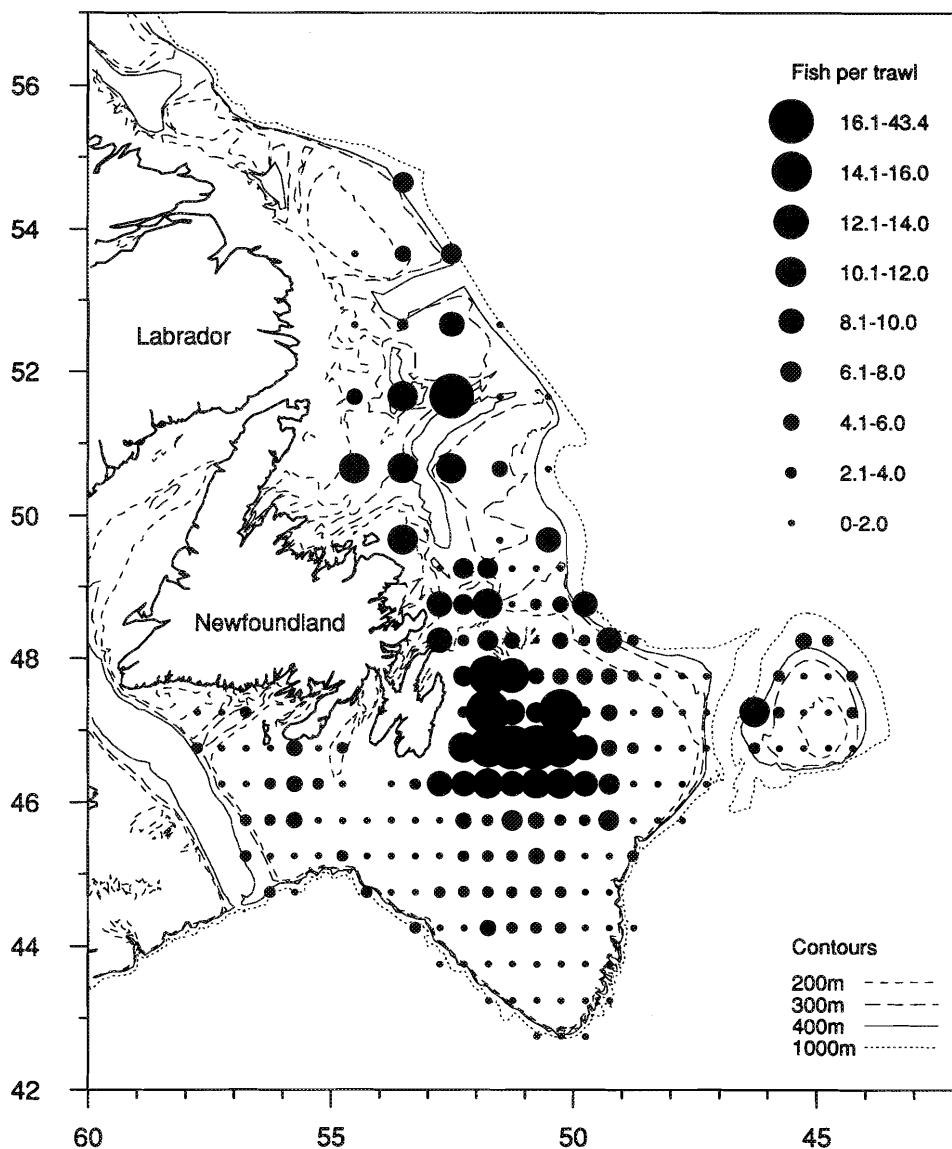


FIG. 4. Relative abundance of spawning Atlantic cod (sexes combined) on the continental shelf and slope off Newfoundland and Labrador. The circles represent the median number of spawning fish caught per trawl in each unit area during potential spawning periods (see text) from 1946 to 1992.

( $2.38 \pm 2.64$ ,  $n = 61$ ); the difference was highly significant ( $F_{[1,194]} = 12.32$ ,  $p < 0.001$ ).

#### Inshore Spawning

Spawning cod have been captured throughout the coastal regions of southeastern Newfoundland and in southeastern Labrador and northern Newfoundland (Fig. 5). The experimental gillnet surveys in St. Mary's, Placentia, Trinity, and Bonavista bays yielded an abundance of spawning cod in both the inner and outer reaches of each bay (Table 2). The percentage of catches composed of spawning individuals was higher in the May–June sampling period than it was during the April–May period in all but St. Mary's Bay (in which catch rates were similar between periods). The relative abundance of spawning cod, measured as the number of fish per gill net, did not differ significantly among bays (St. Mary's Bay:  $16.1 \pm 25.5$ , Placentia Bay:  $6.7 \pm 3.0$ , Trinity Bay:  $4.0 \pm 2.3$ , Bonavista Bay:

$8.2 \pm 2.3$ ;  $F_{[3,16]} = 0.77$ ,  $p = 0.531$ ). The magnitude of the standard deviation for St. Mary's Bay is inflated due to the extremely high value of 67.5 fish per net in 1964. When this value was excluded, the abundance for St. Mary's Bay decreased to  $5.8 \pm 4.3$  (the abundances among bays remained non-significant,  $F_{[3,15]} = 1.60$ ,  $p = 0.236$ ).

Further evidence of inshore spawning was provided by the sample of mature individuals collected by commercial gill nets fished immediately off Cape Bonavista in May–July 1983 and 1984. Although gonads were not examined to determine the state of maturity, the spawning condition of these fish can be assessed with an index that reflects the proportional allocation of body mass to gonads versus soma. In the absence of data on body weight, we divided gonad weight by  $(\text{body length})^3$  and compared the value of this gonadal index for the fish sampled by the commercial nets with the mean value for fish known to be in spawning condition in 3L (gonadal index in 3L:  $0.143 \pm 0.060$ ,  $n = 275$ , including all research data from 1946 to 1992). Of the

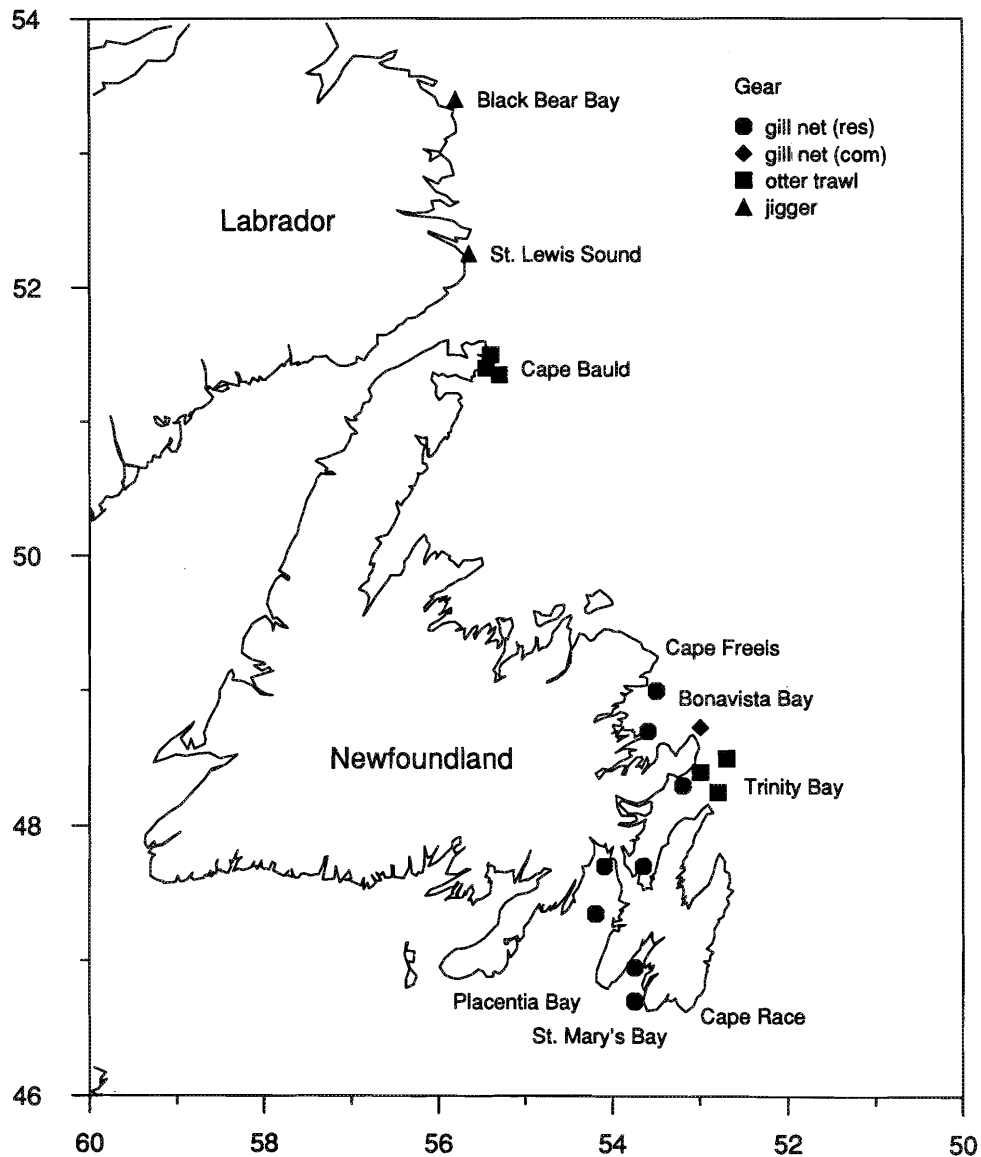


FIG. 5. Inshore locations of spawning Atlantic cod (sexes combined) sampled by gill nets (primarily research), research otter trawls, and research jiggers in coastal Newfoundland from 1946 to 1992.

315 female cod sampled in May–July 1983 and 1984, the gonadal index of 21% of the individuals encompassed 1 SD of the mean gonadal index of spawning cod in 3L, providing evidence of spawning immediately off Cape Bonavista.

Inshore cod in spawning condition have also been captured by research otter trawls and jiggers. Trawl samples containing spawning cod have been conducted in the outer reaches of Trinity Bay and close to shore near Cape Bauld (Fig. 5). Spawning cod have also been collected in Black Bear Bay and St. Lewis Sound, southeastern Labrador, by research jiggers.

## Discussion

### Cod Spawning Locations

Our data indicate that Atlantic cod spawn throughout the continental shelf and slope waters of Newfoundland and Labrador. However, contrary to previous views (Serebryakov 1965, 1967; Templeman 1965, 1981; Fitzpatrick and Miller 1979),

research trawl samples of mature individuals indicate that Newfoundland cod, consistent with Barents Sea stocks (Bergstad et al. 1987), spawn primarily on the shelf. The relative abundance of spawning individuals on the shelf is comparably high: (i) off northeast Newfoundland, (ii) within 100 km of the Newfoundland coast from Cape Freels to Cape Race, (iii) on central Grand Bank, and (iv) on St. Pierre Bank. Slope spawning is largely restricted to the eastern slope of Hamilton Bank, a small section of northern Grand Bank, and Flemish Cap. Spawning is also evident in inshore waters with high concentrations recorded in St. Mary's, Placentia, Trinity, and Bonavista bays in southeastern Newfoundland. Two factors may contribute to the relatively low numbers of spawning fish per trawl in some areas. Experimental observations (Brawn 1961) indicate that cod undergo vertical movements in the water column during spawning. Bottom trawls may not efficiently capture spawning cod. Secondly, the numbers of females classified as in spawning condition, i.e., as containing hydrated eggs, may have been underestimated. Kjesbu et al. (1990) have reported that eggs in

TABLE 2. Numbers of male and female Atlantic cod in spawning condition sampled from experimental gill nets in inshore Newfoundland (nd = no data).

Location	Sampling period	Sample size		Percent in spawning condition		Spawning fish per net
		Male	Female	Male	Female	
Colinet Island, St. Mary's Bay	May–June 1964	295	120	nd	>50	13.4
	May–June 1965	330	98	70	57	4.5
	April–May 1966	247	118	11	65	3.1
Broad Cove, St. Mary's Bay	May–June 1964	337	68	nd	34–91	67.5
	May–June 1965	148	35	82	73	3.6
	April–May 1966	297	94	85	81	4.6
Merashen, Placentia Bay	May–June 1964	131	71	>50	>50	7.8
	April–May 1965	220	138	26	20	4.3
	April–May 1966	277	178	16	22	3.9
Woody Island, Placentia Bay	May–June 1964	39	31	>50	>50	1.8
	April–May 1965	296	111	23	40	4.8
	April–May 1966	88	45	11	22	1.4
Tickle Hr. Point, Trinity Bay	May–June 1967	245	193	47	46	7.3
	April–May 1968	172	226	9	13	2.8
Horse Chops, Trinity Bay	May–June 1967	206	191	38	30	6.6
	April–May 1968	156	243	8	3	10.0
Cabot Island, Bonavista Bay	May–June 1967	102	299	29	5	10.6
	May 1968	218	217	0	13	5.1
Little Denier, Bonavista Bay	May–June 1967	288	121	51	27	9.1
	May 1968	249	235	1	32	8.1

hydrated condition are present only during the latter half of the spawning interval between successive egg batches.

A comparison of the spawning locations of cod (Fig. 4) with the trajectories of satellite-tracked drifter buoys (Fig. 6) suggests that cod spawn in areas in which eggs and larvae are likely to be retained on the shelf (Helbig et al. (1992) provide further information regarding these trajectories). In general, cod probably avoid spawning on the slope, particularly off Grand Bank, because of the high probability that eggs will be transported away from the banks. Spawning would also be avoided on the southern slopes of Grand Bank and St. Pierre Bank because of potential entrainment, and subsequent mortality, of eggs and larvae in warm core rings (Myers and Drinkwater 1989). Alternatively, spawning should not be unexpected on the Labrador and northeastern Newfoundland slopes because of the existence of eddies that can displace water from the slope onto the shelf (Helbig et al. 1992). The meandering trajectories of buoys on the northeastern Newfoundland shelf and on Grand Bank indicate that eggs spawned in these regions will be retained on the shelf (Fig. 6). Our data, in conjunction with the drifter trajectory routes, are consistent with the hypothesis that spawning locations of marine pelagic fish are dependent upon the geographic extent of oceanographically predictable larval retention areas (O'Boyle et al. 1984).

#### Variability in Spawning Distributions: Evidence of Offshore and Inshore Stocks

Disjoint spatial distributions of spawning individuals may lead to or reflect reproductive isolation among cod populations. The spatial distribution of reproductive cod described here might indicate the existence of four such populations on a large scale: a Labrador – northeastern Newfoundland stock, a Grand

Bank stock, a Flemish Cap stock, and a St. Pierre stock (cf. Fig. 4). These geographical divisions are consistent with those suggested by Templeman (1962), based upon variation in vertebral numbers (but see Pepin and Carr 1993) and migration studies, and to a lesser extent with the 2J3KL and 3NO stocks identified by Helbig et al. (1992), based upon physical oceanography. Serebryakov et al. (1987) reported a distribution of spawning individuals on Flemish Cap similar to that reported here.

Our data provide evidence of local, inshore populations of cod. Although such evidence is particularly strong in southeastern Newfoundland, an area encompassing that of Templeman's (1962) Avalon–Burin stock, we cannot discount the possibility that spawning also occurs throughout bays in northeastern Newfoundland, areas where ice has prevented comprehensive sampling during spawning. Our conclusion that these spawning inshore cod have not migrated from offshore areas is supported by hydroacoustic survey data reported by Rose (1993). In 1991 and 1992, cod have been monitored during their migration from the north slope of Grand Bank to inshore waters off Bonavista Bay. Sampling indicated that spawning occurred throughout the migration period and that most fish were spent by the time they approached the coast. Thus, the presence of spawning fish in coastal bays is probably indicative of inshore populations, as has been previously postulated by Templeman (1966). Evidence of inshore cod populations also exists in Nova Scotia (McKenzie 1940) and Norway (Bergstad et al. 1987). It is critical for the management of this species that the existence of such populations be explored throughout coastal Newfoundland. Clearly, the gillnet experiments of the 1960s conducted in St. Mary's, Placentia, Trinity, and Bonavista bays should be repeated. Additional surveys should be conducted in

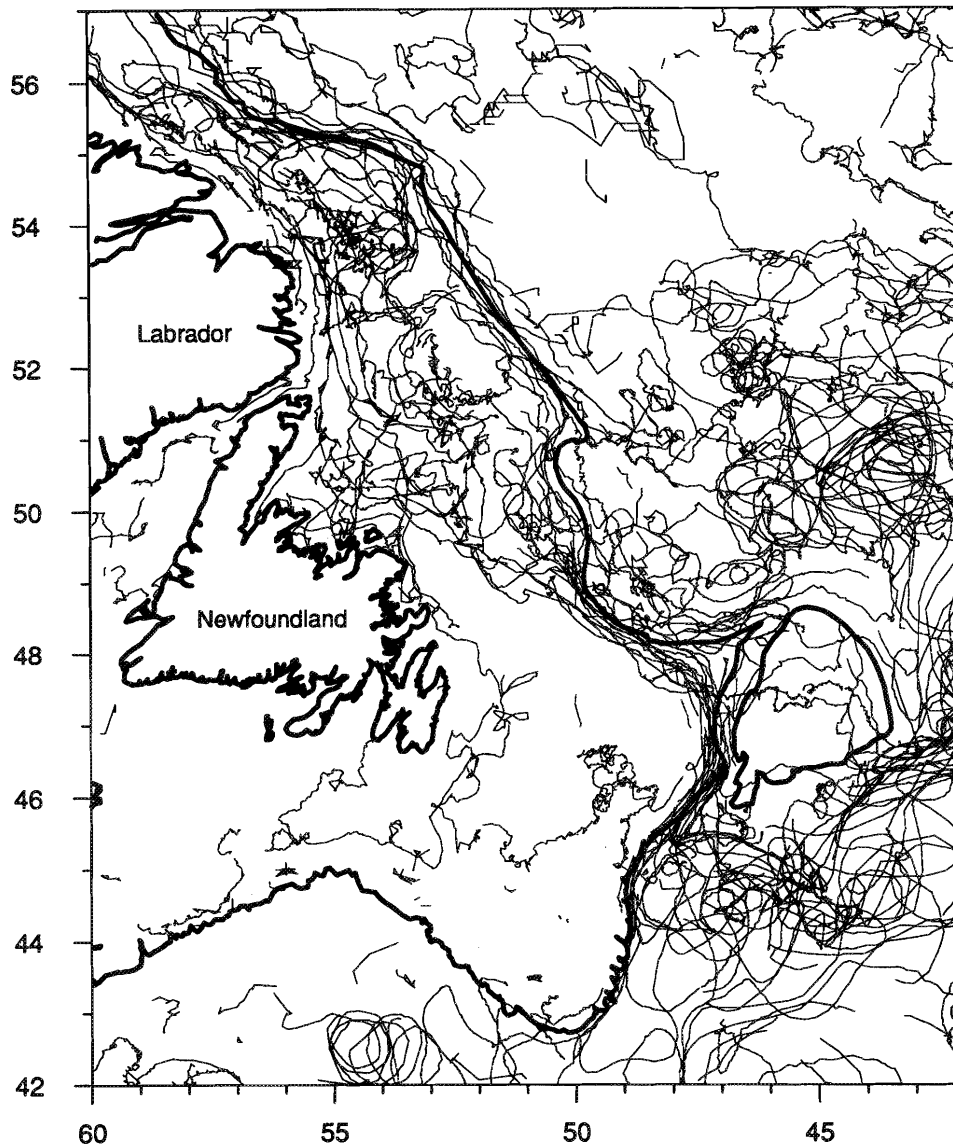


FIG. 6. Trajectories of satellite-tracked drifter buoys off Newfoundland and Labrador. The bold line represents the 1000-m depth contour. Most of the buoys were released on the shelf and slope off Labrador and northeastern Newfoundland; thus the general direction of water flow is from northwest to southeast along the continental slope. Redrawn from Helbig et al. (1992).

Conception, Notre Dame, and White bays. Given the efficient capture of spawning cod inshore by research gill nets (cf. Table 2), questions are raised regarding the degree to which the dramatic rise in the commercial use of gill nets in the early 1960s (Templeman 1966, fig. 19) was responsible for the decline in cod stocks in inshore waters since that time. This is particularly relevant given that, in a mixed-population (or species) fishery, those populations with comparatively high catchability become progressively depleted through time (Clark 1985). The existence of inshore populations and their potential importance to recruitment to the fishery warrant study.

#### A Historical Review of Cod Spawning Locations in the Newfoundland – Labrador Region

A historical review of the data on cod spawning locations suggests that our data are consistent with information compiled over the past century and that the perception that cod spawn pri-

marily on the slope, perpetuated since the early 1960s, can be attributed primarily to biased sampling.

The first reported spawning locations of cod off Newfoundland and Labrador were inshore areas. Harvey (1891, p. 6) noted that cod could be produced at the newly constructed hatchery at Dildo, Trinity Bay, by crossing “the smaller fish of Trinity Bay” with those near Cape St. Mary “where the largest and finest spawning fish are found early in the season.” In fact, broodstock for the hatchery (1890–97) were regularly obtained from the head of Trinity Bay where mature spawning fish “were found in abundance all round Dildo Island” (Nielsen 1895, p. 28) and were collected occasionally from nearby Bull Arm (Nielsen 1894). With regard to the timing of reproduction, Nielsen (1889, cited in Graham 1922) reported that “only during May and June can spawning cod be obtained...in Placentia, Trinity or Conception Bays.” Graham (1922) provided limited evidence of spawning cod immediately off St. John’s in July and noted the

dearth of research on the spawning of cod inshore prior to 1922.

The first account of possible offshore spawning locations was derived from egg and larval surveys conducted during the Canadian Fisheries Expedition (Biological Board of Canada) in 1914–15 (Dannevig 1919). The area sampled covered much of St. Pierre Bank and the nearby slope. Dannevig (1919) reported the relative abundance of *Gadus* spp. eggs and cod larvae collected from surface hauls (10–15 min in duration) of a 1-m-diameter silk net. Eggs were found on St. Pierre Bank in late May – early June and in late July; larvae were collected primarily during the latter sampling period. Eggs were found over the slope during the former sampling period only.

Frost (1938) summarized the next attempt to identify spawning locations of cod off Newfoundland and Labrador. From 1931 to 1935, gadoid eggs and cod larvae were sampled with surface hauls of 2-m-diameter cheese cloth nets from southeastern Labrador, coastal Newfoundland, and from Grand Bank. Eggs and larvae were collected in abundance within 50 km of the coast in virtually all major bays and were evident throughout much of Grand Bank. Frost's (1938, p.14) conclusion that "some spawning probably occurs on all banks" and Thompson's (1943, p. 90) later interpretation of the same data that "a fair proportion of the total spawning takes place at no great distance from the coast" need to be tempered by the facts that eggs were not identified to species and that larvae may have drifted inshore from spawning locations further offshore.

The third research programme, and the one most influential on later accounts of spawning locations (e.g. Fitzpatrick and Miller 1979; Templeman 1981), was conducted by Soviet researchers. They collected juvenile and adult cod (1957–63) and eggs and larvae (1959–63) along transects which sampled the Newfoundland–Labrador slope far more effectively than the shelf (Serebryakov 1965, 1967). For example, from March to May 1962, the ratio of slope-to-shelf sampling stations off Newfoundland and Labrador increased from 1.3:1 in March and April to 7:1 in May (Serebryakov 1965). This period of ichthyofauna sampling (March–May) would exaggerate the importance of slope versus shelf spawning, and positively bias the importance of the Labrador slope as a spawning location for cod in Newfoundland waters. Myers et al. (1993) have recently documented geographical variation in the timing of cod spawning. A comparison of their estimates of the months in which spawning occurs with those in which the Soviet sampling was conducted reveals that Serebryakov (1965, 1967) would have sampled the Labrador and northeastern Newfoundland slopes during the peak spawning months for this area (March–May) but would have inadequately sampled Grand Bank shelf during 2 of 3 mo of peak spawning (April–June)

Serebryakov (1965, 1967) concluded that spawning took place primarily on the slope off Labrador and northeastern Newfoundland and secondarily on the slopes of Grand Bank. Based upon the locations of egg samples, estimates of current velocity, water temperature, and egg developmental stage duration, he constructed the first map to delineate the areas in which cod were thought to spawn. This figure, flawed by spatial and temporal sampling biases, was subsequently reproduced by Fitzpatrick and Miller (1979) and has provided the empirical basis for research atlases that are consulted for fisheries management (FAO 1981), the development of offshore oil production (e.g., McGuire 1978), and for models of cod recruitment (Myers and Drinkwater 1988, 1989; Helbig et al. 1992).

Prior to 1963, there had been no concerted attempt to

determine the spawning distribution of Newfoundland and Labrador cod by Canadian authorities (e.g., May 1959). It may be noteworthy that the first (and only) cruises with an objective of determining cod spawning times and locations in this region encompassed the 1962 dates of 14–18 April in which Serebryakov (1965, p. 425) reported "large quantities of eggs... on the boundary between central and north Labrador waters on the slope of the shelf over depths 380 to 450 m." The Canadian cruises (*A.T. Cameron* Cruise Reports 68 and 69) of 6–9 April and 30 April – 14 May 1963 were conducted in the same region sampled by the Soviets and also located "large concentrations of spawning and post-spawning cod on the extreme eastern slope of [Hamilton] bank" (Templeman and May 1965, p. 149), although a cruise the following year during the same time period, and sampling the 1963 stations, yielded few spawning or post-spawning individuals (Templeman 1965; *A.T. Cameron* Cruise Report 84). Tagging cruises conducted off Grand Bank in 1964 and 1965 yielded spawning cod on the northeastern, southeastern, and southwestern slopes (*A.T. Cameron* Cruise Reports 85, 102, and 103, respectively); these sampling areas corresponded to those described as "intensive" spawning areas by Serebryakov (1967). Finally, with respect to the perceived importance of the Hamilton Bank slope as the primary cod spawning location, it should be noted that Serebryakov's (1965) totals (pooled for two stations at each location) of 1020 and 650 eggs from the extreme northeastern Labrador slope and the Hamilton Bank slope, respectively, are considerably less than the maximum number of eggs ( $n = 1334$ ) caught in a single haul on St. Pierre Bank in 1914 (Dannevig 1919).

In summary, spawning cod can be found throughout the continental shelf and slope although, with the exception of southeastern Labrador, a small section of northern Grand Bank, and Flemish Cap, spawning occurs primarily on the shelf. The preponderance of shelf spawning is consistent with the hypothesis that cod spawn in areas in which their eggs and larvae are likely to be retained. Our review suggests that there have been historical shifts in the perceived importance of various spawning locations and that the predominant view of the past 30 yr — offshore spawning being more important than inshore spawning; slope spawning being more prevalent than shelf spawning — lacks empirical support. The absence of representative sampling from the shelf during the years in which present opinions of spawning locations were being formed, and the apparent identification of the slope as the main location of spawning cod in 2J3KL (Templeman 1965; Serebryakov 1965, 1967) appear to be the primary reasons underlying the general belief that cod spawn predominantly on the slope and do so largely east of the Hamilton Bank (e.g., Fitzpatrick and Miller 1979; Templeman 1981; Helbig et al. 1992). Based upon our analysis of all available data, we conclude that offshore spawning occurs primarily on the shelf, particularly off northeastern Newfoundland and on Grand Bank, and that, given the historical consistency of evidence of inshore spawning, coastal populations of cod exist and may have provided a considerably larger contribution to recruitment than has previously been believed.

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