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

by

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Abstract

We analyzed 47 years (1946-92) of research trawl data and 5 years (1964-68) of research gillnet data to identify offshore and inshore spawning locations of Atlantic cod, *Gadus morhua*, in the Newfoundland-Labrador region. Spawning cod have been captured offshore throughout the continental shelf and slope. When corrected for spatial variation in trawling effort, spawner abundance is common on the shelf but generally rare on the slope. The relative abundance of spawning individuals on the shelf is highest (i) off northeast Newfoundland, (ii) within 100 km of the Newfoundland coast from Cape Freels to Cape Race, (iii) on the central Grand Bank, and (iv) on St. Pierre Bank. Slope spawning is largely restricted to the eastern slopes of Hamilton Bank and Funk Island Bank. Spawning is also evident within 10 km of the coast in eastern Newfoundland and southeastern Labrador. Inshore concentrations of spawning fish are particularly high 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 the Grand Bank and much of the northeastern Newfoundland slope will be transported into shelf and coastal waters. The observed 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. We conclude that Atlantic cod in the Newfoundland-Labrador region spawn primarily on the northeastern Newfoundland shelf, the Grand Bank and the eastern slope of Hamilton Bank, and that inshore spawning may provide a considerably larger contribution to cod recruitment in coastal Newfoundland than has previously been believed.

Introduction

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 juvenile survival (the primary correlate of adult recruitment) cannot be fully assessed. In the northwest Atlantic off Newfoundland and Labrador, the 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 by Templeman (1965) in the early 1960s, 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 those currently accepted as the major spawning locations of cod in the Newfoundland-Labrador region (e.g. Templeman 1981; Helbig et al. 1992). 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 undoubtedly be lost to the population(s).

Our first objective is to address the obvious inconsistency that underlies the reported spawning areas and the predicted trajectories of egg and larval transport. We combine all available 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 which describe the relative abundance of spawning individuals in the Newfoundland-Labrador region. Our third objective is to collate all available research data on spawning cod in coastal areas to assess the prevalence of inshore spawning. Finally, we include a review of extant research spawning records of cod off Newfoundland and Labrador to assess our results within appropriate historical and biological contexts.

Materials and Methods

Offshore Region

Offshore spawning locations were determined from research trawl data collected from 1946-1992 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 the Grand Bank (3LNO), Flemish Cap (3M), and St. Pierre Bank (3Ps) in the south (cf. Fig. 1). We included only those fish deemed to be in spawning condition. Reproductive status 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 days of hydration (Kjesbu 1988), the collection locations of females containing hydrated eggs should closely approximate spawning locations. Males were defined as spawning individuals if their testes and vas deferentia were white and not depleted of milt. Spent individuals were excluded to ensure that capture locations were representative of spawning locations (spent fish may have migrated from their spawning area to the place of capture). These individuals were identified as follows: the ovaries of spent females are whitish-grey or bluish-grey, slack and often wrinkled, residual eggs may be present; the testes of spent males are grey or pink and milt is not evident in the outer edges at the time that all females are spent. 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, 3K not at all).

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 anaylsis 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 conducted in a given unit area during the four primary months in which 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. The number of spawning fish per trawl will, of course, be related to population density. 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 affected the catch in some manner) or fished at depths greater than 500m (below which cod are generally not found, e.g. Baird et al. 1992) were also excluded from the analysis. A total of 8657 trawls met these criteria and were included in the analysis. The size of the unit areas depended upon the region and was designed to maximise the number of trawls per 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 the sampling of spawning cod in the north. Thus, unit areas were relatively small but numerous in the south, being 0.5° latitude X 0.5° longitude on the Grand Bank (n=77, 31, and 31 unit areas in 3L, 3N, and 3O, respectively), St. Pierre Bank (n=29 in 3Ps) and Flemish Cap (n=18 in 3M) (Fig. 2). Unit areas were larger in the north (1° latitude X 1° longitude) and fewer in number (n=14 and 13 in 3K and 2J, respectively). Unit areas in which the number of trawls was less than 10 were not included in the analysis (Fig. 2). This criterion removed 7.5% (n=16) of the unit areas.

We assume that sampling efficiency was similar among research vessels. This assumption is a reasonable one. Of the 6 ships whose trawls were included in the analysis, 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*. Of the remaining ships, the *Investigator II* and *Northern Kingfisher* contributed 212 and 46 trawls, respectively, which represents only 3% of the total number of trawls in the analysis. In addition, neither the months in which the trawls were conducted nor the average number of spawning females per trawl have changed dramatically through time.

The relative abundance of spawning cod on the shelf and the slope was compared with a oneway 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 gill net surveys in southeastern Newfoundland. From 1964-66, the Fisheries Research Board of Canada conducted experimental gill net surveys at two stations in St. Mary's Bay (Colinet Island and Broad Cove) and at two stations in Placentia Bay (Merasheen and Woody Point). Additional gill net 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 1968 (1 and 2)). The gill nets measured 91.4 m in length and contained mesh sizes of 6" (Trinity and Bonavista bays), 6.5" (St. Mary's and Placentia bays) or 7" (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 employed. The relative abundance of spawning cod among bays was compared with a oneway ANOVA and statistical significance with 1000 data randomizations. Maturity data on inshore cod were also obtained from samples collected by research otter trawls and jiggers, and by commercial gill nets off Cape Bonavista in 1983 and 1984.

Results

Offshore Spawning

Spawning cod have been captured throughout the continental shelf and slope of Newfoundland and Labrador (Fig. 3). Shelf spawning is evident on Flemish Cap and on all banks with the possible exception of a corridor extending from St. Mary's Bay east of St. Pierre Bank. The lower concentration of 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 upon the shelf (Fig. 4). Labrador shelf spawning was most evident on southeastern Hamilton Bank and Belle Isle Bank while spawning occurred throughout the northeastern Newfoundland shelf. Off eastern Newfoundland, spawner abundance was highest from Cape Freels to Cape Race within 100 km of the coast and in the central portion of the Grand Bank. Throughout the Grand and St. Pierre banks, spawning fish were encountered more frequently on the shelf than on the slope. The relative abundance of slope spawners was high in only one region. Reproductive individuals were more abundant on the eastern slope of Hamilton Bank in 2J than they were further inshore. The mean relative abundance of spawning cod in unit areas located on the shelf (mean$\pm$SD: 0.59$\pm$0.70, n=150) exceeded the mean for unit areas located on the slope (0.44$\pm$0.59, n=46) although the difference was not significant ($F_{[1,194]}$=1.78, p=0.176). However, when 2J was excluded from the analysis, the relative abundance of shelf spawners (0.57$\pm$0.68, n=145) was almost 70% greater than that of slope spawners (0.34$\pm$0.32, n=43) and the difference was significant ($F_{[1,186]}$=4.81, p=0.026).

Inshore Spawning

Spawning cod were captured throughout the coastal regions of southeastern Newfoundland, and in southeastern Labrador and northern Newfoundland (Fig. 5). The experimental gill net 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 comprised of spawning individuals was higher in the May/June sampling period than it was during the April/May period. The relative abundance of spawning cod (measured as the number of fish per gill net) did not differ significantly among bays (mean$\pm$SD: 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 high standard deviation associated with the mean for St. Mary's Bay can be attributed to the extremely high value of 67.5 fish per net in 1964. When this value was excluded, the mean for St. Mary's Bay decreased to 5.8 $\pm$ 4.3 and the mean abundance among bays remained insignificant ($F_{[3,15]}$=1.60, p=0.236).

Spawning individuals were included in the sample of cod collected from commercial gill nets fishing immediately off Cape Bonavista in May-July 1983 and 1984. Although the

gonads of these fish were not examined to determine the state of maturity, the spawning condition of these fish can be assessed with an index which reflects the proportional allocation of body tissue to gonads. In the absence of data on body weight, we divided gonad weight by (length)^3 and compared the value of this index for the fish sampled by the commercial nets with the mean value for fish known to be in spawning condition in 3L (0.143 ± 0.060, n=275, including all research data from 1946-92). Of the 315 female cod sampled in May-July 1983 and 1984, the gonad index of 21% of the fish encompassed 1SD of the mean value of spawning cod in 3L.

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 thought (Serebryakov 1965, 1967; Fitzpatrick and Miller 1979; Templeman 1965, 1981), 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 highest: (i) off northeast Newfoundland, (ii) within 100 km of the Newfoundland coast from Cape Freels to Cape Race, (iii) on the central Grand Bank, and (iv) on St. Pierre Bank. Slope spawning is largely restricted to the eastern slope of Hamilton Bank. 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. Experimental observations (Brawn 1961) indicate that cod undergo vertical movements in the water column during spawning and may not, therefore, be caught efficiently in bottom trawls. Secondly, the numbers of females classified as in spawning condition, i.e. as containing hydrated eggs, may have been underestimated. Kjesbu (1988) reported that eggs in 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 should avoid spawning on the slope, particularly off the Grand Bank, because of the high probability that the eggs will be transported away from the banks. Spawning should 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 which 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 the Grand Bank indicate that eggs spawned in these regions will be retained on the shelf. Our data, in conjunction with the drifter trajectory routes, are consistent with Iles and Sinclair's (1982) hypothesis that the spawning locations of marine pelagic fish are dependent on the geographic extent of oceanographically predictable larval retention areas.

Variability in Spawning Distributions: Evidence of Offshore and Inshore Stocks

Variability in the distribution of spawning individuals may reflect reproductive isolation among genetically differentiated populations or stocks. The spatial distribution of reproductive cod described here might indicate the existance of four such populations on a large scale: a Labrador-northeastern Newfoundland stock, a Grand Bank stock, a St. Pierre Bank stock, and possibly a Flemish Cap stock (cf. Fig. 4). These geographical divisions are consistent with those suggested by Templeman (1962), based on variation in vertebral numbers and migration studies and with the 2J3KL and 3NO stocks identified by Helbig et al. (1992) based on 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 can prevent

comprehensive sampling during spawning. Our conclusion that these spawning inshore cod have not migrated from offshore areas is supported by unpublished data collected by G.A. Rose (Fisheries and Oceans, P.O. Box 5667, St. John's, NF A1C 5X7). For several years, Rose has monitored a group of cod migrating from the slope to inshore bays off Cape Bonavista and has found that while spawning occurs throughout the migration, most fish are spent by the time they approach the coast. Thus, the presence of spawning fish in coastal bays is probably indicative of inshore populations, whose existence was also postulated by Templeman (1966). Evidence of inshore cod populations also exists in Nova Scotia (McKenzie 1940) and Norway (cf. 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 Conception, Notre Dame and White bays. The efficiency with which the research gill nets caught spawning cod inshore (cf. Table 2) also raises serious questions regarding the degree to which the dramatic rise in the commercial use of gill nets in the early 1960s (Templeman 1966; Fig. 19) contributed to the decline in cod stocks in inshore waters in recent years. The potential importance of inshore populations to recruitment to the fishery warrants 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 of the early 1960s that cod spawn primarily on the slope can be attributed primarily to biassed sampling.

The first reported spawning locations of cod off Newfoundland and Labrador were inshore areas. Harvey (1891:6) 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 (1890-1897) were regularly obtained from the head of Trinity Bay where mature spawning fish "were found in abundance all round Dildo Island" (Nielsen 1895:28) and were collected occassionally from nearby Bull Arm (Nielsen 1894). With regard to the timing of reproduction, Nielsen (1889) 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. 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 atempt to identify spawning locations of cod off Newfoundland and Labrador. From 1931-1935, gadoid eggs and cod larvae were sampled with surface hauls of 2 m diameter cheese cloth nets from southeastern Labrador, coastal Newfoundland and from the 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 the Grand Bank. Frost's (1938:14) conclusion that "some spawning probably occurs on all banks" and Thompson's (1943:90) 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 who collected cod (1957-63) and eggs and larvae (1959-1963) 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). The sampling period of ichthyofauna (March, April, May) introduces a second bias that would 1) exaggerate the importance off slope versus shelf spawning, and 2) 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 Russian 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 the Grand Bank shelf during 2 of its 3 months 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 the 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 biasses, 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 not be coincidental that the first (and only) cruises whose objectives included the determination of cod spawning times and locations in this region encompassed the 1962 dates of 14-18 April in which Serebryakov (1965:425) reported "large quantities of eggs...on the boundary between central and north Labrador waters on the slope of the shelf over depths from 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 1965:149), although a cruise the following year during the same time period, and sampling the 1963 stations, did not yield the large quantities of spawning fish captured the previous year (Templeman 1965). Tagging cruises conducted off the 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).

Summary

Spawning cod can be found throughout the continental shelf and slope although, with the exception of southeastern Labrador, 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 (offshore spawning being more important than inshore spawning; slope spawning being more important than shelf spawning) and that these shifts have not been accompanied by empirical data. The absence of representative spawning 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 on careful analysis of all available data, we conclude that offshore spawning occurs primarily on the shelf, particularly off northeastern Newfoundland and on the Grand Bank and St. Pierre Bank, and that, given the historical consistency of evidence of inshore spawning, coastal populations of cod exist and may provide a considerably larger contribution to recruitment than has previously been believed.

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Table 1. Research vessels and years in which otter trawls were employed, 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	*Investigator II*
	1962-64, 66, 69-71, 73-74	*A.T. Cameron*
	1978-79, 81-83, 86-92	*Gadus Atlantica*
	1991	*Alfred Needler*
	1992	*Northern Kingfisher*
3K (northeastern Newfoundland)	1963-64, 69-71, 74	*A.T. Cameron*
	1978-83, 85-91	*Gadus Atlantica*
	1992	*Northern Kingfisher*
3L (incl. northern Grand Bank)	1946-48, 50-51, 53	*Investigator II*
	1959, 61, 63-78, 80-82	*A.T. Cameron*
	1979-80, 84-90	*Gadus Atlantica*
	1983-92	*Wilfred Templeman*
	1984	*Alfred Needler*
3M (Flemish Cap)	1961, 64, 68, 77	*A.T. Cameron*
	1978-85	*Gadus Atlantica*
3N (southeastern Grand Bank)	1946-48, 50-53, 56-59	*Investigator II*
	1959-62, 64-82	*A.T. Cameron*
	1984-85	*Alfred Needler*
	1985-92	*Gadus Atlantica*
3O (southwestern Grand Bank)	1946-48, 51-52, 55-59	*Investigator II*
	1959-62, 64-66, 68, 71, 73, 75-82	*A.T. Cameron*
	1984-85	*Alfred Needler*
	1985-91	*Gadus Atlantica*
3Ps (St. Pierre Bank)	1947-48, 50-51, 53-54, 56-60, 63, 65	*Investigator II*
	1960, 62, 64, 67-70, 72-82	*A.T. Cameron*
	1984-85	*Alfred Needler*
	1985-87	*Wilfred Templeman*
	1986	*Gadus Atlantica*

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 date	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
Merasheen, 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

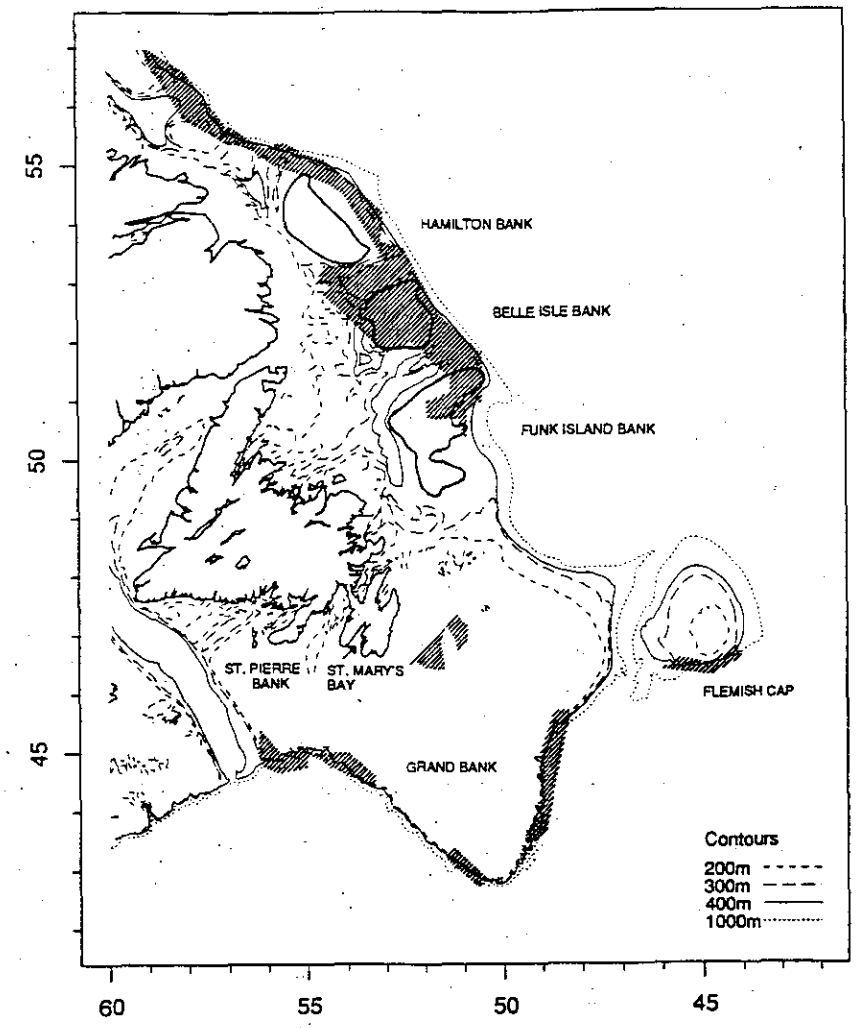

Figure 1. Spawning locations (hatched areas) of Atlantic cod identified by Fitzpatrick and Miller (1979) off Newfoundland and Labrador. Hamilton, Belle Isle and Funk Island banks are delineated along their respective 200m (Hamilton Bank) and 300m depth contours.

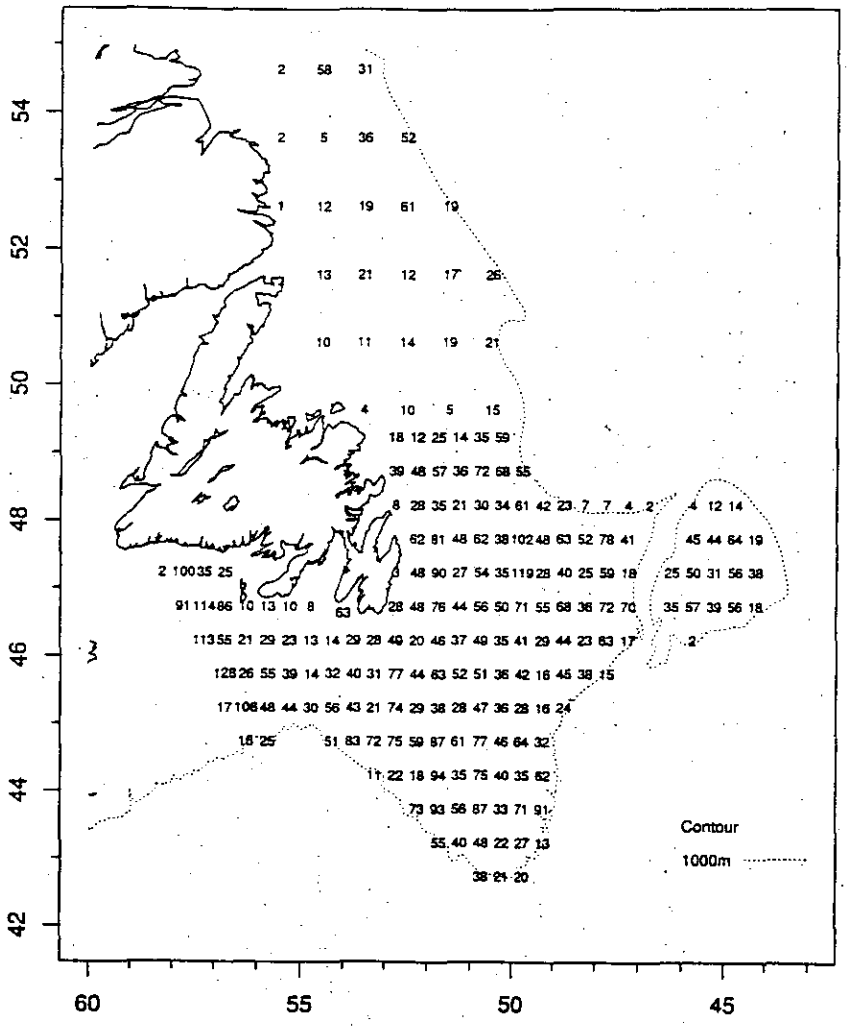

Figure 2. Number of research otter trawls conducted from 1946-1992 during potential cod spawning periods within unit areas of the continental shelf and slope off Newfoundland and Labrador (the sizes of the unit areas and the potential spawning periods specific to different regions, are described in the text).

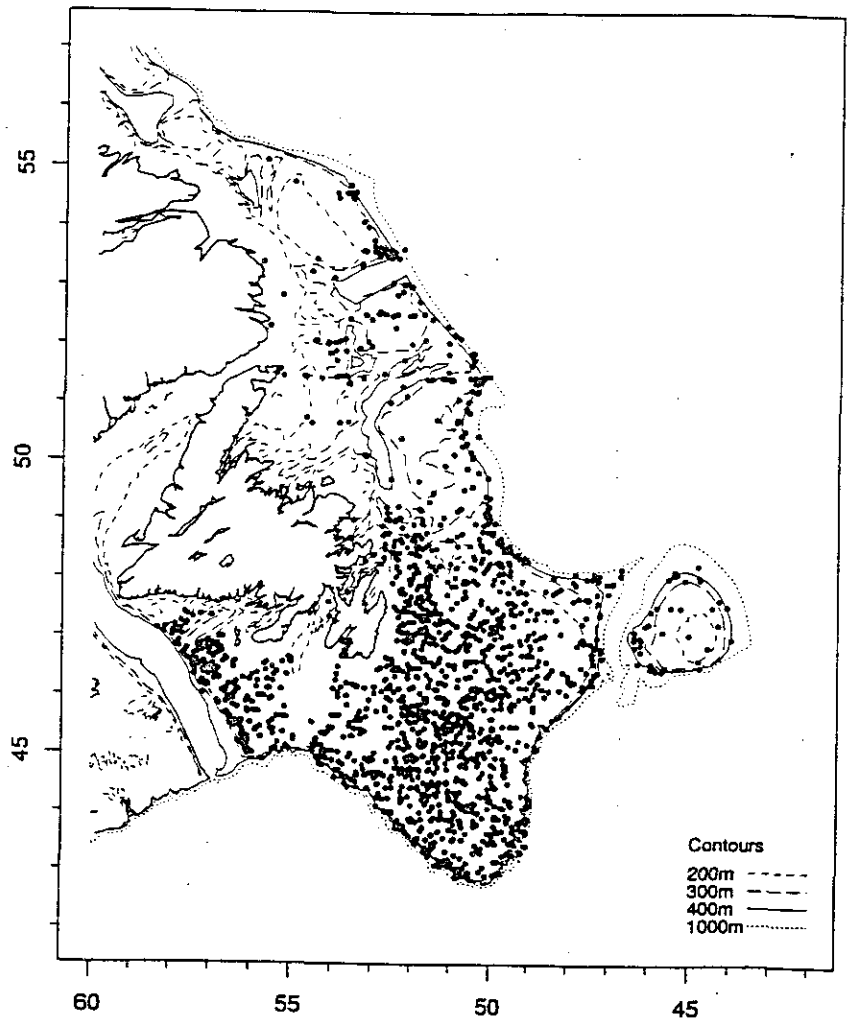

Figure 3. The locations of Atlantic cod (male and female) in spawning condition sampled by research trawls, gill nets and jiggers from 1946-1992 off Newfoundland and Labrador.

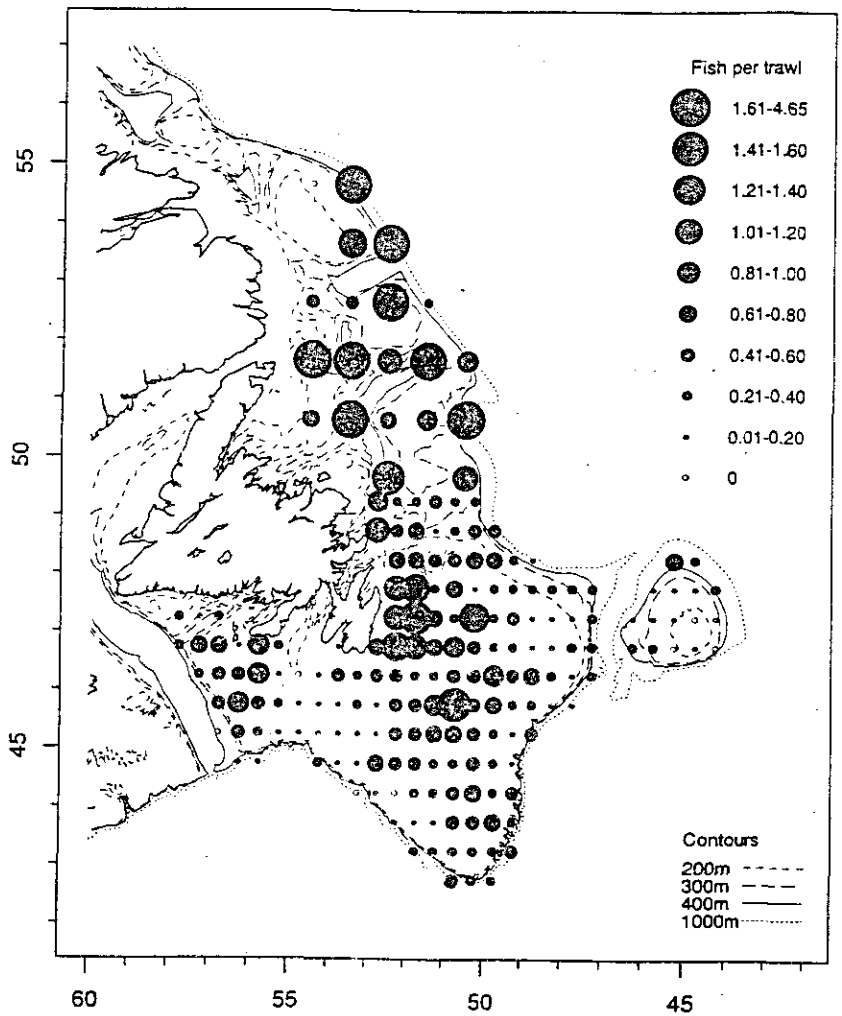

Figure 4. The relative abundance of spawning Atlantic cod (sexes combined) on the continental shelf and slope off Newfoundland and Labrador. The circles represent the total number of spawning fish caught per unit area divided by the total number of research otter trawls conducted in each area during potential spawning periods (see text) from 1946-1992.

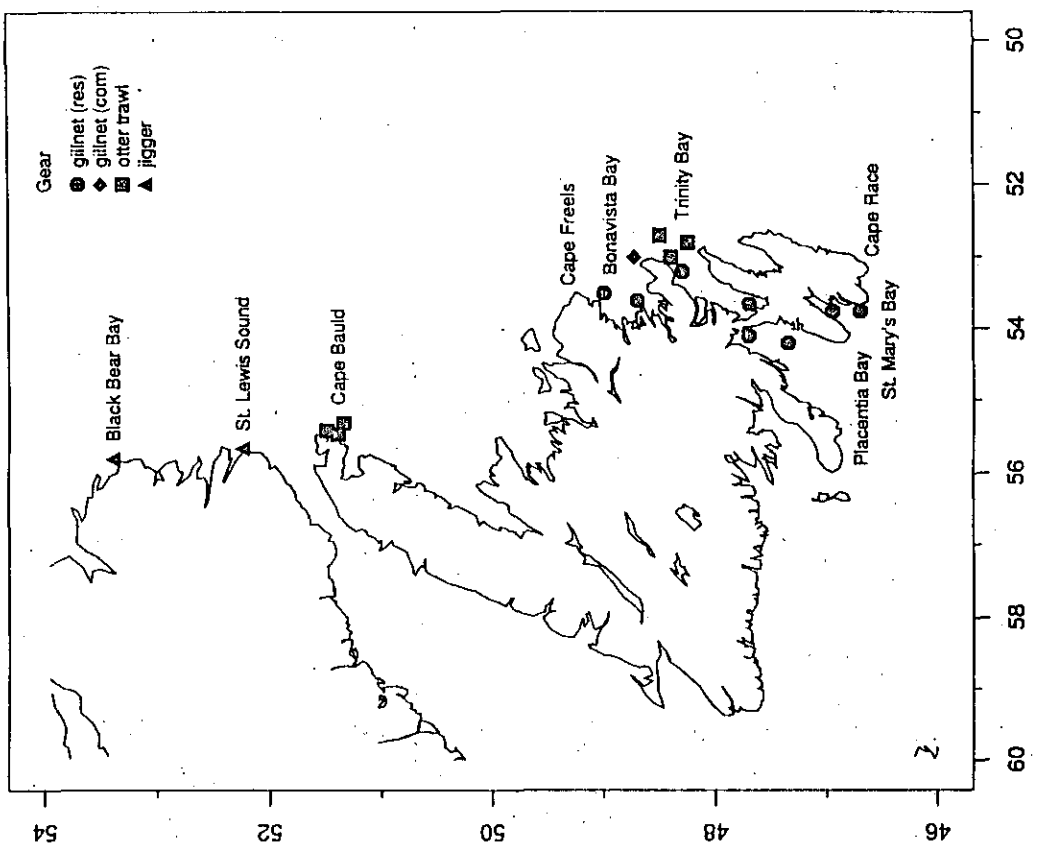

Figure 5. Locations of spawning Atlantic cod (sexes combined) sampled by gill nets (primarily research), research otter trawls, and research jiggers in coastal Newfoundland (1946-1992).

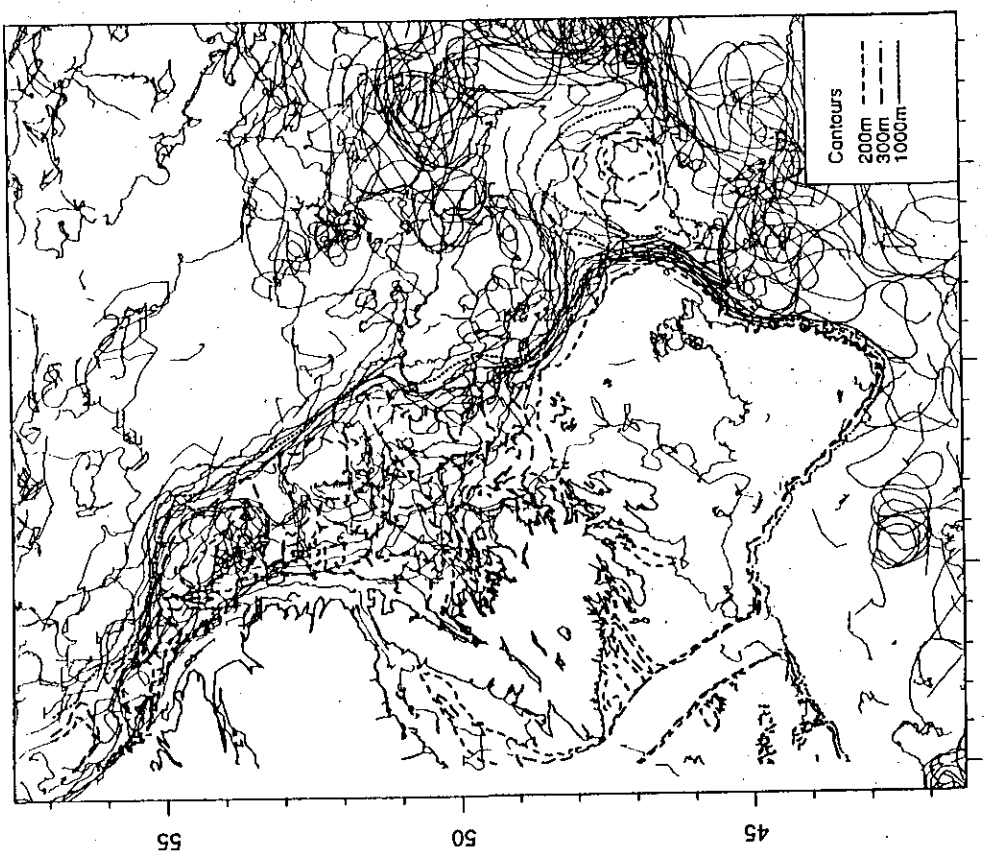

Figure 6. Trajectories of satellite-tracked drifter buoys off Newfoundland and Labrador. Most of the buoys were released on the shelf and slope off Labrador and northeastern Newfoundland. Re-drawn from Helbig et al. (1992).