

Bank-Scale Migration Patterns in Northern Cod

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Abstract

Proper resolution of population structure is necessary not only for the interpretation of temporal and spatial variations in the biology of a species, but also for successful management. This is particularly true for the seriously depleted northern cod (*Gadus morhua*) stock complex (NAFO Divisions 2J, 3K, and 3L). In this paper, data collected over the last three decades from tagging studies conducted in winter on Hamilton and Belle Isle Banks and in the North Cape region of the northern Grand Bank, are employed to assess migration patterns in northern cod and to compare those patterns to the population structure described in recent genetic studies conducted on populations from the same regions. The results reveal that the average geographic distribution of cod tagged in the vicinity of Hamilton Bank in winter overlaps in the offshore winter distribution with those tagged on Belle Isle Bank, showing the populations can intermingle during the offshore spawning period. The average geographic distribution of cod tagged in winter in the North Cape region did not overlap with those fish tagged on either Hamilton or Belle Isle Bank. Likewise, the average winter distributions of cod from the latter two banks did not overlap with those from the North Cape area. These results are entirely consistent with recent and earlier genetic studies of populations from the same regions and suggest that the northern cod stock complex is comprised of at least two discrete offshore populations. The results from this study are used to present a testable hypothesis to explain anomalous distributions in recent years for northern cod in the offshore and inshore areas of Newfoundland.

Keywords: cod, migration, NW Atlantic, stock structure, tagging

Introduction

Proper resolution of population structure in exploited fish species is necessary not only for the interpretation of temporal and spatial variations in the biology of the species but also for successful management (Angel *et al.*, 1994). These issues are exemplified by the seriously depleted (Shelton *et al.*, MS 1996) northern cod (*Gadus morhua*) stock complex in NAFO Div. 2J, 3K and 3L.

Although the distribution and migration patterns of northern cod are recognized as complex, it is generally understood, at least historically, that most mature northern cod overwinter along the edge of the continental shelf where spawning occurs over a 3–4 month period from winter through early-summer (Myers *et al.*, 1993), although spawning also occurs on the interior and landward margins of offshore banks (see review in Taggart *et al.*, 1994). It is also known that some northern cod remain inshore all winter, relying on serum antifreeze proteins to survive in cold ($<0^{\circ}\text{C}$) coastal waters (Goddard *et al.*, 1994) and that these fish appear genetically dissimilar from those fish overwintering offshore (Ruzzante *et al.*, 1996, 1997). In general, cod that have overwintered and spawned offshore migrate inshore in the spring to coastal feeding grounds and then return offshore in late-autumn and early-winter (Templeman, 1966).

Bentzen *et al.* (1996) have briefly reviewed the biological and genetic basis of population structure within the northern cod complex which are equivocal in their implications. On the one hand, geographic surveys (e.g. Hutchings *et al.*, 1993), vertebral data (Templeman, 1981; Lear and Wells, 1984) and tag recovery data (Templeman, 1974 and 1979; Lear, 1984; reviewed in Lear and Green, 1984; and in Taggart *et al.*, 1995) all suggest that northern cod are divided into several distinct offshore spawning units. In particular, cod-tagging studies have provided evidence of population fidelity to particular overwintering/spawning areas on offshore banks and in some inshore bays, as well as evidence of vagrant movements among these areas (Lear, 1984; Taggart *et al.*, 1995; Wroblewski *et al.*, 1996). Thus far, evidence of population structure gained from genetic studies of northern and other western Atlantic cod has been mixed and subjected to various interpretations (see Bentzen *et al.*, 1996). On the other hand, in that same paper, Bentzen *et al.* (1996) report on polymorphism at six microsatellite loci in northern cod sampled from offshore overwintering/spawning locations spanning their range from the northern Grand Bank northwest to Hamilton Bank off Labrador, and they describe evidence that offshore northern cod may comprise more than one population. In particular they show that within the northern cod complex two pooled samples, NORTH consisting of Hamilton, Funk and

Belle Isle Banks) and SOUTH (consisting of northern Grand Bank area including the North Cape area), were distinguishable from each other using a variety of genetic measures applied to the microsatellite data.

In this paper, cod tagging data from Taggart *et al.* (1995) are employed to assess migration patterns in northern cod and to compare those patterns to the population structure described in Bentzen *et al.* (1996). This is achieved using a compilation of tagging experiments conducted over the last three decades in the Hamilton Bank and Belle Isle Bank regions (equivalent to NORTH in Bentzen *et al.*, 1996) and in the North Cape region of the Grand Bank (equivalent to SOUTH in Bentzen *et al.*, 1996).

Methods

Cod tagging data were extracted from the tagging data base described in detail in Taggart *et al.* (1995). Only those tagging experiments that occurred offshore during winter (February to May) on any of Hamilton Bank, Belle Isle Bank, or in the North Cape region of the northern Grand Bank were used for the analyses reported here (Table 1).

For each region/experiment, the latitude and longitude of the tagging location and the reported recapture dates and locations were used to assess

the migration pattern relative to the marking location for each of the three regions. The reported recapture location data in these analyses are resolved at 30 naut. miles (i.e. reported recaptures within a 30'N by 60'W Newfoundland grid area are assigned the latitude $\pm 15'$ N and longitude $\pm 30'$ W of the grid area centroid as the recapture location (see Taggart *et al.*, 1995). These data were ordered sequentially with respect to the recapture date, from earliest to latest, and then the dates and recapture latitudes and longitudes were "smoothed" using a 15-point, uniformly weighted, moving average to calculate the average position of the tagged population on the *average* date of recapture. The standard error around the moving average location was calculated in a similar manner. These data were then employed for each region/experiment to assess the frequency and amplitude of migrations relative to the tagging location.

To estimate the overall annual average pattern of migration ("the normal") for each of the three major regions of tagging, each of the experiments within a region, and regardless of year of tagging, were pooled and then ordered according to the day of the year (1 to 365) of reported recapture. As described above, a 15 point moving average was used to estimate the average location and the standard error around the average throughout the *normal* year. As the number of reported recaptures ranged from about 600 (North Cape) to about 1 500

TABLE 1. Summary of the cod tagging studies used for assessing bank-scale migration patterns in northern cod, during winter only (February to May). Details for each study are provided in Taggart *et al.* (1995).

Experiment number	Year tagged	Location (region)	Latitude ($^{\circ}$ N)	Longitude ($^{\circ}$ W)	Number tagged	Number recaptured	% recaptured
6404	1964	Hamilton Bank	53.5	53.3	1 152	186	16.1
6601	1966	Hamilton Bank	54.9	54.9	1 120	300	26.8
8103, 8104	1981	Hamilton Bank	54.7, 53.4	54.0, 53.2	3 766	450	11.9
8202, 8203	1982	Hamilton Bank	54.7, 53.2	53.7, 52.4	3 160	761	24.1
Overall		Hamilton Bank	54.1	53.6	9 198	1 697	18.4
7801	1978	Belle Isle Bank	52.1	51.8	4 456	843	18.9
8303	1983	Belle Isle Bank	52.1	52.5	3 142	562	17.9
Overall		Belle Isle Bank	52.1	52.2	7 598	1 405	18.5
8003	1980	North Cape	49.1	50.2	1 994	225	11.3
8206	1982	North Cape	49.2	50.6	492	33	6.7
8301, 8304	1983	North Cape	48.5	49.9	3 031	99	3.3
9001	1990	North Cape	49.2	50.1	2 447	115	4.7
9102	1991	North Cape	49.0	50.1	3 466	158	4.6
Overall		North Cape	48.9	50.1	11 430	630	5.5

Differential reporting of tags, and differential fishing effort, within or among tagging experiments, has not been incorporated into these analyses. However, as there was considerable overlap among the years of tagging and among the subsequent years of reported recapture among the three geographic regions (Table 2), particularly in the 1980s, differential fishing effort among regions was assumed to have been minimized (though not absent) at least as it relates to a first approximation for the interpretation of the results presented here.

The average tagging location in the North Cape region was approximately 360 naut. miles South-Southeast of the average tagging location on Hamilton Bank, and approximately 190 naut. miles South-Southeast of Belle Isle Bank, which is itself approximately 175 naut. miles South-Southeast of Hamilton Bank (Table 1).

The overall (normal) annual along-shelf (North–South) pattern of migration, as inferred by the tag return data, was variable through the year (Fig. 1A). In general, during the April through June period (days 90–180), the fish moved southward at the same time as moving landward in a cross-shelf di-

The overall annual normal pattern of cross-shelf migration (East–West) inferred from tag reporting showed the majority of fish located offshore in the vicinity of the tagging location during the winter period of January through April (days 0–120; Fig. 1B). Landward migration appeared to begin near the end of April (day 120) and lasted approximately two months through to the end of June (day 180). The fish remained inshore through to the end of day 270 (September) at which time there was a slow (relative to the landward migration in spring) seaward progression back toward the Bank.

During the winter spawning period, the across-shelf average distribution was of the order of 50 naut. mile (Fig. 1C). In contrast, the along-shelf average distribution was of the order of 175 nm (Fig. 1C) which just extended South–Southeast to the vicinity of Belle Isle Bank. The greater variation in the along-shelf distribution was shown by the larger standard error relative to the average which was of the order of ± 100 naut. mile compared to ± 25 naut. mile in the across-shelf distribution (Fig. 1A, B).

Year	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88
Location																									
Hamilton Bank	■	■	■	■	■	■																			
			■	■	■	■	■	■																	
																		■	■	■	■	■	■		
																				■	■	■	■	■	■
Belle Isle Bank															■	■	■	■	■	■					
																			■	■	■	■	■	■	■
North Cape of Grand Bank																		■	■	■	■	■	■		
																			■	■	■	■	■	■	
																				■	■	■	■	■	■

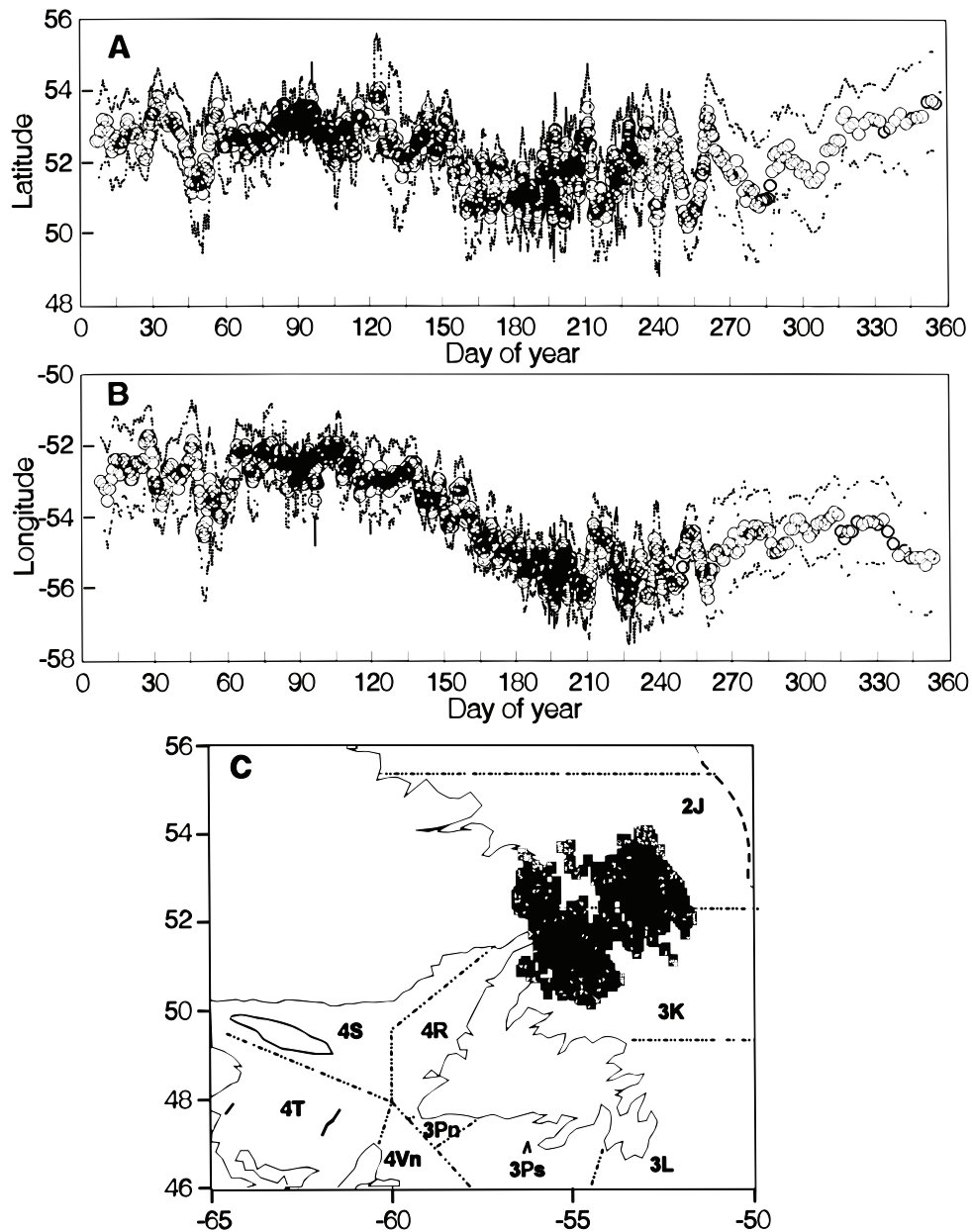


Fig. 1. Combined average (± 2 standard error) latitudinal (A) and longitudinal (B) and progressive vector (C) geographic positions of reported cod-tag returns as a function of day of the year from tagging experiments conducted on Hamilton Bank during the winter periods of 1964, 1966, 1981, and 1982. Data from Taggart *et al.* (1995).

Belle Isle Bank

Data from the two Belle Isle Bank tagging studies revealed an annual migrational pattern very similar to that seen for Hamilton Bank (Fig. 2). During winter (days 0–120; Fig. 2B) most fish were found in the vicinity of the offshore tagging location and began a landward migration in early May (day 120; Fig. 2A). The fish appeared to remain inshore during June through October (days 150–300) after

which they began a seaward migration (Fig. 2B). As seen for Hamilton Bank, the along-shelf variation (Fig. 2A) was greater than the across-shelf variation (Fig. 2B), and as well the landward migration was accompanied by a generally southward migration. Again, as seen with the Hamilton Bank study, after arriving at the coast there was a general northward migration along the coast before the fish moved offshore again for the winter (Fig. 2A). The

greater variation in the along-shelf distribution was shown by the larger standard error relative to the average when compared to the across-shelf distribution.

During the winter period the across-shelf average distribution was of the order of 50 naut. mile (Fig. 2C). In contrast, the along shelf mean distribution was of the order of 125 naut. mile (Fig. 2C), extending northward just to the southern limits of

Hamilton Bank but not southward to anywhere near the vicinity of the North Cape. However, as shown above, the offshore winter distribution of Hamilton Bank fish did extend to the Belle Isle Bank region.

It appears that the distributional patterns described above, particularly in winter and early-spring, were not overly influenced by data from the tags that were reported during the first three months immediately subsequent to tagging and release.

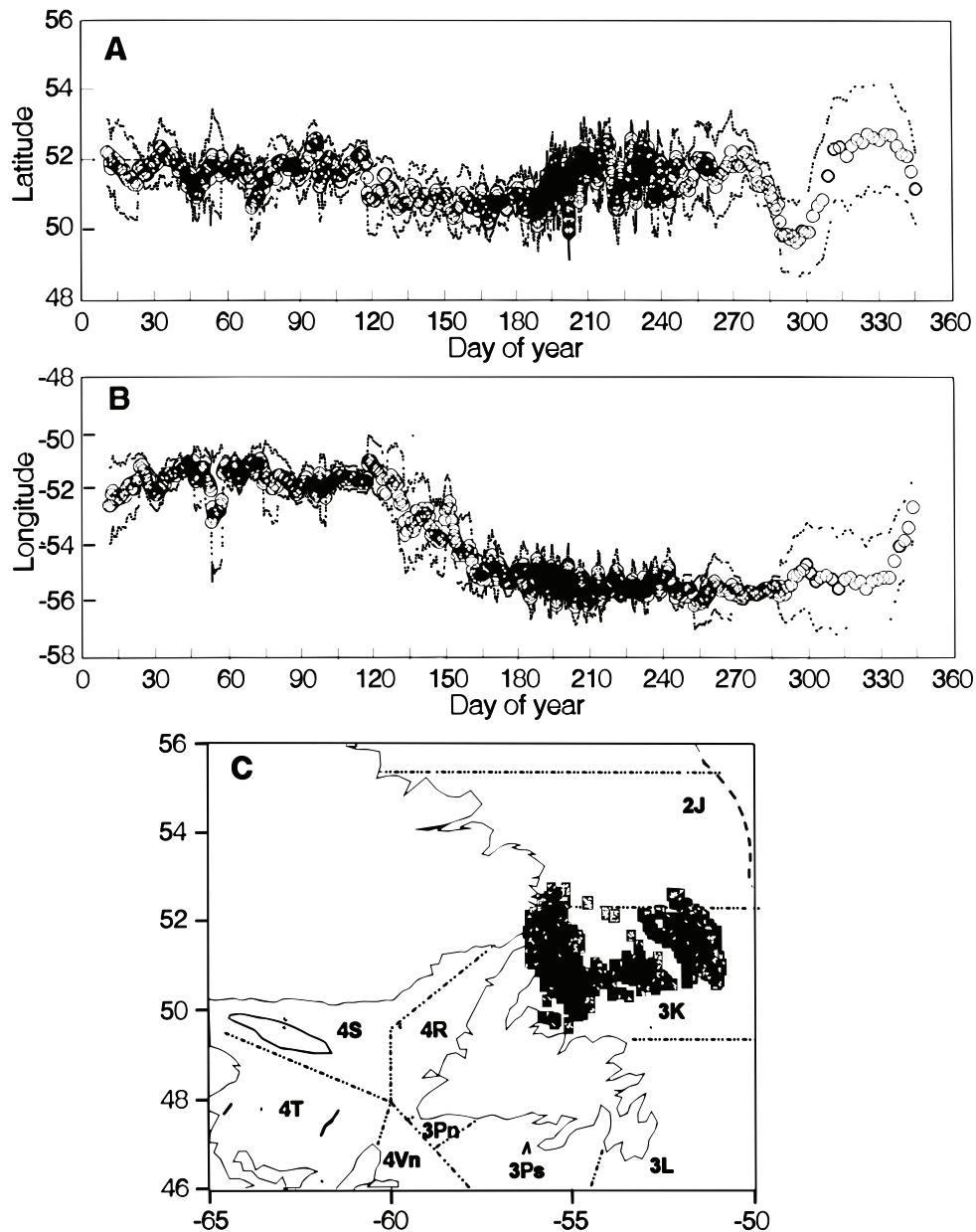


Fig. 2. Combined average (± 2 standard error) latitudinal (A) and longitudinal (B) and progressive vector (C) geographic positions of reported cod-tag returns as a function of day of the year from tagging experiments conducted on Belle Isle Bank during the winter periods of 1978 and 1983. Data from Taggart *et al.* (1995).

When the above analyses were repeated after removing the first three months of reported returns in each experiment, the same annual pattern of migration was revealed, although the standard errors were somewhat reduced (Fig. 3).

The well defined across-shelf annual cyclic pattern described in Figures 2 and 3 resulted from a pattern that was repeated among years within any given region. For example, in the Belle Isle Bank studies there was a very clear cross-shelf pattern of migration from year to year (Fig. 4) until the number of reported returns within a study were no longer sufficient to resolve the cycle (i.e. after 5 years). These results illustrate a clear tendency for a wintertime return to the general vicinity of the offshore tagging location during the spawning period. In this example, there was little evidence to suggest that fish were, on average, found more than 100 miles north of their original tagging location on Belle Isle Bank (Fig. 4A, B), though they appeared further toward the shelf-break during the winter in some years (Fig. 4B, D).

North Cape of the Grand Bank

The annual normal for cross-shelf migration inferred from recaptures of cod tagged in the North Cape region of the northern Grand Bank showed the majority of fish were located offshore in the vicinity of the tagging location during the winter period of January through April (days 0–120; Fig. 5), as seen for tagged populations in the other regions above. Landward migration appeared to begin near the end of April (day 120; Fig. 5B) and lasted, with some oscillations, for approximately two months through to the end of June (day 180). The fish remained inshore through to approximately day 270 (September; Fig. 5B) at which time there was a slow seaward progression back toward the shelf-break.

The along-shelf pattern of migration was much more variable through the year (Fig. 5A). However, in general during the April through June period (days 90–180), when the fish were moving landward, they were also moving southward followed by a generally northward, but oscillatory, movement

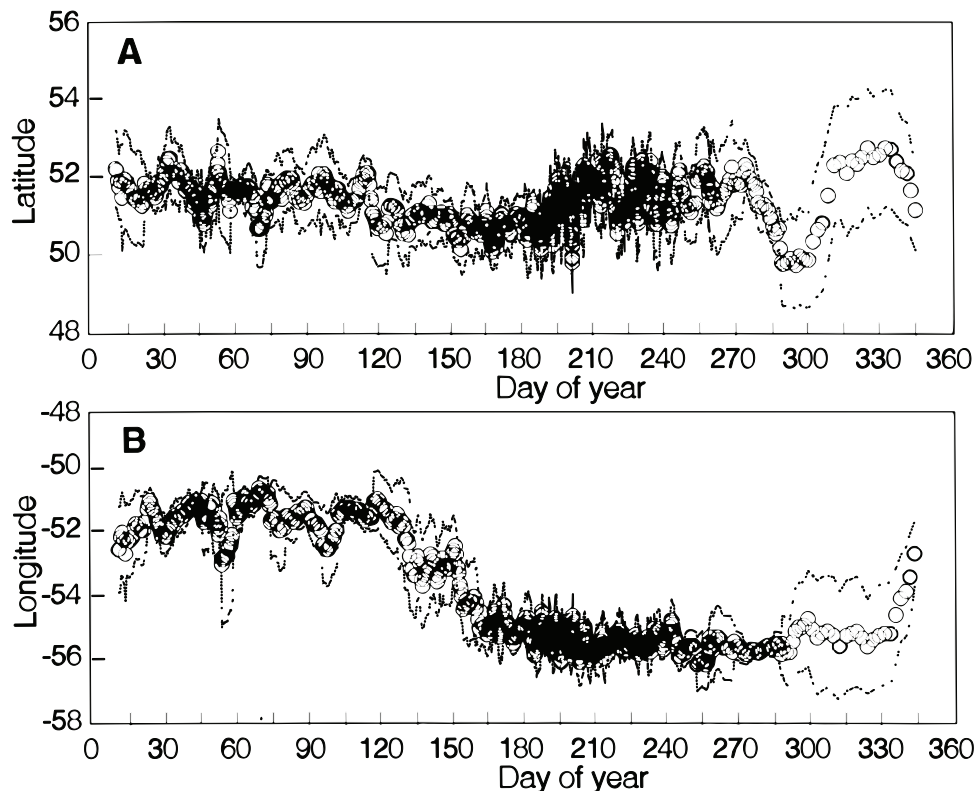


Fig. 3. Combined average (± 2 standard error) latitudinal (A) and longitudinal (B) geographic positions of reported cod-tag returns as a function of day of the year from tagging experiments conducted on Belle Isle Bank during the winter periods of 1978 and 1983 as shown in Fig. 2 but excluding data from reported returns during the first three months immediately following tagging. Data from Taggart *et al.* (1995).

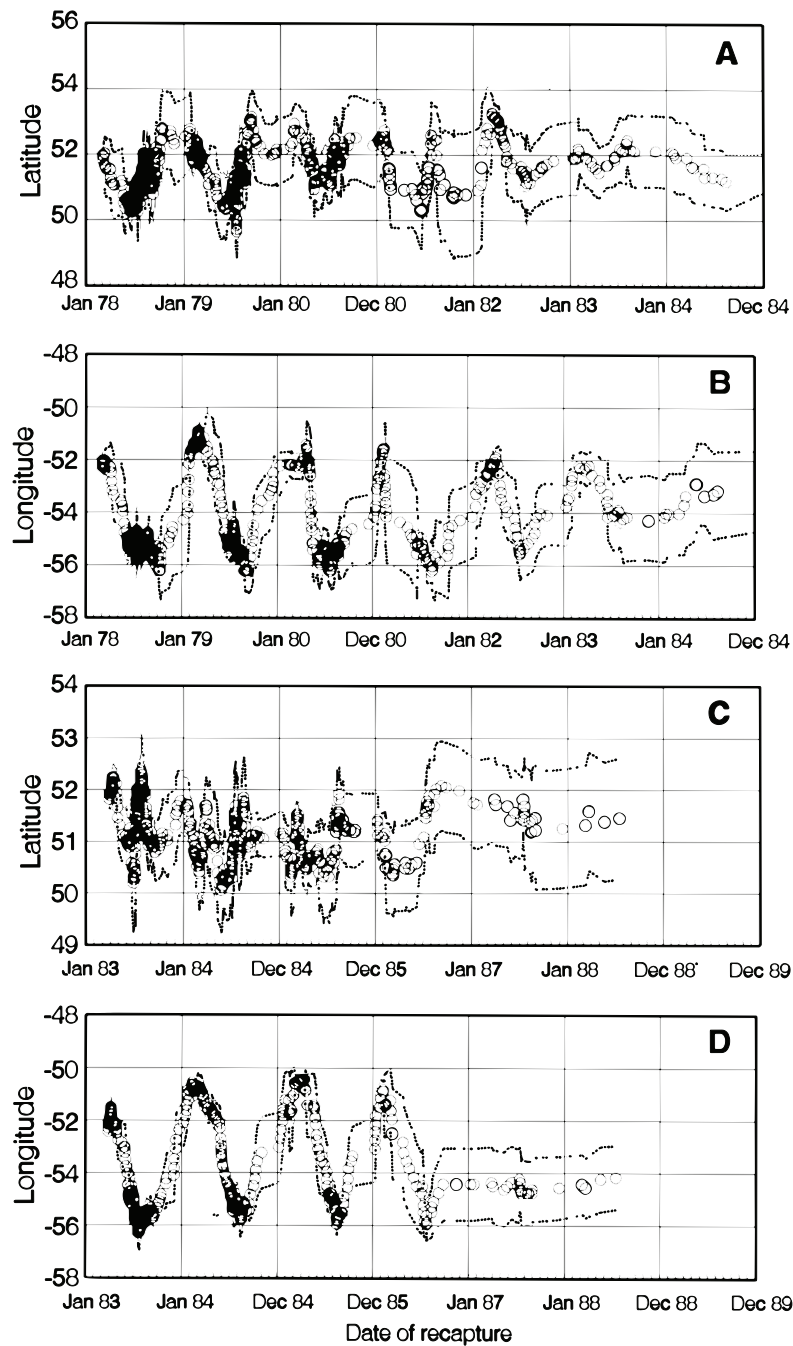


Fig. 4. Average (± 2 standard error) latitudinal (A, C) and longitudinal (B, D) geographic positions of reported cod-tag returns as a function of date after tagging from tagging experiments conducted on Belle Isle Bank during the winter periods of 1978 (A, C) and 1983 (B, D). Data from Taggart *et al.* (1995).

along the coasts and bays of eastern Newfoundland before they moved offshore in September (day 270).

During the winter period, the across-shelf average distribution of the tagged populations was of

the order of 50 naut. mile and the along-shelf average distribution was of the order of 75 naut. mile (Fig. 5C) which clearly did not extend northward to overlap the range of fish tagged on either of Belle Isle Bank or Hamilton Bank (see Fig. 1 and 2 above).

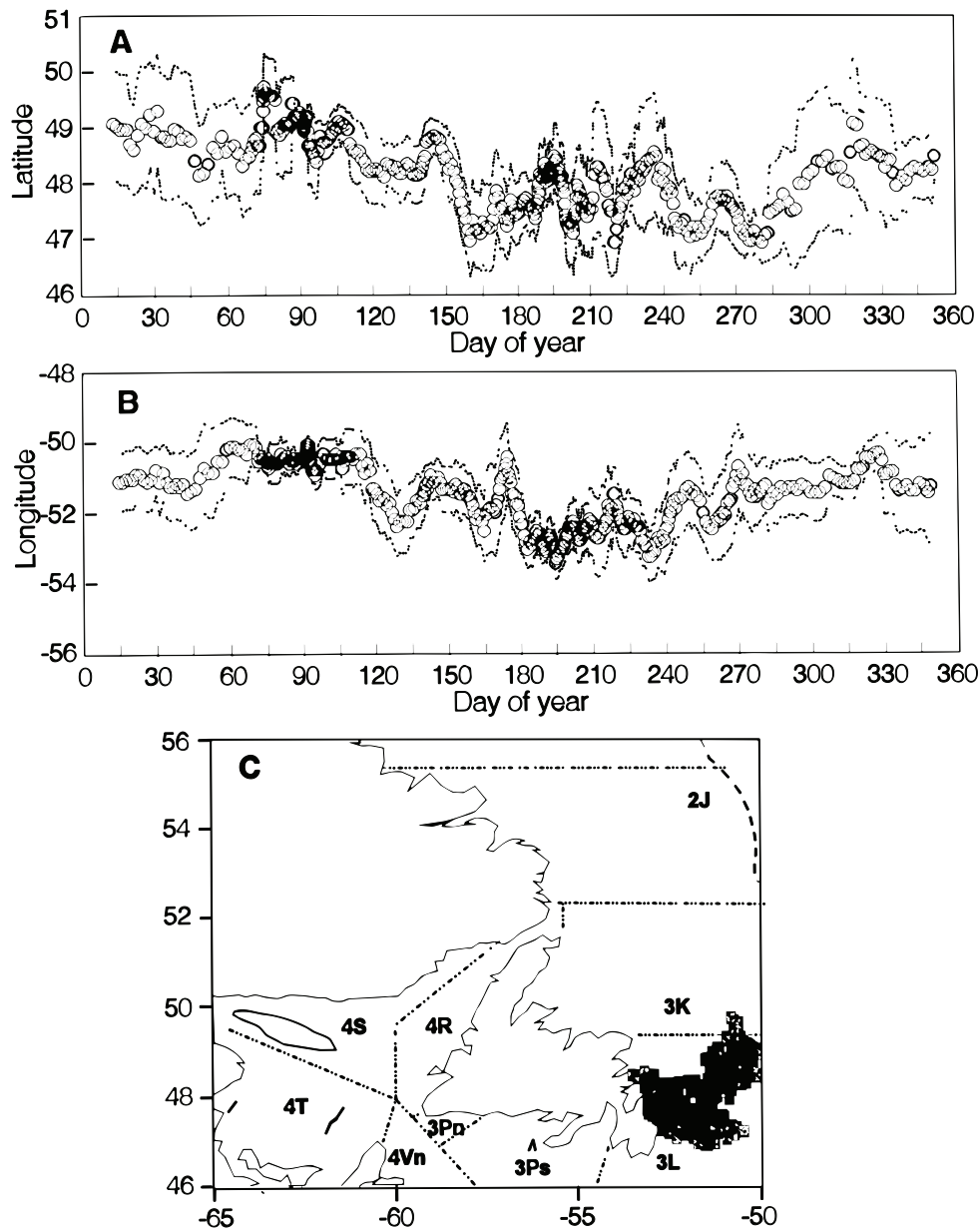


Fig. 5. Combined average (± 2 standard error) latitudinal (A) and longitudinal (B) and progressive vector (C) geographic positions of reported cod-tag returns as a function of day of the year from tagging experiments conducted in the North Cape region of the Grand Bank during the winter periods of 1980, 1982, 1983, 1990, and 1991. Data from Taggart *et al.* (1995).

Discussion

It appears from the results that fish tagged in the vicinity of Hamilton Bank can overlap in their offshore winter distribution with those tagged on Belle Isle Bank, and thus the populations can intermingle during the offshore spawning period. This is consistent with the inability to resolve genetic

differences between these bank-specific populations (Bentzen *et al.*, 1996). However, the same cannot be said for the fish tagged in the North Cape region, for which their average distribution offshore during winter did not overlap with those fish tagged on either Hamilton or Belle Isle Bank. This is also consistent with the genetic results in Bentzen *et al.* (1996) which showed that cod sampled from the

North Cape region in 1992 and 1993 were genetically distinguishable from more northern populations sampled on each of Hamilton, Belle Isle and Funk Island Banks. These results are also consistent with those of Lear (1984) who argued that there was bank-scale population structure, and also those of Cross and Payne (1978) who were able to resolve genetic differences among these same populations. Thus, it appears that the northern cod stock complex is comprised of at least two discrete offshore populations.

Recent Inshore and offshore aggregations: hypothesis

Cod tagged in the winter period in the North Cape region showed a pattern of fish moving from a relatively aggregated distribution offshore in the winter to the inshore region in summer followed by an offshore return to the same location (Fig. 5). The persistence of an offshore winter aggregation in this region is consistent with the offshore aggregations regularly observed over the short period covered by the annual research survey in the late-autumn and early-winter in that region, at least up until 1993 (cf. Fig. 5 and 6 in Taggart *et al.*, 1994 and Fig. 13 in Shelton *et al.*, MS 1996). However, the autumn surveys of 1994 and 1995 failed to reveal these offshore aggregations in the North Cape region (Shelton *et al.*, MS 1996).

One can ask "is it simply a coincidence that it was precisely in the following April and May periods of those years (1994, 1995) when large and anomalous aggregations of cod were located in the Random Island region of Trinity Bay (Bratney, 1996; Rose, MS 1996)?" To answer this question, it must first be recognized that cod have been known historically to overwinter in the inshore regions of eastern Newfoundland (Lilly, MS 1996). In the Trinity Bay region cod show a wintertime fidelity (Taggart *et al.*, 1995; Wroblewski *et al.*, 1996) as well as being genetically different from offshore overwintering populations (Ruzzante *et al.*, 1996, 1997). However, no "large" aggregations such as those seen in the spring of 1995 and 1996 have been previously reported in the region though there have been regular surveys conducted there during the spring periods of 1991, 1992, 1993, and 1994 (Taggart *et al.*, 1995; Taggart, unpublished data, Dalhousie University, N.S., Canada), and prior to those years (Lear, unpublished data, NAFC, St. John's, NF, Canada). Interestingly, Bratney (1996) showed that the large and main aggregation of fish (say P_o) found in the region (Northwest-Arm and Smith Sound) in 1995 and 1996 had relatively low levels of infestation of the parasite *Lernaeocera branchialis* (consistent with what is normally observed for offshore populations), while the other less aggregated cod sampled in the Southwest-Arm area of the region

(say P_i) during the same period had relatively high levels of festation (consistent with what is normally observed for inshore populations). Ruzzante *et al.* (1996, 1997) have shown that inshore overwintering populations from the Random Island region of Trinity Bay are genetically distinguishable from offshore overwintering fish, but those inshore overwintering populations sampled were not from large dense aggregations as seen in recent years (P_o) but from smaller more dispersed presumed overwintering aggregations (P_i). Bratney (1996) has also shown that the here-defined P_i inshore population was not in spawning condition as would be expected for that time of year (see Wroblewski *et al.*, 1996) while the large aggregation (P_o) was in spawning condition (as would be expected for a normally offshore spawning group). It has also been shown (Fig. 5) that fish tagged in the North Cape region habitually migrate from the North Cape region to and from the coasts and bays of eastern Newfoundland, including Trinity Bay.

Taken together, such observations imply that it is reasonable to hypothesize that the large aggregations of cod observed in recent years in the Random Island region of Trinity Bay (P_o) may be those fish that would normally aggregate offshore in the North Cape region but for some reason have ceased their normal migration pattern to offshore for winter. It should be possible to genetically test this hypothesis using tissue samples drawn from the large aggregation (P_o) and comparing their genetic structure to the inshore (P_i) and offshore (P_o) populations documented in Ruzzante *et al.* (1996). This hypothesis would be rejected if these fish were not genetically different from the inshore population. On the other hand, the hypothesis would not be rejected if the aggregation was not distinct from offshore fish sampled in the North Cape region in the winters of 1992 and 1993 (Ruzzante *et al.*, 1996, 1997). If the hypothesis was not rejected, it is not unreasonable to consider the possibility of other populations or aggregations of fish overwintering in inshore regions that would normally overwinter offshore where virtually none have been observed recently.

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