Mixing and migration of overwintering Atlantic cod (*Gadus morhua*) stocks near the mouth of the Gulf of St. Lawrence

S.E. Campana, G.A. Chouinard, J.M. Hanson, and A. Fréchet

Abstract: Millions of Atlantic cod (*Gadus morhua*) migrate distances of up to 500 km each fall to aggregate together in a small overwintering area off eastern Canada. Synoptic research vessel surveys carried out each January between 1994 and 1997 documented dense aggregations of cod along both flanks of the Laurentian Channel in each year, with estimated biomasses exceeding 100 000 metric tons. Using the trace element composition of the otolith ("otolith elemental fingerprint") as a natural tag, we found members of four populations to be present on the overwintering grounds in significant numbers, yet large-scale mixing among the populations was minimal. Individual trawl samples were often composed of a single population, suggesting that population integrity was maintained at a scale of <20 km. Cod from the southern Gulf of St. Lawrence dominated the population composition along the southern flank of the Channel, while cod from the northern Gulf dominated the northern flank; the distributions of both of these populations extended well to the east of their summer habitats and were remarkably similar across years. There was no evidence of large-scale mixing across the Channel. In light of the substantive migration of northern Gulf cod into the management area for the southern Newfoundland population, fishing effort off southern Newfoundland has the potential to reduce the size of the northern Gulf population.

Résumé : Chaque automne, des millions de morues (*Gadus morhua)* parcourent des distances pouvant atteindre 500 km pour se regrouper dans une petite aire d'hivernage située au large de l'est du Canada. Des relevés synoptiques effectués par des navires de recherche océanographique au mois de janvier de chaque année, entre 1994 et 1997, ont documenté des agrégats denses de morue sur chacun des flancs du chenal Laurentien, les biomasses étant estimées à plus de 100 000 tonnes métriques. À l'aide de la composition en oligo-éléments de l'otolithe (« empreinte élémentaire de l'otolithe ») comme marque naturelle, nous avons observé la présence d'un certain nombre d'individus de quatre populations dans l'aire d'hivernage, bien qu'il y ait peu de mélange à grande échelle entre les populations. Les échantillons prélevés par les chaluts étaient souvent composés d'individus d'une seule population, ce qui indique que l'intégrité de la population serait maintenue à une échelle <20 km. La morue du sud du golfe du Saint-Laurent dominait la composition de la population sur le flanc méridional du Chenal, tandis que la morue du nord du Golfe dominait sur le flanc nord; les distributions de ces deux populations s'étendaient nettement à l'est de leurs habitats d'été, et elles étaient remarquablement similaires d'une année à l'autre. On n'a relevé aucune indication de mélange à grande échelle dans le Chenal. Compte tenu de la migration importante de la morue du nord du Golfe dans la zone de gestion visant la population du sud de Terre-Neuve, il est possible que l'effort de pêche mené au large de la partie sud de Terre-Neuve réduise la taille de la population de la partie nord du Golfe.

[Traduit par la Rédaction]

Introduction

The migration patterns of marine fish populations are less understood than the spawning migrations of anadromous fish such as salmon, but the influence on their population dynamics may be just as important. In response to spawning, feeding, or predator avoidance cues, marine fish migrations can extend over scales as small as a few kilometres in the case of flatfish moving offshore to overwinter (MacDonald et al. 1984) to thousands of kilometres for bluefin tuna (*Thunnus thynnus*) crossing the North Atlantic (Lutcavage et al. 1999). The extent and timing of these often-annual migrations are generally both consistent and predictable within a given population, suggesting an evolutionary advantage. However, the exact nature of the survival advantage, as well as the migratory route and destination, is often poorly under-

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Table 1. Summary of Atlantic cod samples collected by area and season.

				Length (cm)		Age (years)	
Area	Season	Date(s)	*n*	Mean	SD	Mean	SD
North Gulf	Spring 1996	Apr. 13–30	155	56.5	10.9	7.6	2.1
	Spring 1997	Apr. 6–30	134	52.9	9.9	6.9	1.8
Southern Newfoundland, offshore	Spring 1996	Apr. 27–29	70	61.4	8.4	6.4	1.0
Southern Newfoundland, inshore (Fortune)	Spring 1997	June 19	42	64.6	15.4	—	—
Southern Newfoundland, inshore (Placentia)	Spring 1997	June 26	61	57.3	6.1	—	—
Southern Gulf	Spring 1996	June 13–15	200	52.1	7.9	7.3	1.4
	Spring 1997	June 11–13	200	53.4	6.1	7.6	1.5
Eastern Shelf (Gully)	Spring 1996	May 1	99	53.0	5.6	6.3	1.3
	Spring 1997	May 2	81	41.3	4.0	4.1	1.1
Northern Shelf (Banquereau)	Spring 1997	May 1	69	42.8	7.8	4.5	1.3
Cabot Strait	Winter 1996	Jan. 3–22	781	46.0	8.0	6.0	1.7
	Winter 1997	Jan. 6–25	866	45.5	9.3	5.8	1.8

Note: All spring samples were collected from spawning grounds around the time of spawning and thus represent populations of known identity. Winter samples of unknown population identity were subsequently classified using the spring samples as the reference.

stood, in part due to the technical limitations associated with tracking the movements of millions of fish deep beneath the ocean's surface.

Shortly after spawning in late spring, several Atlantic cod (*Gadus morhua*) populations off eastern Canada disperse to feed throughout the northern and southern Gulf of St. Lawrence, southern Newfoundland (NF), and the eastern Scotian Shelf. During the autumn, these same populations migrate to the warm deep waters of the Laurentian Channel (Cabot Strait) to overwinter, presumably to avoid near-freezing water temperatures and ice cover in their summer habitat (Templeman 1962; Jean 1964; Fréchet 1990). Cod density is high on the overwintering grounds, since the area occupied is about 10% of that occupied during the summer. However, particularly dense aggregations have been documented at various locations along both the northern and southern flanks of the Laurentian Channel (Templeman 1962; Jean 1964; Chouinard[2]). Although genetic (Bentzen et al. 1996) and tagging (Taggart et al. 1995) studies have both suggested the presence of four to six populations in the overwintering area, the spatial distribution of the populations and the extent of any population mixing are unknown. It seems unlikely that the 400–500 m depth of the Laurentian Channel is a physical impediment to cross-channel migration during the winter. Given that a substantial proportion of the biomass of the potential source populations is believed to overwinter in the area (Chouinard[2]), the likelihood of population mixing would appear to be high. Both mixed-population catches and distributions of populations outside management units can introduce serious error into the stock assessment of any fish species, thus degrading efforts at optimal management (Wood et al. 1989).

Tagging and genetic studies carried out to date lack the resolving power necessary to map the spatial extent of population mixing in the overwintering area. Therefore, we used the trace element composition of the otolith as a more highly resolved natural tag. The otolith is well suited to this application because it grows without resorption throughout the life of the fish (Campana and Neilson 1985) and it accretes trace elements from the environment in a temperature-sensitive manner (Kalish 1989; Edmonds et al. 1995; Fowler et al. 1995). Thus the elemental composition of the whole otolith ("otolith elemental fingerprint") serves as an environmentally induced natural tag of fish that have spent at least part of their lives in different habitats, independent of genetic identity. Recent studies have demonstrated that the elemental fingerprint of cod is not only population specific but that otolith growth and environmental shifts over periods of up to a year have a negligible effect on the fingerprint (Campana et al. 1995, 1999). By using the otolith elemental fingerprint of spawning cod on spawning grounds as a short-term natural tag, we were able to confidently track and identify those same groups of fish on the overwintering grounds with no more assumptions than those associated with genetic markers (Campana et al. 1999).

In this paper, we use the results of 4 years of synoptic research vessel surveys to document the distribution and density of cod on the overwintering grounds near the mouth of the Gulf of St. Lawrence. We then apply otolith elemental fingerprints as natural tags to provide the first description of population structure, distribution, and mixing within the overwintering area and assess the implications of the findings for migration theory and fisheries management.

Materials and methods

A grid sampling design was used to survey the density and distribution of Atlantic cod in and around the approaches to the Gulf of St. Lawrence each January between 1994 and 1997. Surveys were carried out January 13–25, 1994, on the *Alfred Needler* (N197) (southern Gulf), January 8–28, 1994, on the *Gadus Atlantica* (G239) (northern Gulf), January 10–29, 1995, on the *Alfred Needler* (N214), January 3–22, 1996, on the *Wilfred Templeman* (WT182), and January 6–25, 1997, on the *Wilfred Templeman* (WT201). The nominal distance between survey samples was 20 km, although some areas were surveyed at 5-km intervals. Survey biomass (minimum trawlable biomass) was calculated by multiplying the mean weight per standardized tow by the number of trawlable units in the survey area. The resulting biomass distribu-

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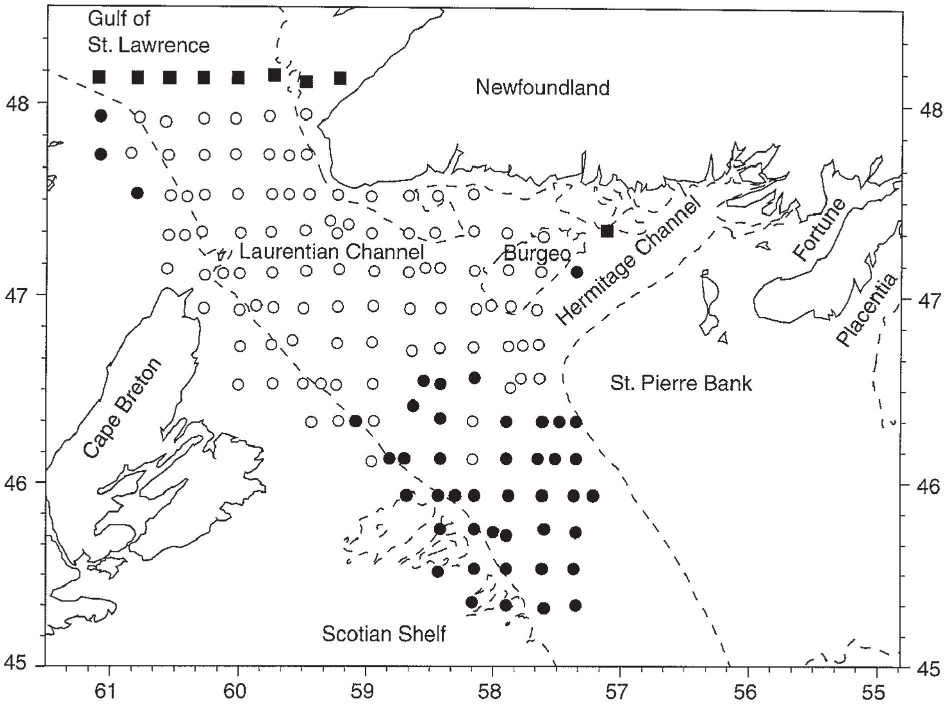
[2] Chouinard, G.A. Unpublished manuscript. Distribution of Atlantic cod (*Gadus morhua*) in Cabot Strait during January 1996 and 1997. Workshop on the Identification of Cod Stocks, Dartmouth, N.S.

Fig. 1. Map of the study area showing the Atlantic cod overwintering grounds sampled in January 1996 (●), January 1997 (■), and January of both years (○). The 200-m contour is shown.



tions were contoured using Delauney triangles in the spatial analysis program ACON.

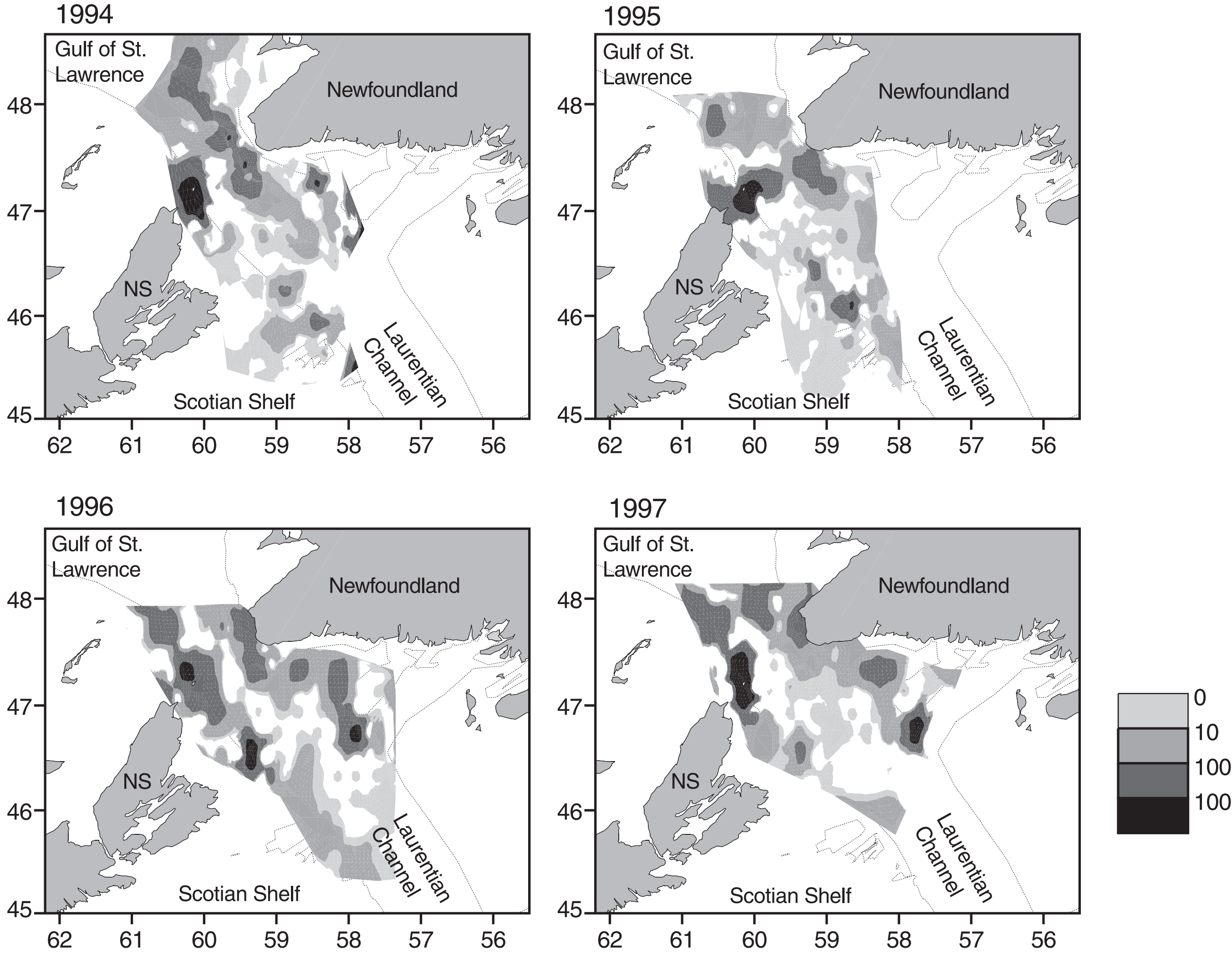
Otoliths for determination of stock identity were collected from adult cod (35–85 cm) on approximately every second set of the 1996 and 1997 surveys (Table 1; Fig. 1). A total of 138 successful sets were made in 1996, of which 60 sets were sampled for otoliths (n = 754). Samples from 1997 came from 104 successful sets, of which 49 sets were sampled for otoliths (n = 866). Additional samples (n = 89) (45°50′ latitude, 58°03′ longitude) to the east of the region surveyed by the *Wilfred Templeman* in 1997 were collected on March 15, 1997, in two sets as part of the *Alfred Needler* N255 spring survey.

Each cod population off the eastern coast of Canada spawns at a distinct site and is thus of known population identity at the time of spawning (Templeman 1962). Since the otolith elemental fingerprints of the 1996 and 1997 spring-spawning aggregations differed significantly among spawning groups (Campana et al. 1999), they were used as population- and year-specific reference markers against which the winter samples could be compared (Table 1). The elemental fingerprint of each otolith was characterized by a suite of five elements (Li, Mg, Mn, Sr, Ba) using isotope dilution inductively coupled plasma mass spectrometry and procedures described in Campana et al. (1999). Elemental assays for both spring spawner (known identity) and winter (unknown identity) samples from each year were systematically randomized with respect to assay sequence and analyzed together at the same laboratory. As a result, spring spawner and winter samples from any given year are completely comparable. To insure that differences in fish length or age among samples were not confused with population-specific differences, the effect of otolith weight was statistically removed from those elemental concentrations in which a size effect was evident (Campana et al. 1999). Detrended elemental concentrations showed no obvious residual relationship with fish size (and by inference, fish age) for most of the sample collections. In any event, relative differences among detrended samples tended to be very similar to those based on original data, with the exception of samples of very small fish. Since small intercalibration differences between laboratories could have introduced artifactual differences among years, only spring spawner samples collected in the same year as that of the January survey were used in classification. Thus the January 1996 samples were classified as to population completely independently and using a different set of reference samples than those in 1997. A second set of 1997 classifications was carried out using the 1997 spring spawner reference samples in conjunction with the 1996 spring spawner sample from St. Pierre Bank, since the latter area was not sampled in 1997. Tests of classification accuracy were also made against collections of cod made throughout the Gulf of St. Lawrence in the fall of 1995 (Campana et al. 1999).

Stock composition analysis of each set in the winter samples was carried out using a maximum likelihood based analysis analogous to that of Millar's (1990) HISEAS program. The reference data for all elemental fingerprints were the spring spawner fingerprints from the same year, for which stock affinity was known. Conceptually, the stock composition analysis used the statistical distribution of the elemental fingerprints in each reference (spawning) group to estimate the proportion of each reference population in the unknown (winter) mixture. As long as all of the possible groups contributing to the group mixture have been characterized, the analysis will produce an unbiased estimate of population proportions, with no more assumptions than those associated with genetic markers (Wood et al. 1987, 1989; Campana et al. 1999). The product of the analysis was the proportion of each reference population in each set, which was subsequently converted to population-specific biomass as described earlier. Unsampled sets were assumed to contain the same population proportions as the nearest neighbouring set along a similar depth contour.

Population-specific biomass estimates from the winter surveys were subsequently compared with those from summer and fall research vessel surveys, which is a time when populations are largely separated. Biomass (all ages) calculations from those surveys were calculated as the mean of the preceding and following years, so as to approximate the biomass in January. Biomass estimates for the northern Gulf population were calculated as the mean of the sum-

Fig. 2. Relative Atlantic cod abundance on overwintering grounds near the mouth of the Gulf of St. Lawrence off eastern Canada as determined with bottom trawl surveys in January of 1994–1997. The densest aggregations were consistently found in the same locations along each flank of the Laurentian Channel. Estimated biomass in each year was between 100 000 and 200 000 tonnes. The 1994 data represent the results of two separate surveys. NS = Nova Scotia. The 200-m bathymetric contour is shown.



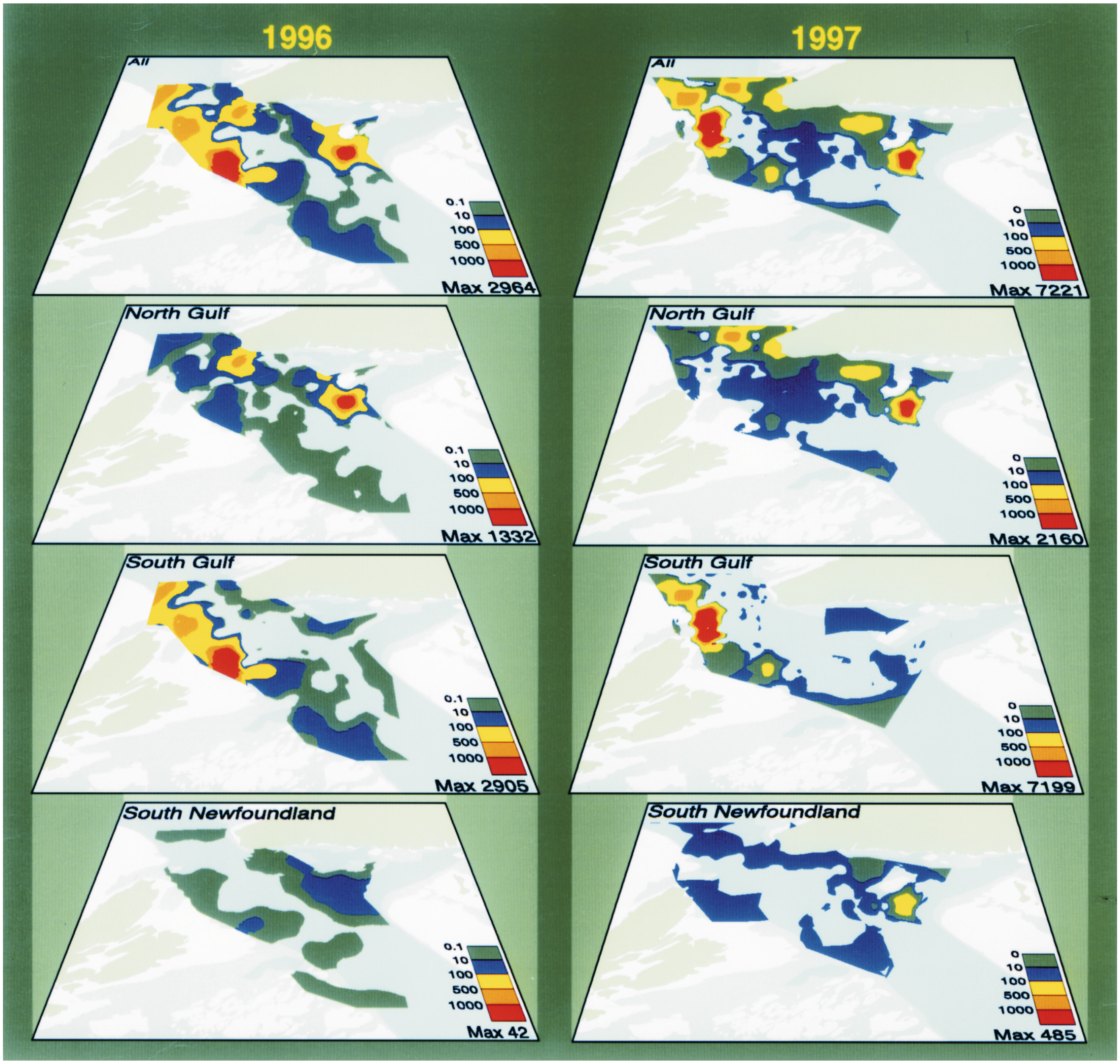
mer and fall mobile gear sentinel surveys in the preceding and following years. The estimate for the southern NF population was based on the April 1996 survey. All biomass estimates represent minimum trawlable biomass, with no adjustment for catchability.

Results

January trawl surveys of the overwintering area documented dense aggregations of Atlantic cod at 250–450 m depth in various locations along the northern and southern flanks of the Laurentian Channel (Fig. 2). The locations of these aggregations were remarkably consistent from year to year, as were the relatively low densities in the centre of the Channel. Water temperature at the sites of large aggregations generally ranged between 4.9 and 5.3°C.

The accuracy and precision of the population identifications based on the otolith elemental fingerprints appeared to be high and were not a source of important error. When the spring-spawning reference samples of 1996 (four populations) were used to classify cod collected in the southern and northern Gulf in the fall of 1995 (which were probably in their own stock area at the time), 98.9% of the cod captured in the southern Gulf were identified as being of southern Gulf origin, while 99.2% of the cod captured in the northern Gulf were identified as being of northern Gulf origin. To the extent that the southern and northern Gulf cod avoided mixing between the fall of 1995 and the spring of 1996, these results suggest that these two groups of fish were easily differentiated. The results of the second test of accuracy were based on classification of the 1996 spring-spawning samples using the 1997 spawners (seven spawning groups) as the reference (Table 1). Classification accuracy for the northern Gulf, southern Gulf, and Scotian Shelf (Gully) spawning groups was 77, 89, and 70%, respectively. Misclassification error for the Scotian Shelf group was primarily associated with southern Newfoundland spawners, indicating that their elemental fingerprints were similar. Accuracy increased to more than 96% for both the northern Gulf and southern Gulf groups when the 1996 spawners (four reference groups) were used to classify the 1997 spawners. The accuracy of all

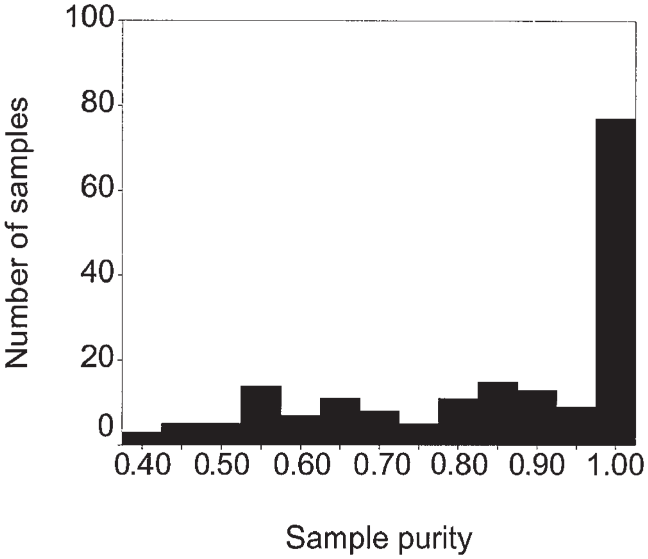
Fig. 3. Population-specific abundance of adult Atlantic cod on overwintering grounds near the mouth of the Gulf of St. Lawrence in January of 1996 and 1997. The top layer shows the overall cod abundance in each year, while each of the following layers shows the abundance attributable to the specific population named on the layer. Total abundance was decomposed into component populations through analysis of otolith elemental fingerprints, which served as natural tags for each of the component populations.



of these tests would be expected to increase as the interval between sampling reference and test groups was reduced, due to the reduced opportunity for otolith growth between the time of initial characterization and testing. Since the interval used in the identification of the winter samples was half of that used above, it would appear that a coefficient of variation of 5–20% is likely in the analyses that follow.

On the basis of the stock composition analysis of the individual trawl samples, it was possible to contour population-specific abundance to show relative abundance and distribution each winter (Fig. 3). The population-specific distribution patterns in the two years were very similar and indicated that the two largest populations in the area remained largely separate in their distribution. Southern Gulf cod dominated the aggregations on the southern flank of the Laurentian Channel, while northern Gulf cod dominated aggregations on the northern flank and in the central part of the Channel. There was no evidence of large-scale mixing across the Channel, although northern Gulf cod were more prevalent in the centre of the Channel than were southern Gulf cod. The overall representation of the population from offshore southern Newfoundland (St. Pierre Bank) was relatively low and restricted to the area immediately adjacent to St. Pierre Bank. On the other hand, two other populations from inshore southern Newfoundland (Fortune Bay and Placentia Bay), as well as that from the eastern Scotian

Fig. 4. Purity of each bottom trawl sample in terms of Atlantic cod population composition. The population mixture analysis indicated that four populations contributed significantly to the overwintering grounds; hence, the estimated proportion of the dominant population in each sample should vary randomly between 0.25 and 1.00. Instead, 69% of the 183 samples consisted of essentially only one population (>80% purity), indicating that the populations did not intermix on a local scale. Both 1996 and 1997 samples where the catch was ≥10 fish are presented.



Shelf, were not present in significant numbers (< 5% of total numbers) anywhere in the survey area. The poor representation of the eastern Scotian Shelf population may have been amplified by its extremely low current population size, although all of the characterized populations except those from southern Newfoundland are thought to be at low abundance levels.

The segregation among populations occurred on a scale even finer than that indicated by the contoured population distributions. Samples from a single tow were generally dominated by a single population and, in 69% of samples containing at least 10 individuals, were essentially pure (Fig. 4). This was the case even where adjacent samples were characterized by completely different population compositions. Allowing for unavoidable integration of closely spaced schools across the 2-km tow length, the overall purity of the samples suggests that population integrity was maintained at a scale of < 20 km, corresponding to the mean distance between sites in the sampling grid. The one area in which true population mixing may have occurred is the Hermitage Channel to the west of St. Pierre Bank. There, both the northern Gulf and southern Newfoundland populations were present in significant numbers, but we were unable to determine if individual schools were pure in composition but tightly packed or of mixed composition.

Minimum trawlable biomass in the 1996 and 1997 winter surveys was estimated at 102 800 and 134 200 tonnes (metric tons), respectively, which is a substantial proportion of the biomass of the potential source populations (Table 2). When calculated on a population-specific basis, the northern Gulf and southern Gulf populations together comprised more than 91% of the biomass of the surveyed region in each year, with the rest being made up of cod from the remaining populations. Population-specific biomass estimates differed relatively little between years for the northern Gulf, southern Newfoundland, and Scotian Shelf populations. The interyear difference was more marked for the southern Gulf population; however, much of this difference was attributable to greater survey coverage of the southern Gulf in 1997. Comparisons with biomass estimates made in summer and fall, at a time when the various populations were largely separated, suggested that a large proportion of the southern and northern Gulf populations were present in the survey region during the winter (Table 2). In contrast, < 20% of the southern Newfoundland and Scotian Shelf populations were present in the survey region, suggesting that their overwintering grounds were elsewhere.

The distribution of population-specific biomass was not in keeping with current stock management units (Table 2). In particular, less than half of the northern Gulf biomass was determined to be present in the northern Gulf management unit during the winter, with most of the remainder being found well inside the boundaries of the southern Newfoundland region, mixed with the resident fish. This pattern was similar in both years. Similarly, <13% of the cod collected in the surveyed region of the Scotian Shelf were actually of Scotian Shelf origin, with most of the remainder (74% in 1996; 83% in 1997) being from the southern Gulf. In contrast, the portion of the southern Newfoundland population that was surveyed seemed to be largely restricted to the southern Newfoundland management unit (NAFO Division 3Ps), and >91% of the southern Gulf population was found in the appropriate management unit (4TVn, November–April). Very few differences in biomass distribution were evident between the years.

Discussion

It has been known for some time that the approaches and mouth of the Gulf of St. Lawrence serve as the overwintering grounds for several large Atlantic cod populations in the area (Templeman 1962; Jean 1964). However, the distribution of cod on the overwintering grounds was not evident until the detailed winter surveys reported in this study had been completed. Over the 4 years of surveys, cod showed remarkable year-to-year consistency in the location of their overwintering aggregations along the slopes of the Laurentian Channel, suggesting that some feature of the bottom topography or environment made the location a preferred habitat. Preferred depths tended to be close to the mean depth of the Channel (400–500 m), suggesting that depth was not a physical impediment to cross-channel migration during the winter. Nor did distribution appear to be a function of water temperature alone, since the preferred temperature of 4.9–5.3°C was widely available in the Laurentian Channel (Swain et al. 1998). Other fish species also migrate out of the Gulf each winter (Swain et al. 1998), suggesting that the ecological or evolutionary motivation for migration is broadly shared.

Table 2. Population-specific Atlantic cod biomass (tonnes) from the January 1996 and 1997 research vessel surveys in each of the management areas based on classification of the otolith elemental fingerprints.

	1996 reference population				
January 1996 area of capture	Southern Newfoundland	Northern Gulf	Southern Gulf	Scotian Shelf (Gully)	Total
Southern Newfoundland	3 269	23 955	516	542	28 643
Northern Gulf	870	12 519	2 145	798	16 330
Southern Gulf	0	1 018	5 845	368	7 230
Cape Breton (4Vn)	107	4 440	43 028	950	48 525
Scotian Shelf	140	222	1 152	153	1 668
Total	4 746	42 154	52 685	2 810	102 800
Biomass from summer surveys	41 100	34 500	88 000	14 000	

	1997 reference population							
	Southern Newfoundland					Scotian Shelf		
January 1997 area of capture	St. Pierre Bank	Fortune	Placentia	Northern Gulf	Southern Gulf	Banquereau	Gully	Total
Southern Newfoundland	5 882	93	2237	24 396	45	0	273	32 963
Northern Gulf	655	115	2	23 061	92	0	549	23 960
Southern Gulf	38	0	0	923	28 547	1037	0	30 549
Cape Breton (4Vn)	263	1	0	1 288	43 898	417	18	45 880
Total	6 839	209	2238	49 801	72 583	1454	840	133 900
Biomass from summer surveys	-------------------41 100-------------------			43 000	86 000	-----------------7800---------------		

Note: Mean population-specific biomass estimates from the the summer–fall surveys of the preceding and following years are tabled for comparison. The biomass for 3Ps cod is from the April 1996 research vessel survey. Discrepancies between the total survey biomass and the sum of the population-specific biomasses are due to rounding errors during classification.

Our results indicate that four major cod populations (northern Gulf, southern Gulf, southern Newfoundland, and eastern Scotian Shelf) contributed fish to the overwintering grounds in the Laurentian Channel, dominated by contributions from the northern and southern Gulf populations. Although the presence of these populations had previously been suspected based on otolith elemental fingerprints (Campana et al. 1999), genetics (Bentzen et al. 1996), and tagging studies (Taggart et al. 1995), the location and relative contribution of the populations in winter were unknown. Historic tagging studies suggested that small numbers of an additional population (Cape Breton cod, 4Vn) may also have been present (McKenzie 1956). However, we could not address that issue because the elemental fingerprints of spawning fish sampled from the Cape Breton area were not distinguishable from those of the southern Gulf (Campana et al. 1999).

The otolith elemental fingerprints used in this study performed well as natural tags and provided population-specific distributions with a resolving power that was simply not possible in previous tagging and genetic studies. Our findings indicated that Gulf cod overwinter along the flanks of the Laurentian Channel, resulting in population extensions well to the east of their summer habitats. In general, these findings reinforce expectations based on tagging studies (McKenzie 1956; Taggart et al. 1995), fleet dynamics (Sinclair and Currie 1994), research vessel surveys (Rollet et al. 1994), and analyses of size composition (Hanson 1995). In particular, the near absence of cross-channel migration is completely consistent with past tagging studies, which reported on average <5% movement across the channel from either direction (McKenzie 1956; Templeman 1962; Martin and Jean 1964; Taggart et al. 1995). Several other results came as a surprise, however. The first was the relative purity of the population composition in the individual survey tows, suggesting that population integrity was maintained at a scale of <20 km. With the exception of the area to the west of St. Pierre Bank, there was little evidence of population mixing either across or on any given side of the Channel. Such a degree of population segregation is remarkable given the 100- to 500-km migration distance of many of the individuals in the two Gulf populations. Few analogies exist in the marine groundfish literature, although the homing capabilities of Atlantic herring (*Clupea harengus*) and other pelagic fishes to spatially segregated spawning grounds are well documented (Wheeler and Winters 1984). In the only reported parallel, Rose (1993) used hydroacoustic gear to monitor a portion of a 250-km migration by a 500 000-tonnes school of cod from an offshore spawning ground to an inshore feeding area during which the integrity of the school was maintained. The migration pathway of the cod in the current study was not monitored. However, in light of the relationship between size of cod and distance from the mouth of the Gulf (Chouinard[2]), larger cod apparently migrated further out of the Gulf than did smaller cod, consistent with Rose's (1993) suggestion that older, more experienced cod lead the way for others to follow. Alternatively, larger cod may simply have migrated further, due to the energetic efficiencies of a larger body size (Dodson 1997). Tagging studies on cod in and around the Gulf of St. Lawrence indicate that homing to spring-spawning grounds after overwintering is carried out with relatively little loss to other spawning groups (Taggart et al. 1995). If migration to and from the overwintering grounds is indeed a learned response, it could be that spatial segregation of cod populations on the overwintering grounds is a behavioural mechanism through which faithful returns to spawning grounds are maximized. Such a mechanism would presumably supplement or reinforce philopatry brought on by imprinting at an early life history stage (Cury 1994). However, the role of imprinting and learning in the development of migratory patterns remains unclear (Quinn and Brodeur 1991), particularly given the increasing evidence for innate directional mechanisms in many fishes (Walker et al. 1997).

A second unexpected result was the extent of the eastward distribution of both the southern and northern Gulf populations. The result indicating movement of southern Gulf cod as far east as Banquereau Bank on the eastern Scotian Shelf is consistent with previous reports (McKenzie 1956; Martin and Jean 1964; Sinclair and Currie 1994; Campana et al. 1995; Hanson 1995), although the relative dominance of the southern Gulf population had never been quantified in such detail. On the other hand, there was no prior suggestion that the winter distribution of northern Gulf cod extended so completely to the southeast of Burgeo Bank, despite having previously been noted as a stock mixing area (Templeman 1962; D'Amours et al. 1994; Rollet et al. 1994). The distance between Burgeo Bank and St. Pierre Bank is relatively small and is probably not meaningful in a biological context. However, the relative concentration of northern Gulf cod in this area was large, characterized by the highest densities of this population in both survey years. It is difficult to discount these findings as anomalies, given that the reconstructed population distributional patterns were virtually identical between years, despite being based on completely independent reference collections. Of course, historic distributional patterns may have differed from those present now, perhaps in response to different environmental conditions or abundance. However, the results of synoptic research survey distributions in the 1980s (Rollet et al. 1994) and historic and current tag returns as reported by Taggart et al. (1995) were completely consistent with our findings: the Hermitage Channel area to the west of St. Pierre Bank often served as the easternmost boundary for the northern Gulf migration, as well as the westernmost boundary for movements of more westerly groups of cod. Thus, there is no evidence to suggest that large-scale movement of northern Gulf cod to the Hermitage Channel is merely a recent phenomenon.

Substantive migration of northern Gulf cod into the southern Newfoundland management unit has significant management implications. With more than half of the northern Gulf population biomass present in the southern Newfoundland management unit during the winter, fishing effort in southern Newfoundland to the west of St. Pierre Bank has the potential to reduce the relative abundance of the northern Gulf population. Indeed, a given unit of fishing effort in this area in the winter of 1996 or 1997 would have caught three to four times more northern Gulf cod than resident southern Newfoundland cod. Maximal influence would be associated with fishing activity in the winter, since this is the period during which the largest numbers of northern Gulf cod are present in the management area for the southern Newfoundland population, but some effect would also be expected in the spring before the return migration of northern Gulf cod has been completed.

As noted by Shelton et al. (1996), the extension of northern Gulf cod into the southern Newfoundland area also poses problems for the interpretation of the winter research surveys previously used to estimate the abundance of the southern Newfoundland population. Current research surveys of the region are carried out in April, under the assumption that most northern Gulf cod have left the area. However, it is not clear that the return migration has necessarily been completed by April. Research survey abundance indices based on mixed populations would provide an inflated abundance estimate for the resident population.

While differences undoubtedly exist, the migration patterns of southern Gulf cod appear to parallel those of northern Gulf cod, making the southern flank of the Laurentian Channel biologically analogous to that of the northern flank. Along the southern flank, fisheries management has made accomodations for this migration pattern by acknowledging that fishing off Cape Breton (4Vn) and the eastern Scotian Shelf (4Vsb) in winter–spring is likely to catch high proportions of southern Gulf cod. Research surveys of the Scotian Shelf are carried out in July, long after the return migration to the Gulf has been completed, thus avoiding contamination of abundance indices due to the presence of southern Gulf cod. However, no such accomodations have yet been made on the northern edge of the Channel, despite the close analogy to the southern Gulf cod. Further examination of this issue appears warranted.

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