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Homing and group cohesion in Atlantic cod *Gadus morhua* revealed by tagging experiments

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Homing behaviour and group cohesion in Atlantic cod *Gadus morhua* from the northern Gulf of St Lawrence were studied based on tagging–recapture data from two periods, the 1980s and a recent period from 1996 to 2008. Two or more tags from a single tagging experiment were frequently recovered together in subsequent years. The null hypothesis was tested that the frequency of matching tag recoveries occurred by chance only through random mixing of tagged *G. morhua* before their recapture by the commercial fishery. The alternative hypothesis was that non-random, positive association (group cohesion) existed among tagged individuals that persisted through time and during migrations. Results show that the *G. morhua* population exhibits a homing behaviour, with temporal stability across seasons and years: 50% of recaptured fish in the recent period were caught <34 km from their mark site, even 3 years after release. In the 1980s, *G. morhua* were located at <10 km from their release site 1 year after tagging during summer and at <16 km during spring and autumn combined. Despite the increasing distance between the mark and recapture sites over time, the difference was not significant. In addition, occurrences of two or more tagged fish from the same release event that were caught together indicated a non-random association among individual fish for periods of one to several years and through migrations over several hundred kilometres. Hence *G. morhua* showed group cohesion in addition to site fidelity. These two interacting behaviours may be fundamental for the rebuilding and conservation of depleted fish stocks.

Key words: migrations; northern Gulf of St Lawrence; stock rebuilding; sub-stock structure.

INTRODUCTION

Marine fishes show great variability in population richness despite the common occurrence of larval dispersal and adult migratory phases (Sinclair, 1988). Some species such as Atlantic cod *Gadus mohrua* L. 1758 and Pacific halibut *Hippoglossus stenolepis* Schmidt 1904 exhibit intraspecific differences in migratory behaviours and spatial distribution patterns (Neat *et al*., 2006; Loher, 2008). Moreover, marine fishes may show great variability in movements, from sedentary coastal species such as blennies to transoceanic migrants such as tunas (Metcalfe *et al*., 2002). Movements will also determine the spatial scale over which population processes take place.

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Knowledge of both the migration patterns and spatial distribution of commercial fish stocks is important for understanding population dynamics and for effective fisheries management and stock conservation (Stephenson, 1999; Wroblewski *et al*., 2005; Levin, 2006).

Much work to date has provided evidence that many *G. morhua* populations undertake long migrations (hundreds of kilometres) for spawning or feeding purposes (Templeman, 1979; Hanson, 1996; Wright *et al*., 2006). Furthermore, *G. morhua* populations are capable of precise and repeated homing migrations; combined with site fidelity, this leads to a persistent spatial structure (Godø, 1984; Lear, 1984). Indeed, recent studies have shown that *G. morhua* populations can migrate along the same route (Rose, 1993) and return to the same spawning or feeding grounds in subsequent years (Robichaud & Rose, 2001; Wright *et al*., 2006; Svedäng *et al*., 2007; Heath *et al*., 2008). In addition, homing behaviour, combined with site fidelity, has been shown to lead to a mosaic of small, genetically distinct *G. morhua* populations in Norway (Fevoldon & Pogson, 1997), Newfoundland and the Gulf of St Lawrence (Ruzzante *et al*., 1999; Beacham *et al*., 2002), Labrador (Morris & Green, 2002), the Gulf of Maine (Howell *et al*., 2008) and the Atlantic coast of the U.S.A. (Kovach *et al*., 2010), particularly in coastal areas. Like many other *G. morhua* populations, the northern Gulf of St Lawrence stock presents the same homing behaviour in summer as revealed by tagging studies (Templeman, 1979; Moguedet, 1994; Gascon *et al*., 1997; Yvelin *et al*., 2005). In the present study, *G. morhua* recaptured in the same location and at the same time in subsequent years is considered homing. In other words, homing is fidelity to specific locations during the migration process. This definition is in agreement with Gerking (1959), who defined homing as 'the choice that a fish makes between returning to a place formerly occupied instead of going to other equally probable places' (Righton *et al*., 2007; Loher, 2008).

There is a substantial scientific literature that deals with the topic of schooling and aggregations of small pelagics and other fishes. Schooling behaviour is common among fishes (Pitcher, 2001). The tendency to form shoals or schools, however, varies both between and within species, depending on ecological niche and other factors linked to species behaviours (Fréon & Misund, 1999). The behaviour of individuals within shoals or schools and the functional significance of schooling have been described by Fréon & Misund (1999). The dynamic of schooling behaviour, however, is largely driven by a different set of needs and preferences that may affect migratory habits, as noted by Bakun & Cury (1999) and Cury *et al*. (2000). It is not known if shoal or school cohesion is maintained during migrations or whether schools visit specific locations with precise seasonal timing for feeding or spawning. Social cohesion and how it might occur is not understood but may be fundamental to understanding issues related to the assessment and conservation of *G. morhua* stocks and other depleted fish stocks. MacKinnell *et al*. (1997) developed an approach to quantify or estimate the probability of non-random tag aggregations for steelhead trout *Oncorhynchus mykiss* (Walbaum 1792) in the North Pacific Ocean. This approach is based on a description of the coincidence of recovery of tagged fish that were released at the same times and locations, and recovered together after some time at liberty. It has also been used for Pacific herring *Clupea pallasi* Valenciennes 1847 recaptured 6 months after their release (Hay & MacKinnell, 2002).

A recovery strategy and better fisheries management should consider both migratory behaviour patterns and other factors related to *G. morhua* behaviour. The

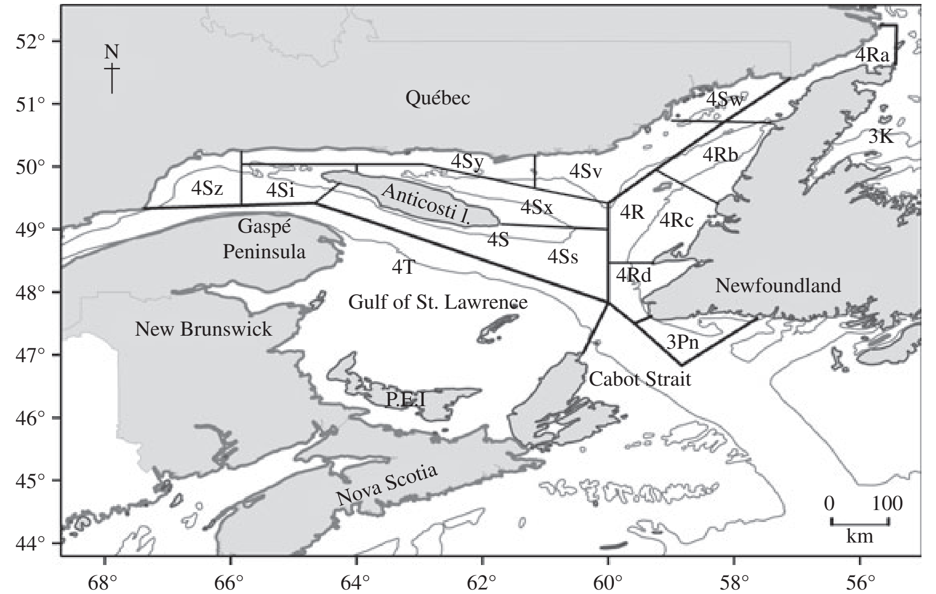

Fig. 1. The Gulf of St Lawrence and Northwest Atlantic Fisheries Organization (NAFO) Divisions. The study area is the northern Gulf of St Lawrence, which includes divisions 4R and 4S and subdivision 3Pn. Unit areas such as 4Ra, 4Rb, 4Rc and 4Rd are also shown. The grey lines delineate the 200 m isobath.

migration pattern of *G. morhua* in the northern Gulf of St Lawrence (divisions 3Pn4RS; Fig. 1) is well known. In winter, *G. morhua* is located outside the Gulf of St Lawrence on the northern side of Cabot Strait off the south-west coast of Newfoundland, including Burgeo Bank (Campana *et al.*, 1999; Méthot *et al.*, 2005). In spring, they move to the north (divisions 4R and 4S) for spawning (Ouellet *et al.*, 1997). They then disperse along the shore during the postspawning feeding period. They migrate back to the northern side of Cabot Strait (division 3P) outside the Gulf of St Lawrence in late autumn and early winter (Chouinard & Fréchet 1994; Castonguay *et al.*, 1999; Yvelin *et al.*, 2005). This study was based on tagging–recapture data collected in a period of high abundance (1983–1986) by the Department of Fisheries and Oceans Canada (DFO), and the Ministère de l'Agriculture et des Pêcheries et de l'Alimentation du Québec (MAPAQ) as well as on tagging–recapture data collected in a period of low abundance (1995–2008) by DFO. The first goal of the present work is to characterize and quantify the homing of *G. morhua* in the northern Gulf St Lawrence between two periods, the 1980s and 1996–2008, as well as across seasons. For the first time, the temporal stability of homing, beyond 1 year after release was examined. The second goal was to examine the occurrence of matching tag recoveries (*i.e.* fish tagged and recaptured together) to test the hypothesis that the frequency of matching tag recoveries occurred by chance only through random mixing of tagged fish before their recapture during fishing operations. In other words, all *G. morhua* recovered from a release event occurred with no more co-ordination among their recovered members than with members of other release events. The alternative hypothesis is that at least some of the recovered tagged fish of a given release event remain together and stay associated with other fish from the same release site.

MATERIALS AND METHODS

STUDY AREA

The Gulf of St Lawrence is a semi-enclosed sea located in eastern Canada that includes Northwest Atlantic Fisheries Organization (NAFO) divisions 4R, 4S and 4T (Fig. 1). The study area is the northern Gulf of St Lawrence (NAFO divisions 4R and 4S) and NAFO subdivision 3Pn, which represents a total surface area of 130 000 km^2 (Fig. 1). The northern Gulf of St Lawrence is physically and topographically heterogeneous and characterized by highly variable bathymetry, with a maximum depth of *c*. 500 m; it is dominated by shallow coastal shelves with deep trenches that bisect both the eastern and northern extensions (Koutitonsky & Bugden, 1991). As a boreal marine ecosystem and semi-enclosed sea, the Gulf of St Lawrence experiences strong interannual variability in water and ice properties (Smith *et al*., 2006). This variability may potentially hinder the migrations of several fish species, including *G. morhua*.

TAGGING AND RECAPTURE DATA

The first tagging programme was operated mostly in July and August from 1983 to 1985 by MAPAQ. About 15 000 tagged fish were released on the lower north shore of Gulf of St Lawrence (division 4S). A second tagging programme was run by DFO primarily during July and August from 1983 to 1985. Nearly 29 000 tagged fish were released throughout the northern Gulf of St Lawrence (divisions 4RS). For both programmes, fish were initially captured using bottom trawls or *G. morhua* traps. Details concerning tagging methods are presented in Gascon *et al*. (1990).

In the recent period (tagging years 1995–2007), over 60 000 tagged *G. morhua* were released by DFO in the northern Gulf of St Lawrence. The tagging programme operated annually from February to December in division 3Pn and from June to December in divisions 4RS. Fish were captured by the fixed gear commercial fishery (long lines, feathered hooks and *G. morhua* traps). Only fish >43 cm (≥4 years) total length (L_T) and in good condition were used for tagging. Further details concerning tagging methods are presented in Bérubé & Fréchet (2001).

The present study considers only fish that had made a complete migration cycle before recapture, *i.e.* at least 1 year after tagging (≥365 days). It also compares two periods, the 1980s, characterized by a high abundance of *G. morhua* and the recent period (recapture years 1996–2008) of low abundance.

ESTABLISHING EVIDENCE FOR HOMING BEHAVIOUR

In the search for evidence of homing, only fish that were recovered 1, 2 and 3 years after tagging ±15 days were considered from the total tagging data set (Yvelin *et al*., 2005). The ±15 day lag was defined arbitrarily, but is expected to allow a better characterisation and quantification of homing beyond 1 year after release. For the 1980s data, there were insufficient recaptures within 2 years of tagging to allow statistical analysis. Estimates of the distance between release and recovery for each release and recovery event were made by comparing the latitude and longitude of positions for each release and recovery record. Simple triangulation was used to estimate the distance (km) between release and recovery. This approach has been used for *H. Stenolepis* (Loher, 2008), *G. morhua* (Yvelin *et al*., 2005; Howell *et al*., 2008) and *Clupea pallasii* (Hay & MacKinnell, 2002). As always with tagging studies, the actual distances travelled by *G. morhua* are underestimated because a straight line is assumed between the mark and recapture locations.

Recapture data were then subdivided in two groups according to the recapture seasons: spring and autumn and summer. In this paper, spring and autumn were combined to have enough recaptures. The cumulative distribution of recapture percentages according to the distance from the release site was calculated considering the two periods (1980s and 1996–2008) and the two seasons (spring and autumn and summer). Most of the recaptures (70·3%) by the commercial fishery were made in summer (July, August and September) when *G.*

morhua are known to disperse on their feeding grounds. Kolmogorov–Smirnov tests (Zar, 1984) were used to test the temporal stability of homing between the 1980s and the recent period, and between 1, 2 and 3 years after tagging in the recent period and within the same season.

ESTIMATING THE PROBABILITY OF NON-RANDOM MATCHES

The approach was originally developed by MacKinnell *et al*. (1997) for *O. mykiss* and was also used for *C. pallasii* (Hay & MacKinnell, 2002); it was adapted for *G. morhua*. Three different events were defined, each with specific dates and locations: (1) a tag release event was the release of tagged fish at a specific location and date, (2) a tag recovery event was the recovery, at a specific location, of one or more tagged fish originating from one or more release events and (3) a release–recovery event was the number of unique combinations of release and recovery events. For instance, single recovery events often recovered two or more tagged *G. morhua* from several release events. Tag recoveries were considered to be matching (*e.g.* pairs and triples) if two or more tagged fish from the same release event were caught in the same recovery event and specific area. While tag recoveries ±15 days of the tagging date were used for establishing homing, all recoveries made at least 1 year after tagging were used for the study of non-random matches. In order to avoid the possible bias induced by individuals that do not migrate (*e.g.* residents in 3Pn area), or that were re-associated due to homing behaviour, only fish recaptured outside their tagging region were considered in the analyses. The regions refer to the fishing statistical areas shown in Fig. 1. The average distance between tagging and recapture sites was estimated to be 98·5 km. It should be noted that the ±15 day recapture window was not used in this analysis of cohesion.

To quantify how the observed numbers of matching recoveries were distributed, the probability distribution was tested under the null hypothesis that all *G. morhua* recovered from any release group migrated in the northern Gulf of St Lawrence with no co-ordination with any other *G. morhua*. This means that the observed distribution of matches would only be due to a random mixing of fish. The alternative hypothesis (the alternative distribution) is that recovered individuals originated from the same tagging event and that the observed distribution could be due to group cohesion (*i.e.* individual fish travelling together between capture and recapture). It was assumed that *G. morhua* tagged in the 1980s and fish tagged recently (*i.e.* separated by at least 10 years) could not possibly mix.

For both time periods, the observed distribution resulting from the number and size of successful recovery events and their matching recoveries (*e.g.* pairs and triples) was determined. In order to test the null hypothesis, a random mixing of tag recoveries was simulated according to the method described by MacKinnell *et al*. (1997). A series of random distributions of tagged fish, was simulated from 10 000 Monte-Carlo trials, and the numbers and types of matches were recorded in each distribution (Hay & MacKinnell, 2002). To test the null hypothesis, the observed distribution was compared to the simulated one, using a right-tail χ^2 test, as was done for *O. mykiss* (MacKinnell *et al*., 1997). The same hypothesis was tested from data of each time period for three categories: fish at large for 1 year, for 2 years and for ≥3 years. Analyses were done with an algorithm developed in the R software, using the nperm function (www. r-project.org).

RESULTS

Between 1983 and 1986, a total of 458 tags were at large for ≥1 year (Table I). This subset of the data included tags released and recovered in the northern Gulf of St Lawrence and northeast of Newfoundland (division 3K; Fig. 1). From 11 to 86% of tags were recovered in their release subarea for the period 1984–1986 (Table I). In the recent period, a total of 1848 tagged and recovered *G. morhua* had made at least one complete migration cycle, *i.e.* at least 1 year after tagging (Table II). This

TABLE I. Subset of tag recovery data used for the Monte-Carlo test of non-random association among individual *Gadus morhua* for the 1984–1986 period. The release and recovery regions are broken down by unit areas identified in Fig. 1

	Recovery region										
	3K	3Pn	4Ra	4Rb	4Rc	4Rd	4Si	4Sv	4Sw	4Sy	Total
Release region											
4Ra	63	5	**35** (44%)	1	0	6	0	0	2	1	113
4Rb	0	0	4	**7** (44%)	1	4	0	0	0	0	16
4Rc	0	0	2	0	**5** (38%)	1	0	1	0	0	9
4Si	0	0	1	0	0	0	**7** (11%)	0	0	2	10
4Sv	0	0	1	0	0	0	0	**6** (35%)	5	0	12
4Sw	2	3	21	1	1	0	0	1	**81** (86%)	9	119
4Sy	0	6	15	7	6	7	57	9	6	**66** (85%)	179
Total	65	14	79	16	13	18	64	17	94	78	458

Note: Only tags recovered ≥1 year after tagging were used. Tags recovered in the release area are shown in bold, with percentages in parentheses.

subset included tags released and recovered from all regions of the northern Gulf of St Lawrence. From 28 to 81% of tagged *G. morhua* were recaptured within their release unit area (Table II).

HOMING BEHAVIOUR

In the 1980s, 163 tagged *G. morhua* were recaptured during three seasons (spring, autumn and summer) and that had been at liberty for 365 ± 15 days. The majority of such recaptures (94) occurred in the summer, with 50% of recaptures located

TABLE II. Subset of tag recovery data used for the Monte-Carlo test of non-random association among individual *Gadus morhua* for the 1996–2008 period. The release and recovery regions are broken down by unit areas identified in Fig. 1

	Recovery region							
	3Pn	4Ra	4Rb	4Rc	4Rd	4Sv	4Sw	Total
Release region								
3Pn	**484** (81%)	41	69	74	160	6	10	844
4Ra	33	**149** (54%)	47	10	11	13	50	313
4Rb	22	32	**194** (53%)	23	14	4	3	292
4Rc	29	12	42	**75** (38%)	22	1	2	183
4Rd	25	1	6	10	**82** (28%)	0	0	124
4Sv	0	5	2	1	0	**9** (35%)	3	20
4Sw	2	33	4	0	3	0	**30** (30%)	72
Total	595	278	368	189	292	26	100	1848

Note: Only tags recovered ≥1 year or more after tagging were used. Tags recovered in the release area are shown in bold, with percentages in parentheses.

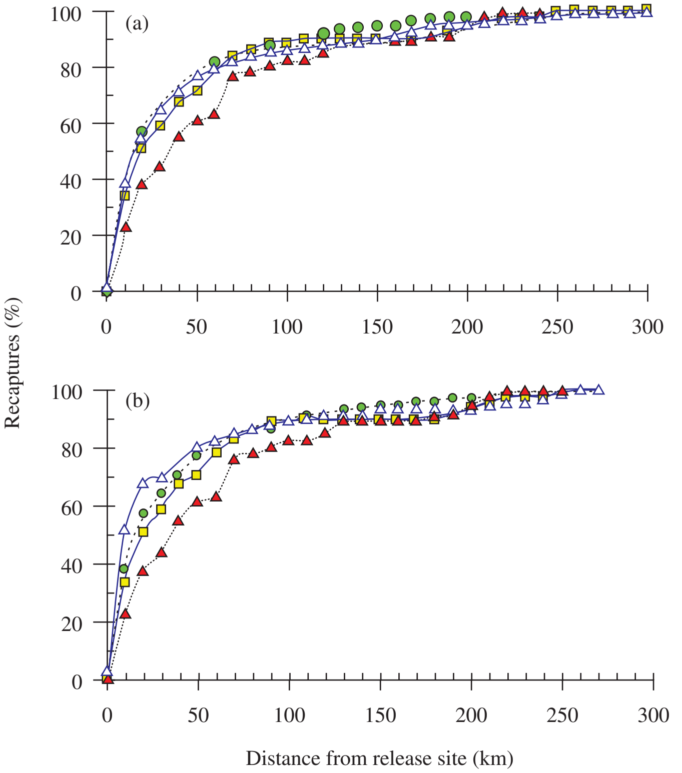

FIG. 2. Cumulative distribution (%) of recaptures according to distance travelled, for 1 year (—△—) in 1984–1986 and 1 (··●··), 2 (—■—) and 3 (····▲····) in 1996–2008 in years ±15 days after release (a) spring and autumn combined and (b) summer.

<9·6 km and 75% within 40·8 km of their release locations (Fig. 2). For spring and autumn, 50 and 75% of recaptures were located at <16·3 and <43·7 km of their release sites (Fig. 2).

In the recent period, 140 tagged fish were recaptured in summer 1 year ± 15 days after tagging, 80 were recaptured after 2 years and 47 were recaptured after 3 years; for spring and autumn, 91, 44 and 11 fish were recaptured after 1, 2 or 3 years. One year after tagging, 50 and 75% of recaptures were located within 15·4 and 40·5 km of their release location for spring and autumn, and at 16·3 and 46·7 km for summer [Fig. 2(a), (b)]. Two years after release, recaptures were located within 17·9 km (50%) and 41·3 km (75%) for spring and autumn and within 19·3 km (50%) and 55·0 km (75%) for summer. After 3 years, the recaptures were located within 32·5 km (50%) and 52·5 km (75%) for spring and autumn and within 33·8 km (50%) and 68·8 km (75%) for summer [Fig. 2(a), (b)].

Comparing cumulative distributions of distances between mark and recapture sites between the 1980s and the recent period 1, 2 and 3 years after tagging, homing fish showed no significant difference. Moreover, although a slight degradation of homing through time (1, 2 and 3 years after tagging) for the recent period was observed, it was not significant. Differences between seasons were also not significant.

TABLE III. Results of tests of association of *Gadus morhua* recaptures calculated separately for the 1996–2008 and 1984–1986 periods. For example, in the 1996–2008 period, there were 27 cases where three tagged fish were recaptured together, with 23 of those triplets being fish that had been tagged together (same time and place)

Period	Number of tags in recovery events	Frequency	Total number of tags	Observed number of matches	Probability of random mixing
	1	557	557		
	2	99	198	58	
1996–2008	3	27	81	23	$P < 0{\cdot}001$
	4	6	24	7	
	5	2	10	3	
	All	691	870	91	
	1	135	135		
	2	30	60	25	
1984–1986	3	14	42	13	
	4	6	24	7	$P < 0{\cdot}002$
	5	4	20	5	
	All	189	281	50	

Note: Only tags recovered ≥1 year after tagging and outside their release region were used.

PROBABILITY OF ASSOCIATION OCCURRING BY CHANCE

The maximum number of *G. morhua* tagged that was observed in a single recovery event was five tagged fish. This occurred four times in the 1980s and twice in the recent period (Table III). The observed matches in all recovery events were 17·8 and 10·5% for the 1980s and the recent period (Table III). The Monte-Carlo test of the non-random co-occurrence hypothesis for all *G. morhua* recovered and for those that had completed at least one migration cycle in the 1980s and the 1996–2008 period was significant ($P < 0{\cdot}001$; Table III). These results show that the released cod groups remain together for >1 year after release during both periods, *i.e.* the association of individuals of the same group over time is not due to chance.

For the recent period, after 1, 2 or ≥3 years at liberty, the observed matches in all recoveries were *c*. 11·5, 11·6 and 7·1% for 1, 2 and 3+ years. Over time, the numbers of matches observed tended to decrease. The Monte-Carlo test of the hypothesis was significant (1 and 2 years: $P < 0{\cdot}001$; 3 years: $P < 0{\cdot}01$; Table IV). These results show that *G. morhua* groups remain together for 1, 2 or 3 years after release. This behaviour appears to be stable at least over the medium term and probably also over a longer term.

DISCUSSION

It is important, while interpreting the results, to consider biases and limitations linked to the use of mark–recapture data. Recapture data are related to fishing activities and the distribution of fishing effort. In the northern Gulf of St Lawrence, fishing activities are only prosecuted by fixed gears, and are, therefore, spatially localized. In

TABLE IV. Results of tests of association of *Gadus morhua* recaptures calculated separately for 1–3 years after release and outside their release region in the recent period (1996–2008)

Recapture years after tagging	Number of tags in recovery events	Frequency	Total number of tags	Observed number of matches	Probability of random mixing
1	1	264	264		
	2	47	94	28	
	3	18	54	15	$P < 0.001$
	4	3	12	4	
	5	2	10	3	
	All	334	434	50	
2	1	145	145		
	2	29	58	19	
	3	6	18	6	$P < 0.001$
	4	1	4	1	
	All	181	225	26	
≥3	1	148	148		
	2	23	46	11	
	3	3	9	2	$P < 0.01$
	4	2	8	2	
	All	255	380	15	

addition, because tagging data come from fishermen, the precision of recapture location and date may vary. Spatial and temporal coverage is incomplete, and, therefore, the inference of conclusions to the entire population should be made with caution. Recaptures, however, are actual observations that can be interpreted, and the overall conclusions should not be affected by the possible bias induced by the fishing effort.

The *G. morhua* population in the northern Gulf of St Lawrence undertakes regular long distance (hundreds of kilometres) seasonal migrations between feeding, overwintering and spawning locations (Templeman, 1979; Castonguay *et al*., 1999; Yvelin *et al*., 2005). Despite this long-distance migration, between 11 and 86% returned in subsequent years to the same feeding or spawning ground based on fish recaptures after at least 1 year at liberty in the 1980s and the 1996–2008 period (see Tables I and II). *Gadus morhua* populations exhibiting similar homing behaviour have been documented elsewhere (Godø, 1984; Taggart, 1997; Robichaud & Rose, 2001, Windle & Rose, 2005; Wright *et al*., 2006; Righton *et al*., 2007).

The present results confirm that *G. morhua* populations in the northern Gulf of St Lawrence exhibited homing behaviour, and show, for the first time, the relative stability of this homing behaviour through seasons and years. There were no differences in homing between the pre-collapse period of the 1980s and recent post-collapse period. Furthermore, there was no significant difference between seasons. Given the variable spatial resolution of the tagging data in the literature, the distance at which recaptures were considered to be near the release locations or regions could not be held constant across experiments. For example, McKenzie (1956) considered recaptures within 22 km to be near the release site, while Taggart *et al*. (1998) used 54 km; other authors considered recaptures within 100 km to be near the release site (Lear, 1984; Hovgård & Christensen, 1990). The present results are in the range defined by Taggart *et al*. (1998): 50% of recaptured fish were caught <34 km from their mark site, even 3 years after release within the same season. The same homing behaviour and stability through seasons in the 1996–2008 period were also observed for *G. morhua* recaptured 1, 2 and 3 years after their release. A slight degradation of homing, however, was observed as the time between mark and recapture increased. For example, during summer, 50% of recaptured *G. morhua* were caught within 16·3, 19·3 and 33·8 km of their release site 1, 2 and 3 years after their release. Despite the increasing distance between the mark and recapture sites over time, the difference was not significant, suggesting that the *G. morhua* population in the northern Gulf of St Lawrence exhibits relative stability in homing behaviour through time and for comparable seasons.

On the basis of migratory tendencies, four categories of *G. morhua* populations were proposed by Robichaud & Rose (2004): 'sedentary residents' that exhibit year-round site fidelity, 'accurate homers' that return to specific spawning or feeding areas, 'inaccurate homers' that home to a much broader area around the original release region in subsequent years, and 'dispersers' that move and spawn in a haphazard pattern over large geographical areas. The *G. morhua* population in the northern Gulf of St Lawrence could be described as accurate homers since they seem to return to the same areas year after year. Homing behaviour has been observed in a number of pelagic and demersal species, most notably anadromous species. Species include salmonids (Dittman & Quinn, 1996; Candy & Beacham, 2000), yellowfin tuna *Thunnus albacares* (Bonnaterre 1788) (Klimley & Holloway, 1999), Atlantic herring *Clupea harengus* L. 1758 and *C. pallasii* (McQuinn, 1997; Hay *et al*., 2001), *H. stenolepis* (Loher, 2008) and *G. morhua* (Gascon *et al*., 1997; Robichaud & Rose, 2001, 2004; Svedäng *et al*., 2007). Understanding the processes involved in these homing behaviours is fundamental for effective management measures to enable the conservation and to rebuild depleted fish stocks, such as Canadian *G. morhua* stocks.

Co-occurrence of individual *G. morhua* in time and space was found to be significantly non-random for fish that had made at least complete migration cycle. The results, based on fish recaptured outside their tagging area, confirm that the positive association is neither due to sedentary individuals (such as in 3Pn area) nor to homing behaviour. These results show that there is a positive association among tagged fish released in the same region. In the recent period, the positive association persists even 3 years after release. Such results suggest that tagged *G. morhua* from a single release region continue to associate with each other during seasonal movements throughout the northern Gulf of St Lawrence and that such associations persist through time, for at least 3 years. The same behaviour has been reported for at least 6 months after release for both *C. pallassii* (Hay & MacKinnell, 2002) and *O. mykiss* (MacKinnell *et al*., 1997) in the Pacific Ocean. An alternate explanation for the present results is that some *G. morhua* tagged and released together do not necessarily associate at all, but rather mix randomly and then home to the same spawning or feeding region. In this case, the incidence of matched tags could be a consequence of a re-association of tagged fish homing to the spawning or feeding grounds, since the degree of homing (fidelity) of *G. morhua* to specific locations is relatively high (Gascon *et al*., 1997; Robichaud & Rose, 2001, 2004; Wright *et al*., 2006). The fact that re-associations were obtained from individuals recaptured in following years outside their tagging region, however, indicates that group cohesion rather than site fidelity is responsible for the observed re-associations between individual fish.

Group cohesion suggests that there may be a level of structure in sub-groups or metapopulations constituting larger populations that prevents thorough mixing. If so, most *G. morhua* aggregations observed overwintering, spawning and feeding in Newfoundland and Labrador (Lawson & Rose, 2000; Morris & Green, 2002; Rose *et al*., 2011) and on Georges Bank (Mountain & Murawski, 1992) could represent aggregations of different stock components, each with its own sub-population characteristics. According to Bakun & Cury (1999), the ability to return to suitable locations could be due to certain individuals that would guide the smaller components in which the others would be entrained (school trap effect). The disappearance of these guides could have a negative effect on the rebuilding of different sub-stocks of *G. morhua*, such as the abandonment of habitats even if they are suitable.

The present study suggests that there may be even smaller structures within *G. morhua* populations in the northern Gulf of St Lawrence. This structure at a fine spatial scale within cod populations has been already reported by Swain & Frank (2000) in the southern Gulf of St Lawrence (division 4T), based on a study of vertebral numbers. In the future, genetic methods such as microsatellite markers could be used to examine the degree of affinity of such small groups and determine if siblings are present, as was found for brook charr *Salvelinus fontinalis* (Mitchill 1814) groups in Mistassini Lake in Québec (Fraser *et al*., 2005).

Homing behaviour and group cohesion may be fundamental for developing strategies to rebuild northern Gulf of St Lawrence *G. morhua* and other similarly depleted fish stocks. The study demonstrates that these fish exhibit group cohesion in time and space, which can be characterized as homing. The stability of homing and cohesion may lead to resistance to mixing, expansion and colonization of new habitat, as reported by Svedäng *et al*. (2007). It could, however, promote the recovery of local populations at small scales. In addition, density-dependent habitat selection could promote recovery strategies, especially with respect to rebuilding *G. morhua* in the northern Gulf of St Lawrence (Tamdrari *et al*., 2010). Homing as well as group cohesion and density-dependent habitat selection are important population features that need to be taken into account for managing depleted populations such as northern Gulf of St Lawrence *G. morhua* for the purpose of promoting management policies to allow collapsed fish stocks to rebuild.

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