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Genetic Characterization of the Northern Shrimp, *Pandalus borealis*, in the Northwest Atlantic

by

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Abstract

The genetic variability of the northern shrimp, *Pandalus borealis*, collected in the Saguenay Fjord, in six areas of the Estuary and the Gulf of St. Lawrence, and in two areas off the Labrador-Newfoundland coast was assessed using eight enzymatic loci. Males, primiparous and multiparous females were sampled at all but the Rimouski site in order to determine if gene frequencies within these regions of the Northwest Atlantic are temporally stable. For this species, variation of the genetic characteristics on a geographic scale and among maturity stages was largely determined by the variation occurring at the *EST**, *HEX-1** and to a lesser extent at the *HEX-2** loci. The other loci did not vary significantly either on a geographic or temporal scales. Deviations from Hardy-Weinberg expectations, all of them due to deficits in heterozygotes, were observed mainly at the same three loci and the number of deviations increases when males, primiparous and multiparous females were pooled. A cluster analysis of genetic distance did not reveal geographic patterns in the clustering of the samples. Although some rare private alleles were detected in the Gulf of St. Lawrence samples, the data suggest that gene flow is extensive across the study area.

Introduction

The northern shrimp (*Pandalus borealis*) is an amphiboreal protandric hermaphrodite crustacean found in the high latitude of the Atlantic and the Pacific Oceans (Ivanov, 1972; Shumway *et al.,* 1985). The species is commercially exploited in both oceans. In the Northwest Atlantic, it is distributed from the Gulf of Maine to the Davis Strait. In the St. Lawrence system, this species can be found from West Newfoundland to the Saguenay fjord. The exploited aggregations are found in the Maritime Estuary and, in the Western Gulf of St. Lawrence, around Anticosti Island and in the Esquiman Channel, in NAFO Divisions 4RS and the western part of 4T (Lambert *et al.,* 1998). In the Labrador and Newfoundland system, northern shrimp is exploited off Baffin Island, Labrador (Hopedale, Cartwright and Hawke Channels) and northwestern Newfoundland in NAFO Divisions 0B, 2GHJ and 3K (Parsons *et al.,* 1999).

Despite the economic importance of the northern shrimp, there has been only few studies that have attempted to describe its population genetic structure. Most of these studies were carried out in the Far Eastern Seas (Kartavtsev *et al.*, 1991; Kartavtsev *et al.*, 1993) and the Northeast Atlantic (Jónsdóttir *et al.*, 1998). Some of these studies have shown that shrimp originating from distant seas such as the Barents and the Bering seas, the sea of Japan and the Gulf of St. Lawrence are clearly genetically differentiated from each other (Kartavtsev *et al.*, 1991; Kartavtsev *et al.*, 1993; Kartavtsev, 1994). However, the possibility of observing genetically differentiated populations over shorter distance is not well established. Indeed, while some studies have shown that populations of shrimp were homogeneous within seas and that this homogeneity appears to be stable through time (Kartavtsev *et al*., 1991; Kartavtsev *et al*., 1993; Kartavtsev, 1994), another has detected differences in allelic frequencies at allozyme loci between shrimp collected inshore Iceland and those collected offshore Iceland and in the Denmark Strait (Jónsdóttir *et al*., 1998). Our knowledge of the genetic structure of the northern shrimp in the Northwest Atlantic is more limited as the geographic coverage of the few studies conducted so far have been largely restricted to the Gulf of St. Lawrence. These preliminary studies have pointed at the possible existence of heterogeneity in allelic frequencies among samples collected in the Gulf of St. Lawrence (Savard, 1989; Savard *et al*., 1993; Sévigny, 1994).

The goal of the present study was to describe genetic variability of the northern shrimp in different areas of the Northwest Atlantic, more specifically in the St. Lawrence system and along the east Labrador-Newfoundland coast, to determine if the genetic variation patterns observed support the hypothesis that genetically differentiated populations are present in Eastern Canada. The description of genetic variation presented in this study is based on allozyme loci and includes samples collected over a large geographic area. Males, primiparous and multiparous females were sampled at several sites in order to assess the importance of the temporal variability, since these maturity stages are believed to represent different cohorts or age groups as sex inversion is assumed to be synchronous within cohorts. Indeed, genetic difference on geographic scale will indicate that populations are relatively isolated and self-recruiting if the difference observed is stable through time. By contrast, if temporal variation is important, the genetic difference observed among sites might be modified between generations if genetically different cohorts are recruited (David *et al*., 1997; Li and Hedgecock, 1998 for discussion). More specifically, the objectives of the present study were to determine:

1) if genetically isolated populations are present within the Gulf of St. Lawrence;
2) if genetically isolated populations are present along the Labrador-Newfoundland coast;
3) if the populations from the Gulf of St Lawrence are isolated from those of the Atlantic coast;
4) if the genetic characteristics described are temporally stable.

Material and Methods

Sampling and sample preservation

Samples were collected within commercially exploited shrimp aggregations in the Estuary and the Gulf of St. Lawrence as well as in Hawke and Hopedale channels on the Labrador coast. Samples were also collected in the Saguenay fjord, which sustains a peripheral unexploited population. In the St. Lawrence system and in the Atlantic, the samples were collected using a bottom trawl from August to September 1990 (Fig. 1). They were collected in one tow at the Rimouski site, in two different tows at Pointe-des-Monts, Sept-Îles, North and South Anticosti sites and, over much larger areas from 10 to 12 different tows in the Esquiman Channel, Hawke Channel and Hopedale Channel. Samples from the Saguenay fjord were collected with baited traps during the summer 1990 in the Baie des Ha! Ha!, at Sainte-Rose-du-Nord and at Baie Trinité (Sévigny 1994). For the present study, these three sampling stations are considered part of the same site.

Sampled shrimp were classified into three maturity stages representing at least three different age groups: males, primiparous and multiparous females (Table 1). Individuals were sexed from the characteristics of the first pleopod endopodite (Rasmussen, 1953). The separation between primiparous and multiparous females was based on the presence or absence of sternal spines located on the midventral face of the first four abdominal segments (McCrary, 1971). Specimens were dissected on board and samples of abdominal muscle and hepatopancreas tissue were frozen either in liquid nitrogen or in dry ice and transported to the Maurice Lamontagne Institute, where they were transferred to an ultracold freezer (-80°C) pending genetic analyses. Whole specimens from the Esquiman Channel and of the Saguenay Fjord where frozen on board in liquid nitrogen and dry ice respectively. They were dissected in the laboratory prior to electrophoresis analyses.

Allozyme analysis

Tissue homogenates were prepared according to the procedure described in Roby *et al*. (1991). All allozymes were assayed on cellulose acetate gels using the technique of Hebert and Beaton (1989), except for esterases which were studied on discontinuous polyacrylamide slab gels (Ornstein, 1964). Enzyme activities were visualised according to the standard staining procedure described by Murphy *et al*., (1990). All staining solutions other than esterases were incorporated in a 1% agar overlay. The bands of activity which were consistently detected in the hepatopancreas extracts without specific substrat and with MTT and PMS were tentatively attributed to the activity of the tetrazolium reductase (TR). Specimen of known genotype were used as standards on every gel to assess both the quality of the electrophoretic separation and to ensure the accuracy of allele identification. Uncommon alleles at each locus were re-run simultaneously to ascertain their classification.

Statistical analysis

Allele frequencies and other population genetic statistics such as the F statistics (F_{IS} and F_{ST}) observed and expected heterozygosities were calculated for each locus using the Biosys-1 computer program of Swofford and Selander (1989). This program was also used to test for deviations from Hardy-Weinberg expectations at all sites using the chi-square (χ^2) test of goodness-of-fit. When more than two alleles were observed at a locus, genotypes were pooled into three classes representing the homozygotes for the most common allele, the heterozygotes for the most common allele and all other genotypes. Tests of conformance to Hardy-Weinberg equilibrium were carried out for each maturity group within sites and for all the maturity stages pooled at each site. These tests could not be performed for the *GPI** and *PGM** loci for any of the maturity stages and for the maturity stages pooled due to the low variability detected at these loci. Furthermore, these could not be performed at the site Rimouski for the primiparous and the multiparous females due to the low number of individuals belonging to these maturity stages collected at this site.

Differences in allelic frequencies between males, primiparous and multiparous females within sites and heterogeneity in allelic frequencies among sampling sites within the Gulf of St. Lawrence, within the Labrador Sea and across the study area were tested for significance using the Monte Carlo randomization procedure (Rohlf and Bentzen, 1989) described in the software Reap (McElroy *et al*., 1992). The advantage of this procedure is that it allows testing without grouping rare alleles. Despite this procedure, comparison of allelic frequencies among maturity stages could not be carried out at the loci *GPI** and *PGM** because the variability detected at these loci was too low. Furthermore, the comparison among maturity groups could not be carried out at the site Rimouski for any loci because of the low number of primiparous and multiparous females collected at this site. Sequential Bonferroni tests were used to maintained the overall significance level $\alpha = 0.05$ as recommended by Rice (1989). However, since this procedure has been challenged (Perneger, 1998), the results of all statistical tests are provided when it is relevant.

The F statistic analysis was used to characterise the genetic variance into that occurring within populations (F_{IS}) and that occurring between populations (F_{ST}). The chi-square tests described in Waples (1987) were used to evaluate the null hypothesis of $F_{ST} = 0$. In these tests, the χ^2 values were calculated according to the equation: $2nF_{ST}(K\text{-}1)$ with degrees of freedom equals to $(K\text{-}1)(S\text{-}1)$. Similarly, the significance of F_{IS} was tested using the equation: $n(F_{IS})^2(K\text{-}1)$ with degrees of freedom equals to $(K(K\text{-}1))/2$. In these equations n is the total number of individuals sampled, K is the number of alleles at the locus and S represents the number of populations sampled.

Gene flow and the number of migrants were estimated from Wright's fixation index according to the formula:

$$F_{ST} = 1/(1 + 4N_e m),$$

where m is the migration rate and N_e is the effective number of individuals (Wright, 1969).

Absolute differentiation between populations was estimated using Nei (1978) unbiased and Cavalli-Sforza and Edwards (1967) chord genetic distances.

Results

Genetic variability was detected at eight enzymatic systems four of which were better resolved in the hepatopancreas (Table 2). The number of alleles observed at these loci varies from 2 to 6 (Table 2). Genetic variability was the lowest at the *GPI** locus which was variable in only two sites. For this locus, one heterozygous individual only was detected at the site Rimouski and two at Esquiman Channel. This locus was analysed despite its low variability for comparison with previous studies (Kartavtsev *et al*., 1991; Kartavtsev *et al*., 1993; Kartavtsev, 1994; Jónsdóttir *et al*., 1998). Genetic variability was also low at the locus *PGM** with observed heterozygosities varying between 0.007 for the pooled maturity stages in Saguenay Fjord and 0.063 for the primiparous females in the Hopedale Channel (Table 3). When the maturity stages are considered separately, the lowest value of mean observed heterozygosity was 0.164 for the primiparous females collected at the site South Anticosti while the highest value of 0.258 was estimated for the males from Hawke Channel (Table 3). Mean observed heterozygosity evaluated for all the maturity stages pooled varied from 0.204 for the site South Anticosti to 0.242 for the site Esquiman Channel. There was no apparent trend in heterozygosity change among maturity stages within sites or on the geographical scale (Table 3).

Conformance to Hardy-Weinberg expectations

A general pattern emerges when deviation from Hardy-Weinberg expectations is considered for each maturity stage. Indeed, for all 3 stages, significant deviations were observed mainly at the loci *EST**, *HEX-1** and *HEX-2**. All the deviations were caused by deficits in the number of heterozygotes. For the males, significant departure were detected at the *EST** locus at the sites Rimouski (χ^2 = 20.55, P = 0.000), Septs-Iles (χ^2 = 6.35, P = 0.000), South Anticosti (χ^2 =10.46, P = 0.001) and at Hopedale Channel (χ^2 = 17.07, P = 0.000). Deviations were also observed at the locus *HEX-1** at the sites Sept-Iles (χ^2 = 21.14, P = 0.000) and Hawke Channel (χ^2 = 7.42, P = 0.006) and at the locus *HEX-2** at the sites Rimouski (χ^2 = 33.11, P = 0.000) and Pointe-des-Monts (χ^2 = 7.93, P = 0.005). For the primiparous females, deviations were detected at the *EST** locus at the sites Sept-Iles (χ^2 = 14.81, P = 0.000), South Anticosti (χ^2 = 26.40, P = 0.000), Hawke (χ^2 = 7.834, P = 0.005) and Hopedale (χ^2 = 11.45, P = 0.001) Channels. There was also significant departure from Hardy-Weinberg at the *HEX-1** at Sept-Iles (χ^2 = 10.35, P = 0.001) and North Anticosti (χ^2 = 13.795, P = 0.000). For the multiparous females, deviations from Hardy-Weinberg were observed at the locus *EST** in Sept-Iles (χ^2 = 11.45, P = 0.001), South (χ^2 =24.18, P = 0.000) and North (χ^2 = 8.69, P = 0.003) Anticosti, Esquiman (χ^2 =9.66, P = 0.002) and Hopedale (χ^2 =9.89, P = 0.002) Channels as well as at the locus *HEX-1** in the Saguenay Fjord (χ^2 = 26.22, P = 0.000) and at South (χ^2 = 23.43, P = 0.000) and North (χ^2 = 18.17, P = 0.000) Anticosti. Significant deviation was also observed at the locus *PGDH** in South Anticosti (χ^2 = 8.72, P = 0.003).

Deviations from Hardy-Weinberg were more frequent when all the maturity stages were pooled. Significant deviations were observed at 17 site-loci (Table 4). In this case, significant deviations were largely restricted to the loci *EST** (all sites) and *HEX-1** loci (5 sites). In addition, deviations were observed at the *HEX*-2* (2 sites) and at the locus *MDH** (one site).

The values of F_{IS}, indicating the within-sample genetic structuring differed significantly from zero at the loci *EST**, *HEX-1** and *HEX-2** for maturity stages pooled. All values were positive indicating a deficit in heterozygotes (Table 5).

Genetic variability among maturity stages within sites

A total of 48 randomisation tests were carried out. Of these, significant difference was detected at the *TR** locus in Saguenay Fjord sample (χ^2 = 8.91; P = 0.011) and North Anticosti (χ^2 = 6.22; P = 0.038), at the *HEX-2** locus at Pointe-des-Monts (χ^2 = 11.05; P = 0.002), at the *EST** locus (χ^2 = 24.99; P =0.0000) and *HEX-1** (χ^2 = 15.27; P = 0.004) in Hawke Channel and at the *MDH** locus (χ^2 = 8.54; P = 0.011) in Hopedale Channel. When the Bonferroni procedure (Rice 1989) is applied for each site (critical value of α = 0.008), difference remains significant for the loci *EST**, *HEX-1** and *HEX-2**.

Macrogeographic variation

Significant heterogeneity in allelic frequencies was observed among the sites at the scale of the Northwest Atlantic as well as within each of the two large scale areas investigated, the Gulf of St. Lawrence and the Labrador Sea (Table 6). It is worth noting that all differences in allelic frequencies on the geographic scale are observed at the loci *EST** and *HEX-1** for some but not all the maturity stages and not all the areas investigated. Indeed, in the Gulf of St. Lawrence, significant difference could be detected only at the *HEX-1** locus for the males and at the *EST** and *HEX-1** loci for the pooled samples. In the Labrador Sea, differences were observed only at the *EST** locus for the males, primiparous and maturity stages pooled. At the scale of the Northwest Atlantic, differences were detected at the *EST** locus for the males and the maturity stages pooled and at the *HEX-1** for the males, primiparous and for the pooled maturity stages. No difference could be detected for the multiparous females at any locus in any of the studied area (Table 5). Values of F_{ST} indicating population subdivision ranged from 0.001 to 0.052 for the maturity stages pooled and were significantly different from zero at the loci *EST** and *HEX-1** only (Table 5).

Nine alleles in low frequency (≤ 0.01 at some sites after pooling the maturity stages) were detected (Table 3). Of these alleles, four (*EST*C, EST*D, HEX-1*D, PGM*B*) were present in one or more sites of both the St. Lawrence System and the Labrador Sea. The five other (*EST*C, GPI*B, HEX-1*C, PGDH*C, PGM*C*) were private to the St. Lawrence system. They were often detected at sites separated by large geographic distances and were absent at intermediary sites.

Absolute differentiation among the sampling sites is weak. Unbiased Nei's genetic distances for pooled maturity stages range from 0.000 to 0.011 while that of Cavalli-Sforza and Edwards genetic distances vary from .034 to .099 (Table 7). UPGMA cluster analysis of Cavalli-Sforza and Edwards genetic distances calculated for each maturity stage and for all maturity stages pooled show that genetic differences that exist among shrimp samples do not reveal geographic patterns in the clustering of the samples (Fig. 2). For example, the two samples from the Labrador Sea appear to be more similar to some samples from the Gulf of St. Lawrence than they are to each other. It thus seems that samples separated by large geographic distances are more similar to each other than they are to geographically contiguous samples. The correspondence between genetic and geographic distances does not improve when the analyses are carried out without the loci *EST** and *HEX-1** (results not shown).

Gene flow estimation

Values of N_em calculated at each locus were high except for *HEX-1** (Table 5). An overall value of 25 was estimated from F_{ST} mean value calculated over all loci. The lowest values of N_em were observed at the *EST** and *HEX-1** loci. However, disequilibrium of genotypic proportion as well as significant differences in allelic frequencies among maturity stages were observed at these loci in many samples. The possibility that these changes could result from environmental effects cannot be ruled out. Therefore, the mean N_em was recalculated without taking into account these two loci. When these two loci are omitted, the mean N_em increase to 83 (Table 5).

Discussion

The present study differs from previous ones (Kartavtsev *et al*., 1991; Kartavtsev *et al*., 1993; Kartavtsev, 1994; Jónsdóttir *et al*., 1998) as eight loci from either the squeletal muscle tissue or the hepatopancreas were used to assess genetic variability of the northern shrimp, *P. borealis* in the Northwest Atlantic. Using the hepatopancreas has allowed the resolution of four additional polymorphic loci (Table 2). The loci *GPI**, *PGM** and *MDH** were the only one that were used in all studies that have been carried out so far on the northern shrimp. As it was the case for previous studies, the *GPI** locus showed the lowest variability of all as only three heterozygous individuals were detected in the analyzed samples. Variability at the *PGM** locus is also low in all samples.

There are some differences in the number of alleles detected at the three loci common to all studies carried out in the North Atlantic. In the Barents Sea, Kartavtsev *et al*. (1991) detected two alleles at the *GPI**, the *PGM** and at the *MDH** loci. In the present study, three alleles were detected at the *PGM** locus (Table 2 and 3). Such difference is not surprising given the distance separating the study areas and the fact shrimps from different seas are genetically differentiated (Kartavtsev *et al*., 1991; Kartavtsev *et al*., 1993; Kartavtsev, 1994). There are however, important differences with the study of Jónsdóttir *et al*., (1998) who detected four, six and five alleles at the *GPI** *PGM** and *MDH** loci respectively in samples collected in the Denmark Strait and inshore and offshore Iceland. These differences may be due to the techniques involved, as isolectric focusing was used by Jónsdóttir *et al*., (1998) while cellulose acetate was used in the present one. These differences may also indicate that genetic differentiation has taken place between Northwest (Gulf of St. Lawrence and the Labrador Sea) and Northeast Atlantic populations.

Further studies will be necessary to assess the interaction between populations from both sides of the North Atlantic.

A general picture emerges from the present study.The changes in the genetic statistics such as deviation from Hardy-Weinberg expectations, differences among maturity stages and macrogeographic heterogeneity of allelic frequencies are almost exclusively the results of variation occurring at the *EST** and *HEX-1** loci. This observation applies even though the variability at most of the other loci is high enough to allow the detection of changes in the genetic characteristics of the species. The fact that the pattern of variation detected at the *EST** and *HEX-1** differ from that detected at the other loci suggests that these two loci may not be neutral. Furthermore, it is also at these two loci that significant differences were observed between maturity stages at some sites, an indication that selection may be influencing the variability at these loci. However in the present study, the relevant factors generating the genetic variation observed at these two loci cannot be identified. This study is not the first one that has observed such patterns of variation. For example, deviation from Hardy-Weinberg caused by deficit in heterozygotes was observed at an *EST** locus in the estuarine population of the mud crab (*Macrophthalmus hirtipes*) and was attributed to selection against the heterozygotes (Sin and Jones, 1983). Heterozygote deficiency was also observed at the *EST**, *HEX-1**, *GPI** and *Pt-2** in the crab *Trapezia* (Huber, 1987) and in the spiny lobster (*Panulirus marginatus*) at the *EST-3** and *MPI** locus (Seeb *et al*., 1990). In this species, heterogeneity on the geographical scale as well as difference between years was detected at the *EST-3** loci. Multilocus studies involving other types of molecular markers will be necessary to understand the dynamics of the *EST** and *HEX-1** loci in the northern shrimp.

When the *EST** and *HEX-1** loci are not taken into consideration for the above reasons, there is strong evidence that the northern shrimp belong to a panmictic population in the Northwest Atlantic. This conclusion can be drawn from various lines of evidence. First, none of the other loci showing substantial amount of genetic variability (*HEX-2**, *MDH**, *PGDH** and *TR**) has allow discrimination of differentiated populations at any of the geographical scales considered in this study; within the St. Lawrence system and the Labrador Sea and between these two systems. The variability detected at the loci *HEX-2**, *MDH**, *PGDH** and *TR** should be sufficiently high to confer discrimination power to these loci. Second, the estimate of gene flow (N_em) estimated from the mean F_{ST} values is high (25) across the study area even when *EST** and *HEX-1** loci are included in the calculation. It is worth noting that the smallest N_em value (5) was observed at the *HEX-1** locus. The value further increases to 83 when *EST** and *HEX-1** are not taken into account. Third, among the nine low frequency alleles detected at different loci, four (*EST*C, EST*D, HEX-1*D, PGM*B*) were present in one or more sites of both the St. Lawrence System and the Labrador Sea. The other five alleles (*EST*C, GPI*B, HEX-1*C, PGDH*C, PGM*C*) were private to the St. Lawrence system. Although these may indicate restrictied gene flow (Slatkin, 1985), they were often detected at sites separated by large geographic distances and were absent at intermediary or adjacent sites. Therefore, they may not have been detected at other sites or in the Labrador Sea because of inadequate sample size. Our results are thus in general agreement with those obtained in previous studies that have shown homogeneity within seas (Kartavtsev *et al*., 1991; Kartavtsev, 1994) and differs from that of Jónsdóttir *et al*., (1998) who detected difference over much shorter distances. The genetic distances estimated in that study were however very small.

The lack of genetic differentiation over large geographic distance is not unusual for marine species (Shaklee and Bentzen, 1998; Bohonak, 1999) and several factors may account for the homogeneity observed for the northern shrimp *P. borealis* in the Northwest Atlantic. The geographic distribution of the species in the Northwest Atlantic, although it is characterised by aggregations of commercial importance, is continuous in the deep waters at approximately 300-500 m from the northern tip of the Labrador Shelf to eastern Newfoundland (3L) (Lilly *et al*., 1998). Within the Gulf, the species is continuously distributed from Newfoundland coast to the Saguenay Fjord (Lambert *et al*., 1998). Such a distribution pattern favours gene flow. Furthermore, gene flow in *P. borealis* is most likely determined by the interaction between the duration of the pelagic larval stage and the circulation patterns observed in the Northwest Atlantic (Fig. 3). The two-three month duration of the larval phase provides a mechanism by which stock can recruit from distant populations. The surface circulation patterns would favour such dispersion and subsequent homogenisation not only in the Gulf of St. Lawrence but also throughout the Northwest Atlantic. In the Gulf of St. Lawrence, Ouellet *et al*., (1990) have shown that although the emergence of larvae takes place in areas corresponding to the main aggregations of adults shrimps, they are afterward dispersed by currents and the exchanges may take place between aggregations. *Pandalus borealis* larvae are also broadly distributed along the

Labrador coast; dispersion that may be caused by the circulation patterns in the area (Chaput, 1984). Gene flow does not need to be constant over time to prevent differentiation through random drift. Episodic events of expansion and shift in the geographic distribution of the aggregations of northern shrimp as the one that were observed recently in the Gulf of St. Lawrence (Lambert *et al*., 1998) and in the Labrador Sea (Parsons *et al*., 1999) may constitute a very efficient mechanism to increase gene flow among aggregations.

The distribution of genetic variability observed in *P. borealis* may be comparable to some extent to that observed for the Greenland halibut *Reinhardtius hippoglossoides* that also possess a long-lived pelagic larva (Vis *et al*., 1997 and references therein). The various approaches used (allozymes, mt-DNA, parasites, morphometrics, meristics) for stock discrimination of this species suggest that there is one panmictic population in the Northwest Atlantic and that the Gulf of St. Lawrence population is a self-sustained population which is not completely isolated since migration seems to occur from Labrador Sea. The conclusion regarding the status of the Gulf of St. Lawrence Greenland halibut population was mainly based on the presence of private alleles in the Gulf of St. Lawrence population (Vis *et al*., 1997 and references therein). In the present study, some private alleles were also observed in the Gulf of St. Lawrence while none was observed in the samples collected in the Labrador Sea. As mentioned previously, the presence of private alleles may indicate restricted gene flow but it is very difficult to sample these alleles adequately.

From the present study, it can be concluded that *P. Borealis* is panmictic in the Northwest Atlantic as might be expected from a marine invertebrate with high dispersal potential (Bohonak, 1999). Furthermore, this genetic homogeneity appears to be stable through time. Additional studies will be necessary to describe further the interaction between the Gulf of St. Lawrence and the Northwest Atlantic populations. These future studies should also extend the sampling program to include the Gulf of Maine that was not considered in the present one.

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Table 1. *Pandalus borealis* samples collected for allozyme analyses.

	Maturity stage			
	Male	Female		
Sampling Sites		Primiparous	Multiparous	Total
Saguenay Fjord	30	34	225	289
Rimouski	70	3	7	80
Pointe-des-Monts	50	50	50	150
Sept-Iles	50	50	50	150
South Anticosti	50	50	50	150
North Anticosti	50	50	50	150
Esquiman Channel	13	58	50	121
Hawke Channel	50	49	21	120
Hopedale Channel	47	48	48	143

Table 2. Enzymatic systems used in the genetic characterisation of the northern shrimp, *Pandalus borealis*. The number of observed alleles corresponds to those detected in the samples. H = hepatopancreas; M = muscle.

Enzyme	EC. No.	Observed Loci	Tissue	No of Observed Alleles
Esterase (EST)	3.1.1	1	H	6
Glucose-6-phosphate isomerase (GPI)	5.3.1.9	1	M	2
Hexokinase (HK)	2.7.1.1	*HEX-1**	H	4
		*HEX-2**	H	2
Malate dehydrogenase (MDH)	1.1.1.37	1	M	2
Phosphogluconate dehydrogenase (PGDH)	1.1.1.44	1	H	3
Phosphoglucomutase (PGM)	5.4.2.2	1	M	3
Tetrazolium reductase (TR)		1	H	2

Table 3. Allelic frequencies, observed (H_o) and expected (H_e) heterozygosities and mean observed (H_o) and expected (H_e) heterozygosities at polymorphic loci for the northern shrimp, *Pandalus borealis* (n = sample size). Genetic data for the ma les only are shown for the site Rimouski since sample size of primiparous and multiparous females was low; these data were included in the total.

Locus	Sampled sites																																	
	Saguenay Fjord				Rimouski		Pointe-des-Monts				Sept-Îles				South Anticosti				North Anticosti				Esquiman Channel				Hawke Channel				Hopedale Channel			
	M	PF	M.F.	Tot.	M.	Tot.	M.	P.F.	M.F.	Tot.	M.	P.F.	M.F.	Tot.	M.	P.F.	M.F.	Tot	M.	P.F.	M.F.	Tot	M.	P.F.	M.F.	Tot	M.	P.F.	M.F	Tot.	M.	P.F.	M.F.	Tot.
*EST**																																		
N	28	32	202	262	67	74	50	50	50	150	48	47	48	143	49	49	50	148	50	49	50	149	13	57	50	120	48	46	16	110	43	48	47	138
A	.625	.609	.579	.588	.642	.649	.670	.780	.660	.703	.677	.617	.604	.633	.755	.673	.670	.699	.670	.724	.720	.705	.577	.632	.650	.633	0.7	.826	.563	.741	.581	.604	.638	.609
B	.286	.391	.324	.328	.306	.304	.290	.180	.260	.243	.250	.340	.365	.318	.235	.296	.310	.280	.310	.255	.220	.262	.346	.342	.300	0.3	0.2	.130	.281	.186	.337	.354	.287	.326
C	.018	0	.050	.040	.022	.020	.020	0	.010	.010	.063	.011	.021	.031	0	0	0	0	.020	0	.030	.017	0	0	0	0	0.1	.033	.031	.050	0	0	.011	.004
D	0	0	.012	.010	.022	.020	0	.020	.010	.010	.010	0	0	.003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	.012	0	.011	.007
E	0	0	.007	.006	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	.010	.004	0	0	0	0	0	0	0	0
F	.071	0	.027	.029	.007	.007	.020	.020	.060	.033	0	.032	.010	.014	.010	.031	.020	.020	0	.020	.030	.017	.077	.026	.040	.038	0	.011	.125	.023	.070	.042	.053	.054
Ho	.357	.344	.441	.420	.239	.243	.300	.240	.380	.307	.188	.234	.250	.224	.204	.122	.140	.155	.320	.265	.260	.282	.538	.351	.280	.342	0.3	.174	.500	.282	.186	.250	.255	.232
He	.532	.484	.557	.545	.497	.489	.471	.362	.498	.446	.480	.508	.507	.499	.378	.463	.459	.433	.459	.414	.436	.436	.563	.488	.491	.494	0.4	.303	.607	.415	.550	.513	.512	.522
*GPI**																																		
N	30	34	224	288	70	80	50	50	50	150	50	50	50	150	50	50	50	150	50	50	50	150	13	58	50	121	50	49	21	120	47	48	48	143
A	1	1	1	1	.993	.994	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	.991	.990	.992	1	1	1	1	1	1	1	1
B	0	0	0	0	.007	.006	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	.009	.010	.008	0	0	0	0	0	0	0	0
Ho	0	0	0	0	.014	.013	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	.017	.020	.017	0	0	0	0	0	0	0	0
He	0	0	0	0	.014	.013	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	.017	.020	.016	0	0	0	0	0	0	0	0
*HEX-1**																																		
N	24	31	203	257	69	78	48	50	48	146	47	50	47	144	50	47	47	144	50	49	48	147	12	55	43	110	41	39	12	92	28	41	38	107
A	.938	.952	.926	.930	.652	.686	.958	.900	.927	.928	.904	.880	.904	.896	.980	.947	.936	.955	.840	.745	.760	.782	.958	.909	.837	.886	0.7	.936	.875	.826	.875	.805	.882	.850
B	.042	.048	.067	.062	.333	.301	.042	.100	.073	.072	.096	.110	.085	.097	.020	.053	.064	.045	.160	.255	.229	.214	.042	.073	.140	.095	0.3	.064	.125	.168	.107	.171	.092	.126
C	0	0	0	0	.014	.013	0	0	0	0	0	0	0	0	0	0	0	0	0	0	.010	.003	0	0	0	0	0	0	0	0	0	0	0	0
D	.021	0	.007	.008	0	0	0	0	0	0	0	.010	.011	.007	0	0	0	0	0	0	0	0	0	.018	.023	.018	0	0	0	.005	.018	.024	.026	.023
Ho	.125	.097	.089	.093	.406	.372	.083	.160	.104	.116	.064	.120	.191	.125	.040	.106	.043	.063	.240	.184	.167	.197	.083	.182	.233	.191	0.2	.077	.250	.174	.250	.244	.132	.206
He	.121	.094	.138	.131	.467	.441	.081	.182	.137	.134	.175	.216	.177	.189	.040	.102	.121	.087	.272	.384	.373	.343	.083	.169	.282	.206	0.4	.122	.228	.291	.227	.326	.216	.261
*HEX-2**																																		
N	26	34	203	263	65	74	50	49	50	149	47	49	49	145	50	50	50	150	49	50	50	149	12	58	49	119	43	46	14	103	42	46	47	135
A	.673	.529	.623	.616	.377	.581	.430	.643	.620	.564	.596	.582	.541	.572	.640	.630	.640	.637	.592	.580	.520	.564	.708	.595	.602	.609	0.6	.511	.679	.573	.619	.533	.585	.578
B	.327	.471	.377	.384	.623	.419	.570	.357	.380	.436	.404	.418	.459	.428	.360	.370	.360	.363	.408	.420	.480	.436	.292	.405	.398	.391	0.4	.489	.321	.427	.381	.467	.415	.422
Ho	.269	.412	.409	.395	.138	.541	.300	.388	.360	.349	.383	.429	.347	.386	.600	.340	.520	.487	.449	.360	.400	.403	.417	.397	.469	.429	0.6	.37	.357	.466	.476	.326	.532	.444
He	.449	.506	.471	.474	.473	.490	.495	.464	.476	.494	.487	.492	.502	.491	.465	.471	.465	.464	.488	.492	.504	.494	.431	.486	.484	.478	0.5	.505	.452	.492	.477	.503	.491	.490
*MDH**																																		
N	30	34	224	288	70	80	50	50	50	150	50	50	50	150	50	50	50	150	50	50	50	150	13	58	50	121	50	49	21	120	47	48	48	143
A	.467	.353	.422	.418	.471	.481	.430	.460	.410	.433	.390	.520	.480	.463	.420	.560	.430	.470	.430	.390	.490	.437	.462	.457	.480	.467	0.4	.459	.476	.438	.564	.354	.438	.451
B	.533	.647	.578	.582	.529	.519	.570	.540	.590	.567	.610	.480	.520	.537	.580	.440	.570	.530	.570	.610	.510	.563	.538	.543	.520	.533	0.6	.541	.524	.563	.436	.646	.563	.549
Ho	.467	.412	.487	.476	.429	.438	.460	.560	.580	.533	.500	.560	.520	.527	.520	.400	.540	.487	.540	.500	.540	.527	.308	.500	.480	.471	0.4	.347	.476	.375	.362	.458	.500	.441
He	.506	.464	.489	.488	.502	.502	.495	.502	.489	.493	.481	.504	.504	.499	.492	.498	.495	.500	.495	.481	.505	.494	.517	.501	.504	.500	0.5	.502	.511	.494	.497	.462	.497	.497
*PGDH**																																		
N	23	33	202	258	64	72	49	48	50	147	49	50	48	147	50	50	50	150	48	50	49	147	12	58	50	120	50	49	21	120	46	48	45	139
A	.87	.848	.881	.876	.906	.917	.857	.875	.870	.867	.898	.900	.875	.891	.860	.900	.910	.890	.865	.900	.878	.881	.792	.836	.850	.837	0.8	.847	.952	.863	.859	.896	.889	.881
B	.13	.152	.119	.124	.094	.083	.143	.125	.130	.133	.102	.100	.125	.109	.140	.100	.090	.110	.135	.090	.122	.116	.208	.147	.150	.154	0.2	.153	.048	.138	.141	.104	.111	.119
C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	.010	0	.003	0	.017	0	.008	0	0	0	0	0	0	0	0
Ho	.261	.182	.218	.217	.188	.167	.286	.167	.260	.238	.163	.200	.250	.204	.240	.200	.100	.180	.271	.200	.204	.224	.250	.293	.260	.275	0.3	.224	.095	.225	.196	.125	.178	.165
He	.232	.261	.210	.218	.171	.154	.247	.221	.228	.231	.185	.182	.221	.195	.243	.182	.165	.196	.237	.184	.217	.211	.344	.281	.258	.276	0.3	.262	.093	.238	.245	.189	.200	.210
*PGM**																																		
N	30	34	224	288	70	80	50	50	50	150	50	50	50	150	50	50	50	150	50	50	50	150	13	58	50	121	50	49	21	120	47	48	48	143
A	1	.971	.996	.993	.979	.981	.980	.990	1	.990	.980	1	.970	.983	.990	1	.970	.987	.990	.980	1	.990	1	.991	.980	.988	1	.990	1	.992	1	.969	.979	.983
B	0	.029	.004	.007	.021	.019	.020	0	0	.007	.020	0	.030	.017	.010	0	.030	.013	.010	.020	0	.010	0	.009	.020	.012	0	.010	0	.008	0	.031	.021	.017
C	0	0	0	0	0	0	0	.010	0	.003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ho	0	0	.009	.007	.043	.038	.040	.020	0	.020	.040	0	.060	.033	.020	0	.060	.027	.020	.040	0	.020	0	.017	.040	.025	0	.020	0	.017	0	.063	.042	.035
He	0	.058	.009	.014	.042	.037	.040	.020	0	.020	.040	0	.059	.033	.020	0	.059	.026	.020	.040	0	.020	0	.017	.040	.025	0	.020	0	.017	0	.061	.041	.034
*TR**																																		
N	30	34	224	288	70	80	50	50	50	150	50	50	50	150	50	50	50	150	50	50	50	150	13	58	50	121	50	49	21	120	47	48	48	143
A	.950	.985	.882	.901	.957	.944	.890	.940	.920	.917	.890	.910	.920	.907	.850	.930	.870	.883	.940	.920	.840	.900	.923	.879	.870	.880	0.9	.878	.833	.871	.894	.906	.833	.878
B	.050	.015	.118	.099	.043	.056	.110	.060	.080	.083	.110	.090	.080	.093	.150	.070	.130	.117	.060	.080	.160	.100	.077	.121	.130	.120	0.1	.122	.167	.129	.106	.094	.167	.122
Ho	.100	.029	.210	.177	.086	.112	.220	.120	.120	.153	.180	.180	.160	.173	.300	.140	.260	.233	.120	.160	.200	.160	.154	.207	.180	.190	0.2	.245	.238	.242	.213	.188	.292	.231
He	.097	.029	.209	.178	.083	.107	.198	.114	.149	.153	.198	.165	.149	.170	.258	.132	.228	.207	.114	.149	.272	.181	.148	.214	.228	.212	0.2	.217	.285	.226	.192	.172	.281	.216
Mean Ho	.197	.184	.233	.223	.193	.240	.211	207	.226	.215	.19	.215	.222	.209	.241	.164	.208	.204	.245	.214	.221	.227	.219	.245	.245	.242	.258	.182	.240	.223	.210	.207	.241	.219
S.E.	.060	.064	.069	.067	.055	.068	.056	.066	.073	.064	.061	.069	.058	.062	.080	.061	.075	.068	.068	.058	.065	.063	.069	.061	.060	.060	.068	.050	.070	.057	.057	.052	.069	.057
Mean He	.242	.237	.26	.256	.281	.279	.253	.233	.247	.246	.256	.258	.265	.259	.237	.231	.249	.239	.261	.268	.288	.272	.261	.272	.288	.276	.292	.241	.272	.272	.274	.278	.28	.279
S.E.	.079	.078	.077	.077	.079	.078	.074	.068	.075	.073	.071	.076	.074	.074	.071	.075	.070	.071	.072	.070	.072	.071	.082	.072	.069	.070	.071	.069	.083	.068	.076	.071	.072	.073

Table 4. Values of the χ^2 tests of goodness of fit for deviation from Hardy-Weinberg expectations for the maturity stages pooled at all sampled sites.

Locus		Sampled sites								
		Saguenay Fjord	Rimouski	Pointe-des-Monts	Sept-Îles	South Anticosti	North Anticosti	Esquiman Channel	Hawke Channel	Hopedale Channel
*EST**	χ^2	10.33	21.04	12.17	41.28	59.62	19.19	9.86	9.1	36.89
	P	0.001	0	0	0	0	0	0.002	0.004	0
*GPI**	χ^2	n.t.	n.t	n.t	n.t	n.t	n.t	n.t	n.t	n.t
	P									
*HEX-1**	χ^2	21.36	3.23	2.61	16.42	11.97	29.19	0.37	14.98	4.2
	P	0	0.072	0.106	0	0.001	0	0.545	0	0.04
*HEX-2**	χ^2	7.26	0.79	12.87	6.67	0.35	5.08	1.29	0.29	1.16
	P	0.007	0.373	0	0.01	0.552	0.024	0.256	0.593	0.281
*MDH**	χ^2	0.17	1.35	1.02	0.47	0.11	0.68	0.41	7.05	1.85
	P	0.68	0.245	0.311	0.495	0.746	0.411	0.524	0.008	0.173
*PGDH**	χ^2	0.002	0.54	0.15	0.36	1.08	0.67	0.01	0.38	6.42
	P	0.961	0.462	0.702	0.551	0.298	0.413	0.946	0.539	0.011
*PGM**	χ^2	n.t.	n.t.	n.t	n.t	n.t.		n.t.	n.t.	n.t.
	P									
*TR**	χ^2	0.02	0.25	0	0.07	2.53	2.01	1.32	0.6	0.73
	P	0.881	0.616	0.997	0.796	0.111	0.156	0.251	0.438	0.393

Sequential Bonferronni tests were used to keep the overall significance threshold $\alpha = 0.05$ for the multiple comparisons.
For each site (6 loci) $\alpha/k = 0.008$.

Table 5. *F* statistics calculated for each locus and estimated values of the number of migrants per generation ($N_e m$) for all age groups pooled.

Locus	F_{IS}	F_{ST}	$N_e m$
*EST**	0.417*	0.010*	25
*GPI**	-0.007	0.005	50
*HEX-1**	0.259*	0.052*	5
*HEX-2**	0.103*	0.002	125
*MDH**	0.040	0.002	125
*PGDH**	0.013	0.004	62
*PGM**	0.017	0.001	250
*TR**	-0.017	0.005	50
Mean over loci	0.155	0.010	25
Mean over loci Excluding *EST** and *HEX-1**	0.050	0.003	83

*: $P < 0.001$

Table 6. Geographic heterogeneity of allelic frequencies for *Pandalus borealis* male, primiparous and multiparous females and for all individuals pooled for the samples collected in the Gulf of St. Lawrence, the Labrador Sea and for all the sampled sites (Northwest Atlantic)

Locus		Gulf of St. Lawrence				Labrador Sea				Northwest Atlantic			
			Female				Female				Female		
		Male	Prim.	Multi.	All	Male	Prim.	Multi.	All	Male	Prim.	Multi.	All
*EST**	χ^2	41.49	29.18	36.10	66.84	18.19	17.66	6.13	27.77	65.04	60.03	50.22	104.72
	P	0.017	0.130	0.217	0.000	0.000	0.000	0.178	0.000	0.001	0.030	0.163	0.000
*GPI**	χ^2	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
	P												
*HEX-1**	χ^2	91.87	40.06	45.14	152.9	6.04	6.52	0.83	3.4	99.3	47.55	49.19	164.13
	P	0.000	0.014	0.016	0.000	0.029	0.015	0.685	0.199	0.000	0.002	0.470	0.000
*HEX-2**	χ^2	14.35	10.31	5.85	6.47	0.04	1.00	0.79	0.01	14.89	14.24	6.65	7.05
	P	0.030	0.118	0.449	0.386	0.759	0.328	0.272	0.837	0.047	0.085	0.567	0.529
*MDH**	χ^2	2.01	11.56	3.51	4.37	5.21	2.22	0.18	0.1	8.38	15.71	3.71	4.47
	P	0.894	0.075	0.753	0.608	0.018	0.096	0.564	0.707	0.409	0.040	0.886	0.823
*PGDH**	χ^2	0.49	9.34	3.47	16.75	0.13	0.57	1.40	0.41	4.55	12.95	5.63	20.76
	P	0.382	0.621	0.76	0.126	0.707	0.398	0.192	0.56	0.788	0.619	0.695	0.171
*PGM**	χ^2	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
	P												
*TR**	χ^2	0.064	8.13	4.85	6.48	0.09	0.41	0.00	0.05	12.50	9.70	7.33	9.75
	P	0.090	0.214	0.538	0.347	0.660	0.490	0.800	0.787	0.125	0.266	0.511	0.278

Sequential Bonferronni tests were used to keep the overall significance threshold $\alpha = 0.05$ for the multiple comparisons.
For each site (6 loci) $\alpha/k = 0.008$.

Table 7. Matrices of genetic distances between samples for all maturity stages pooled over all loci. Nei (1978) genetic distances are shown above diagonal and Cavalli-Sforza and Edwards (1967) chord distances are shown below the diagonal.

Populations	1	2	3	4	5	6	7	8	9
1 Saguenay Fjord	***	.010	.001	.000	.001	.005	.000	.005	.001
2 Rimouski	.094	***	.009	.006	.011	.001	.007	.005	.005
3 Pointe-des-Monts	.047	.088	***	.000	.001	.002	.001	.001	.001
4 Sept-Iles	.034	.076	.043	***	.001	.002	.000	.002	.000
5 South Anticosti	.063	.105	.046	.056	***	.005	.000	.003	.002
6 North Anticosti	.072	.056	.060	.052	.072	***	.002	.000	.001
7 Esquiman Channel	.064	.099	.064	.061	.056	.070	***	.003	.000
8 Hawke Channel	.063	.080	.059	.049	.077	.042	.076	***	.002
9 Hopedale Channel	.052	.084	.054	.044	.062	.062	.046	.063	***

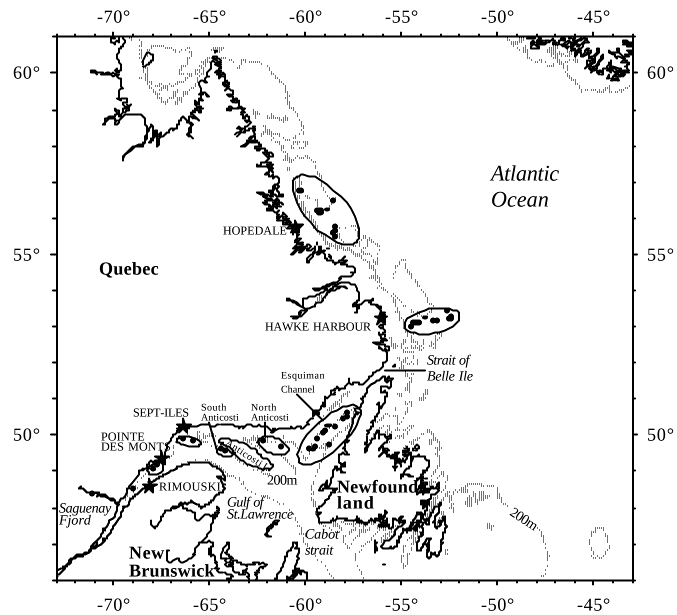

Fig. 1. Location of the sampling sites in the Gulf of St. Lawrence and east of the Newfoundland-Labrador coast. Samples enclosed in a circle were considered to be part of the same sampling site.

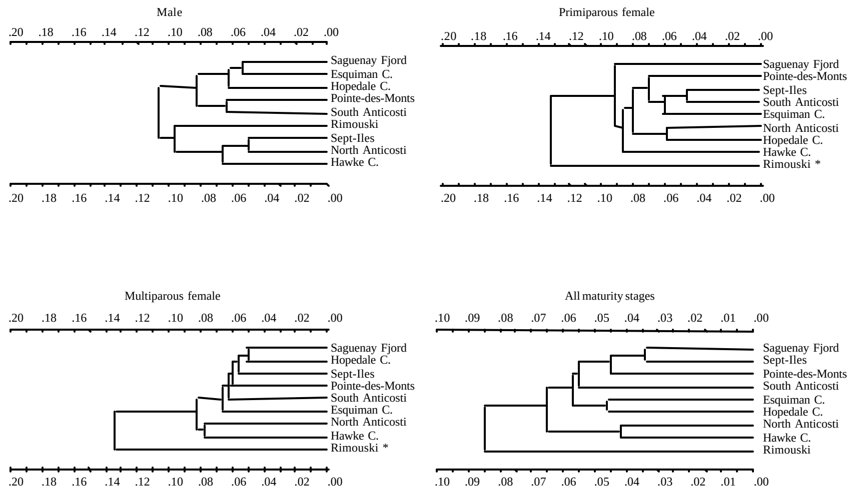

Fig. 2. Dendrogram constructed from Cavalli-Sforza and Edwards (1967)'genetic distance summarising the genetic relationship among the nine northern shrimp samples from the gulf of St. Lawrence and the Labrador Sea.

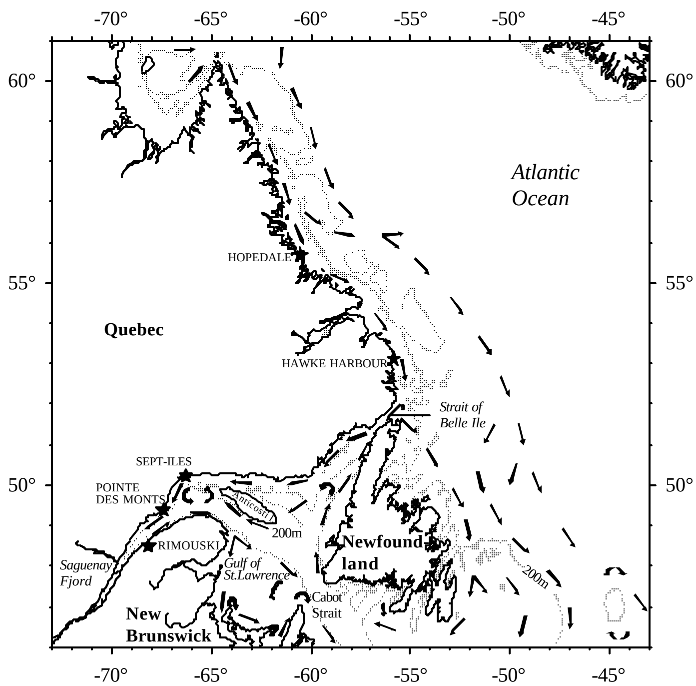

Fig. 3. General circulation patterns of the Northwest Atlantic.