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GENETIC POPULATION STRUCTURE OF NORTHERN SHRIMP, *PANDALUS BOREALIS*, IN THE NORTHWEST ATLANTIC

by

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ABSTRACT

Fisheries and Oceans Canada. 2014. Genetic population structure of northern shrimp, Pandalus borealis, in the Northwest Atlantic. Can. Tech. Rep. Fish. Aquat. Sci. 3046: iv + 27 p.

This is a report on genetic variability patterns of northern shrimp (*Pandalus borealis*) sampled along the Northwestern Atlantic coast, from Hudson Strait to the Gulf of Maine. A total of 1384 female shrimp from 14 sample locations were genotyped at 10 microsatellite loci for the purpose of identifying potential population structure of relevance for the management of Canadian shrimp fisheries. We detected highly significant genetic structure in parts of the sampled area, with genetically distinct shrimp in the Gulf of Maine and on the Flemish Cap. These locations were therefore concluded to harbour separate shrimp populations. The Newfoundland and Labrador shelf areas appeared much more genetically homogenous, which we attributed to population intermixing as a result of the Labrador Current. Some genetic differences were detected among samples from these areas, but this putative structuring was comparable in magnitude to that observed among temporal replicates, and was therefore not considered robust evidence for population subdivisions.

RESUME

Pêches et Océans Canada. 2014. Structure génétique de la population de la crevette nordique (*Pandalus borealis*) dans l'Atlantique Nord-Ouest. Rapp. tech. can. sci. halieut. aquat. 3046: iv + 27 p.

Il s'agit d'un rapport sur les schémas de variabilité génétique des crevettes nordiques (*Pandalus borealis*) prélevées le long de la côte de l'Atlantique Nord-Ouest, du détroit d'Hudson jusqu'au golfe du Maine. Au total, 1 384 crevettes femelles de 14 emplacements d'échantillonnage ont été génotypées à 10 loci microsatellitaires afin de déterminer la structure potentielle de la population qui représente un intérêt pour la gestion des pêches à la crevette au Canada. Nous avons repéré une structure génétique très importante dans certaines parties de la zone échantillonnée, avec des crevettes génétiquement distinctes dans le golfe du Maine et au Bonnet Flamand. Il a donc été conclu que ces endroits abritaient des populations distinctes de crevettes. Les zones de plateau de Terre-Neuve-et-Labrador semblaient beaucoup plus homogènes sur le plan génétique, ce qui, selon nous, était attribuable à l'entremêlement des populations dû au courant du Labrador. Quelques différences génétiques ont été détectées entre les échantillons de ces zones, mais cette structure hypothétique était comparable en ampleur à celle observée dans les réplicats temporels, et n'a donc pas été considérée comme une preuve solide des subdivisions de population.

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1.0 INTRODUCTION

Worldwide there are fourteen major stocks, or management units, of Northern Shrimp (*Pandalus borealis*) (hereafter synonymous with shrimp) (Hvingel 2006). The division into management units is generally based on geographical separation and economical units. In Canadian waters the resource is divided into 17 shrimp fishing areas (SFAs) with separate assessment, management and total allowable catch (TAC) (DFO 2010, Fig. 1). The shrimp resource in SFAs 4-7 covers a broad band from Davis Strait to the Grand Banks along the eastern coast of Newfoundland and Labrador (Fig. 1). The Canadian shrimp fishery within SFAs 4-7 was worth approximately $400 M to the Atlantic Canadian economy during 2012 (B. Fitzpatrick, pers. comm.). SFAs 4-6 are located entirely within the Canadian 200 Nmi limit and, as such, are managed by Canada. Shrimp within SFA 7 straddle the 200 Nmi limit and are managed by the Northwest Atlantic Fisheries Organization (NAFO). NAFO Divisions 2GHJ and 3KLNO cover SFAs 4-7 (Figs. 1 and 2).

Shrimp is assessed and managed by individual SFA. Managing the fishery on an SFA basis ensures that shrimp is exploited over the whole geographic range of the resource. However, most assessment models are based upon the belief that a closed population is being assessed, with negligible immigration or emigration and that internal exchanges take place rapidly enough that a single number with no spatial component suffices to describe and forecast the population (Begg et al. 1999, Cadrin and Friedland 1999). Assessing only a portion of a stock, e.g., a single SFA, may therefore be misleading and bias analyses of growth, mortality and migration: key factors when estimating yields. On the other hand, assessing a 'whole' stock and making inferences about the fate of its different component parts may also lead to misleading results, if these components are demographically independent. Therefore, knowledge of population structure and exchange is essential for sustainable management of fisheries and for understanding the effects that fishing has upon stock dynamics.

The need to establish stock boundaries and study the spatial organization of shrimp was emphasised by the ICES “Study group on life histories and assessment of *Pandalus* stocks in the North Atlantic” (Anon. 1994), and more recently by Bergström (2000). Investigations of shrimp stock structure carried out in the 1960-1980s (refs. in Kartavtsev et al. 1993, Skúladóttir and Pétursson 1999) were based on phenotypic (morphologic) variation which is affected by environmental conditions. Population structure should instead be defined by molecular genetic approaches (e.g., Ryman and Utter 1987). Molecular approaches allow for characterization of different genetic variants (alleles) and their distribution within and among samples of individuals. Inference of population structure can then be made for the sampled geographic area by statistical tests of allele frequency differences and by estimates of genetic differentiation among sample localities. Precision of such estimates depends on the true levels of differentiation and improves with increasing sample sizes, sample localities, and the number of gene loci studied. Briefly, genetic differences are expected among demographically separate populations because, in the absence of repeated intermixing, directed (natural selection) and random errors (mutations and genetic drift) in the transmission of genes from parents to offspring will accumulate over generations. Hence, observed genetic differences give evidence for samples being drawn from different biological populations that have been separated for some time. Conversely, apparent lack of differentiation could arise from samples being collected from a single biological population, from just recently separated populations, from populations that regularly exchange individuals (and genes) or from lack of statistical power in the analyses.

As a first approach in this direction, protein electrophoresis and Random Applied Polymorphic DNA (RAPD) fingerprinting methods were applied in the 1990s in a number of studies to investigate genetic variation among and within shrimp stocks in the Barents Sea, along the Canadian east coast, and around Iceland (Kartavtsev et al. 1991, Rasmussen et al. 1993, Kartavtsev 1994, Jónsdóttir et al. 1998, Drengstig et al. 2000, Sévigny and Savard 2000, Martinez et al. 2006). These studies, based on limited genetic information, did detect genetic differentiation among shrimps from different ocean basins: inshore and offshore Iceland, Norwegian fjords and the Barents Sea, and among Norwegian fjord populations. On the other hand, they failed to detect genetic differentiation within basins, or along the Canadian coast.

In the present work, we have used a more powerful genetic method - DNA microsatellites - to investigate the population structure of shrimp in the Northwest Atlantic, including the economically important stock(s) along the east coast of Canada. Microsatellites are non-coding nuclear genes, consisting of tandemly repeated short DNA sequences (2-6 base pairs), that vary greatly in copy number among individuals and populations and are thus highly informative in population genetic studies.

2.0 MATERIAL AND METHODS

The species: Northern shrimp (*Pandalus borealis* Krøyer 1838) is found on the continental shelves throughout most of the North Atlantic. In the Northwest Atlantic, shrimp is distributed from Davis Strait in the north to the Gulf of Maine in the south. The species is a protandric hermaphrodite, and in the Northwest Atlantic males become sexually mature by age 2, changing sex to female at age 3 and remaining as sexually mature females for the rest of their lives. Spawning normally takes place during late summer or early autumn and females carry the eggs on their pleopods for the next 9 – 10 months, depending on sea temperature (Koeller et al. 2009). After hatching in spring or early summer, the pelagic larvae drift in the water currents before settling to the bottom at one to four months, depending on ambient temperature (Shumway et al. 1985).

Study area and oceanographic conditions: Pelagic larvae are subject to advective forces due to ocean currents. Dominant near-surface mean flow features off Northwest Atlantic are the equator ward-flowing Labrador Current (Fig. 3). The equator ward shelf currents are generally stronger in the north than in the south. The shelf-edge Labrador Current interacts with the Gulf Stream and the North Atlantic Current off the Newfoundland Slope (Han et al. 2008). The shelf-edge current off Nova Scotia (also called the Labrador Current Extension) also interacts with the Gulf Stream (Han 2007). The Labrador Current transport has strong interannual variability (Han et al., 2010) and can, in some years, have a strong influence on the hydrography and circulation over the Scotian Shelf and in the Gulf of Maine. The Labrador Current carries colder and fresher water of Arctic origin equatorward. The bottom temperature pattern (Fig. 3) shows an equatorward warming with two distinct regimes: below 4^{o}C over the Labrador and Newfoundland Shelf and 6-8^{o}C over the central and western Scotian Shelf and in the Gulf of Maine.

Sampling: Fourteen samples of shrimp were collected from Hudson Strait to Gulf of Maine during 2009 to 2012, covering a large portion of the species' distributional range along the eastern coast of North America (Fig. 2, Table 1). Where possible, samples were taken onboard scientific cruises by scientists or technicians. Observers, onboard commercial factory

freezers, collected shrimp in NAFO Divisions 2G and 2H (along the Labrador Shelf) during autumn 2012. The 2010 sample from Flemish Cap was collected by a Canadian patrol vessel boarding a non-Canadian fishing vessel, while the Nova Scotia sample was collected onboard a commercial trap vessel (Appendix, Table A1). Samples from the Grand Banks, Newfoundland, Labrador, and Hudson Strait were collected in October-December, while samples from Gulf of Maine, Nova Scotia, and Flemish Cap were collected in July-September. From each locality we selected approximately 100 shrimps from multiple (typically 5, ranging from 1 to 9) trawl hauls in order to obtain representative samples from the area. Only female shrimp were selected for this study. Females include several age classes (cohorts), ensuring that individuals from multiple spawning events were included in each sample. The oblique carapace length for each shrimp was measured to 0.1mm accuracy (Appendix, Fig. A1).

On scientific cruises, tissue samples were stored directly in ethanol at sea. Shrimp collected by observers/patrols were frozen onboard and tissue samples were later transferred to ethanol before being shipped to the Institute of Marine Research (IMR) in Tromsø, Norway. Shrimp from Nova Scotia and the 2012 sample from Gulf of Maine were shipped frozen to the IMR lab where they were stored in ethanol. The latter sample was obtained frozen from the Maine Department of Marine Resources lab after the survey was completed, and the trawl stations are unknown for the individual shrimps collected in that sample (Appendix, Table A1). All samples were genotyped at the IMR lab.

Genetic analyses: DNA was isolated from ethanol fixated muscle tissue using the commercial E-Z 96 Tissue DNA kit (Omega Bio-Tek Inc., USA). A total of 12 microsatellite loci, arranged in three multiplexes, were analyzed based on the Pereyra et al. (2012) protocol. During a preliminary screening two loci (PbD8 and PbA104a) were found to display large heterozygote deficiencies relative to Hardy-Weinberg expectations and were therefore judged unreliable and excluded from the present analyses, which were based on the following 10 loci: PbC105, PbC8, PbA110, PbC109, PbD9, PbA1, SD1-41, SD2-14, SD2-68, and SD3-62.

Statistical analyses: Levels of genetic variability within samples were characterized from microsatellite genotypes by calculating average (over loci) estimates of allelic richness (*Ar*: Kalinowski 2004) and expected heterozygosity (H_S: Nei and Roychoudhury 1974) for each sample. Deviations from Hardy-Weinberg genotype proportions were tested for by an exact probability test, using GENEPOP (version 4.0.6, Raymond and Rousset 1995) and quantified by Wright's fixation index (F_{IS}), separately for each locus and averaged over loci (Nei and Roychoudhury 1974).

Genetic differentiation (F_{ST}) at single alleles, loci and averaged over loci were estimated with Weir and Cockerham's (1984) estimator theta. Averaged over loci, F_{ST} gives an estimate of the amount of genetic differentiation among samples relative to the maximum amount, i.e., the amount under complete fixation (Wright 1978, p. 82). Theoretically, F_{ST} varies between zero (no differentiation: all samples have the same allele frequencies) and unity (samples fixed for different alleles), but in practice estimates can be less than zero because of sampling errors, and may be limited upward by high levels of within-population variability (Hedrick 1999). Analysis of genetic differentiation patterns focused on NAFO Divisions (Fig. 2). Samples from different years from within the same Division were treated as temporal replicates, and used to assess temporal stability of observed genetic differences. Temporal replicates were obtained from Divisions 2J (years 2009, 2011, and 2012), 3L (2009 and 2012), 3M (2010 and 2011), and 5Y (2010 and 2012) (Table 1, further details in Appendix,

Table A1). Standard errors (SE) for average F_{ST}-estimates were calculated by jackknifing over loci, and used to set confidence limits and intervals for the point estimates, assuming a normal distribution. Lower 5% confidence limit (CL) was calculated as F_{ST} - 1.64*SE, and used to judge if the point estimate was "significant" (i.e., greater than zero), and the 95% confidence interval (CI) was calculated as F_{ST} +/- 1.96*SE. Genetic differentiation was further tested for significance with the GENEPOP exact allele frequency homogeneity test.

The problem of excess false positive test results that arise in multiple testing situations was handled by two different approaches, depending on context. First, when multiple tests concerned the exact same null-hypothesis, as when combining data from multiple gene loci to address the null-hypothesis of samples being drawn from the same population, we joined information over loci (assumed to be independent) as recommended by Ryman and Jorde (2001). This was done following Fisher's summation procedure, i.e., by summarizing twice the natural logarithm of single-locus p-values and comparing this sum with the theoretical chi-square distribution for the relevant number of degrees of freedom (d.f. = twice the number of tests) and the desired 5% significance level. Second, when performing multiple tests representing different null-hypotheses we instead applied the False Discovery Rate (FDR) approach to each table of p-values. When test concerned pairwise comparisons that cannot be assumed independent, e.g., when testing equality of allele frequencies between pairs of sample locations (dependence arises because each sample is included in multiple pairs), we applied the FDR approach of Benjamini & Yekutieli (2001). This was done separately for each table of m p-values (each p-value being the result of summation over all loci, as described above) by calculating the quantity $\alpha / \sum_{i=1}^{m} (1/i)$, where $\alpha = 0.05$was the desired rejection level, and accepting as significant pairs with a p-value smaller than or equal to this quantity. In situations where multiple tests could be assumed independent, as when testing genotype proportions against Hardy-Weinberg expectations, we instead used the original FDR procedure of Benjamini and Hochberg (1995). Briefly, the procedure was to arrange all of the m p-values in increasing order (i = 1 to m) and finding the largest number, $k = i$, for which the i'th ordered p-value was smaller than or equal to the quantity $i/m = \alpha$. All of the ordered i = 1 to k tests were then considered significant.

Inference on population structuring was drawn from pairwise F_{ST}-estimates and outcomes of allele frequency homogeneity tests (above), and from phylogenetic relationships. The phylogenetic relationship among samples was reconstructed from Nei's genetic distance metric *Da* (Nei et al. 1983), using the neighbour-joining method (Saitou and Nei 1987). Calculations and graphical visualizations were done with POPTREE and POSTREE software (distributed by Prof. N. Takezaki, Kagawa University). Support for particular phylogenetic relationships was evaluated by bootstrapping using 50,000 replicates.

Computer simulations, using POWSIM software (version 4.0; Ryman and Palm 2006), were used to calculate statistical power of detecting low levels of genetic differentiation. Simulations were based on observed allele frequency profiles at 10 microsatellite loci (arbitrarily using CAN_2G sample frequencies), and carried out for different sets of POWSIM input parameters (t and Ne) to achieve a range of F_{ST} from 0 to 0.005. Pairwise tests were simulated among samples, using sample sizes of n = 100, similar to those used for analyzing shrimp (Table 1). Simulations were repeated 5000 times, and the proportion of replicates that resulted in a significant test result (joint test over loci: above) was taken as the statistical power of the test (or alpha error in the case of true $F_{ST} = 0$).

3.0 RESULTS

Genetic variability: All 10 microsatellite loci were highly polymorphic, segregating for eight (at locus SD3-63) to 53 (PbC109) alleles in the combined sample, comprising 1384 shrimps. The average heterozygosities (H_S) varied among loci from 0.246 (SD3-62) to 0.943 (PbC109) (data not shown). Averaged over loci, genetic variability within each of the 14 samples was similar, as estimated either by allelic richness (*Ar*) or heterozygosity (Table 2). However, there was a slight trend of reduced allelic richness towards the north (linear regression of *Ar* on sample latitude: $R^2 = 0.269$, p-value = 0.033). No such trend was seen among the heterozygosity estimates ($R^2 = -0.058$, p-value = 0.60).

Genetic equilibrium: All samples displayed a slight overall departure from genotype proportions expected under Hardy-Weinberg equilibrium, representing 0.5% to 3.9% deficiencies of heterozygotes (F_{IS}: Table 2). The deviations were statistically significant at the 5% level in 7 out of 14 samples when tests were considered separately, three of which (GOM10, GOM12, and FLC10) remained significant when allowance was taken for multiple tests using the FDR-approach. There was no apparent geographical trend to deviations from Hardy-Weinberg (regression of F_{IS} on sample latitude: $R^2 = -0.077$; p-value = 0.80). Deviations from Hardy-Weinberg expectations within NAFO Divisions appeared to fluctuate among temporal replicates, as exemplified by the two samples from Flemish Cap where p-values varied from 0.006 to 0.517 from one sample year to the next (cf. Table 2). Such fluctuations indicate an ephemeral nature of the deviations, perhaps reflecting technical problems.

Genetic structure: Levels of genetic differentiation (F_{ST}) and associated tests for significance among all pairs of samples are detailed in the Appendix (Table A2). Here, we focus on patterns of differentiation among nine areas, represented by eight NAFO Divisions and Hudson Strait, lumping replicate samples within areas (cf. Table 1). The average F_{ST} among the nine areas was 0.010 (95% CI from 0.002 to 0.019). However, closer inspection revealed that Division 5Y (Gulf of Maine) accounted for the larger part of this diversity, as eliminating the two 5Y samples reduced average F_{ST} five-fold, from 0.010 to 0.0018 (data not shown).

The results from pairwise estimates of genetic differentiation among areas (Table 3) may be summarized as follows. First, and as noted above, Division 5Y (Gulf of Maine) was highly differentiated from all Canadian samples, with pairwise estimates of F_{ST} that were typically >0.020 and an order of magnitude greater than between any other areas. Likewise, shrimp from Division 3M (Flemish Cap) differed from all other samples, albeit at a lower level than did those from the Gulf of Maine: F_{ST} ranged from 0.0034 (between 3M and 2G) to 0.0079 (3M and 2H). All these pairwise genetic differences were statistically significant, both as judged by their 5% confidence limits not overlapping zero (Table 3, below diagonal: estimates in bold) and from their significant joint p-value over loci (Table 3, above diagonal). Further, the sample from 2H (Hopedale Channel) differed significantly from other areas as judged by the probability tests (Table 3, above diagonal), even though the confidence limit for the point estimates of F_{ST} overlapped zero (i.e., non-bold values in Table 3, below diagonal). Similar observations pertained to 2G (Saglek Bank), but with fewer significant comparisons. All other Divisions resulted in low F_{ST}-estimates (0.0009 or lower), similar in magnitude to comparisons among replicate samples from the same Division (see below and Fig. 4), and none were found statistically significant.

For four Divisions (2J, 3L, 3M, and 5Y: Table 1), two or more samples from different years were available for testing temporal stability of allele frequencies over time. As indicated by the results tabulated in Appendix (Table A2), samples from within the same Division were genetically similar to each other, as judged by the low pairwise F_{ST}-estimates (0.0017 or lower: mean 0.0003, standard error 0.0004). None of these estimates were statistically significant when allowance was made for multiple tests (cf. Appendix, Table A2, above diagonal).

The neighbour-joining dendrogram (Fig. 5) largely concurred with the patterns revealed by the F_{ST}-analysis above. In addition to identifying Gulf of Maine (Division 5Y) and Flemish Cap (3M) samples as distinct groups, supported by 99 and 65% of bootstrap replicates, respectively, the dendrogram also indicated that the Nova Scotia (4W) sample was partly associated with the Gulf of Maine branch (57% bootstrap support). While the Nova Scotia sample did not stand out in terms of pairwise F_{ST}-values, we note that the probability tests (Appendix, Table A2, above diagonal) yielded moderately low p-values to several other samples, although none were judged significant under a multiple test scenario (FDR). Finally, sample CAN_2H appeared in the dendrogram branching off from the geographically non-adjacent CAN_3L sample, with 62% bootstrap support. The remaining samples, representing Hudson Strait and the Labrador and Newfoundland shelf areas, appeared intermingled with respect to geographic position, and all branches had low bootstrap support (9 to 34%) among them, indicating weak or absence of genetic structure.

The results of computer simulations for evaluating statistical power (Table 4) revealed that true F_{ST}-values smaller than about 0.0010 have a relatively low probability (<0.4) of yielding a statistical significant (at the 5% level) outcome in tests of allele frequency homogeneity, even before taking allowance for multiple tests. This value thus gives a rough indication of the lower detection limit for genetic differentiation among samples in the present study. Similar limits obviously exist for other types of statistical inference (confidence limits, bootstrap support, etc.), although the performance of these methods was not evaluated herein.

4.0 DISCUSSION

The analyses reported several genetically different samples of shrimp from along the east coasts of the U.S. and Canada. In particular, samples from the Gulf of Maine and Flemish Cap differed from all other sample localities, their differences confirmed by temporal replicates. We note, however, that all observed genetic differences in the present study must be described as minor. First, F_{ST} estimates, the mean as well as pairwise estimates, were all lower than the average (0.062) reported for various marine species (Ward et al. 1994). Second, very few alleles (gene variants) were unique to particular samples or NAFO Divisions and those that apparently were unique always occurred in very low frequencies (in one or two heterozygote individuals out of the 1384 screened). Such rare alleles contributed little if anything to the overall level of genetic differentiation (F_{ST}), which instead largely reflected differences in frequency of alleles that were common to all samples and Divisions. Nevertheless, the existence of significant, and sometimes highly significant, allele frequency differences clearly demonstrate that exchange (gene flow) among localities is restricted and implies existence of multiple shrimp populations in the study area.

Theoretically, gene flow is a highly potent homogenizing force, requiring only a modest number of successful exchanges per generation in order to reduce genetic differentiation

among populations to a very low level. Exact numbers depend on the (unknown) patterns of dispersal, but approximate numbers can be calculated if we make some simplifying assumptions regarding dispersal and population structure, e.g., an "island" model of dispersal (Wright 1931). While perhaps biologically unrealistic (Whitlock and McCauley 1999), this simple model can nevertheless give an indication of the level of genetic differences that can be expected from a set of selectively neutral loci under various assumptions of population size and dispersal rates. For shrimp, population size is generally counted in the billions, and theory (Wright 1931, Hössjer et al. 2013) tells us that an exchange of even a tiny fraction (say, 0.000025%, or 250 individuals) among populations per generation is sufficient to keep genetic differentiation among them at or below the lower detection limit (F_{ST} = 0.0010, approx.) of the present study. As demonstrated by the computer simulations (Table 4), such low levels cannot readily be detected by present methods, since the probability of obtaining a significant test result is not much above the alpha level, i.e., the probability of making a statistical Type I error. This means that apparent genetic homogeneity and absence of statistically significant differences can result even from a very low rate of exchange. Conversely, where we do detect significant genetic differences, genetic exchange is likely to be very low, unless such differences arose from unrepresentative sampling or technical errors in the genotyping. Temporal replicate samples are a powerful means of guarding against such problems and, when genetic differences are thusly confirmed, the constituent populations may safely be concluded to be demographically independent. This is the case for the Gulf of Maine and Flemish Cap and implies that, if these populations were to be overexploited, the rescuing effect from immigration from neighbour areas may be too low to rebuild the resources in a timely manner.

In contrast to the well-separated populations in the Gulf of Maine and at the Flemish Cap, the shelf areas of Labrador and Newfoundland (NAFO Divisions 2GHJ3KL) appear largely homogenous genetically, as judged by the low F_{ST}-estimates among samples and Divisions, and whose lower confidence limits always overlapped zero (but see below). These shelf areas are mostly situated in the strong Labrador Current (cf. Fig. 3), and the possibility for transport of pelagic shrimp larvae with currents is obvious. Reduced genetic structure among shrimp collections from this area is thus likely a reflection of gene flow caused by transport of pelagic larvae among putative spawning aggregations. Such larval drift, or transfer, as the transport is unidirectional towards the south, implies that demographic events in the north (e.g., a large year-class) may influence the stock situation in the south, while not in the opposite (up-current) direction. On the other hand, the numerical calculations above indicate that for a species as numerous as shrimp, exchange and transfer of only a minute fraction of a population may be sufficient to eradicate genetic differences, yet is likely to have minor impact on the demography of the recipient. Hence, supplementary studies, including larval drift studies, should be carried out to elucidate the rate of exchange of individuals between the different NAFO Divisions (e.g., Pedersen et al. 2003).

Despite low levels of genetic differentiation among samples in the Labrador and Newfoundland shelf areas, several pairwise comparisons from this area came out as statistically significant in tests of allele frequency differences (Tables 3 and A2: above diagonal). These comparisons involve the two samples from Divisions 2H and 2G. Yet, these samples differed weakly at best from other Labrador and Newfoundland shelf samples, and were associated with low F_{ST}-estimates whose confidence limits overlapped zero. How are we to reconcile these apparent conflicting observations (F_{ST} vs. allele frequency homogeneity test), and do the shelf areas harbor genetically different shrimp populations or not? There are several issues to consider here. First, it is not uncommon for different statistical tests to differ

in power and in various underlying assumptions that may affect their outcomes. In the present case, the confidence limits to F_{ST} were calculated from the variation among single-locus estimates, and the limits will therefore be broad if this variation is large for some reasons. Broad confidence limits translate to a weak, and perhaps overly conservative, judgment of "significance" when based on F_{ST}. Second, statistical tests assume representative (i.e., random) sampling of the population(s), and may otherwise yield biased outcomes. We made attempts to sample as representative as possible for this study, using multiple trawl hauls to represent each sample locality and also replicating over years, but this was not always practical. Thus, some sampled localities, including 2H and 2G (cf. Table A1), were based on collections from observers on commercial vessels, possibly from a single trawl haul. No temporal replicates from these locations were available for genotyping in the present study, and genetic divergence patterns for them cannot presently be verified. Third, some scoring errors cannot be ruled out in a study with tens of thousands of individual genotypes. Such errors could contribute to a false positive test outcome when real differences are small or absent, as for the Labrador and Newfoundland shelf areas. Lastly, conclusions based on multiple tests, such as our pairwise tables, are sensitive to how this multiplicity is dealt with statistically.

One solution to the problem of how to interpret small, and sometimes statistical significant, estimates of genetic divergence among localities is to compare such spatial estimates with temporal estimates among replicate samples taken from the same location and otherwise treated similarly as for spatial samples. Errors arising from genotyping and non-representative sampling are then expected to also be replicated in temporal estimates, and real spatial effects should yield an additional contribution to the estimated F_{ST}. Comparing spatial estimates among samples from different Divisions within the Labrador and Newfoundland shelf areas with temporally replicated samples from within the same Divisions, we found that spatial and temporal patterns are broadly overlapping in the present case (Fig. 4). From this broad overlap there does not seem to be any compelling evidence for spatial population structure within the Labrador and Newfoundland shelf areas, using the available data. This conclusion is consistent with our computer simulations, which indicated a lower detection threshold around $F_{ST} = 0.0010$, as the great majority of pairwise estimates from the shelf area are at or below that magnitude. Further research should be directed towards addressing possible substructure of shrimp in the shelf areas by including more replicate samples and perhaps also employing a larger number of genetic markers to increase statistical power.

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Boothbay Harbor). The sample from Nova Scotia was provided with assistance from Michelle Theriault (Université Sainte-Anne, Petit de Grat). We thank Tim Siferd and Geoff Evans for valuable comments on an earlier version of this manuscript.

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Table 1. Shrimp samples taken along the northeastern coasts of the U.S. and Canada for genetic analyses. Latitude and Longitude refer to the start position of trawl hauls for each year and locality. Sample size refers to number of genotyped females. Sample abbreviations prefixed with "CAN" were provided specifically for this report, while other samples were collected within the "POPBOREALIS" project (see Acknowledgments). For more details, refer to Appendix, Table A1.

NAFO Division	Feature	Sample abbrev.	Year	Month	Sample Size	Latitude	Longitude	Depth
-	Hudson Strait	HUS	2009	10	85	61.23N	68.54W	216-481m
2G	Labrador, north (Saglek Bank)	CAN_2G	2012	12	99	58.12N	59.98W	236m
2H	Labrador, middle (Hopedale Channel)	CAN_2H	2012	12	99	56.61N	59.99W	274m
2J	Labrador, south	LAB09	2009	11	96	53.79N	54.39W	205-435m
	(Hamilton Bank)	LAB11	2011	10-11	77	55.08N	55.82W	214-270m
		CAN_2J	2012	11	97	53.7N	53.59W	207-363m
3K	Newfoundland	CAN_3K	2012	12	100	49.47N	50.95W	310-324m
3L	Grand Banks	GRB	2009	11	99	47.21N	47.63W	168-303m
		CAN_3L	2012	11	100	49.48N*	52.14W	285-322m
3M	Flemish Cap	FLC10	2010	8	96	47.52N	44.06W	450m
		FLC11	2011	7	84	48.06N	44.65W	342-800m
4W	Nova Scotia	NSC	2011	9	80	45.45N	61W	70m
5Y	Gulf of Maine	GOM10	2010	7	180	43.28N	69.51W	129-177m
		GOM12	2012	7-8	92	42.93N	70.34W	81-167m

*) Two sampling stations (cf. Appendix Table A1) extended slightly into Division 3K (at 49.15N).

Table 2. Genetic characteristics of shrimp samples, averaged over 10 microsatellite loci. *Ar* is the allelic richness, normalized to a common sample size of n = 72; H_S is the average heterozygosity over loci; F_{IS} measures the average deviation from Hardy-Weinberg genotype proportions (a positive value indicates a deficiency of heterozygotes), and p-value represents the joint tests for significance over all loci (**bold italics** value: significant deviation from H-W also under Benjamini & Hochberg's FDR approach). Sample abbreviations as in Table 1. SD is the standard deviation among samples.

	Genetic variability		Genetic equilibrium	
Sample	*Ar*	H_S	F_{IS}	p-value
HUS	13.0	0.754	0.024	0.314
CAN_2G	13.0	0.744	0.027	0.119
CAN_2H	13.0	0.747	0.016	0.233
LAB09	12.9	0.736	0.039	0.047
LAB11	13.2	0.744	0.012	0.434
CAN_2J	12.8	0.751	0.052	0.025
CAN_3K	13.0	0.747	0.017	0.240
FLC10	14.0	0.737	0.038	***0.006***
FLC11	12.8	0.744	0.005	0.517
GRB	13.4	0.753	0.024	0.013
CAN_3L	13.8	0.745	0.047	0.026
NSC	14.0	0.755	0.020	0.318
GOM10	13.3	0.736	0.028	***0.011***
GOM12	13.6	0.747	0.036	***0.001***
Average	13.3	0.746	0.027	<0.001
SD	0.4	0.006	0.013	

Table 3: Pairwise genetic differences among shrimp between NAFO Divisions, with replicate samples combined (number of samples in parentheses; cf. Table 1). Below diagonal: estimated F_{ST} (Weir & Cockerham's 1984 estimator, theta; ***bold italics*** values represent estimates with a lower 5% confidence limit greater than zero). Above diagonal: p-values resulting from test for genetic differentiation (GENEPOP option 3/2 with MCMC parameters 50000, 500, 50000), summarized over loci (Fisher's summation procedure; ***bold italics*** values represent test results that were significant also under Benjamini & Yekutieli's FDR approach).

Division	HUS (1)	2G (1)	2H (1)	2J (3)	3K (1)	3L (2)	3M (2)	4W (1)	5Y (2)
HUS	-	***0.0079***	***0.0000***	0.9375	0.6633	0.9710	***0.0000***	0.5618	***0.0000***
2G	0.0004	-	0.0274	***0.0013***	0.2431	0.0233	***0.0000***	0.0380	***0.0000***
2H	0.0027	-0.0002	-	***0.0000***	0.0278	***0.0099***	***0.0000***	***0.0000***	***0.0000***
2J	-0.0006	0.0002	0.0017	-	0.6664	0.1537	***0.0000***	0.0368	***0.0000***
3K	0.0000	-0.0013	0.0004	-0.0003	-	0.2707	***0.0000***	0.1674	***0.0000***
3L	-0.0008	-0.0008	0.0017	-0.0003	-0.0008	-	***0.0000***	0.4432	***0.0000***
3M	***0.0036***	***0.0034***	***0.0079***	***0.0051***	***0.0056***	***0.0055***	-	***0.0000***	***0.0000***
4W	0.0002	0.0015	0.0027	-0.0001	0.0012	0.0009	***0.0038***	-	***0.0000***
5Y	***0.0219***	***0.0280***	***0.0287***	***0.0239***	***0.0274***	***0.0270***	***0.0245***	***0.0187***	-

Table 4. Computer simulations of statistical power (proportion of significant tests) to detect various levels of true genetic differentiation (F_{ST}), in pairwise comparisons among samples (n = 100 individuals each) scored for 10 microsatellite loci. Simulations were carried out with POWSIM (Ryman and Palm, 2006) using 5000 replicate runs for each parameter set.

True F_{ST}	POWSIM parameters	Proportion significant tests
0	(t=0; Ne=5000)	0.051*
0.0001	(t=1; Ne=5000)	0.074
0.00025	(t=5; Ne=10000)	0.106
0.0005	(t=5; Ne=5000)	0.170
0.001	(t=5; Ne=2500)	0.395
0.0025	(t=25; Ne=10000)	0.504
0.005	(t=25; Ne=5000)	0.909

* = alpha error.

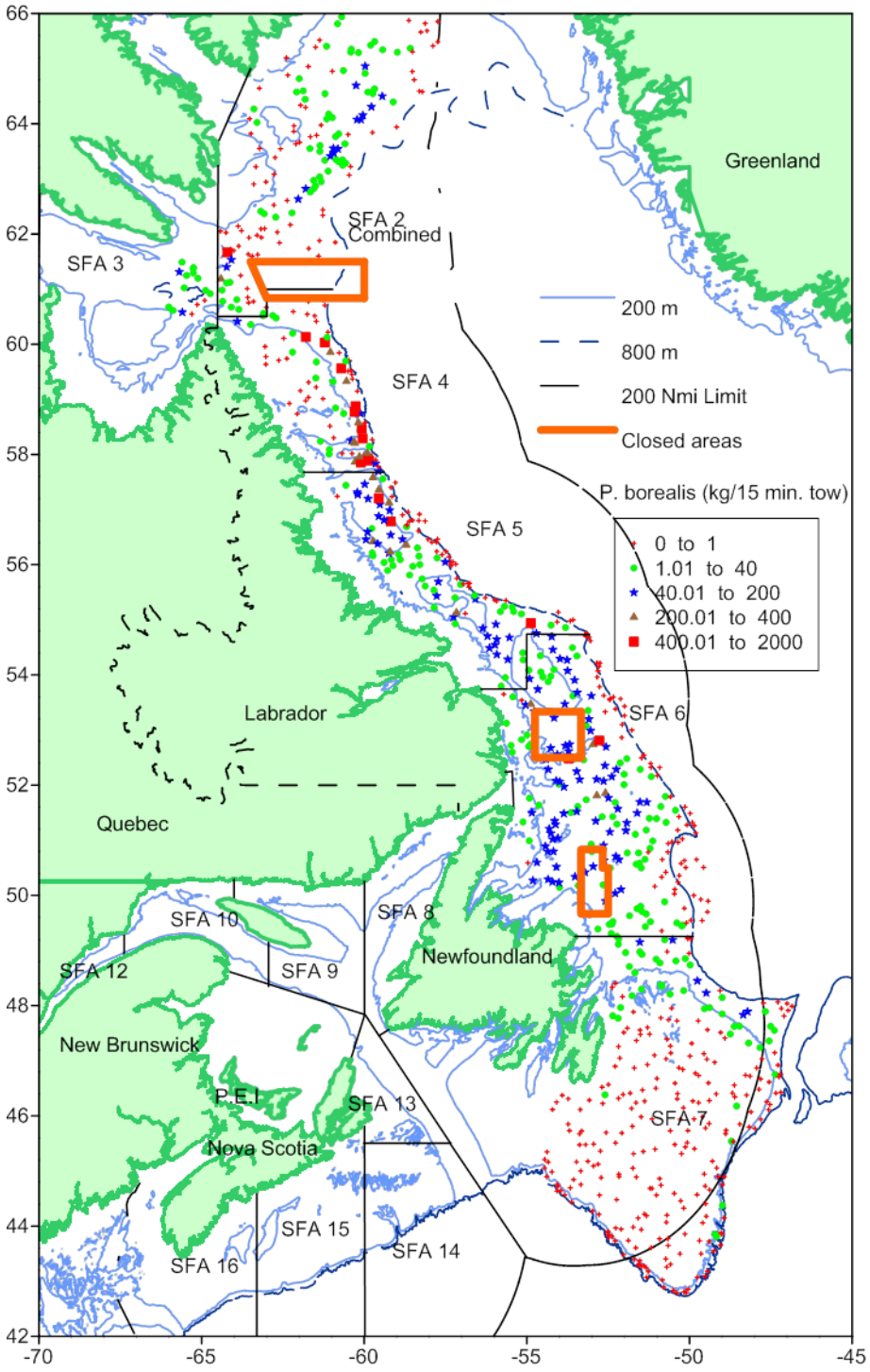

Figure 1. Distribution of the northern shrimp (*Pandalus borealis*) resource within shrimp fishing areas (SFAs) 2 to 7 in 2012.

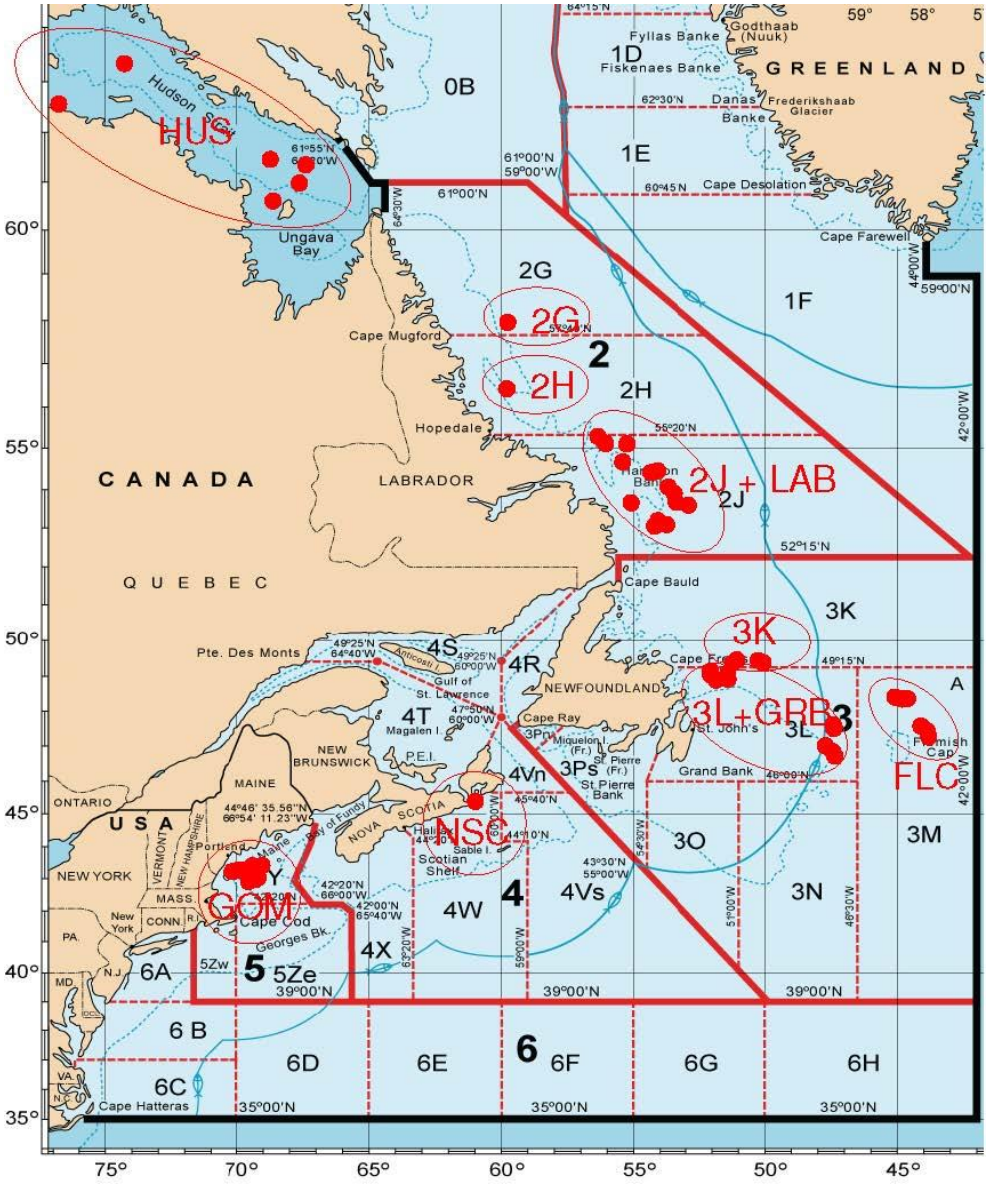

Figure 2. The NAFO convention area with NAFO Divisions and gross bathymetric features (blue dotted line: 200m isocline). The area outside the 200 Nmi limit (blue line) is the NAFO Regulatory Area (NRA). Red dots indicate collection sites for the various samples (for details, refer to Appendix, Table A1). Courtesy of NAFO.

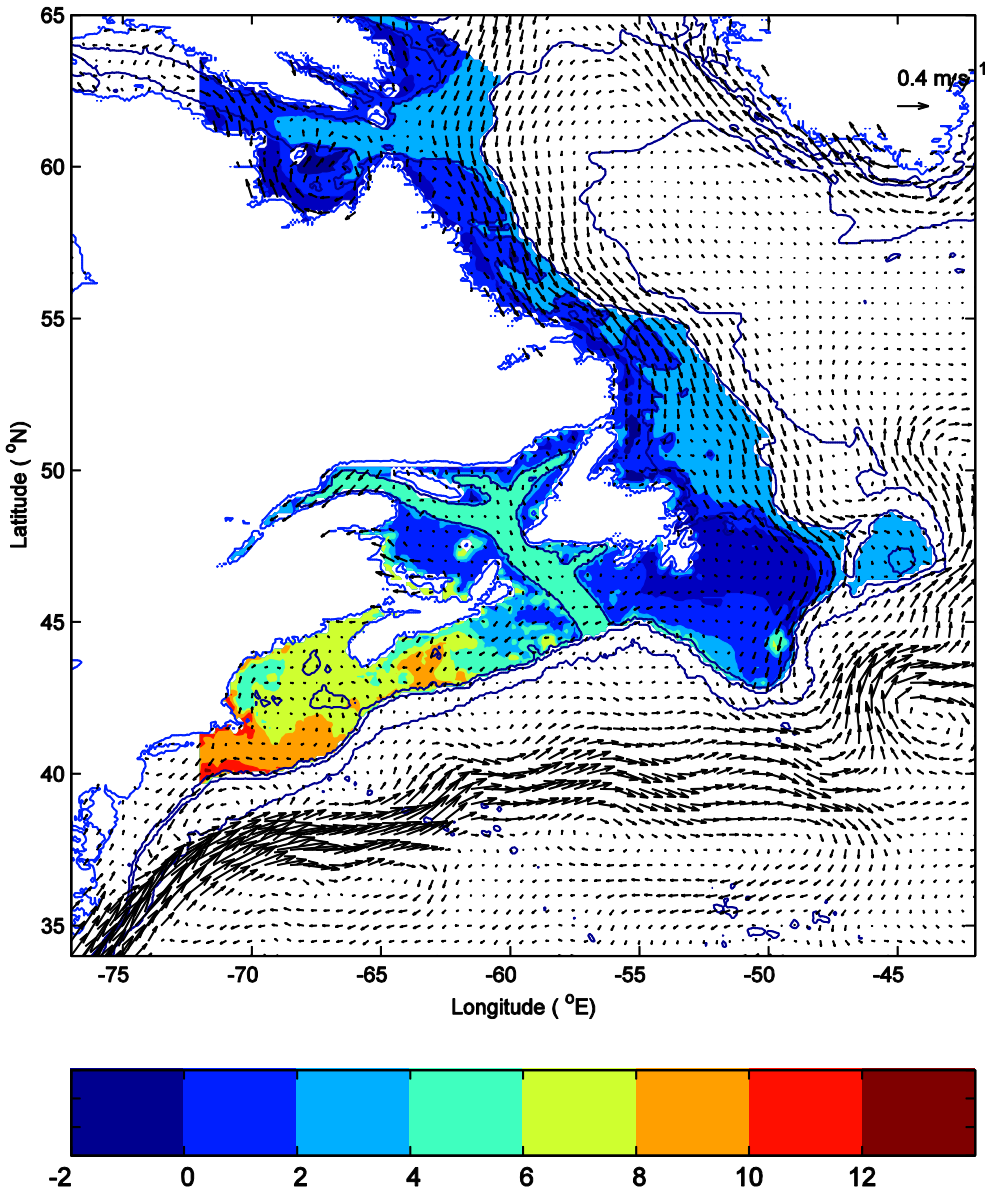

Figure 3: Near-surface mean currents (arrows, m s^{-1}) and climatological-mean bottom temperature (colour image, ^{o}C) in the study region and adjacent waters. The currents are derived from satellite observations (an update of Tapley et al. 2003, Han 2011) and the bottom temperature from Tang (2007). The bottom temperature shown is for waters shallower than 1000 m only. The 200, 1000 and 3000 m isobaths are also depicted.

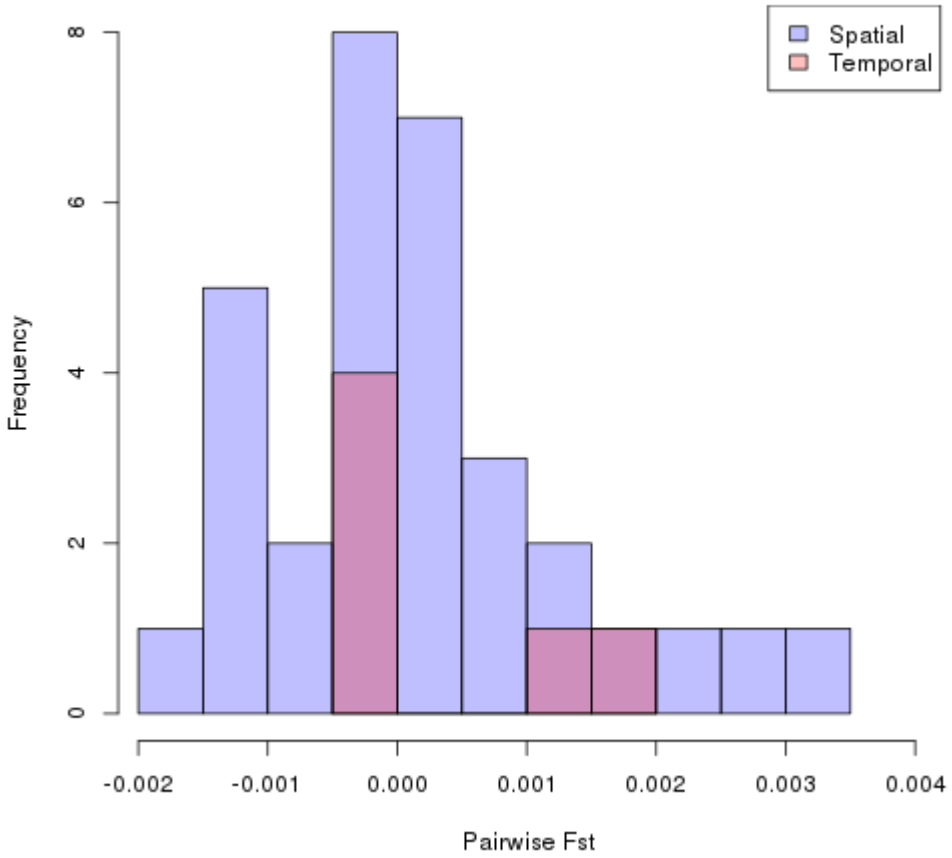

Figure 4. Histogram of pairwise F_{ST}-estimates (averaged over 10 microsatellites: from Table A2) among samples from the Newfoundland and Labrador shelf areas (nine samples from HUS, 2G, 2H, 2J, 3K, and 3L). Estimates are separated into temporal (i.e., for pair of samples from the same NAFO Division: mean F_{ST} = 0.0003, Standard Error = 0.0004) and spatial components (sample pairs from different Divisions: mean = 0.0001, SE = 0.0002). Note the broad overlap of estimates from the two components.

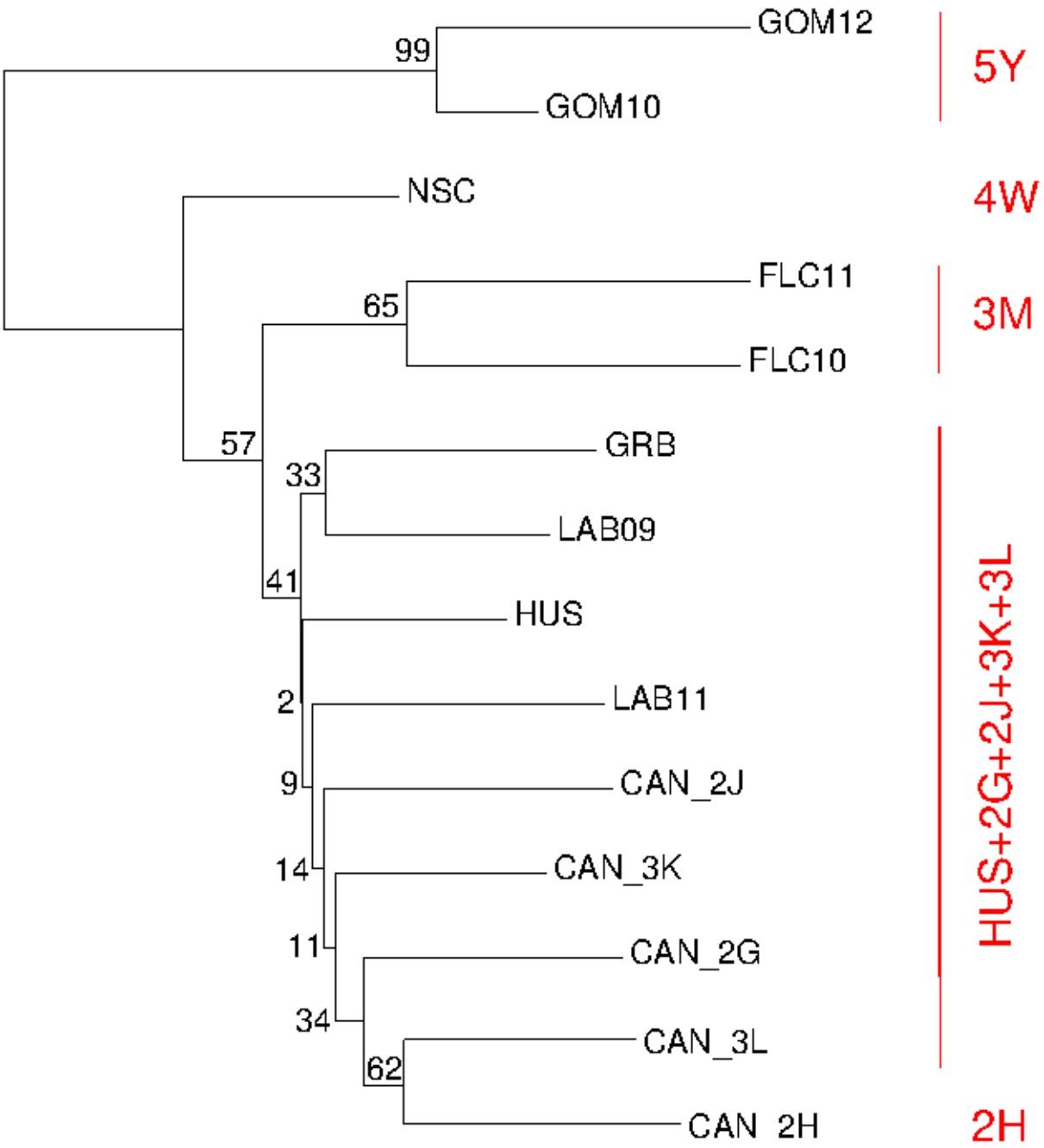

Figure 5. Phylogenetic relationship among 14 shrimp samples (Table 1), reconstructed from genetic distances (*Da*) with the neighbour-joining method. Numbers at nodes indicate percentage of bootstrap support.

7.0 APPENDIX 1 - TABLES

Table A1. Station details for all samples of shrimp for genetic analyses: NAFO Division (where applicable), descriptive name of sample, abbreviated name, date of sampling, sample size (number of successfully genotyped individuals), geographic position, depth (m), bottom temperature (°C), and means of sample collection (scientific survey, observer onboard commercial vessel, patrol vessel inspecting commercial vessel, and scientist onboard commercial vessel). Samples with abbreviations prefixed with "CAN" were provided specifically for this report, while other samples were collected within the Research Council of Norway project POPBOREALIS. The 2012 sample from Gulf of Maine was obtained frozen from the lab at Maine Department of Marine Resources after the survey was completed, and at that stage it was no longer possible to trace the different shrimp to particular trawl stations.

NAFO Division	Name	Sample abbrev.	Year	Month	Day	Sample size	Latitude	Longitude	Depth range (m)	Temp. (°C)	Collector
-	Hudson Strait	HUS	2009	10	13	20	60.63767N	68.603W	216	-0.27	survey
					13	20	61.0149N	67.60737W	481	1.01	
					15	20	61.38883N	67.36317E	379	1.09	
					16	20	61.48533N	68.70367W	383	0.68	
					21	4	62.60467N	76.64033W	398	-0.87	
					24	1	63.38517N	74.183W	297	-0.86	
2G	Labrador, north	CAN_2G	2012	12	NA	99	58.1297N	59.9733W	236		observer
2H	Labrador, middle	CAN_2H	2012	12	14	99	56.6067N	59.9882W	274		observer
2J	Labrador, south	LAB09	2009	11	13	20	54.4392N	54.4098W	205	2.3	Survey
				11	13	20	54.4752N	54.1748W	220	2.5	

Table A1 (Cont'd.)

				11	14	20	53.6822N	55.1638W	288	1.8	
				11	15	20	53.0852N	54.2833W	384	3	
				11	16	19	53.13N	53.8297W	435	3.8	
		LAB11	2011	10	29	20	55.315N	56.412W	214	2.4	Survey
				10	29	20	55.153N	56.117W	270	3.4	
				10	31	20	54.698N	55.483W	263	3.5	
				11	23	20	55.140N	55.3248W	265	3.8	
		CAN_2J	2012	11	4	19	54.07N	53.74W	208-219	1.2	Survey
				11	4	19	53.90N	53.53W	218	1.5	
				11	5	20	53.62N	53.01W	221-222	2.3	
				11	5	20	53.68N	53.44W	207-209	1.6	
				11	5	19	53.22N	54.16W	360-363	3.5	
3K	Newfoundland	CAN_3K	2012	12	2	20	49.523N	51.20W	323	3.2	Survey
				12	2	20	49.43N	51.3575W	324	3	
				12	3	20	49.502N	50.390W	322	3.7	
				12	3	20	49.458N	50.210W	314	3.7	

Table A1 (Cont'd.)

				12	3	20	49.448N	50.238W	310	3.9	
3L	Grand Banks	GRB09	2009	11	14	20	47.0905N	47.8658W	168	-0.30	Survey
				11	14	20	46.9235N	47.5997W	188	0.50	
				11	14	20	46.7933N	47.5157W	189	0.90	
				11	15	20	47.5898N	47.5602W	277	2.80	
				11	16	19	47.6995N	47.5822W	303	2.40	
		CAN_3L	2012	11	26	20	48.9612N	51.9655W	320	3.6	Survey
				11	26	20	49.1125N	52.1890W	313	2.3	
				11	26	20	49.2092N	52.1767W	299	3.2	
				11	26	20	49.1520N	51.5290W	310	3.5	
				11	26	20	48.9770N	51.5258W	285	3.2	
3M	Flemish Cap	FLC10	2010	8	7	100	47.5227N	44.0572W	450	3.80	Patrol
		FLC11	2011	7	6	20	48.4905N	45.257W	780		survey
				7	6	20	48.4352N	44.790W	800		
				7	7	20	48.4152N	44.9778W	707		
				7	31	20	47.6592N	44.2892W	342		

Table A1 (Cont'd.)

				7	31	20	47.341N	43.9893W	419		
4W	Nova Scotia	NSC	2011	9	8	80	45.45175N	61.00168W	70		scientist
5Y	Gulf of Maine	GOM10	2010	7	19	20	43.485587N	69.384945W	148		survey
				7	20	20	43.504458N	69.013858W	133		
				7	20	20	43.334918N	69.354007W	168		
				7	20	20	43.118342N	69.15518W	177		
				7	21	20	43.064592N	69.274202W	174		
				7	21	20	43.013282N	69.518022W	155		
				7	22	20	43.304803N	70.125178W	129		
				7	22	20	43.331192N	69.93476W	138		
				7	22	20	43.35836N	69.862015W	163		
		GOM12	2012	7-8	NA	96	43.05N	70.20W	167	6.60	survey
				7-8	NA		42.93N	70.38W	120	6.00	
				7-8	NA		42.87N	70.45W	116	6.00	
				7-8	NA		42.78N	70.37W	81	6.10	
				7-8	NA		42.92N	70.33W	139	6.10	
				7-8	NA		42.97N	70.25W	158	6.40	
				7-8	NA		42.98N	70.42W	104	6.40	

Table A2. Estimates and tests for genetic differentiation among all sample pairs based on 10 microsatellite loci. Below diagonal: average F_{ST} over loci (***bold italics*** values represent estimates with a lower 5% confidence limit above zero). Negative estimates indicate absence of genetic difference between samples. Above diagonal: p-values resulting from test for genetic differentiation (GENEPOP option 3/2 with MCMC parameters 50000, 500, 50000), summarized over loci (Fisher's summation procedure) (***bold italics*** values are significant also under Benjamini & Yekutieli's FDR approach). Sample information in Table A1.

Division	-	2G	2H	2J			3K	3L		3M		4W	5Y	
Sample	HUS	CAN_2G	CAN_2H	CAN_2J	LAB09	LAB11	CAN_3K	CAN_3L	GRB	FLC10	FLC11	NSC	GOM10	GOM12
HUS	-	***0.0055***	***0.0000***	0.5414	0.5909	0.8375	0.6601	0.6917	0.6026	***0.0000***	***0.0002***	0.5322	***0.0000***	***0.0000***
CAN_2G	0.0004	-	0.0286	***0.0038***	***0.0095***	***0.0040***	0.2308	0.0421	***0.0062***	***0.0000***	***0.0000***	0.0359	***0.0000***	***0.0000***
CAN_2H	0.0027	-0.0002	-	***0.0010***	***0.0000***	0.0284	0.0326	0.3527	***0.0000***	***0.0000***	***0.0000***	***0.0000***	***0.0000***	***0.0000***
CAN_2J	-0.0011	0.0001	0.0011	-	0.1121	0.2156	0.2872	0.0457	***0.0038***	***0.0000***	***0.0000***	0.0508	***0.0000***	***0.0000***
LAB09	0.0002	0.0007	0.0021	-0.0004	-	0.2290	0.1865	0.0950	0.4484	***0.0000***	***0.0000***	0.1608	***0.0000***	***0.0000***
LAB11	-0.0014	-0.0008	0.0016	-0.0003	-0.0004	-	0.6836	0.6869	0.5421	***0.0000***	***0.0000***	0.4322	***0.0000***	***0.0000***
CAN_3K	0.0000	-0.0013	0.0004	-0.0010	0.0002	-0.0006	-	0.1496	0.0741	***0.0000***	***0.0000***	0.1626	***0.0000***	***0.0000***
CAN_3L	-0.0016	-0.0003	0.0010	-0.0003	0.0001	-0.0014	-0.0003	-	0.0420	***0.0000***	***0.0000***	0.1365	***0.0000***	***0.0000***
GRB	0.0007	-0.0004	0.0033	0.0011	0.0004	-0.0003	-0.0004	0.0017	-	***0.0000***	***0.0000***	0.3006	***0.0000***	***0.0000***
FLC10	***0.0042***	***0.0039***	***0.0091***	***0.0046***	***0.0051***	***0.0056***	***0.0066***	***0.0057***	***0.0068***	-	0.0176	***0.0000***	***0.0000***	***0.0000***
FLC11	***0.0034***	***0.0035***	***0.0072***	***0.0047***	***0.0067***	***0.0048***	***0.0050***	***0.0052***	***0.0071***	0.0013	-	***0.0001***	***0.0000***	***0.0000***
NSC	0.0002	0.0015	0.0027	-0.0006	-0.0001	0.0001	0.0012	0.0016	0.0011	***0.0049***	***0.0032***	-	***0.0000***	***0.0000***
GOM10	***0.0212***	***0.0268***	***0.0276***	***0.0231***	***0.0229***	***0.0222***	***0.0262***	***0.0242***	***0.0291***	***0.0266***	***0.0212***	***0.0182***	-	0.4642
GOM12	***0.0228***	***0.0302***	***0.0306***	***0.0244***	***0.0270***	***0.0251***	***0.0294***	***0.0264***	***0.0308***	***0.0292***	***0.0221***	***0.0194***	-0.0004	

8.0 APPENDIX 2 - FIGURE

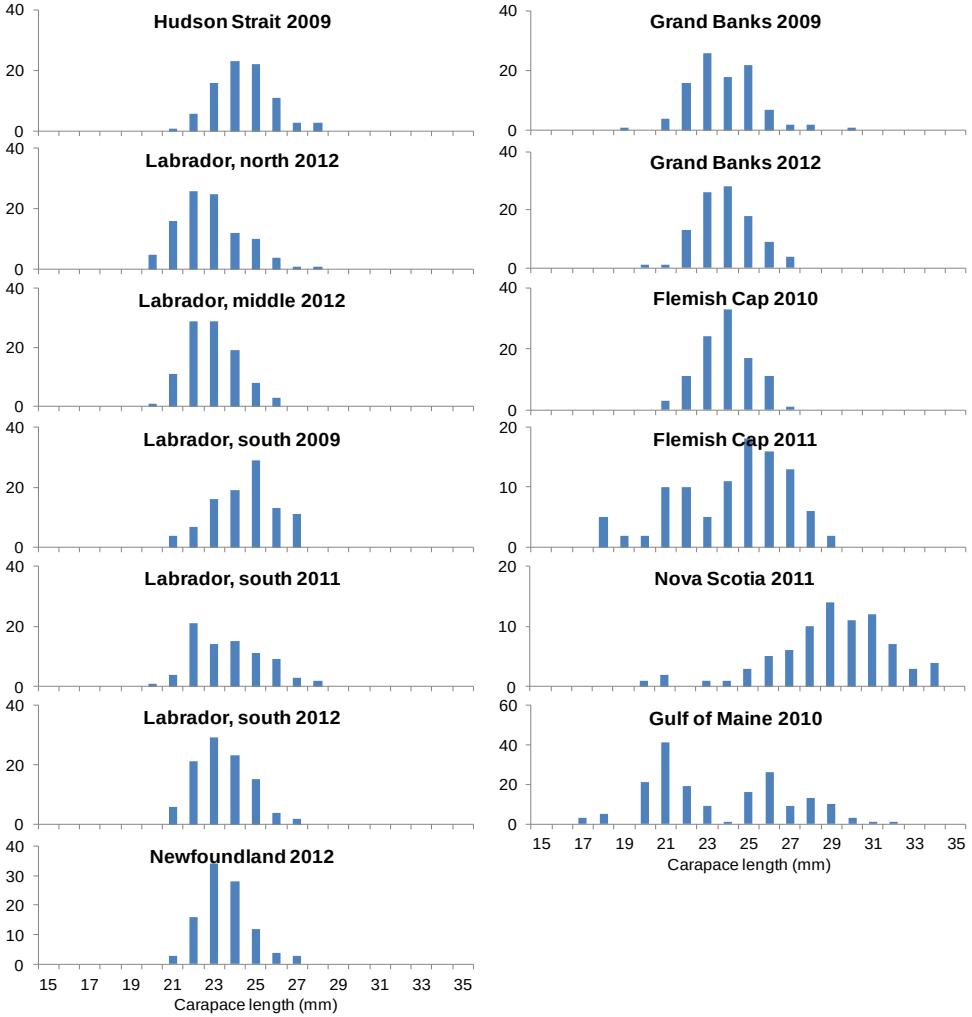

Fig. A1. Length frequency distribution of samples of female shrimp for genetic analyses. Sample sizes are given in Table A1. Note different scales of y-axes (number of shrimp.