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Redfish Species Distribution and Population Genetic Structure in the Northwest Atlantic: Preliminary Results

by

Séverine Roques[1], J.-M. Sévigny[2], L. Bernatchez[1] and D. Power[3]

[1] GIROQ, Département de biologie, Université Laval, Ste-Foy
Québec, G1K 7P4 Canada

[2] Direction des Invertébrés et de la Biologie expérimentale, Ministère des Pêches et des Océans
Institut Maurice-Lamontagne, 850, Route de la Mer, Mont-Joli, Québec G5H 3Z4 Canada

[3] Science, Oceans and Environment Branch, Department of Fisheries and Oceans
P.O. Box 5667, St. John's, Newfoundland A1C 5X1 Canada

SUMMARY

Redfish species distribution and population differentiation in the Northwest Atlantic are described using variability at the *MDH** locus and microsatellite DNA markers. The distribution of the MDH genotypes shows that *S. fasciatus* dominates the southern part of the redfish distribution while *S. mentella* is the most abundant species in the northern part of the distribution area. The distribution of both species overlaps mainly in Units 1 and 2, in NAFO divisions 3O, 3LN and 3M. The presence of *S. fasciatus* in the Labrador Sea is also observed and some *S. mentella* specimens are present on the Scotian Shelf. The distribution of the heterozygous individuals at the *MDH** locus is largely restricted to Units 1 and 2 indicating that hybridization between the two species does not occur across the area of sympatry.

Analyses of the variability at eight microsatellite loci reveal the existence of structure although weak in some cases. Within *S. fasciatus*, significant differences in allelic frequencies were observed between samples from the Gulf of Maine and those of Unit 3 but no difference was found between samples from the Gulf of St. Lawrence (Unit 1) and those collected in Unit 2 (Laurentian Channel Southeast of Newfoundland). Within *S. mentella*, no genetic difference could be detected among samples from the Div. 3LNO and those from the Subarea 2 + Division 3K. No difference could be detected either among samples collected in the Unit 1 (MES5-MES7) and those of Unit 2 (MES1 and MES2). However, significant differences were observed between the Newfoundland sample MES4 and the other samples from the same region, MES1-MES3 (mean $\theta = 0.013$). The sample MES3 was also significantly different from MES1 and MES5. These results may indicate that weak structuring exists for *S. mentella* in these areas.

INTRODUCTION

The management of several marine exploited species is based on the assumption that these species distribution comprises different stocks and that these stocks represent populations with particular patterns of recruitment and mortality (Carvalho and Hauser 1995). It is also assumed that the fishery will target unique stocks. Understanding the population structure (geographical structuring) is thus a prerequisite to the proper management and conservation of those species.

In the case of redfish, the description of stock structure may be quite complex since these stocks may comprise different sibling species each of them being characterised by different life history patterns. Indeed, three species are currently recognized in the Northwest Atlantic: *Sebastes mentella* Travin, 1951, *S. fasciatus* (Storer, 1854) and *S. norvegicus* (Ascanius, 1772). For the fishery management however, *S. fasciatus* (Acadian redfish) and *S. mentella* (deep-water redfish) are the two most important species in the Northwest Atlantic and show differential ecological preferences. *Sebastes fasciatus* occurs in shallower waters (150-300m) with a distribution mainly restricted to the southern regions (Gulf of Maine, Scotian Shelf), whereas *S. mentella* is distributed all over the North Atlantic ocean at depths varying between 350 and 500m (Atkinson 1987). The two species overlap in regions south of Newfoundland, and off the Scotian Shelf, but particularly in the Gulf of St. Lawrence, where there are both known to extrude their larvae (Sévigny *et al*. 2000).

In the Northwest Atlantic, there are eight redfish management areas: Subarea 2 + Division 3K, Division 3M (Flemish Cap), divisions 3LN, Division 3O, Unit 1 (Gulf of St. Lawrence), Unit 2 (Laurentian Channel, South of Newfoundland), Unit 3 (Scotian Shelf) and Gulf of Maine. In these areas, except for Flemish Cap and in the Gulf of Maine, Canada has prosecuted redfish fisheries to varying degrees since the late 1940s. The most commonly fished areas were Subarea 2 + Division 3K, as well as units 1, 2 and 3.

Several morphological and genetic characters were used to assess the redfish species identification and distribution in the Northwest Atlantic. However, anal fin ray counts (AFC), extrinsic gasbladder muscle (EGM) rib passage patterns and the malate dehydrogenase (MDH) electrophoretic mobility patterns (Ni 1981; Ni 1982; Payne and Ni 1982; McGlade *et al*. 1983) are those currently used to discriminate among redfish species. Recently Desrosiers *et al*. (1999) used ribosomal DNA to discriminate between *S. fasciatus* and *S. mentella* and they have shown that introgression occurs between these two species in the Gulf of St. Lawrence. However, the above mentioned studies did not allow for the fine description of the population genetic structure. Recently, microsatellite DNA markers were developed for redfish (Roques *et al*. 1999 a and b) and used to assess the importance of introgressive hybridization between *S. fasciatus* and *S. mentella* in the Northwest Atlantic (Roques *et al*. in preparation).

In this study, we present the results on the distribution of *S. fasciatus* and of *S. mentella* in the Northwest Atlantic as identified by the MDH electrophoretic patterns of this enzyme and we assess the population structure of these two species using microsatellite DNA markers in this area.

MATERIAL AND METHODS

Sampling

Sampling was carried out from 1994 to 1998 between May and November and covered most of the redfish distribution area in the Northwest Atlantic i.e. from the Gulf of Maine to the Labrador Sea and the Gulf of St. Lawrence. Redfish samples were obtained from 552 bottom trawl tows. In order to increase the sample size, all the tows that were carried out within a rectangle of 0.4 degree of latitude and longitude were pooled. The result of this grouping is represented in Figure 1. For the present study, however, all the individuals collected within each NAFO division were pooled in order to provide a broad picture of the species distribution as described by the variability at the *MDH** locus. More detailed results of this study will be presented elsewhere.

All redfish collected were classified into *S. fasciatus* and *S. mentella* based on the examination of meristic (anal fin ray count, AFC), morphological (gasbladder musculature, GBM) and genetic characters (*MDH* locus*). Laboratory analyses of the MDH electrophoretic patterns were carried out as described in Sévigny *et al*. (2000) using liver tissue. Two alleles segregated at the *MDH** locus, resulting in the presence of three phenotypes (Rubec *et al*. 1991 and references therein). Homozygotes for the slow allele (*MDH*A2*) were assigned to *S. fasciatus,* and homozygotes for the fast allele (*MDH*A1*) were classified as to *S. mentella*. Heterozygous individuals were kept separated, as they are most likely of hybrid origin. Statistical analyses of the MDH variability were limited since the MDH data are used to provide a broad picture of the species distribution in the study area. The adequacy of genotypic proportions to Hardy-Weinberg proportions were tested for the whole NAFO divisions where genotypic variation was observed using the *G*-test of goodness-of-fit. Differences in genotypic frequencies between Units 1 and 2 were tested using heterogeneity χ^2 test.

For the microsatellite analyses, redfish larger than 20 cm of both *S. fasciatus* and *S. mentella*, sampled and identified as described, were selected from samples collected in a large region encompassing distribution areas of these species in the Northwest Atlantic and different NAFO management units. Sample sizes averaging 47 fish were chosen. A total of 803 fish were collected from 1995 to 1998, including four *S. mentella* samples from the northern regions (ALLOMEN), two *S. fasciatus* from the southern regions (ALLOFAS), three *S. fasciatus* (SYMPFAS) and seven *S. mentella* (SYMPMEN) from Units 1 and 2. Information about the sampling is presented in Table 1 and Figure 2.

DNA was extracted from muscle tissue, frozen at -80^{o}C or stored in 95% ethanol, using phenol-chloroform (Sambrook *et al.* 1989) Chelex (Walsh *et al.* 1991) methods. Samples were screened for variation at eight specific microsatellites loci, as detailed in Roques *et al.* (1999a).

Descriptive Statistics for microsatellites

The extent of intra- and inter sample genetic diversity based on allelic composition of the 17 samples was first documented. Number of alleles (A), observed heterozygosity (H_o) and unbiased gene diversity (H_e) corrected for sampling bias (He_{nb}, Nei (1987)) were calculated using the GENETIX program, version 4.0 (Belkhir *et al.* 1998). A, H_o and H_e were compared between both redfish taxa using the non-parametric t-test of Student available using STATISTICA, version 4.5 (Statistica 1994). For those comparisons, the number of alleles was adjusted to an equal sample size of 47 per population (averaged number of individuals per sample) using the equation 11 in Ewens (1972).

Deviation from Hardy-Weinberg (HW) proportions were assessed for both alternatives of deficit and excess of heterozygotes using the multisample score test available in the GENEPOP program, version 3.1 (Raymond and Rousset 1995). Probabilities of significance (P) were computed using the Markov chain method through 1000 iterations (Guo and Thompson 1992) as implemented in GENEPOP. The extent of HW departures was estimated in each sample using *f*, the Weir and Cockerham's (1984) estimator of F_{is}. Significance levels were tested using the permutation procedures available in GENETIX. The null hypothesis of no linkage disequilibrium was tested in all samples, and significance values were computed for each locus pair by unbiased estimates of Fisher's exact tests using the Markov Chain method available in GENEPOP.

Population differentiation

To test for genetic differentiation among the 17 samples, homogeneity tests of allele frequency distribution were performed using GENEPOP. Multilocus values of significance were obtained following Fisher's method. The extent of gene flow among samples was estimated by the unbiased Fst estimator (θ) of Weir and Cockerham (1984). Disjunct allelic size distributions, in which alleles were separated by numerous base pairs, were observed for several loci (see Roques *et al.* 1999b), suggesting that they probably do not follow a strict stepwise mutational model (DiRienzo *et al.* 1994; Angers and Bernatchez 1997). We therefore did not estimate the extent of genetic differentiation based on molecular variance. Probability values calculated in all the tests above were adjusted for multiple test comparisons using the sequential Bonferroni adjustments (Rice 1989). The extent of divergence among the 17 samples of *S. fasciatus* and *S. mentella* was also quantified by the (Cavalli-Sforza and Edwards 1967) chord distance (D_{ce}), to test whether sympatric samples were intermediate between allopatric samples of each taxa, due to introgression. The use of chord distance generally lead to a higher probability of obtaining the correct tree topology under either the infinite allele model (IAM) or SMM assumptions (Takezaki and Nei 1996; Angers and Bernatchez 1998). Pairwise distances were used to construct a populations phenogram using the neighbour-joining (NJ) algorithm (Saitou and Nei 1987) available in PHYLIP version 3.5c (Felsenstein 1993). SEQBOOT, GENDIST, NEIGHBOR, CONSENSE programs were successively conducted to build the tree. Confidence estimates on tree topology were estimated by the percentage of 1000 bootstraps performed resampling allelic frequencies.

Dynamics, extent and patterns of introgression

Two different multivariate analyses were used to investigate the extent and patterns of introgression between *S. fasciatus* and *S. mentella*. We first conducted a Principal Components Analysis (PCA) (Greenacre 1984) to visualize the relationships between the 17 samples based on their allelic frequency, using STATISTICA. This approach involves a linear transformation of the observed allele frequencies, where the axes (components) are chosen as to

maximize the variation of the transformed data, measured along each axis. To test whether the intermediate samples observed in the PCA were composed of an admixture of individuals from the two taxa, or of individuals from mixed allelic composition, a Factorial Correspondence Analysis (FCA) was carried out using GENETIX, that allows the projection of all the individuals in a space defined by the components. Briefly, the method is based on the similarity of individuals in their allelic state for each allele. A code is attributed to each individual whether it is heterozygote (1), homozygote (2) or if the given allele is absent (0). The main advantage of the FCA is that each individual can be represented using each allele as an independent variable, contrary to other multivariate analyses that generally use a combined parameter as descriptor.

RESULTS

Species distribution based on MDH variation

Figure 3 shows clearly that, in the Northwest Atlantic, the distribution of the two most important redfish species differs significantly. Indeed, *S. fasciatus* is almost the only species represented in the southern part of the distribution; the Gulf of Maine and the Scotian Shelf. In these two units, the frequencies of the allele **A2* which is characteristic of *S. fasciatus* is equal to 1 and 0.98 respectively (Table 2). In these two divisions, only 14 individuals out of 675 belong to the *S. mentella* species. In the northern part of the Northwest Atlantic redfish distribution (Subarea 2 + Div 3K), *S. mentella* is the most important species although *S. fasciatus* was also observed in small proportion (Fig. 3; Table 2). Both species are well represented in all the other NAFO divisions (3M, 3N, 3LN, 3O, Units 1 and 2). The change in the species distribution across the NAFO divisions is reflected in the allelic frequency changes that take place from north to south. Indeed, allele **A1* characteristic of *S. mentella* is the most frequent in the northern part of the species distribution while allele *A2* is almost fixed in the southern part. The presence of the two redfish species in most NAFO divisions translate not surprisingly in significant deviations from Hardy-Weinberg expectations; all of them being associated with deficits in heterozygotes (Table 2).

One of the most important feature of the genotypic distribution observed in the present study is the presence of heterozygous individuals (*MDH*A1A2*) in Units 1 and 2. In fact their distribution is almost exclusively restricted to these two areas (Fig. 3, Table 2). These heterozygous individuals are most likely the results of hybridization between *S. fasciatus and S. mentella* in this part of the area of sympatry. There are however difference in the genotypic frequencies between Units 1 and 2 (χ^2 = 111.8; $P < 0.001$).

Patterns of genetic variability of S. fasciatus and S. mentella

For microsatellites, high genetic variability was generally observed across the 17 samples, with a total number of observed alleles (A) ranging from 104 to 165 (mean = 135), and unbiased heterozygosity values ranging from 0.748 to 0.914 (mean = 0.831) (Table 1). A highly significant difference in allelic diversity (t = -9. 895, P< 0.00001) was observed between *S. fasciatus* and *S. mentella*, with mean number of alleles being respectively 115 (ranging from 94 to 124) and 155 (ranging from 146 to 171). Fewer alleles at relatively high frequencies were observed for *S. fasciatus*, while *S. mentella* was characterized by numerous alleles at low frequencies (not shown), as previously observed in a smaller number of samples (Roques *et al*., 1999b). Unbiased heterozygosity values were also significantly different between taxa (t = -6.131, P= 0.00019), ranging from 0.748 to 0.843 (mean = 0.803) in *S. fasciatus*, and from 0.794 to 0.914 (mean = 0.869) in *S. mentella*.

Higher polymorphism is generally expected in sympatry, compared to allopatry, since introgression should increase genetic variability. Here, however, this was expected for *S. fasciatus*, but not necessarily for *S. mentella*, given the lower polymorphism observed in *S. fasciatus*. Indeed, we observed in *S. fasciatus* a mean unbiased heterozygosity value significantly higher for SYMPFAS (0.832) compared to ALLOFAS group (0.757) (t = -3.69, P= 0.021), although mean allelic diversity (A = 115) was identical for both groups. The reverse pattern was observed for *S. mentella*, with a number of alleles significantly lower for sympatric (SYMPMEN) (A=149) compared to allopatric (ALLOMEN) (A=160) (t= -2.748, P= 0.022) (Table 1), whereas mean unbiased heterozygosity was similar for both groups (t= 0.461, P= 0.655). This overall pattern provided a first indication of introgressive hybridization between both taxa in the zone of sympatry (Roques *et al*. in preparation).

Patterns of genetic differentiation

Highly significant differences in allelic frequencies were observed for all pairwise comparisons involving samples of the two taxa (data not shown). Those differences translated into moderate estimates of θ varying from 0.074 to 0.164 with a mean value of 0.103 (Table 3). It has recently been proposed that the maximum value of θ will be greatly reduced when using highly polymorphic markers, such that, the maximum potential differentiation should roughly not exceed the average level of homozygosity (Hedrick 1999). The mean θ value observed here between the two taxa was indeed very similar to the approximate maximum estimate of the parameter (average homozygosity = 0.117). In contrast, much smaller differences were found among samples within taxa. Within *S. fasciatus*, significant differences in allelic frequencies were observed between allopatric samples from the Gulf of Maine (FAA1) and from Unit 3 (FAA2) ($\theta = 0.0132$), but no difference was found among SYMPFAS samples (averaged $\theta = 0.0006$) (Table 3). The θ values, however, were neither significant within SYMPFAS, or between FAA1 and FAA2. Within *S. mentella*, no genetic difference was found among ALLOMEN samples (3LN, 3O, Subarea 2 + Division 3K), with non-significant values of θ ranging from – 0.0006 to 0.0062 (mean = 0.0056) (Table 3). For sympatric samples (SYMPMEN), no difference was observed between samples in the Gulf of St. Lawrence (MES5-MES7) and the two samples from the Laurentian Channel south of Newfoundland (MES1 and MES2) (Figure 2, Table 1). However, significant differences were observed between the Newfoundland sample MES4, and the other samples from the same region, MES1-MES3 (mean $\theta = 0.013$). MES3 was also significantly different from MES1 and MES5. Altogether, these results suggested that samples within SYMPFAS and ALLOMEN were genetically homogeneous, whereas weak structuring may exist within the other two groups (ALLOFAS, SYMPMEN).

A general pattern in hybrid zones studies is that the exchange of genes from one species to another is expected to decrease divergence between them. Hence, *S. fasciatus* and *S. mentella* were expected to be more closely related in sympatry than in allopatry. Indeed, we found that the sympatric groups, SYMPMEN and SYMPFAS, were genetically more similar (average $\theta = 0.088$, ranging from 0.074 to 0.107), than were allopatric samples (ALLOMEN/ALLOFAS, average $\theta = 0.134$, ranging from 0.109 to 0.164) (t-Student, $P < 0.001$). Altogether, these results further indicated the occurrence of introgression between *S. fasciatus* and *S. mentella* when found in sympatry.

Pattern, extent and level of introgression in the hybrid zone

The intermediate genetic composition of sympatric samples was illustrated by the NJ tree in which the two allopatric groups (ALLOMEN and ALLOFAS) clustered at the opposite ends of the network, and the sympatric ones (SYMPFAS and SYMPMEN) in between (Figure 4). The distinction of the two taxa was supported by high bootstrap values (100%). Within taxon, allopatric samples formed highly supported groups (72% and 100% respectively) relative to sympatric samples. In contrast, bootstrap values were generally low within the four groups, and particularly within SYMPMEN.

This intermediate position of sympatric samples was further supported by the PCA analysis (Figure 5). The first component (not shown) essentially separated *S. fasciatus* and *S. mentella*, and explained most of the total variance (60%). More information on the position of samples within species was gained by the others components. The second component summarising 26.9% of the variation, mainly accounted for the differentiation between *S. fasciatus* and *S. mentella*, but also separated sympatric from allopatric samples of *S. mentella*. Considering this axis, sympatric *S. mentella* samples were closer to *S. fasciatus* than were the allopatric ones. The third component (3.2% of the variation) differentiated allopatric from sympatric samples within each taxon (ALLOMEN from SYMPMEN, and ALLOFAS from SYMPFAS), and also accounted for the intermediate position of SYMPFAS between the two allopatric groups. The fourth component represented a small percentage of the total variance (1.7 %), but accounted for the difference between the allopatric groups of both taxa, and also brought SYMPFAS and SYMPMEN samples together, relative to allopatric samples.

The factorial correspondence analysis, based on 569 individuals, revealed that intermediate samples were composed of individuals of mixed specific allelic composition of both *S. fasciatus* and *S. mentella*, rather than of an admixture of individuals from the two taxa. Figure 6A represented the projections in the FCA space of all the allopatric individuals (ALLOMEN and ALLOFAS). The first axis accounted for 66.5% of the total variance and totally separated the two groups, except for two individuals of *S. mentella* found in *S. fasciatus*, possibly due to a

priori misclassification. Figures 6B and 6C represented the same allopatric individuals, to which sympatric *S. fasciatus* and *S. mentella* individuals were added. This showed that sympatric individuals of a given species tended to position closer to the cluster of individuals of the other species, than did allopatric individuals. They also created a continuum between the two species groups, further supporting an admixed allelic composition in individual fish of both *S. fasciatus* and *S. mentella* when found in sympatry.

The exact tests of Hardy-Weinberg equilibrium revealed highly significant deficits of heterozygotes in 6 out of the 17 samples, following sequential Bonferroni corrections (k=17, α= 0.05/17=0.0029) (Table 1). This was unlikely imputable to a particular locus, as 4 out of the 8 loci analysed were significantly deviating from HW proportions (k=8, α= 0.05/8=0.00625). A trend towards more important heterozygote deficiency was found in the sympatric *S. mentella* group, as four of the six deficits were observed in SYMPMEN (Table 1). In contrast, a single sample (FAS2) deviated from HW proportions within *S. fasciatus.* The highest deficit value (f = 0.087) was observed in the MES4 sample. The results of population differentiation also showed that this sample was the most genetically distinct *S. mentella* sample (Table 2). It was also the most introgressed sample with 22.89 % of specific *S. fasciatus* alleles (Table 1). These observations are suggestive of ongoing and more pronounced introgressive hybridization in this location.

DISCUSSION

Different studies have suggested previously that *S. fasciatus* and *S. mentella* hybridize in the Gulf of St. Lawrence (Rubec *et al*. 1991; Desrosiers *et al.* 1999; Valentin, 1999). Recently, Roques *et al*. (in preparation) have shown the importance of introgressive hybridization in the determination of genetic diversity, inter-specific difference and population structuring among redfish species in the Northwest Atlantic. In the present study, we have shown that hybridization does not occur across the area of sympatry but is limited to Units 1 and 2. Indeed, the distribution of the heterozygous individuals at the *MDH** is largely restricted to these two units (Fig. 3) implying either that the capacity of these individuals to migrate outside the hybridization area is limited or that other factors such as natural selection are acting (Roques *et al*. in preparation).

The overall high genetic variability quantified in this study corroborates observations of microsatellite analyses in other marine organisms (Ruzzante *et al.* 1998; Bagley *et al.* 1999; Lundy *et al.* 1999; Shaw *et al.* 1999). Rocha-Olivares *et al.* (1999) proposed that the high variability generally observed in redfish may be due to their exceptional longevity, high degree of generational overlap, and low temporal variability in effective population size. Large geographic range of distribution, along with high dispersal capabilities are also regularly invoked to explain the high genetic variability of marine organisms (Smith and Fujio 1982; Planes 1998). This last assumption could explain the significantly higher polymorphism found in *S. mentella* relative to *S. fasciatus.* Indeed, with these assumptions, S. *mentella* is distributed over a much larger area than *S. fasciatus* throughout the North Atlantic, the latter taxon being restricted to a relatively small geographic range in the southwestern regions.

The patterns of population structure observed in both *S. fasciatus* and *S. mentella* were also congruent with weak genetic structuring usually reported for marine organisms (Gyllensten 1985; Palumbi 1994; Palumbi 1996). Differential patterns of population structure, however, were observed between *S. fasciatus* and *S. mentella,* which may be partly explained by their respective life histories. For instance, lower population structure is expected for pelagic and largely distributed marine species compared to more benthic ones or those more geographically restricted (Avise *et al.* 1987; Doherty *et al.* 1995). As mentioned above, *S. mentella* is more largely distributed than *S. fasciatus* and is more frequently encountered in the pelagic zone, in deeper waters, while *S. fasciatus* is more associated with the epibenthic zone of shallower waters (Litvinenko 1980).

As it has been stressed by Roques et al. (in preparation), our results highlighted the predominant role of introgressive hybridization in shaping the extent of genetic diversity, inter-specific differences and population structuring among *S. mentella* and *S. fasciatus.* Hence, the homogenizing effect of introgressive hybridization first resulted in lower genetic divergence between both taxa in the main zone of sympatry (in the area of the sympatric zone where hybridization occurs), compared to what was observed elsewhere. Secondly, all samples of the "sympatric group" in each taxon were genetically distinct from their allopatric congeners whereas almost no population structuring was observed among samples of the latter group. Third, higher polymorphism was observed in sympatric samples of *S. fasciatus,* compared to allopatric ones, as a direct consequence of introgression from *S. mentella*. The observed level of introgression between both redfish taxa was relatively important, averaging 15%

over all samples (Roques *et al*. in preparation). Strict comparisons with previous studies in other marine organisms remain difficult however, given their scarcity and the differential use of genetic markers and/or measures of introgression. Based on the percentage of allozymic conspecific alleles, the estimated level of introgression (average = 7%) observed between three Pacific redfishes, *S. auriculatus*, *S. caurinus* and *S. maliger*, was twice lower than observed in this study (Seeb 1998), whereas the level of introgression observed between two flatfishes, *S. aegyptiaca* and *S. senegalensis* (average = approximately 14%) was comparable to that observed between *S. mentella* and *S. fasciatus* (She *et al*. 1987).

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Table 1. Sample names, geographical origins, sizes (N), number of alleles (A), observed (H_o) and expected (H_e) unbiaised heterozygosities, mean *f* values and probability of significance (D), probability of heterozygote deficiency (P), estimated proportion (in percent) of *S. fasciatus* (AFA) and *S. mentella* (AME) allelic composition in 17 redfish samples pooled in four groups : ALLOFAS and ALLOMEN (allopatry), SYMPFAS and SYMPMEN (sympatry), standard errors on estimates (SE)

Samples	Geographical origin	N	A	A^a	H_0	H_e	P	*F*	D	AME	AFA	SE
ALLOFAS												
FAA1	Gulf of Maine	30	94	109	0.769	0.791	0.3969	0.028	0.150	0	100	0
FAA2	Nova Scotia	35	109	121	0.748	0.757	0.0995	0.011	0.310	0	100	0
SYMPFAS												
FAS1	Newfoundland	54	108	104	0.831	0.809	0.1786	-0.027	0.891	10.18	89.82	4.44
FAS2	St. Lawrence	49	124	122	0.832	0.821	0.0554	-0.013	0.747	11.16	88.84	3.21
FAS3	St. Lawrence	48	117	116	0.843	0.827	0.0857	-0.020	0.846	13.57	86.43	3.39
FAS4	St. Lawrence	47	118	118	0.824	0.815	0.4752	-0.011	0.071	10.25	89.75	2.95
ALLOMEN												
MEA1	Grands Banks	44	150	153	0.868	0.843	0.0613	-0.029	0.915	100	0	0
MEA2	Grands Banks	47	159	159	0.833	0.873	0.0001*	0.045	0.007	100	0	0
MEA3	Labrador (U2G)	52	171	165	0.872	0.883	0.4890	0.012	0.196	100	0	0
MEA4	Labrador (U2H)	52	168	162	0.856	0.891	0.0001*	0.039	0.012	100	0	0
SYMPMEN												
MES1	South Newfoundland	48	160	159	0.84	0.873	0.0112	0.038	0.018	81.78	18.22	4.22
MES2	South Newfoundland	51	153	149	0.844	0.854	0.1496	0.007	0.356	85.68	14.32	3.92
MES3	South Newfoundland	51	153	148	0.811	0.848	0.0001*	0.044	0.007	85.62	14.38	3.99
MES4	South Newfoundland	48	142	141	0.794	0.869	0.0001*	0.087	0.0001*	77.11	22.89	5.02
MES5	St. Lawrence	49	160	157	0.914	0.895	0.6249	-0.022	0.931	82.82	17.18	3.85
MES6	St. Lawrence	48	146	145	0.86	0.882	0.0022*	0.025	0.086	78.97	21.03	4.12
MES7	St. Lawrence	50	149	146	0.847	0.848	0.0001*	0.001	0.516	82.74	17.26	4.11

* indicate significant values following sequential Bonferroni corrections (k=17, α=0.05/17=0.0029).

A^a indicates adjusted number of alleles for an equal sample size (n=47) using equation 11 in Ewens (1972).

Table 2. Observed (Obs.) and expected (Exp.) number of individuals of each of the three genotypes and allelic frequencies in samples collected between 1994 and 1998 in each NAFO division. *n* = sample size.

		Genotype						Allelic Frequency	
		A1A1		*A1A2*		*A2A2*			
NAFO Divisions	*n*	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	**A1*	**A2*
Subarea 2 + Div. 3K	784	671	580	5	189	108	15	0.86	0.14
3M (Flemish Cap)	23	16	12	1	9	6	2	0.72	0.28
3LN	152	81	44	1	76	70	32	0.54	0.46
3O	258	74	22	1	106	183	130	0.29	0.71
Unit 1 (Gulf of St. Lawrence)	1617	743	454	231	806	643	357	0.53	0.47
Unit 2 (Laurentian Channel)	3593	1251	575	348	1725	1994	1293	0.40	0.60
Unit 3 (Scotian Shelf)	586	14	0	0	23	572	563	0.02	0.98
Gulf of Maine	89	0	0	0	0	89	89	0	1

Table 3. Pairwise sample differentiation estimates based on allelic variance at 8 microsatellites loci in 17 redfish samples. Dotted lines circumscribe between taxa comparisons q values.

Sample	FAA1	FAA2	FAS1	FAS2	FAS3	FAS4	MEA1	MEA2	MEA3	MEA4	MES5	MES6	MES7	MES1	MES2	MES3	MES4
FAA1																	
FAA2	0.0132*																
FAS1	0.0091*	0.0196															
FAS2	0.0185	0.0235	(-0.0050*)														
FAS3	0.0196	0.0274	(-0.0003*)	(-0.0058*)													
FAS4	0.0093*	0.0152	(-0.0043*)	(-0.0013*)	(0.0040*)												
MEA1	0.1355	0.1636	0.1354	0.1219	0.1178	0.1255											
MEA2	0.1154	0.1412	0.1113	0.1042	0.0991	0.1067	(-0.0039*)										
MEA3	0.1189	0.1504	0.1145	0.1101	0.1023	0.1105	(-0.0008*)	(0.0026*)									
MEA4	0.1085	0.1424	0.1125	0.1032	0.0974	0.1059	(0.0062*)	0.0014*	(-0.0006*)								
MES5	0.0830	0.1118	0.0817	0.0777	0.0741	0.0743	0.0063*	0.0153	0.0082	0.0044*							
MES6	0.0778	0.1095	0.0883	0.0846	0.0819	0.0792	0.0103	0.0154	0.0096	0.0090	(0.0002*)						
MES7	0.1009	0.1313	0.1015	0.0977	0.0941	0.0927	0.0109	0.0167	0.0156	0.0181	(0.0011*)	(-0.0005*)					
MES1	0.0794	0.1135	0.0829	0.0829	0.0794	0.0766	0.0052*	0.0149	0.0125	0.0103	(0.0020*)	(0.0020*)	(-0.0030*)				
MES2	0.1035	0.1349	0.1016	0.1005	0.0962	0.0933	0.0077	0.0181	0.0117	0.0146	(0.0003*)	(0.0017*)	(-0.0046*)	(0.0000*)			
MES3	0.1065	0.1410	0.1035	0.1070	0.1027	0.0987	0.0078*	0.0224	0.0158	0.0163	0.0093	0.0043*	0.0038*	0.0101	0.0045*		
MES4	0.0817	0.1143	0.0836	0.0865	0.0839	0.0793	0.0169	0.0274	0.0193	0.0213	0.0095	(0.0036*)	0.0057*	0.0098	-0.0094	0.0186	

( ) indicates non significant allelic frequency heterogenity following the method of Fisher (α=0.001).
* indicates non significant following Bonferroni corrections (k=120, α=0.05/120=0.00042)

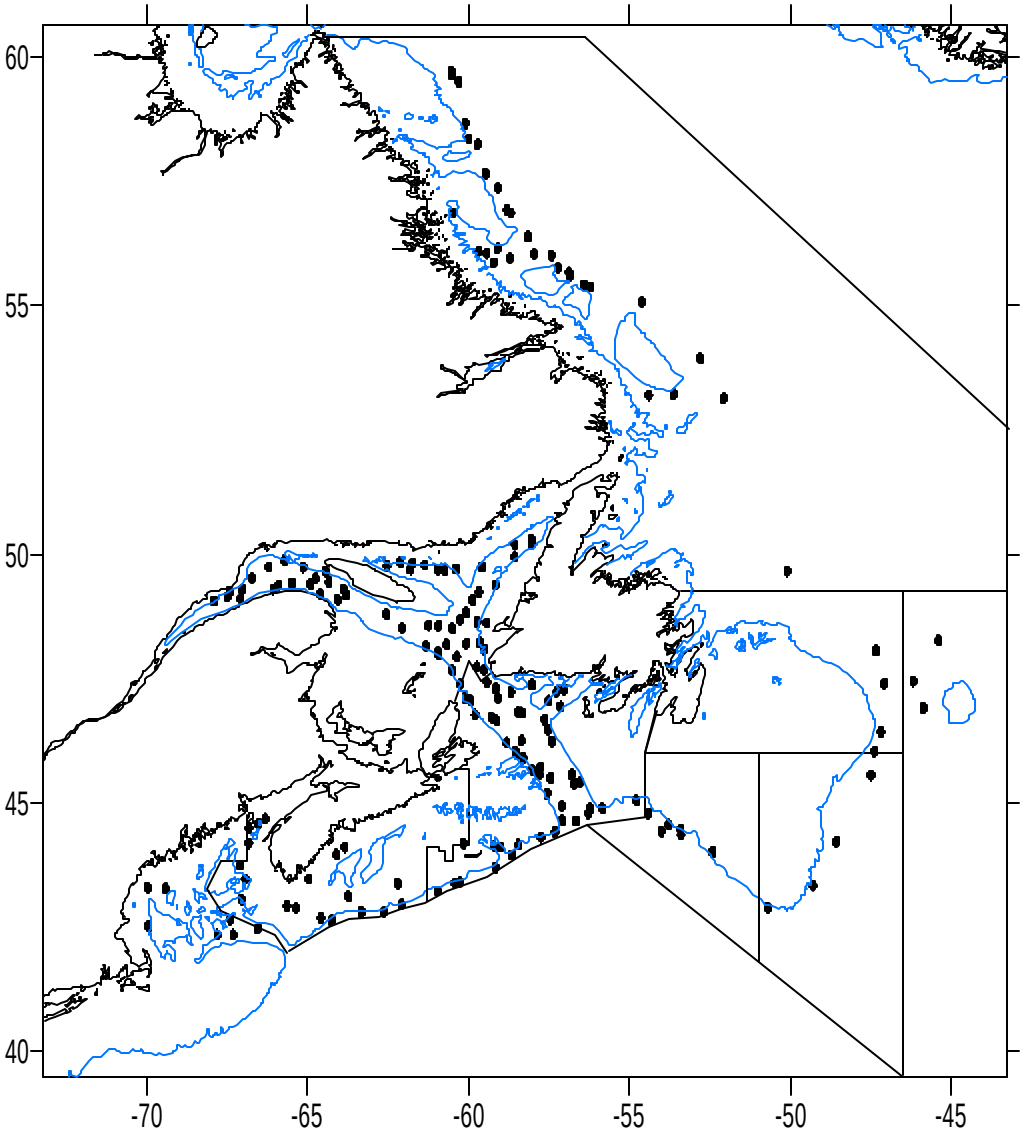

Figure 1. Map of the Northwest Atlantic showing the location of the 184 sites representing the 552 bottom trawl tows carried out between 1994 and 1998.

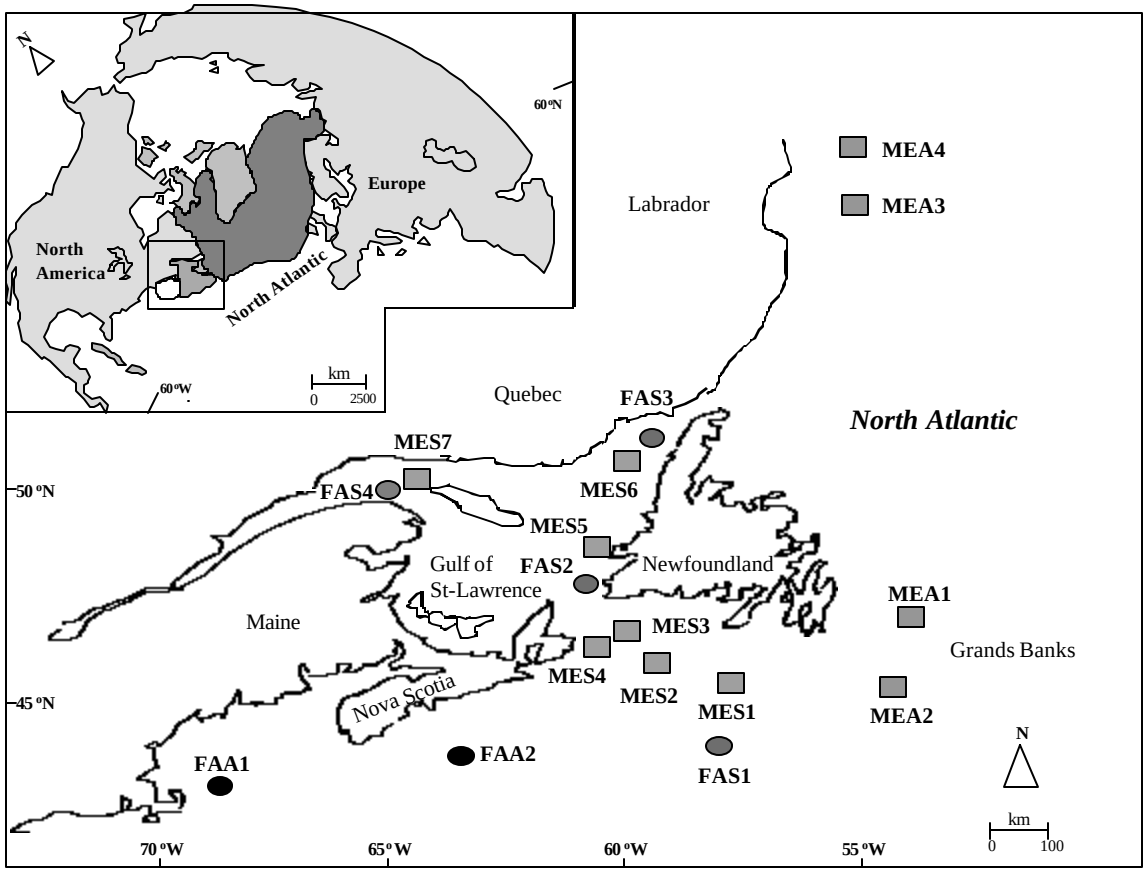

Figure 2. Inset map: geographic distribution of *S. mentella* (dark grey), *S. fasciatus* (white), zone of sympatry (striped), and study area (framed). Below, sampling localities of *S. mentella* (ME) and *S. fasciatus* (FA) samples. Grey squares : allopatric *S. mentella* (ALLOMEN); striped squares : sympatric *S. mentella* (SYMPMEN); black circles : allopatric *S. fasciatus* (ALLOFAS); striped circles : sympatric *S. fasciatus* (SYMPFAS)

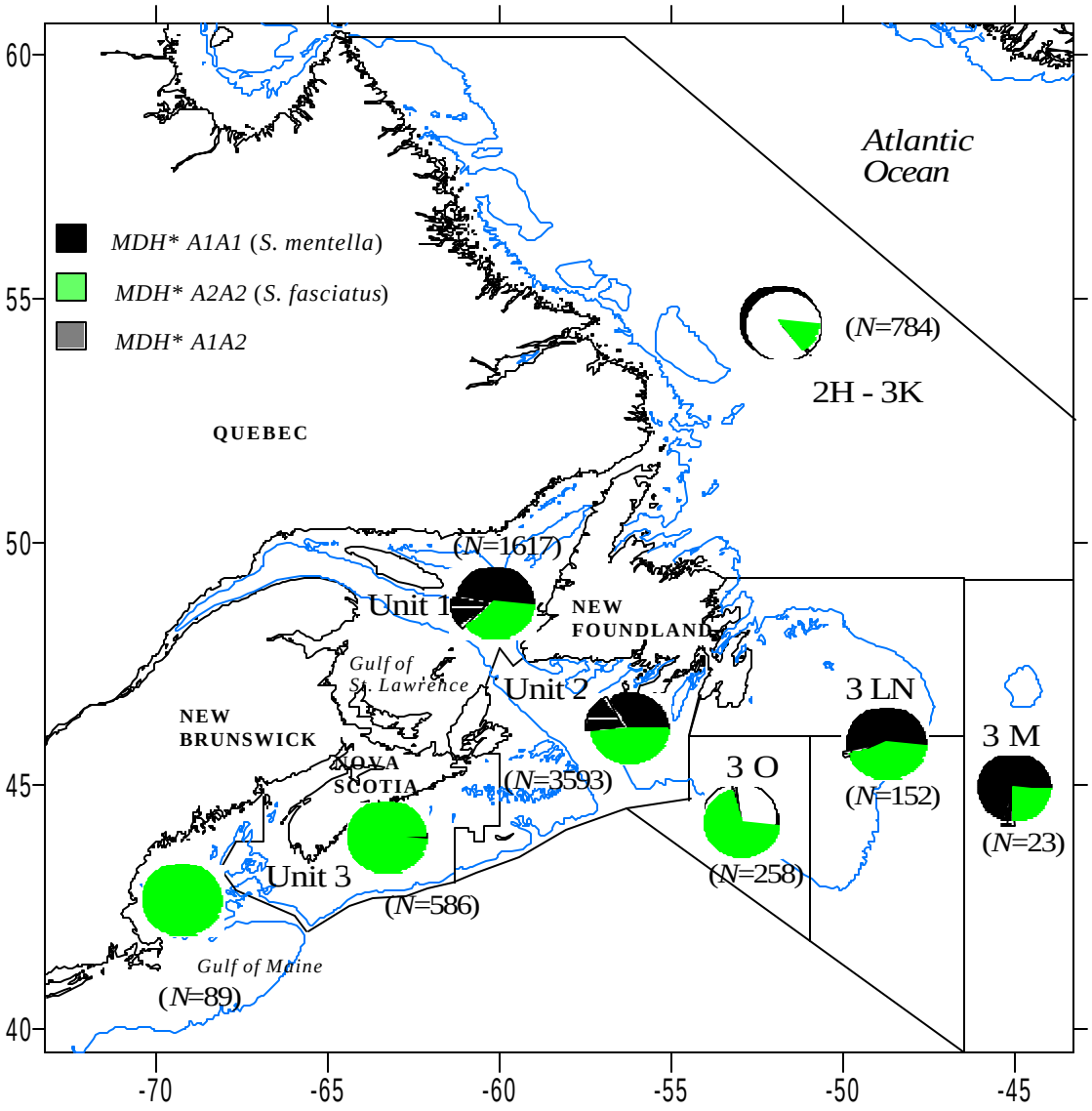

Figure 3. Map of the Northwest Atlanic showing the geographic distribution of the three MDH genotypes in the different NAFO management units.

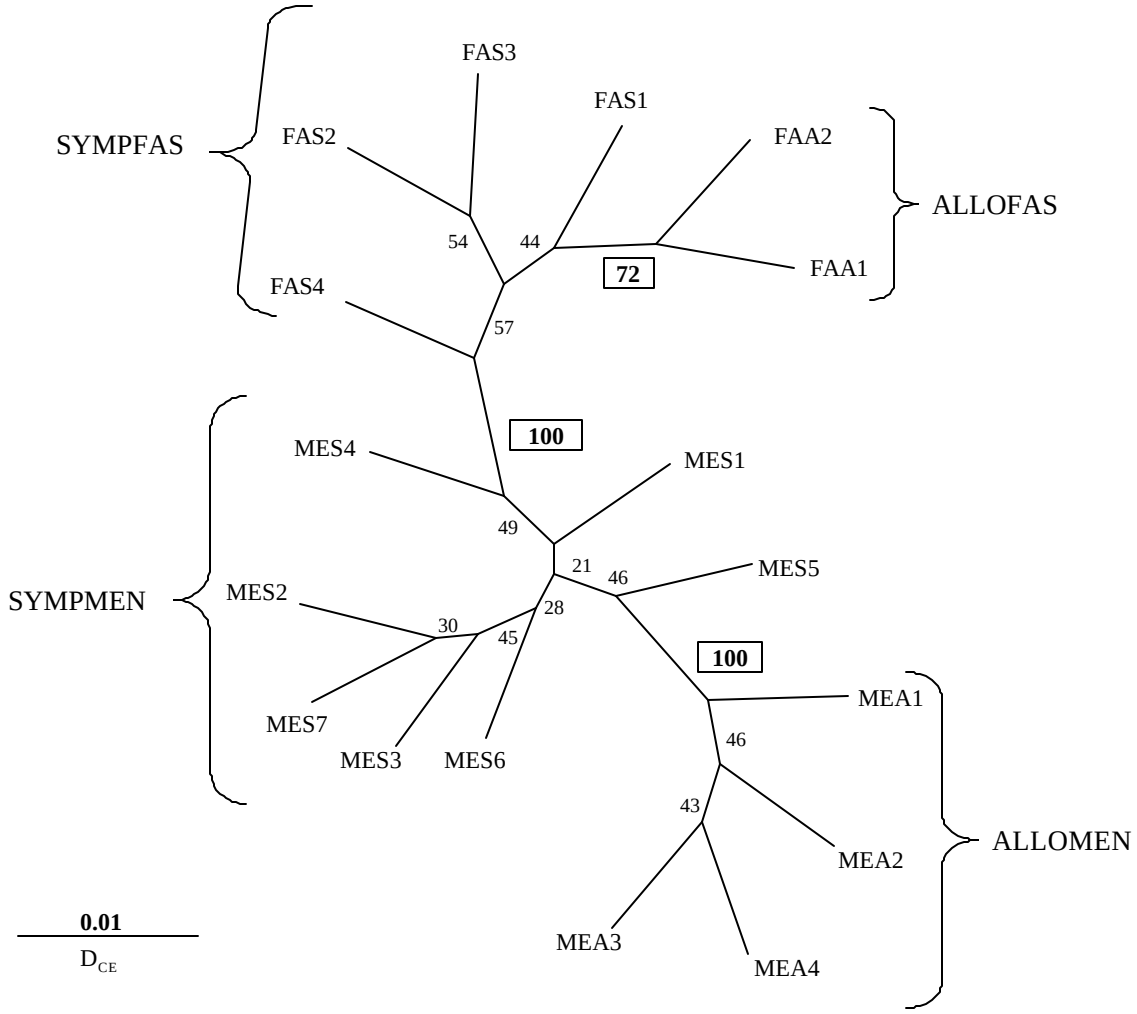

Figure 4. Neighbour-joining tree illustrating the relationships among 17 redfish samples based on pairwise D_{CE} genetic distances. Bootstrap values indicate the degree of support for each branch after 1000 resampling over loci.

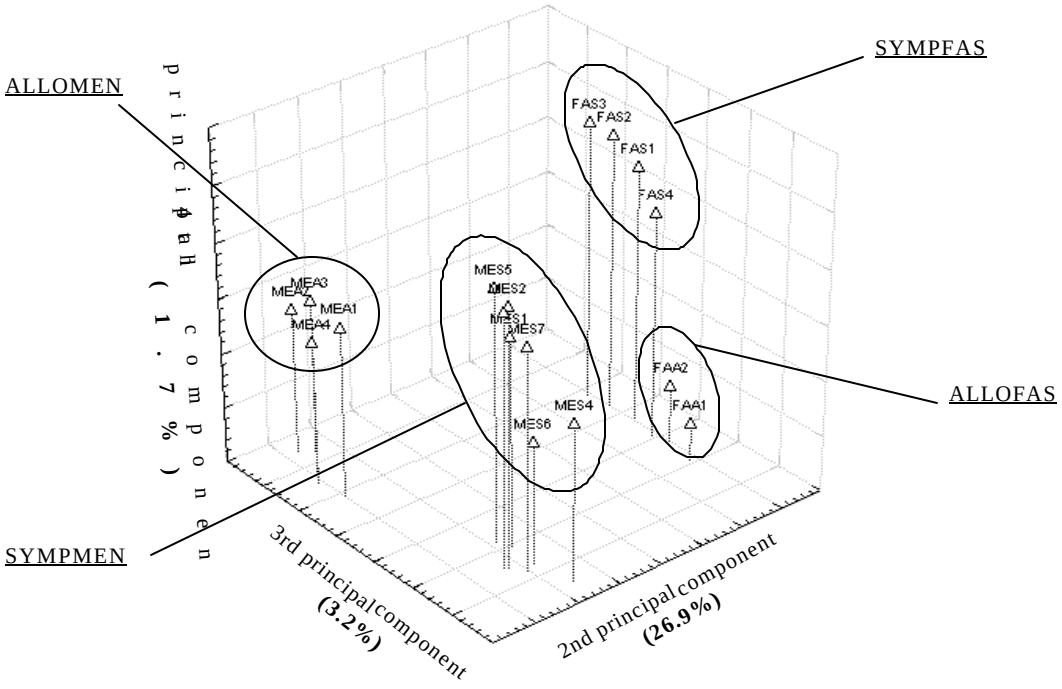

Figure 5. Diagram of the Principal Components Analysis (PCA) showing the 17 redfish samples in a three multidimensional space defined by the second, third and fourth components. Their respective contributions to the grouping are shown in percentage (%). The four groups correspond to the sympatric and allopatric *S. mentella* and *S. fasciatus* samples described in Table 1.

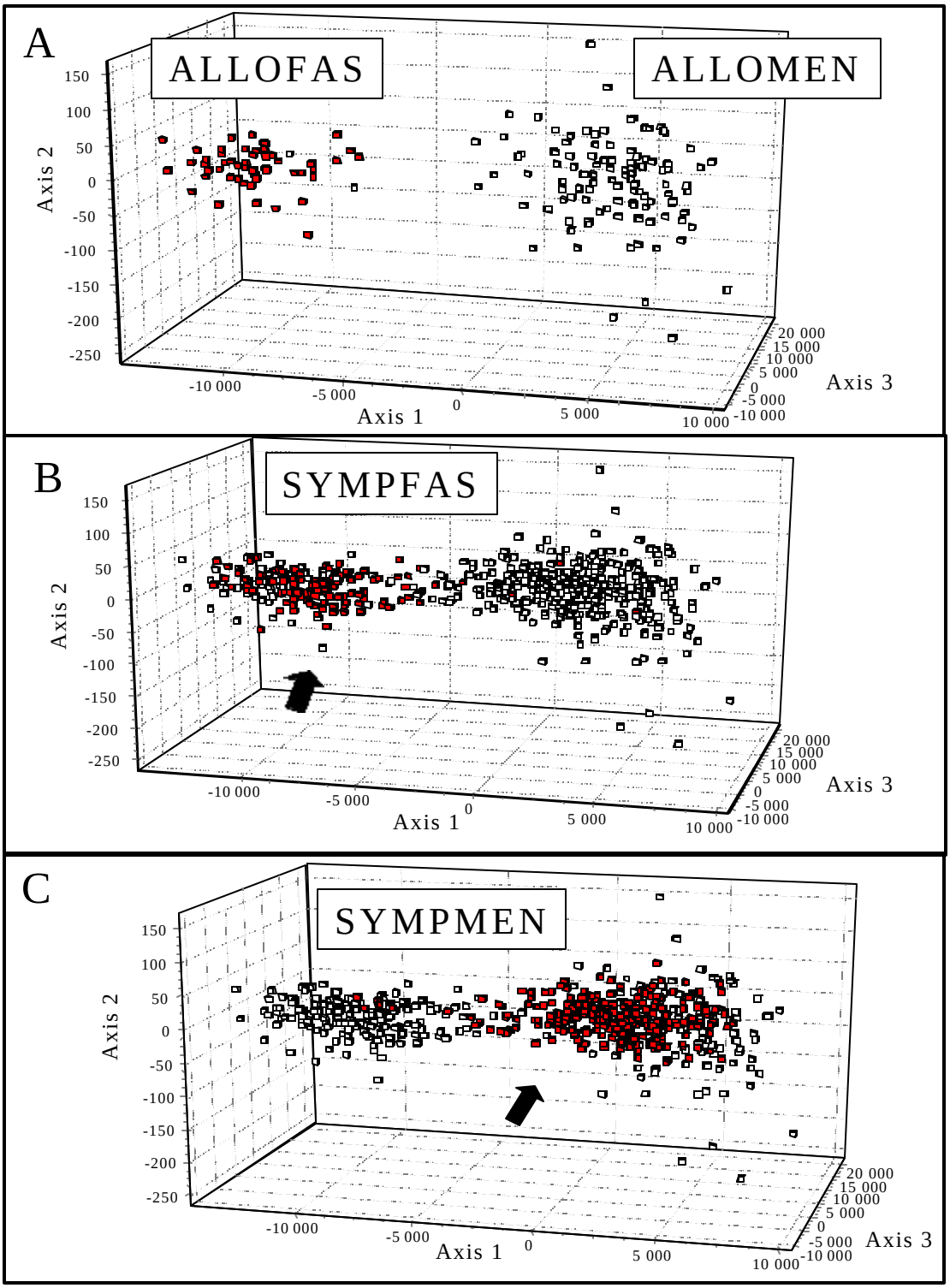

Figure 6. Diagram of the Factorial Correspondence Analysis (FCA) showing redfish individuals in a multidimensional space.

A : Allopatric samples of *S. fasciatus* (in white) and *S. mentella* (in dark)

B : Sympatric *S. fasciatus* samples (in dark)

C : Sympatric *S. mentella* samples (in dark)