Received: 30 August, 2012

Microsatellite and mtDNA markers were unable to reveal genetic population structure of swordfish (*Xiphias gladius*) in the Indian Ocean

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THE VERSION OF THIS PAPER IS STILL UNDER IMPROVEMENT BY THE AUTHORS IN ORDER TO BE SUBMITTED TO A PEER-REVIEWED JOURNAL

Abstract

Genetic population structure of swordfish *Xiphias gladius* was examined among three major sampling areas within the Indian Ocean (twelve sites), Atlantic (two sites) and Pacific (one site) Oceans using analysis of nineteen microsatellite loci and mitochondrial ND2 sequence data. Sample collection was stratified in time and space in order to investigate the stability of the genetic structure observed with a special focus on the South West Indian Ocean. Significant AMOVA variance was observed for both markers indicating genetic population subdivision was present between oceans. Overall value of F-statistics for ND2 sequences confirmed that Atlantic and Indian Ocean swordfish represent two distinct genetics stocks. Indo-Pacific differentiation was also significant but differentiation between these two oceans was less than that observe between Atlantic and Indian Oceans. However, microsatellite F-statistics failed to reveal clear level of structure even at the inter-oceanic scale, indicating that resolving power of our microsatellite loci was insufficient for detecting population subdivision. At the scale of the Indian Ocean, results obtained from both markers are consistent with the swordfish of the IO belonging to a single unique panmictic population or at least several breeding grounds with significant exchange of genetic material. Partitioning of analysis, by sampling areas, seasons, or by sex failed to identify any clear structure within this ocean. Such spatial and temporal homogeneity on genetic structure of the large pelagic swordfish confirms that the current management of swordfish as a single stock in the Indian Ocean is in agreement with our findings.

Keywords: *Xiphias gladius*, large pelagic fish, microsatellite, mitochondrial DNA, population genetics, Indian Ocean, management

Introduction

Large pelagic species have commonly been thought to lack genetic spatial structure of their cosmopolitan distributions due to their large population sizes, high fecundity, production of numerous pelagic larvae, their ability to easily migrate inter-ocean distances (Nakamura, 1985). The wahoo *Acanthocybium solandri,* which showed a single panmictic worldwide distributed population (Theisen et al., 2008), is however one of the rare cases of a cosmopolitan population. Recent genetic studies indicated much more restricted level of connectivity in most of large pelagic fishes. Structure was more often observed at the ocean scale like for the albacore tuna *Thunnus alalunga* (Viñas et al., 2004) and even at the intra-oceanic level like for the blue marlin *Makaira nigricans* (Buonaccorsi et al., 2001) or the white marlin *Tetrapturus albi*dus (Graves & McDowell, 2006). Geographic partition have also been shown in the swordfish *Xiphias gladius* with two subdivisions in the Pacific Ocean (North-west versus South-East; Reeb et al., 2000), as well as in the Atlantic Ocean (northwest versus south with a mediterranean population isolated from those of the Atlantic Ocean (Kotoulas et al., 1995)). Furthermore, the structure between a northwest and a south Atlantic populations was supported by parasitological data (Garcia et al., 2011) thus confirming the existence of discrete stocks in this large pelagic fish at the intra-oceanic scale.

The broadbill swordfish *Xiphias gladius* is one of the most widely distributed species of pelagic fishes, commonly found in the tropical and temperate oceanic waters of the world. Tag-recapture studies and satellite telemetry experiments revealed long distance migration abilities for this species across the North Atlantic - 2500km (Sedberry & Loefer, 2001; see also Tag-recapture ICCAT results presented in Neilson et al. (2009)) and even larger migration in the Indian Ocean with one swordfish recaptured 6670 km south-eastward from the point of release (975 releases – 29 recaptures over the last 20 years; Kadagi et al., 2011). However, a significant number of tagged swordfish were recaptured near the release site

(Carey & Robinson, 1981; Takahashi et al., 2003; Sedberry & Loefer, 2001). For instance, in the North Atlantic, Neilson *et al.* (2009) showed evidence of precise homing from nesting to feeding areas on 4 swordfishes over 25 tracked individuals. This homing behaviour thus explained the population structure observed within this species as shown with the genetic study of Alvarado Bremer *et al.* (2005) on samples from known breeding and feeding grounds in the Atlantic Ocean.

The swordfish population structure of the Indian Ocean is less known. While some genetic substructure have been identified (Jean et al., 2006; Bradman et al., 2011; Lu et al., 2006; Muths et al., 2009), these studies were incongruent probably due to geographic scale, few individuals analyzed, reproduction pattern not taken in consideration and often because of a single genetic marker used. They did not appear conclusive in terms of stock structure and therefore management implications.

While swordfish spawning appears to occur throughout the year in equatorial waters and is progressively restricted to spring-summer at higher latitudes in the Atlantic and Pacific Oceans (Govoni et al., 2003; Mejuto et al., 2008), reproduction data are scarce for this species in the Indian Ocean. From now, only 3 spawning grounds were described: the Gulf of Bengal (Yabe et al., 1959), off the Somalia coast (Mejuto et al., 2006) where spawning is supposed to occur after April for both areas, and at last around Reunion island where spawning is supposed to take place from October to April (Poisson & Fauvel, 2009; and references within). According to the homing hypothesis, a genetic differentiation between these different spawning grounds or between a northern and a southern stock like in the other oceans is therefore expected for the Indian Ocean. The identification of such structure should be of great importance in term of fish management as one of the challenging issue commonly recognized is to match the artificial spatial scale of stock assessment with the natural spatial structure of the species (Francis et al., 2007).

Swordfish has the greatest commercial value of the billfish resource and is currently heavily exploited by commercial fisheries in the Indian Ocean. On the basis of the last swordfish stock assessment (IOTC, 2011), levels of catches in the whole Indian Ocean for 2006-2010 (average of 23 799 tons) were considered below the estimated maximum sustainable yield (MSY; 29-34 000 tons). Nevertheless, when some level of structure was considered and when the assessment focused on the southwest Indian Ocean as an independent stock – a case considered by the IOTC on the basis of the fishery data (IOTC, 2011), most of the evidence indicated that the resource has been overfished in the past decade. Therefore, deeper investigation on the swordfish stock structure have been one of the most important recommendation made by the IOTC Scientific Comity to reduce the uncertainty in assessments (IOTC, 2011).

The present study aims to determine the swordfish genetic population structure in the Indian Ocean. For this purpose, an intensive sampling was conducted over the whole Indian Ocean, at two periods of two consecutive years. We examined genetic variation of more than two thousands swordfish using newly developed genetic markers, supposedly more discriminating than older ones: 19 microsatellite loci (Bradman et al., 2010; Reeb et al., 2003) and mitochondrial sequences of the Nicotinamine Dehydrogenase subunit 2 (ND2; Bradman et al., 2011).

Materials and methods

Sampling area

The present study focuses on the Indian Ocean (IO) – usually defined by international conventions as the waters delineated from the Atlantic Ocean by the 20° east meridian, from the Pacific by the meridian of 146°55' east and a southern limit at 60°S (International

Hydrographic Organization, 1953). Oceanic current patterns are complex in the IO (see Figure 1), with globally strongest variation in the northern hemisphere than in the southern according to summer and winter monsoon period (Schott & McCreary, 2001). IO is dominated by the global westward South Equatorial Current (SEC) that splits at the east coast of Madagascar (near 17° S) into a northward and a southward currents, the first branch generating the strong eastward South Equatorial Counter Current (SECC) (Schott et al., 2009). IO global circulation is primarily controlled by inflows from the Pacific Ocean with the Indonesian Throughflow (ITF) flowing from the north west Pacific to the IO through the Indonesian Sea and supplying to a large part the SEC (Schott et al., 2009). Leakages from IO to the South Atlantic take place with the Agulhas Current (AC), one of the strongest current in the world (Lutjeharms, 2005), with large westward current rings pinching off and translating into the Atlantic but where also is created the Agulhas Current Retroflexion (ACR) that flows back into the IO (Richardson et al., 2003).

Sample Collection

Sampling for the present study focused on the Indian Ocean (IO) – as defined by international conventions as the waters delineated from the Atlantic Ocean by the 20° east meridian, from the Pacific by the meridian of 146°55' east and a southern limit at 60°S (International Hydrographic Organization, 1953). Swordfish samples were collected from different zones within the Indian and adjacent Oceans (Figure 1 and Table 1) by onboard observers on commercial fishing vessels or at landing (with due care collecting the related fishing information). For each sample, muscle tissue biopsies were done and stored in ethanol 90% and frozen until DNA was isolated. Information on sample location (exact latitude and longitude or 5° square) was systematically noted. Whenever it was possible fish sex and size (Law Jaw Fork Length, LJFL) were collected.

Initial sampling strategy was to sample one hundred of fish per zone at two targeted seasons (April-June, non-spawning) and (October-December, fish in spawning condition) over two consecutive years (2009 and 2010). Sampling seasons were defined based on known information of swordfish reproductive condition in IO (see Introduction; Mejuto et al., 2006; Poisson & Fauvel, 2009; Yabe et al., 1959). Due to field realities, not all samples were collected during those periods but were in fact collected over 46 months from February 2008 to November 2011.

Genetic analysis

Total genomic DNA was extracted using DNAeasy Tissue Kit (Qiagen) following the manufacturer instructions. A 1007 bp fragment of the mitochondrial ND2 gene was amplified by PCR using the primers and recommended conditions defined in Bradman *et al.* (2011). PCR products were purified and sequenced forward and reverse on an ABI 3100 sequencer (Macrogen Inc.). Sequences were edited using Chromas version 1.6 (McCarthy, 1997) and aligned using ClustalW (Thompson et al., 1994) in BioEdit Sequence Alignment Editor (Hall, 1999). Sequences were submitted to GenBank (Accession numbers JQ353203 to JQ353484).

Nineteen microsatellite loci were also used, three from (Reeb et al., 2003) (Xg-66, Xg-144, Xg-166) and sixteen from Bradman *et al.* (2010): A3, A4, A7, A8, A10, A113, A115, B108, B112, B6, C10, C4, C7, C8, D11, D2B. Reactions were performed in 20 µl containing 1X PCR buffer, 2.5 mM $MgCl_2$, 2 µM of each dNTPs, 0.3 µM of each primer, 0.5 U of SilverStar Polymerase Taq (Eurogentec), 25 ng of genomic DNA. Cycling parameters were 93°C for 3 min, followed by 35 cycles of 93°C for 30 s, 50-62°C for 50 s, and 72°C for 50 s and a final elongation at 72°C for 30 min. Amplified fragments were separated on an ABI Prism 3100 genetic analyser. Alleles were scored using a co-migrating size standard (Genescan500, Applied Biosystems, Inc.) and identified using GeneMapper4 (Applied Biosystems Inc.).

155 **Data analyses**

156 Data analysis was first conducted on the whole dataset to identify global level of
157 structure. However, we also defined spatially and temporarily stratified sampling sets (*i.e.*
158 swordfish sampled in a given area at a given time; each sample set was named as
159 XXX_00_## (XXX for the area name (see Figure 1b), 00 for the sampling year, ## for the
160 period within the respective 00 year - see details in Table 1) for more meaningful
161 comparisons (e.g. comparison from a same area at different times or from different areas at a
162 same time).

163 For ND2 sequences, haplotype (*h*) and nucleotide (π) diversities and Fu's (Fu, 1997)
164 F-statistic were estimated per sampling sets with DNAsp 5.0 (Librado & Rozas, 2009). Fu's F-
165 statistic tests for departure from equilibrium between the addition of variation by mutation
166 and the removal of variation by genetic drift; theoretically, mutation-drift equilibrium should
167 be reached if the effective population size has remained stable in the past. Phylogenetic
168 relation between all available ND2 sequences were represented by a neighbour-joining tree
169 constructed using Mega 5 (Tamura et al., 2011). Correlations between haplotype frequencies
170 and longitude were tested using Pearson coefficient. For microsatellites, allele frequencies,
171 mean number of alleles (*Nall*), and the observed (*Ho*) and expected (*He*) heterozygosities
172 (Nei, 1987) were calculated per samples sets with Arlequin 3.5 (Excoffier & Lischer, 2010).
173 To account for differences in sample size, allelic diversity was adjusted by estimating the
174 allelic richness (*Rs*) using the rarefaction process of the standArich package (available at
175 http://www.ccmar.ualg.pt/maree/software.php?soft=sarich) for R (R Development Core
176 Team, 2010). Deviations from Hardy-Weinberg equilibrium were examined for each
177 sampling set, at each locus, by calculating Wright's (1969) fixation index F_{is} as estimated by
178 Weir and Cockerham (1984) and tested using exact tests performed with Arlequin 3.5
179 (Excoffier & Lischer, 2010). Micro-Checker 2.2.3 (Van Oosterhout et al., 2004) was used to
180 detect possible null alleles. Microsatellite dataset was analysed using the software

STRUCTURE 2.3.2 (Pritchard et al., 2000) to determine if the genotypes could be partitioned in one or more genetic pools. For this analysis, an admixture model assuming independent allele frequencies was used and ten replicates were run (each with 1.10^5 burn-in samples/generations and 5.10^5 iterations) for *K* values from 1 to 5.

For both ND2 sequence and microsatellite data, the analysis package Arlequin 3.5 (Excoffier & Lischer, 2010) was used to estimate pairwise values of genetic differentiation. A total of 10 000 permutations were used with the fixation index for sequence data Φ_{st} and Wright's F_{ST} statistic for microsatellite data. In both cases, critical significance levels for multiple testing were corrected using in agreement with Narum (2006), using a sequential Benjamini-Yekutieli procedure (2005). Pairwise values of genetic differentiation between sample sets were used as input data in order to construct neighbour-joining trees with the program Mega 5 (Tamura et al., 2011). Jost's (2008) unbiased estimator of divergence (D, based on the effective number of alleles rather than on the expected levels of heterozygosity) was also calculated per pair of localities using the software SPADE (available at http://chao.stat.nthu.edu.tw/softwareCE.html) for ND2 sequences and or SMOGD (Crawford, 2009) for microsatellite data. To test for patterns of isolation-by-distance, marine distances between localities (estimated on the http://www.geodistance.com website) were plotted against genetic distance (using $\Phi_{st}/(1- \Phi_{st})$ for mitochondrial data or $F_{ST}/(1- F_{ST})$ for microsatellite data following the recommendations of Rousset (1997).

Arlequin 3.5 (Excoffier & Lischer, 2010) was also used to perform analysis of molecular variance (AMOVA) with *a priori* grouping based on geographical or temporal proximity, within or between oceans. The software SAMOVA 1.2 (Dupanloup et al., 2002) was finally used to perform spatial analysis of molecular variance (SAMOVA) on localities that were sampled within a same period. This approach detects genetic barriers in a sampling region without *a priori* definition of groups and identifies geographic partitions that maximize

genetic differences between groups and geographic homogeneity within groups; it was tested for *K* group values ranging from 1 to 4, with 100 annealing replicates each time.

At last, same analytical approaches (pairwise values of genetic differentiation and AMOVA) were processed to assess whether or not sex of individual had an effect on the genetic structure.

Results

A total of 2,231 swordfish were sampled from the three major study areas during this study (2,008 from the IO; 168 from Atlantic Ocean; and 125 from the Pacific Ocean). a total of 2,146 were genotyped with microsatellites and 2,001 were examined for sequence information at the mitochondrial ND2 gene. Sampling details are provided in Table 1.

Genetic diversity

ND2 sequences

A total of 195 variable sites, constituting 282 haplotypes were detected among the ND2 sequences (1007 bp) among 2001 swordfish. Approximately 48 % these 282 haplotypes, were represented more than once. Mean haplotype diversity (H_d) and mean nucleotide diversity (π) were high, respectively 0.886 (± 0.04) and 0.0022 (± 0.0004), and similarly high within each sample set (Table 1). The most common haplotype (named #11) was well represented in all localities (all except AFS_10_3 where it was absent), with a mean frequency of 31% (± 7), varying from 16% in NAM_11_1 to 44% in AUS_09_1, ROS_10_3 and RUN_09_1 (Table 1). The private haplotypes constituted a small proportion of the individuals, with a mean frequency of 4% (± 4) per sample set (Table 1). Fu's F values were highly negative and significant ($F = -682.3$; $p < 0.001$).

The relationship between ND2 sequences as represented by a neighbor-joining tree has been presented in Figure 2. Sequence analysis revealed two divergent clades, a dominant one, which contained 98% of the samples, and a second clade separated by seven fixed mutations from the main clade. The proportion of the rare clade observed within each sample was significantly and negatively correlated to longitude (Pearson test $p < 0.02$). The binomial clade structure observed in this study was similar to one previously described from examination of mitochondrial cytochrome *b* sequence data (Alvarado-Bremer et al., 2005a) by homology with this study, the clades herein were called clade I and clade II respectively for the common and the rare clades. The clade I is equally represented in all sample sets while the clade II is absent from the Pacific Ocean sample sets (COR_09_1 and COR_09_3).

Microsatellites

Allelic richness was of the same order between the different sample sets, with a mean at 6.16 (± 0.19) varying from 5.8 for MAD_10_1 to 6.50 for COR_09_1 (Table 1). Fixation indices *Fis* were highly significant in most sample sets with values ranging from 0.02 to 0.14 (Table 1), mostly because of significant heterozygote deficiencies at the three loci A3, B6 and B108. These loci were indeed characterised by the presence of null alleles ($p < 0.05$); consequently, following analyses excluded these three loci and were therefore run using 16 loci. No loci were in disequilibrium ($p < 0.001$) over the whole dataset, supporting the independent assortment of alleles at different loci.

The analysis made with Structure suggested that the highest likelihood of obtaining such data was to consider that only one genetic pool existed ($K = 1$). The likelihood decreases when estimates were made with more than one pool (over ten independent simulations: LnP(D) for $K = 1$ and $K = 2$ were −109850 and −110440, respectively). When considering two genetic pools, the mean assignment value per individual is 0.50 (± 0.04) providing more evidence against subdivision.

Inter-ocean structure

ND2 sequences

Overall Φ_{ST} was 0.006 ($p < 0.001$) when considering all the samples; it decreased to 0.001 and was non-significant ($p > 0.05$) when considering only the swordfish sampled within the IO (*i.e.* excluding all the sample sets from NAM, AFS and COR areas). Pairwise genetic distance estimates (Φ_{ST}) between sample sets are summarized by a neighbor-joining (NJ) tree in Figure 3. This analysis clearly segregated NAM_11_1 and AFS_09_1 from all the others sets but showed no clear structure among the Indo-Pacific sample sets. Of the 630 pairwise comparisons used in this NJ tree (see complete table in appendix 1), 80 were significant ($p < 0.05$) from which 64 concerned interoceanic comparisons (*i.e.* including at least one sample set from NAM, AFS or COR areas in the pairwise comparisons). The highest Φ_{ST} values were observed for the NAM (mean $\Phi_{ST} = 0.098$), followed by COR and AFS comparisons (0.012 and 0.010 respectively). Consistent with these significant differentiation results, values of Jost's D were very high when comparisons included NAM samples ($D > 0.25$), even if the highest values of Jost's D regarded AFS_10_3 (mean D = 0.74). An AMOVA analysis undertaken with grouping made per ocean also demonstrated a small but significant level of structure between oceans ($\Phi_{CT} = 0.011$, $p < 0.001$; see Table 2). This inter-ocean differentiation could be partly explained by the geographical distribution of haplotypes (shown on Figure 4). On one hand, all areas except NAM (Atlantic Ocean) were dominated by the most common haplotype (#11) while NAM area was dominated by a secondary haplotype (#4; 33.3 %), present in most areas but in a lower proportion. The proportion of the haplotype #4 in the AFS sample sets is highly variable according to sampling sets (from 0% in AFS_10_1 to 10% in AFS_10_3 with intermediate values of 2% in AFS_10_2 and 8% in AFS_09_1). On the other hand, the COR area (Pacific Ocean) showed an absence of the haplotypes #4 and #41 and a higher proportion of haplotype #21 (Figure 4). The isolation-by-distance of NAM versus the other sample sets was significant (Pearson test, $p<0.01$) as well

as COR area (AFS_09_1 (Pearson test, $p<0.01$). It is worth noting that there is no significant isolation by distance of AFS area (Pearson test, $p>0.05$).

Microsatellites

Overall F_{ST} was 0.0028 ($p < 0.001$) when considering all the sample sets and 0.0026 ($p < 0.001$) when considering only the swordfish sampled within the IO suggesting the same low level of structure within and between oceans. While using ND2 marker NAM sample set was strongly different from all other sample sets, it is worthwhile noting than using microsatellites, NAM is not different from most others, including Pacific Ocean ones (Appendix 2). The neighbor-joining tree based on the pairwise F_{ST} estimates (Figure 3b) failed to reveal any clear structure within the dataset. Of the 630 pairwise comparisons used in this NJ tree (see complete table in appendix 2), 96 were significant ($p=0.000$) from which 39 concerned interoceanic comparisons (*i.e.* including at least one sample set from NAM, AFS or COR areas). Consistent with these lack of clear structure, values of Jost's D were very low (all $D < 0.03$) even between oceans. However, as for ND2 sequences, an AMOVA analysis made with grouping done per ocean demonstrated a significant F_{CT} value (0.0008, $p < 0.01$; see Table 2). The mean F_{ST} values for the NAM, COR and AFS comparisons were higher than for intra-ocean comparisons (0.006, 0.004 and 0.004 respectively while it was 0.003 for the Indian Ocean samples). A last, using all there is no significant isolation by distance ($p > 0.05$) using all localities.

Within IO analysis

Sampling site areas that we considered part of the IO excluded only three of our sampling regions from the Atlantic Ocean (NAM and AFS) and Pacific Ocean (COR). Irrespective of which markers were examined, the AMOVA analysis conducted within the IO showed that more than 99% of the variance was observed within the samples with no variance significantly associated with the partition into any kind of grouping (Φ_{CT} and $F_{CT} < 0.001$,

306 $p > 0.05$; see Table 2). Similarly, the SAMOVA analysis also failed to demonstrate any
307 population sub-division using the two markers to identify any significant between-group
308 structure (less than 1% of genetic variance, $p > 0.05$); without any *a priori* geographic
309 grouping, between-group variance was maximized when one sample set was considered
310 isolated from all the others.

311 Most ND2 pairwise values of differentiation were low and not significant, even
312 between the most distant areas (*e.g.* AUS_08_1 versus RUN_10_1, $\Phi_{ST} = -0.0064$, $p > 0.05$).
313 There was no significant differences observed between years or seasons sampled at any site
314 (*e.g.* AUS_08_1, AUS_08_2, AUS_09_1 and AUS_11_1; $p > 0.05$*)* neither there was
315 significant differences observed between different sites within a season (*e.g*. IND_09_1,
316 MAD_09_1 ROS_09_1, MAY_09_1 and RUN_09_1; $p > 0.05$). When looking at
317 microsatellite pairwise F_{ST} values (Appendix 2), the situation is by far different, with 139
318 upon the 240 significant values ($p < 0.05$) that are related to intra IO, including 61 that where
319 highly significant ($p < 0.000$). However, values of Jost's D were very low with only 19 values
320 above $D = 0.01$ (Appendix 2) at the intra IO level and no clear pattern of structure could be
321 detected (Figure 3b). When investigating temporal differentiation with microsatellite marker,
322 there is no clear structure at a same site over several seasons nor between different sites
323 within a season.

324 For both sets of markers, there was no general trend for higher genetic divergence
325 with increasing geographic or time separation; in other words, no isolation-by-distance nor
326 isolation-by-time pattern were identified ($p > 0.05$).

327 Genetic structure partitioning by sex was also investigated for sample sets where
328 information was available, *i.e.* the South West Indian Ocean region (SWIO; see Table 1).
329 Overall Φ_{ST} was 0.0018 (not significant; $p > 0.05$) when considering all the samples from this
330 area; it was still not significant and decreased to 0.0009 ($p > 0.05$) when considering only
331 females and increased to 0.0020 ($p > 0.05$) when considering males. A similar trend but

significant was observed with microsatellite data as overall F_{ST} was 0.0023 ($p < 0.001$) when considering all the samples, decreased to 0.0010 ($p < 0.05$) when considering only the female and increased to 0.004 ($p < 0.005$) when considering the male. This trend indicated a higher genetic homogeneity between females than between males at the scale of the SWIO. Moreover, as previously concluded, there is no clear spatial structure for both males and females withneither isolation-by-distance nor isolation-by-time pattern when considering only females and males ($p > 0.05$).

Discussion

Homogeneity within the Indian Ocean

This study aimed to evaluate genetic structure of the swordfish *Xiphias gladius* within the Indian Ocean (IO) and the relations with the adjacent oceans. Analyses of mitochondrial ND2 sequences and microsatellite polymorphisms both indicated a low but significant isolation among ocean basins , however, there was a high level of genetic homogeneity within IO.

The results obtained from both ND2 sequences and microsatellites failed to demonstrate evidence that swordfish have multiple discrete populations within the Indian Ocean. Analysis, of multiple sampling areas over multiple seasons, failed to identify any clear and significant structure. This result may be expected for a large highly fecund and migratory pelagic species (Waples, 1998) and in agreement with the long distance migration observered for Indian Ocean swordfish using tag-recapture approach (Kadagi *et al.* (2011). The existence of at least two distinct stocks observed for this species in the Atlantic and Pacific Oceans (Alvarado-Bremer et al., 2005b; Reeb et al., 2000b) could be mainly explained by the ability of swordfish to feed in cold and productive waters in both North and South extremes of these oceans. The main difference between these two oceans and the IO is that this last could be defined as a “closed” ocean, with a lack of cold water in the north that should contribute to

explain lack of finding major differentiated stocks and finding what appears to be a singles pan-mictic wordfish population.

According to the Longhurst (1998)'s world oceans partitioning on the basis of global hydrodynamics and water colour data (Figure 1b), the IO is mainly comprised of two large hydro geographic oligotrophic areas, the Indian Monsoon Gyre Province (*MONS*) in the north and the Indian South Subtropical Gyre Province (*ISSG*) south, both being separated around 12°S by the hydrochemical front known as South Tropical Front. *MONS* is bordered in the Northwest by the Northwest Arabian Sea Upwelling Longhurst province (*ARAB*). This province is also included in the Arabian Large Marine Ecosystem considered a highly productive ecosystem (Heileman et al., 2009); Figure 1b). This is one of the most intense large scale seasonal costal upwelling (Bakun et al 1998) and productive phytoplanktonic bloom system in the world (Codispoti, 1991; Lévy et al., 2007). In fact, for both summer and winter seasons, the main areas are found in the ALME. Such a specific oceanographic pattern makes *ALME* a serious candidate for a discrete swordfish feeding area. Unfortunately, our sampling scheme did not allow us to identify whether this north-western area is a specific foraging ground for some IO swordfish. However, if we assume this to be the case then we suspect our dataset would have revealed the influence of a differented swordfish population. Investigation into the the origin of swordfish caught in this area that showed significant level of capture by drifting nets may reveal an interesting finding (IOTC, 2011).

Genetic analysis made by sex also failed to reveal a clear structure, however, it indicates a higher genetic homogeneity (significant using the nuclear marker but not using the mtDNA one) between females than between males at the scale of the SWIO. The fact that the genetic information given by the two genders is not the same could indicates a sex-biased dispersal in which gene flow between populations is accomplished primarily by one gender (Prugnolle & de Meeus, 2002). In the present case, one could speculate there was a higher dispersal for females than for males. However, this is in disagreement with a previous study

undertaken in the SWIO which showed more pronounced homing behaviour in females (Muths et al., 2009) and in disagreement with the common pattern of higher dispersal abilities for male recognized in swordfish (Hoey, 1986). The discrepancy in conclusions between these two SWIO studies, associated with a low level structure observed and the unclear genetic structure found using microsatellites even at the inter oceans scale may so be better viewed as an indication of a global lack of structure within the SWIO and *in extenso* is suggestive ofa homogeneous single population in the IO.

Interoceanic isolation

Both molecular markers indicate a significant level of genetic variance associated when comparing samples by oceans, with a level of differentiation higher between Atlantic Ocean (AO) and IO than between IO and Pacific Oceans (PO). The high frequency of the haplotype #4 in the Namibia area (NAM; 30%) that decreased to less than 5% in the IO and absent in the PO and the consequent high Φ_{ST} values observed between NAM and the Indian sample sets are elements that strongly indicate an Indo-Atlantic differentiation. Such differentiation observed is consistent with previous studies (Alvarado-Bremer et al., 2005a; Chow & Takeyama, 2000). That being pointed out, Indo-Pacific differentiation could however be discussed here, as Indo-Pacific swordfish was considered until now to belong to a unique stock (Lu et al., 2006; Alvarado-Bremer et al., 2005a; Chow & Takeyama, 2000). The fact that the IO was poorly sampled in most of these previous studies as well as the supposedly more discriminating ND2 marker (Bradman et al., 2011) used in this study could both contribute explaining why this differentiation between Indian and Pacific samples was not detected before. Even if most of the water in the PO is recirculated within the Pacific itself (Lukas et al., 1996), some enters the Indonesia Seaway and flows westward into the IO, creating the Indonesian Throughflow current. That current pattern therefore potentially transports swordfish larvae and juveniles from the important spawning ground of western

410 tropical Pacific (Nishikawa et al., 1985), supposedly homogenizing the Indian and Pacific
411 swordfish populations and justifying a unique Indo-Pacific population (Chow & Takeyama,
412 2000; Alvarado Bremer et al., 2005; Lu et al., 2006). Assuming that, our results suggest
413 however a significant part of genetic variance associated with the Indo-Pacific differentiation
414 (as well as low but still significant values of Φ_{ST} and F_{ST}), and therefore it should be more
415 appropriate to consider the Indian and the Pacific samples from this study as possibly
416 belonging to separated population. A mark-recapture study around Australia also suggested
417 this interoceanic disruption as the swordfish were recaptured in the ocean where they have
418 been released (Stanley, 2006).

419 One of the criteria previously used to discuss the interoceanic differentiation and
420 consider the swordfish from Indo-Pacific as one population was the shared absence of Clade
421 II in both oceans (Alvarado-Bremer et al., 2005a). In our study, Clade II was still unobserved
422 in the PO but was observed in the IO (at the low frequency of 2% but in all the IO areas); this
423 could be viewed again as an argument against a unique Indo-Pacific population and suggests
424 also potential asymmetric exchange between the two oceans. In fact, the Clade I was
425 supposed to originate in the Pacific and the Clade II originated in the Atlantic, the co-
426 occurrence of these two clades previously observed only in the Atlantic being explained by
427 unidirectional gene flow from the Indo-Pacific into the South Atlantic (Alvarado-Bremer et
428 al., 2005b), a phylogeographic pattern analogous to that reported for the bigeye tuna (Chow et
429 al., 2000), the sailfish *Istiophorus platypterus* and the blue marlin *Makaira nigricans* (Graves
430 & McDowell, 2003). The presence of swordfish Clade II in the IO tends therefore to indicate
431 that a flux of Atlantic swordfish into the IO could also occur. Such dispersal events from the
432 Atlantic into the Indo-Pacific were observed in only few species, because it necessitated
433 strong swimming capacities to go against the Agulhas Current; it is the case of the
434 hammerhead shark *Sphyrna lewini* (Duncan et al., 2006) or the green turtle *Chelonia mydas*
435 (Bourjea et al., 2007), both being active swimmer at all stage of life.

The four sample sets from South Africa (AFS, Figure 6) showed contrasted mitochondrial signature, even if no genetic differences could be identified among them (Φ_{ST} and $F_{ST} > 0.05$). The sample sets AFS_09_1 (July 29 to November 1st 2009) and AFS_10_2 (from April 21th to 26th 2010) showed a mtDNA signature more related to AO while the two others sets from 2010 (AFS_10_1 and AFS_10_3) were more similar to IO (see NJ tree on Figure 3a and Appendix 1, partly congruent with a frequency of the haplotype #4 varying between 0 and 10%). This indicates that the boundary between the two oceans and/or the level of migration between them might fluctuate through time. This could be attributed to oceanographic features variability in this area, mainly driven by the Agulhas current (Richardson et al., 2003). This greater warm and saline Agulhas system from the IO influences temperature and salinity of the AO over the full depth of the water column (see review in: Beal et al., 2011), creating an important gradient of temperature/salinity in short distance (up to 6° in less than 20 km; Lutjeharms, 2007), and therefore being a front in different pelagic habitats characteristics. Based on the fact that this front is highly variable in space and time(Lutjeharms, 2006), we suspect that the variability observed in mitochondrial signature of samples from AFS could be attributed to specific pelagic habitats respectively used by Indian and Atlantic swordfish around South Africa, rather than an ontogenetic migration of individuals from the AO to the IO. Such influence of Agulhas current features on pelagic fishes was not yet demonstrated, but was already shown on marine megafauna, more specifically on leatherback turtles using satellite tracked individuals (see review in Luschi et *al.*, 2006). Therefore, the limit between Atlantic and Indian swordfish populations is not strict and rather could be considered as being a transition zone variable in space and time around African southern tip.

Perspectives & incidence in terms of management

While the mitochondrial ND2 sequences clearly identified the sample from Namibia (Atlantic Ocean) as the most divergent, the microsatellite information failed to reveal clear level of structure between oceans. Some genetic studies already showed discrepancies when using several genetic markers and proposed various explanations: sex-biased dispersal (Keeney et al., 2005), hybridization and introgression (Arnold, 1993) or population size changes (Larmuseau et al., 2010), among others. The example of the marine goby *Pomatoschistus minutus* (Larmuseau et al., 2010) showed large differences in the degree of population differentiation in Europe between the nuclear and mitochondrial markers (at least 30 times higher with mtDNA) that might mainly be explained by a recent demographic expansion. Such mitochondrial-nuclear discrepancies could have important consequences for interpretation and implications in terms of management (Monsen & Blouin, 2003). These studies highlight the strong limitations of identifying population structure on a single genetic marker and the obvious advantages of using combined molecular approaches, especially when such studies have concrete conservation implications such as definition of Management Units.

In the present study, as the female-inherited mtDNA marker showed a clearer population structure pattern than the bi-parentally inherited microsatellite marker, it might indicate a migration from an ocean to the other one more important for male than for female, but it could also underline the fact that our microsatellite loci were not so discriminating as they were expected to and that the use of Single Nucleotide Polymorphisms (Lao et al., 2006) or High Resolution Melting Analysis (Smith et al., 2009) approaches might be more relevant for swordfish or more generally to large pelagic stock identification.

However, even without samples from the Arabian LME, it seems almost evident that the IO Swordfish population acts as a single population. All the analysis focused on the huge sampling done in the SWIO and stratified in time and space failed to identify any significant structure, revealed that the SWIO swordfish clearly belongs to the Indian Ocean population. One matter of concern in term of the management of this species remains the location of the

boundary between Atlantic and Indian Oceans, the first one being managed by the International Commission for the Conservation of Atlantic Tunas, the second by the Indian Ocean Tuna Commission, both legally being separated by the 20° east meridian. In a biological point of view, our study showed that this boundary is not so strict and have to be considered as a large transition area that could be comprised between 17° and 23° east and spatio temporarily driven by the Agulhas current activity. It still could be then very interesting to investigate the migration and spatial dynamic of swordfish in the South African waters, with a special focus on the sex-biased dispersal.

Acknowledgements

This work was funded by the European Union - the FEP and the French State (DMSOI La Réunion; N°31122/DRAM/2009), La Réunion Council (Région Réunion; N°DAE4/20090164), the EU 7th Funding Program - Capacities, Research Potential (project RUNSeaSciences) and Ifremer.

We are very grateful to all people and organization that helped us in the collection of samples: Miguel Neves Santos (IPIMAR, Portugal); IRD UMR 212 colleagues involved in the large pelagic resources component of the South West Indian Ocean Fisheries Project and the La Reunion longline observer program of the EU Data Collection Framework; Andaman Sea Fisheries Research and Development Center, Department Of Fisheries, Thailand and SEAFDEC; We wish to send special thanks to the CapFish SA (Pty) Ltd (South Africa) team; Jan Wissema, Willem Louw and all the scientific observers who participated with the collection of samples from large scale tuna longline vessels and to all the technicians at the Seychelles Fishing Authority and to Mr. Patrick Hoareau (skipper of MV PISCES) and Mr. Elvis Hoarau (skipper of MV ALBACORE) and their crew for their help with the collection. Joao Paulo Machado Torres (Universidad Federale do Rio de Janeiro). The authors would also like to express their gratitude to the skippers from La Réunion (Franck Vandernoorgate, Jean-Marie François, Frederic Le Pape, Alain Le Franc, Gérard Tardet, Franck, Frederic PAYET, Dominique Le Guilloux, Didier Aoustin, Thierry Popovick, Mathieu Perrin) and their crew who welcomed scientific observers on their longliners (Brahma, JustAtao, Laksmi, Hanuman, La fournaise, Cap Tristan, Parvati, Cap Sud) and to the fishing companies for their collaboration (Martin pêcheur, Maevasion, Pêcheries du Sud, Enez, Compagnie réunionaise de pêche au large).

We wish to send special thanks to the CIRAD-3P team: L. Gagnevin and K. Vital from for their help at the genotyping plateform as well as the support of Jean-François

Ternon, Frederic Menard and Michel Potier for their oceanography/Indian Ocean bioregion expertise. At last, we wish to thank the XX anonymous reviewer for their input to the manuscript.

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Table 1. Swordfish samples collected in the Indian and adjacent Oceans and genetic characteristics of the samples. Samples are grouped by sampling sets.

- Sampling: Dates (begin – end) is the temporal range of he sampling set; corresponding season: season 1 from April 10 to July 8 2009; season 2 from September 26 to December 17 2009; season 3 from January 3 to February 4 2010; season 4 from April 6 to July 31 2010; Season 5 from October 12 2010 to January 22 2011; mean fish length (Lower Jow Fork Length in cm) and sex ratio (number of females on the total number of swordfish sexed).
- ND2 sequences: N: Number of samples sequenced; *Nhap*: number of haplotypes; *h*: haplotype diversity; π x 10^3:nucleotide diversity, Main and private hap. %: percentage of main ***(#11)*** and private haplotypes; Fu's F statistic.
- Microsatellites: N: Number of samples genotyped; Nb all/locus: mean number of alleles per locus (19 locus); Rs: allelic richness estimated using rarefaction process; *He* and *Ho*: expected and observed heterozygosities; *Fis*: fixation index.

Significance for Fu's F and Fis statistics is at $p < 0.001$ is indicated in bold characters.

			Sampling						ND2 sequences							Microsatellites					
Ocean	**Sample set name**	**Geographic area**	**Dates (begin - end)**		**Corres-ponding season**	**Ntot**	**LJFL in cm (mean ± SD)**	**Sex ratio (F/(F+M))**	**N**	**Nhap**	***h***	**π (x 10^3)**	**Main hap.#11 %**	**Private hap. %**	**Fu's F**	**N**	**Nb all/ locus**	**Rs**	***He***	***Ho***	***Fis***
INDIAN OCEAN	**AUS_08_1**	Australia (West)	22/02/08	02/03/08	-	38	NA	NA	36	16	0.866	2.202	33	0	**-9.5**	38	9.2	6.4	0.707	0.646	**0.088**
	AUS_08_2	Australia (West)	25/11/08	30/11/08	-	28	130.4 (±34.0)	NA	27	16	0.866	1.573	37	0	**-15.5**	28	8.4	6.3	0.694	0.620	**0.108**
	AUS_09_1	Australia (West)	12/12/09	15/12/09	2	29	162.1 (±30.5)	NA	27	14	0.803	1.954	44	0	**-9.3**	29	8.7	6.0	0.704	0.627	**0.110**
	AUS_11_1	Australia (West)	28/05/11	31/05/11	-	19	163.6 (±33.9)	NA	17	9	0.860	1.544	35	0	**-5.1**	19	7.2	5.8	0.666	0.596	**0.107**
	CA1_10_1	Mozambic chanel (North)	06/04/10	17/04/10	4	48	124.2 (±40.4)	0.55	42	26	0.914	2.213	28	0	**-26.7**	47	9.8	6.1	0.691	0.627	**0.092**
	CA2_10_1	Mozambic chanel (South)	03/01/10	04/02/10	3	54	157.3 (±25.0)	NA	53	29	0.912	2.735	28	5	**-26.1**	53	10.6	6.4	0.685	0.612	**0.108**
	GB1_09_1	Gulf of Bengal (West)	27/09/09	09/12/09	2	48	220.7 (±44.1)	NA	40	23	0.890	2.097	32	2	**-22.9**	48	9.6	5.9	0.691	0.617	**0.107**
	GB1_10_1	Gulf of Bengal (West)	27/06/10	30/07/10	4	83	139.3 (±44.8)	NA	77	43	0.927	2.231	25	0	**-27.1**	83	10.8	6.1	0.676	0.608	**0.100**
	GB2_10_1	Gulf of Bengal (central)	21/01/10	21/01/10	3	38	135.2 (±33.4)	NA	31	19	0.944	2.361	19	3	**-15.8**	38	8.8	5.8	0.671	0.628	**0.064**
	GB2_10_2	Gulf of Bengal (central)	12/12/10	22/01/11	5	21	127.4 (±27.0)	NA	19	11	0.888	1.731	31	0	**-7.2**	21	7.2	6.0	0.687	0.645	**0.061**
	IND_09_1	Indonesia	02/05/09	12/06/09	1	42	143.8 (±43.2)	NA	41	22	0.891	1.995	31	7	**-21.1**	40	9.3	6.2	0.711	0.620	**0.128**
	MAD_09_1	Madagascar (South-east)	28/04/09	10/05/09	1	94	141.7 (±26.1)	0.74	42	21	0.890	2.918	30	7	**-13.4**	91	11.4	6.2	0.693	0.637	**0.080**
	MAD_09_2	Madagascar (South-east)	07/11/09	18/11/09	2	97	152.5 (±31.2)	0.74	93	45	0.838	1.945	39	5	**-27.4**	97	12.2	6.1	0.710	0.628	**0.116**
	MAD_10_1	Madagascar (South-east)	21/04/10	01/05/10	4	96	112.7 (±35.0)	0.70	93	40	0.908	3.456	27	11	**-26.1**	94	11.5	5.8	0.666	0.627	**0.060**
	MAY_09_1	Mayotte	26/10/09	11/12/09	2	96	134.5 (±28.6)	NA	85	39	0.881	2.210	32	10	**-27.1**	95	10.9	6.2	0.704	0.632	**0.103**
	MAY_10_1	Mayotte	12/10/10	18/11/10	5	82	129.6 (±32.1)	NA	76	30	0.892	2.149	30	3	**-27.0**	68	10.3	5.8	0.632	0.591	**0.064**
	RON_09_1	Rodrigues (North)	26/09/09	06/10/09	2	81	157.5 (±30.5)	0.66	70	39	0.906	2.730	30	8	**-26.6**	81	10.6	6.0	0.685	0.587	**0.143**
	ROS_09_1	Rodrigues (South)	09/10/09	18/10/09	2	15	178.6 (±35.8)	NA	11	8	0.927	2.109	27	0	**-4.2**	15	6.7	5.9	0.660	0.586	**0.116**
	ROS_10_1	Rodrigues (South)	19/05/10	24/05/10	4	35	152.1 (±36.4)	0.70	34	20	0.921	2.046	26	5	**-18.6**	35	9.1	6.2	0.687	0.652	**0.051**
	ROS_10_2	Rodrigues (South)	20/07/10	26/07/10	4	45	148.3 (±28.9)	0.71	44	23	0.887	2.001	31	13	**-22.3**	45	9.6	6.1	0.683	0.650	**0.049**
	ROS_10_3	Rodrigues (South)	12/10/10	18/10/10	5	88	156.7 (±31.3)	0.67	84	35	0.801	2.177	44	8	**-27.1**	78	11.0	6.2	0.682	0.659	**0.033**
	RUN_09_1	Reunion island	29/05/09	03/06/09	1	65	134.9 (±34.3)	0.5	63	26	0.795	1.746	44	7	**-26.4**	63	9.8	6.0	0.686	0.602	**0.123**
	RUN_09_2	Reunion island	15/10/09	29/11/09	2	73	138.5 (±27.1)	0.67	59	27	0.916	2.891	23	5	**-20.3**	73	10.0	5.9	0.686	0.612	**0.108**
	RUN_10_1	Reunion island	16/06/10	31/07/10	4	93	147.3 (±29.8)	0.56	78	39	0.921	2.695	25	8	**-26.6**	93	11.6	6.1	0.697	0.664	**0.046**
	RUN_10_2	Reunion island	21/10/10	22/11/10	5	96	147.5 (±22.7)	0.47	92	41	0.903	1.999	28	8	**-27.4**	85	11.2	6.1	0.686	0.638	**0.069**
	SEY_09_1	Seychelles	22/11/09	17/12/09	2	92	158.0 (±19.5)	0.93	85	34	0.826	2.017	40	0	**-27.3**	91	12.0	6.1	0.700	0.636	**0.092**
	SEY_10_1	Seychelles	02/07/10	08/07/10	4	68	153.5 (±26.0)	NA	67	28	0.874	1.888	32	0	**-27.2**	68	10.2	6.2	0.673	0.599	**0.109**
	SEY_10_2	Seychelles	04/11/10	17/11/10	5	21	167.8 (±33.9)	NA	21	11	0.814	1.581	42	0	**-7.2**	21	8.0	6.2	0.657	0.601	**0.087**
	SEY_11_1	Seychelles	21/01/11	21/01/11	5	30	142.8 (±19.4)	NA	24	15	0.837	2.228	41	0	**-11.0**	30	8.9	6.3	0.700	0.636	**0.092**
ATLANTIC OCEAN	**AFS_09_1**	South Africa	29/07/09	01/11/09	2	67	178.8 (±34.8)	NA	64	32	0.929	3.064	23	9	**-26.1**	53	10.5	6.4	0.703	0.650	**0.075**
	AFS_10_1	South Africa	24/01/10	04/02/10	3	15	159.4 (±31.9)	NA	15	11	0.904	2.857	33	0	**-6.0**	15	7.0	6.2	0.699	0.684	**0.021**
	AFS_10_2	South Africa	21/04/10	26/04/10	4	50	165.0 (±29.8)	NA	49	30	0.916	2.493	28	0	**-26.7**	49	9.9	6.2	0.710	0.650	**0.086**
	AFS_10_3	South Africa	25/10/10	30/10/10	5	12	155.2 (±37.1)	0.70	10	9	0.977	2.911	0	0	**-5.6**	12	6.3	5.8	0.697	0.618	**0.117**
	NAM_11_1	Namibia	10/11		-	24	NA	NA	24	13	0.873	1.996	16	0	**-8.2**	23	8.6	6.5	0.706	0.690	**0.023**
PACIFIC OCEAN	**COR_09_1**	Coral Sea	10/04/09	08/07/09	1	53	138.4 (±24.4)	NA	50	20	0.884	2.076	30	10	**-14.4**	53	10.4	6.5	0.694	0.652	**0.061**
	COR_09_3	Coral Sea	26/10/09	08/11/09	2	72	136 (±29.2)	NA	63	33	0.916	2.229	26	15	**-27.0**	72	11.0	6.2	0.700	0.667	**0.047**
	Out Class		04/07/08	27/02/11	-	223	163.2 (±48.3)	0.92	185	65						202					
	TOTAL					2231	148.7 (±37.3)	0.67	2001	282						2146					

Table 2. Results of AMOVAs for both markers ND2 and microsatellites markers according to different grouping: (1) between the 3 oceans (see Table 1 for details); (2) among 3 geographical groups within Indian Ocean (IO), among southeast IO (AUS and IND areas), Gulf of Bengal (GB) and the southwest IO (all the others); (3) among the 5 seasons within the IO (see Table 1 for details). d.f.: degree of freedom.

		ND2 sequences				Microsatellite			
	Source of variation	d.f.	% variation	Fixation index	p	d.f.	% variation	Fixation index	p
(1)	Among oceans	2	1.18	Φ_{CT}=0.0118	< 0.001	2	0.09	F_{CT}=0.0008	0.01
	Among sampling sets within oceans	33	0.30	Φ_{SC}=0.0030	0.02	33	0.26	F_{SC}=0.0026	< 0.001
	Among individuals within sampling sets	1770	98.52	Φ_{ST}=0.0118	< 0.001	3852	99.65	F_{ST}=0.0035	< 0.001
(2)	Among 3 groups within IO only	2	0.08	Φ_{CT}=0.0008	0.21	2	0.03	F_{CT}=0.0003	0.09
	Among sampling sets within the 3 groups	26	0.12	Φ_{SC}=0.0012	0.12	26	0.25	F_{SC}=0.0025	< 0.001
	Among individuals within sampling sets	1502	99.80	Φ_{ST}=0.0020	0.09	3305	99.72	F_{ST}=0.0028	< 0.001
(3)	Among 5 seasons (IO only)	3	-0.14	Φ_{CT}=-0.001	0.98	4	0.02	F_{CT}=0.0002	0.14
	Among sampling sets within seasons	22	0.34	Φ_{SC}=0.0019	<0.05	21	0.25	F_{SC}=0.0025	< 0.001
	Among individuals within sampling sets	1435	99.8	Φ_{ST}=0.0033	<0.05	3138	99.73	F_{ST}=0.0027	< 0.001

Appendix 1: ND2 sequences pairwise ΦST values for swordfish sampling sets are shown in below diagonal (p value < 0.05 are indicated in bold characters, P value = 0.000 are indicated by *). D Jost's value for swordfish sampling sets are shown in above diagonal (values above 0.1 are indicated in bold).

	AFS_09_1	AFS_10_1	AFS_10_2	AFS_10_3	AUS_08_1	AUS_08_2	AUS_09_1	AUS_11_1	CA1_10_1	CA2_10_1	COR_09_1	COR_09_3	GB1_09_1	GB1_10_1	GB2_10_1	GB2_10_2	IND_09_1	MAD_09_1	MAD_09_2	MAD_10_1	MAY_09_1	MAY_10_1	NAM_11_1	RON_09_1	ROS_09_1	ROS_10_1	ROS_10_2	ROS_10_3	RUN_09_1	RUN_09_2	RUN_10_1	RUN_10_2	SEY_09_1	SEY_10_1	SEY_10_2	SEY_11_1
AFS_09_1		-0,062	-0,025	**0,530**	0,041	-0,0110	**0,193**	-0,030	-0,004	0,017	0,094	0,059	0,026	-0,022	-0,073	-0,012	0,015	0,009	0,096	0,001	0,031	-0,040	**0,269**	0,009	-0,048	-0,028	0,041	**0,187**	**0,149**	-0,022	0,002	-0,012	**0,126**	0,012	**0,157**	**0,165**
AFS_10_1	-0,0074		-0,101	**0,784**	-0,039	-0,1720	-0,023	-0,111	-0,118	-0,095	0,026	-0,032	-0,103	-0,097	-0,001	-0,191	-0,101	-0,149	-0,116	-0,062	-0,073	-0,106	**0,472**	-0,121	-0,138	-0,049	-0,097	-0,038	-0,039	-0,026	-0,036	-0,062	-0,058	-0,081	-0,043	-0,070
AFS_10_2	-0,0019	-0,0026		**0,807**	0,036	-0,0720	**0,118**	-0,023	-0,063	-0,031	-0,008	-0,018	-0,059	-0,148	0,017	-0,027	-0,084	-0,010	0,019	-0,024	-0,038	-0,049	**0,409**	-0,059	-0,117	-0,113	-0,016	0,072	0,054	0,043	-0,036	-0,015	0,047	-0,019	0,067	0,033
AFS_10_3	0,0141	0,0012	0,0057		**0,804**	**0,8100**	**0,882**	**0,782**	**0,706**	**0,736**	**0,710**	**0,850**	**0,774**	**0,699**	**0,339**	**0,526**	**0,813**	**0,638**	**0,859**	**0,621**	**0,850**	**0,696**	**0,441**	**0,680**	**0,617**	**0,708**	**0,865**	**0,924**	**0,930**	**0,648**	**0,747**	**0,688**	**0,828**	**0,748**	**1,000**	**0,919**
AUS_08_1	0,0058	-0,0030	-0,0009	0,0130		-0,0840	0,035	-0,142	-0,012	-0,002	0,071	0,011	-0,045	0,048	0,024	-0,056	0,002	-0,015	-0,008	0,017	-0,018	-0,012	**0,437**	0,030	-0,033	0,013	-0,040	0,028	-0,027	-0,018	0,004	-0,010	-0,028	-0,062	-0,059	0,046
AUS_08_2	0,0124	0,0155	-0,0059	0,0252	-0,0065		-0,006	-0,131	-0,089	-0,057	-0,032	-0,049	-0,100	-0,089	0,006	-0,098	-0,088	-0,059	-0,063	-0,030	-0,076	-0,077	**0,373**	-0,063	-0,108	-0,077	-0,095	-0,030	-0,050	-0,039	-0,034	-0,053	-0,054	-0,087	-0,070	-0,054
AUS_09_1	0,0126	0,0002	0,0032	0,0125	-0,0029	0,0011		-0,005	0,055	0,087	**0,168**	**0,198**	0,069	**0,173**	**0,266**	0,034	0,071	0,073	0,000	**0,111**	0,088	0,095	**0,465**	0,089	**0,153**	**0,177**	**0,117**	0,011	-0,007	**0,218**	**0,170**	**0,109**	-0,021	0,038	0,018	-0,037
AUS_11_1	-0,0023	-0,0070	0,0000	0,0150	-0,0163	-0,0020	-0,0123		-0,108	-0,075	0,024	-0,013	-0,106	0,001	-0,067	-0,185	-0,052	-0,103	-0,063	-0,063	-0,039	-0,070	**0,448**	-0,036	-0,007	-0,031	-0,062	0,005	-0,053	-0,081	-0,075	-0,095	-0,075	-0,101	-0,040	0,035
CA1_10_1	0,0269	0,0112	**0,0173**	0,0035	0,0015	0,0115	-0,0074	-0,0188		-0,115	-0,003	-0,008	-0,086	-0,045	-0,030	-0,139	-0,068	-0,081	-0,030	-0,082	-0,018	-0,027	**0,463**	-0,107	-0,053	-0,074	-0,012	0,021	0,021	0,010	-0,061	-0,088	-0,015	-0,037	0,042	0,005
CA2_10_1	0,0068	0,0070	0,0017	-0,0170	-0,0030	0,0055	-0,0022	-0,0080	0,0002		0,076	0,004	-0,048	-0,008	0,016	-0,113	-0,016	-0,049	-0,006	-0,062	-0,015	-0,007	**0,409**	-0,091	-0,060	-0,036	-0,005	0,036	0,032	0,033	-0,023	-0,050	0,027	-0,008	0,053	0,033
COR_09_1	**0,0374***	**0,0338**	**0,0134**	0,0145	**0,0136***	0,0025	0,0162	0,0176	**0,0168**	**0,0201***		0,035	0,018	0,023	0,129	0,082	-0,039	0,103	0,081	0,092	0,027	0,028	**0,478**	0,039	-0,022	-0,114	0,043	**0,100**	0,096	**0,110**	0,030	0,068	0,085	0,034	0,072	0,071
COR_09_3	**0,0335***	0,0151	**0,0124**	0,0014	-0,0014	-0,0054	-0,0026	-0,0039	0,0024	**0,0079**	0,0086		-0,045	-0,029	0,015	0,030	0,004	0,050	0,054	0,032	-0,010	0,012	**0,528**	0,006	-0,127	-0,073	-0,055	0,086	0,075	0,005	-0,023	0,013	0,096	0,034	0,038	**0,101**
GB1_09_1	**0,0248**	0,0060	**0,0095**	0,0129	-0,0049	-0,0046	-0,0027	-0,0214	-0,0068	0,0084	0,0087	-0,0017		-0,050	-0,009	-0,058	-0,048	-0,036	-0,022	-0,036	-0,066	-0,038	**0,508**	-0,049	-0,192	-0,083	-0,084	0,016	-0,014	-0,032	-0,062	-0,050	-0,022	-0,048	-0,038	0,010
GB1_10_1	**0,0113**	0,0104	-0,0111	0,0091	-0,0022	-0,0141	0,0041	-0,0017	**0,0144**	0,0055	**0,0116**	0,0055	0,0032		-0,087	-0,033	-0,045	-0,003	0,055	0	-0,018	-0,026	**0,409**	-0,037	-0,168	-0,106	-0,025	**0,11**	0,094	0,009	-0,027	0,000	0,090	0,009	0,089	0,091
GB2_10_1	**0,0208**	0,0015	**0,0101**	0,0073	-0,0050	-0,0006	-0,0005	-0,0204	-0,0053	0,0082	0,0102	0,0017	-0,0134	0,0026		-0,077	0,043	-0,014	0,147	-0,024	0,053	-0,001	**0,441**	0,022	-0,140	-0,059	0,031	**0,244**	**0,189**	-0,129	-0,083	-0,041	**0,137**	0,021	**0,185**	**0,284**
GB2_10_2	0,0144	-0,0103	0,0019	-0,0113	-0,0015	0,0097	-0,0044	-0,0155	-0,0148	-0,0044	0,0081	-0,0029	-0,0058	0,0016	-0,0073		-0,075	-0,183	-0,047	-0,08	0,014	-0,032	**0,447**	-0,100	-0,041	-0,013	-0,029	0,024	0,031	-0,008	-0,021	-0,087	-0,021	-0,050	0,068	0,045
IND_09_1	**0,0259***	0,0118	**0,0075**	0,0152	0,0004	-0,0039	-0,0108	0,0016	0,0006	0,0072	0,0094	-0,0021	0,0030	0,0054	0,0074	-0,0049		-0,014	0,005	0,002	-0,030	-0,054	**0,490**	-0,029	-0,052	-0,082	-0,020	0,057	0,032	0,049	-0,009	-0,012	0,018	-0,036	0,021	0,029
MAD_09_1	0,0103	-0,0223	0,0093	0,0015	-0,0047	0,0137	0,0025	-0,0068	0,0077	0,0050	**0,0297**	0,0118	**0,0134**	**0,0182***	0,0120	-0,0043	0,0091		-0,005	-0,025	0,027	0	**0,496**	-0,041	-0,119	0,029	0,007	0,056	0,055	0,029	0,012	-0,028	0,010	-0,033	0,076	0,061
MAD_09_2	**0,0144***	0,0032	0,0028	0,0137	-0,0072	-0,0022	-0,0065	-0,0153	-0,0006	0,0005	**0,0145***	0,0011	-0,0003	0,0022	0,0031	-0,0084	-0,0015	0,0061		0,029	0,004	0,019	**0,474**	-0,002	0,006	0,042	-0,001	-0,011	-0,018	**0,105**	0,057	0,028	-0,018	-0,007	-0,024	-0,031
MAD_10_1	0,0108	-0,0123	**0,0093**	0,0010	-0,0006	0,0118	0,0037	-0,0048	0,0102	0,0055	**0,0235**	**0,0177**	0,0133	**0,0205***	0,0123	0,0017	0,0111	-0,0083	**0,0115**		0,019	0,001	**0,404**	-0,049	-0,026	-0,007	0,019	0,086	0,069	0,013	-0,039	-0,051	0,040	0,007	0,097	0,075
MAY_09_1	0,0067	0,0104	-0,0039	0,0144	-0,0070	-0,0061	0,0013	-0,0076	**0,0115**	0,0000	**0,0184***	**0,0078**	0,0044	-0,0029	0,0067	0,0078	0,0050	**0,0133**	-0,0009	**0,0143**		-0,036	**0,385**	-0,021	-0,106	-0,074	-0,054	0,031	0,002	0,015	-0,004	0,003	0,025	-0,029	-0,027	0,011
MAY_10_1	0,0015	-0,0066	-0,0038	0,0153	-0,0048	-0,0042	-0,0013	-0,0150	0,0096	0,0024	**0,0232***	**0,0107**	0,0043	0,0009	0,0044	0,0014	0,0046	0,0033	-0,0014	0,0064	-0,0031		**0,322**	-0,014	-0,074	-0,056	-0,029	0,084	0,04	-0,003	-0,003	-0,017	0,037	-0,046	0,037	0,054
NAM_11_1	**0,0271**	**0,0966**	**0,0455***	**0,0811**	**0,1016***	**0,1082***	**0,1130***	**0,1161***	**0,1254***	**0,0542***	**0,1268***	**0,1226***	**0,1275***	**0,0673***	**0,1167***	**0,1232**	**0,1264***	**0,0991***	**0,1046***	**0,0765**	**0,0700***	**0,0757***		**0,396**	**0,468**	**0,367**	**0,461**	**0,49**	**0,485**	**0,403**	**0,518**	**0,407**	**0,519**	**0,389**	**0,536**	**0,418**
RON_09_1	0,0105	-0,0115	-0,0009	-0,0046	-0,0056	0,0002	-0,0054	-0,0129	-0,0007	-0,0028	0,0122	0,0058	0,0027	0,0053	0,0043	-0,0140	0,0011	-0,0066	-0,0023	-0,0018	0,0030	-0,0011	**0,0823***		-0,106	-0,058	-0,008	0,039	0,038	0,051	-0,021	-0,036	0,032	-0,004	0,060	0,016
ROS_09_1	0,0012	0,0065	-0,0130	-0,0025	-0,0114	-0,0006	0,0180	0,0184	0,0242	-0,0029	0,0007	0,0043	-0,0025	-0,0125	-0,0023	0,0134	0,0154	0,0063	0,0054	0,0051	-0,0047	0,0070	**0,0850***	-0,0037		-0,203	-0,096	0,065	0,021	-0,025	-0,135	-0,017	0,043	-0,103	0,019	0,065
ROS_10_1	0,0171	0,0214	-0,0049	0,0077	-0,0007	-0,0053	0,0040	0,0055	0,0054	0,0030	-0,0058	0,0039	-0,0007	-0,0048	0,0007	-0,0004	0,0005	0,0196	-0,0003	0,0146	-0,0026	0,0074	**0,0993**	0,0016	-0,0136		-0,060	0,076	0,069	-0,034	-0,086	-0,039	0,069	-0,022	0,046	0,062
ROS_10_2	0,0202	0,0044	0,0051	0,0136	-0,0084	-0,0090	-0,0021	-0,0008	0,0104	0,0059	0,0130	-0,0050	0,0001	0,0017	0,0109	0,0022	-0,0035	0,0031	-0,0037	0,0084	0,0006	0,0033	**0,1212**	-0,0009	0,0022	0,0042		0,029	0,01	-0,036	-0,020	-0,013	0,030	-0,015	-0,053	0,038
ROS_10_3	0,0201	0,0090	0,0039	0,0096	-0,0055	-0,0004	-0,0008	-0,0015	0,0076	0,0000	0,0117	0,0036	0,0079	0,0058	0,0122	-0,0034	0,0011	0,0012	-0,0006	0,0039	0,0020	0,0063	**0,1039**	-0,0048	0,0046	0,0015	-0,0048		-0,014	**0,177**	**0,120**	0,086	0,004	0,046	-0,036	-0,061
RUN_09_1	0,0205	0,0202	0,0062	0,0224	-0,0085	-0,0037	-0,0024	-0,0170	-0,0014	0,0008	0,0161	0,0009	-0,0067	0,0010	-0,0010	-0,0026	0,0021	**0,0121**	-0,0058	0,0130	-0,0023	0,0019	**0,1205**	-0,0019	0,0038	0,0007	-0,0010	-0,0004		**0,123**	0,079	0,062	-0,022	0,000	-0,062	-0,033
RUN_09_2	0,0136	-0,0048	0,0079	0,0110	-0,0112	-0,0057	0,0047	-0,0111	0,0108	0,0079	0,0145	0,0058	-0,0001	**0,0085**	0,0007	0,0085	0,0077	0,0011	0,0058	0,0026	0,0013	0,0025	**0,0922**	0,0032	-0,0081	0,0053	-0,0039	0,0020	0,0042		-0,041	-0,026	0,097	0,002	0,096	**0,198**
RUN_10_1	0,0205	0,0072	0,0032	0,0014	-0,0064	-0,0051	-0,0004	-0,0119	-0,0004	0,0068	0,0002	0,0028	-0,0081	0,0024	-0,0066	-0,0061	0,0011	**0,0115**	-0,0001	**0,0110**	0,0030	0,0054	**0,0951**	0,0022	-0,0180	-0,0103	0,0003	0,0033	-0,0034	0,0011		-0,042	0,061	0,006	0,076	**0,131**
RUN_10_2	0,0214	0,0152	0,0069	0,0191	-0,0029	-0,0028	-0,0047	-0,0181	-0,0046	0,0055	**0,0135***	0,0027	-0,0063	0,0036	-0,0020	-0,0057	0,0032	**0,0160**	-0,0033	**0,0169**	0,0020	0,0025	**0,1093**	0,0020	0,0107	0,0002	0,0008	0,0048	-0,0053	0,0072	-0,0007		0,03	-0,019	0,070	0,080
SEY_09_1	0,0216	0,0028	0,0075	0,0179	-0,0045	-0,0016	-0,0059	-0,0159	-0,0030	0,0067	0,0109	0,0029	-0,0063	**0,0074**	-0,0038	-0,0082	0,0008	0,0048	-0,0040	0,0064	0,0051	0,0018	**0,1240**	-0,0039	0,0071	0,0009	0,0007	0,0001	-0,0049	0,0030	-0,0033	-0,0037		-0,013	-0,020	-0,017
SEY_10_1	0,0159	0,0111	0,0013	0,0174	-0,0082	-0,0082	-0,0044	-0,0193	-0,0022	0,0024	0,0117	0,0007	-0,0075	-0,0025	-0,0067	-0,0069	0,0012	0,0102	-0,0052	**0,0138**	-0,0017	-0,0031	**0,1063**	-0,0004	-0,0011	-0,0010	0,0018	0,0028	-0,0076	0,0033	-0,0025	-0,0057	-0,0045		-0,002	0,028
SEY_10_2	0,0176	0,0235	0,0004	0,0254	-0,0105	-0,0148	0,0006	0,0126	0,0141	0,0013	0,0039	-0,0045	0,0044	-0,0055	0,0066	0,0170	-0,0055	0,0126	-0,0032	0,0094	-0,0085	0,0041	**0,1191**	-0,0003	0,0038	-0,0045	-0,0134	-0,0105	-0,0046	-0,0055	-0,0047	-0,0002	0,0014	-0,0006		-0,033
SEY_11_1	0,0074	0,0051	-0,0109	0,0038	-0,0071	-0,0095	-0,0088	-0,0064	0,0018	-0,0071	0,0084	-0,0039	-0,0016	-0,0092	0,0042	-0,0011	-0,0054	0,0023	-0,0051	0,0034	-0,0092	-0,0021	**0,0838**	-0,0084	-0,0040	-0,0065	-0,0096	-0,0104	-0,0064	-0,0024	-0,0050	-0,0055	-0,0020	-0,0047	-0,0167	

Appendix 2: Microsatellites Pairwise FST values for swordfish sampling sets are shown in below diagonal (p value < 0.05 are indicated in bold characters, p value = 0.000 are indicated by *; D Jost's value for swordfish sampling sets are shown in above diagonal (values above 0.01 are indicated in bold).

	AFS_09_1	AFS_10_1	AFS_10_2	AFS-10_3	AUS_08_1	AUS_08_2	AUS_09_1	AUS_11_1	CA1_10_1	CA2_10_1	COR_09_1	COR_09_3	GB1_09_1	GB1_10_1	GB2_10_1	GB2_10_2	IND_09_1	MAD_09_1	MAD_09_2	MAD_10_1	MAY_09_1	MAY_10_1	NAM_11_1	RON_09_1	ROS_09_1	ROS_10_1	ROS_10_2	ROS_10_3	RUN_09_1	RUN_09_2	RUN_10_1	RUN_10_2	SEY_09_1	SEY_10_1	SEY_10_2	SEY_11_1
AFS_09_1		0,0001	0,0003	0,0016	0,0003	0,0000	0,0001	0,0023	0,0077	0,0063	0,0033	0,0047	**0,0135**	0,0086	**0,0140**	0,0011	0,0011	0,0022	0,0050	0,0004	0,0020	**0,0132**	0,0062	0,0029	0,0008	0,0017	0,0000	0,0006	0,0007	0,0003	0,0004	0,0037	0,0000	0,0036	0,0011	0,0045
AFS_10_1	-0,0007		0,0000	0,0037	-0,0070	0,0000	0,0000	0,0000	0,0002	0,0039	0,0000	-0,0015	0,0000	0,0013	0,0022	0,0008	0,0012	0,0001	-0,0003	0,0000	0,0000	0,0021	0,0005	0,0000	0,0000	0,0007	0,0000	0,0000	0,0002	0,0011	0,0003	0,0000	0,0000	0,0000	-0,0001	0,0008
AFS_10_2	0,0007	-0,0037		0,0008	**0,0000**	-0,0010	0,0000	0,0005	0,0000	0,0031	0,0017	0,0003	0,0026	0,0000	0,0047	0,0000	0,0000	0,0060	0,0004	0,0000	0,0007	0,0040	0,0058	0,0016	0,0002	0,0015	0,0003	0,0000	0,0024	0,0015	0,0005	0,0002	0,0002	0,0020	0,0000	0,0005
AFS-10_3	**0,0081**	0,0057	0,0045		0,0045	0,0000	0,0032	0,0043	**0,0145**	**0,0265**	0,0021	0,0099	**0,0197**	0,0097	0,0031	**0,0143**	0,0088	0,0097	0,0084	0,0057	0,0065	0,0055	**0,0105**	0,0012	**0,0164**	0,0029	0,0048	0,0045	0,0099	0,0044	0,0024	0,0070	0,0042	0,0079	0,0038	0,0052
AUS_08_1	0,0022	-0,0072	-0,0003	0,0040		0,0007	0,0000	0,0001	0,0000	0,0029	0,0008	-0,0003	0,0012	0,0000	0,0045	0,0000	0,0000	0,0001	0,0000	0,0002	0,0000	0,0038	0,0050	0,0006	0,0000	0,0022	0,0015	0,0001	0,0008	0,0000	0,0001	-0,0003	0,0000	-0,0006	0,0000	0,0005
AUS_08_2	-0,0002	-0,0027	-0,0039	0,0016	0,0008		-0,0010	0,0014	0,0010	0,0007	0,0000	0,0000	0,0000	0,0004	0,0000	0,0008	0,0019	0,0000	0,0000	-0,0017	0,0024	0,0065	0,0003	-0,0003	0,0077	0,0000	-0,0011	0,0000	0,0010	0,0000	0,0000	0,0000	-0,0029	0,0000	-0,0005	0,0002
AUS_09_1	-0,0001	-0,0043	-0,0003	0,0081	-0,0010	-0,0010		0,0000	0,0000	0,0000	0,0002	0,0000	0,0005	0,0001	0,0047	0,0066	0,0016	0,0000	0,0000	0,0000	0,0000	0,0038	0,0000	0,0000	0,0073	-0,0001	0,0000	0,0000	0,0012	-0,0020	0,0000	0,0001	0,0000	0,0000	0,0000	0,0012
AUS_11_1	**0,0079**	-0,0027	0,0046	0,0152	0,0034	0,0050	0,0007		-0,0003	-0,0008	0,0018	0,0003	0,0020	0,0003	0,0030	0,0000	0,0033	0,0020	0,0007	0,0024	0,0001	0,0011	0,0074	0,0008	0,0003	0,0041	0,0004	0,0002	0,0010	0,0010	0,0003	0,0006	0,0018	0,0014	0,0000	0,0003
CA1_10_1	0,0029	-0,0033	-0,0001	**0,0135**	-0,0014	0,0003	-0,0013	-0,0033		0,0003	0,0055	0,0000	0,0004	0,0000	0,0001	0,0000	0,0046	0,0011	0,0004	0,0033	0,0004	0,0100	**0,0160**	0,0019	0,0029	0,0040	0,0012	0,0000	0,0056	0,0000	0,0002	0,0007	0,0024	0,0006	0,0000	0,0000
CA2_10_1	**0,0065***	0,0053	**0,0070**	**0,0200**	**0,0065**	0,0054	-0,0009	-0,0027	0,0005		0,0033	0,0052	0,0026	0,0007	**0,0194**	0,0036	0,0077	0,0020	0,0036	0,0010	0,0040	**0,0102**	0,0068	0,0050	0,0080	0,0007	0,0017	0,0033	0,0055	0,0020	0,0024	0,0016	0,0025	0,0031	0,0003	0,0010
COR_09_1	**0,0071***	-0,0024	**0,0026**	**0,0077**	0,0032	0,0016	0,0023	0,0043	**0,0031**	**0,0074***		0,0032	0,0038	0,0009	0,0099	0,0081	0,0055	0,0024	0,0016	0,0005	0,0055	0,0067	0,0096	0,0017	0,0038	0,0019	0,0000	0,0019	0,0023	0,0012	0,0032	0,0005	0,0007	0,0010	0,0010	0,0059
COR_09_3	**0,0026**	-0,0054	0,0023	**0,0106**	0,0001	0,0014	-0,0005	0,0031	0,0009	**0,0066***	**0,0038***		0,0016	0,0011	0,0067	0,0026	0,0022	0,0027	0,0003	0,0014	0,0017	**0,0124**	0,0023	0,0027	0,0002	0,0017	0,0001	0,0000	0,0017	0,0002	0,0000	0,0000	0,0003	0,0032	0,0016	0,0027
GB1_09_1	**0,0058**	0,0003	0,0036	**0,0156**	0,0038	0,0008	0,0021	**0,0059**	0,0009	**0,0060***	**0,0053**	0,0018		0,0000	0,0001	0,0001	0,0045	0,0041	0,0026	0,0007	0,0017	0,0073	**0,0105**	0,0012	0,0021	0,0006	0,0002	0,0032	0,0029	0,0000	0,0006	0,0001	0,0000	0,0000	0,0002	0,0009
GB1_10_1	**0,0049***	0,0011	**0,0022**	**0,0134***	0,0012	0,0032	0,0004	0,0033	-0,0002	**0,0043***	**0,0032**	**0,0032**	0,0005		0,0029	0,0000	0,0015	0,0056	0,0041	0,0004	0,0012	0,0035	**0,0151**	0,0040	0,0003	0,0005	0,0000	0,0006	0,0021	0,0000	0,0001	0,0000	0,0005	0,0024	0,0006	0,0003
GB2_10_1	**0,0086***	0,0044	**0,0035**	0,0064	**0,0054**	-0,0012	0,0046	**0,0096**	0,0014	**0,0121***	**0,0084***	**0,0086***	0,0015	**0,0032**		0,0003	**0,0157**	0,0023	0,0041	0,0027	0,0020	0,0039	**0,0203**	0,0024	0,0058	0,0047	0,0053	0,0041	0,0036	0,0000	0,0022	0,0036	0,0021	0,0026	0,0069	0,0000
GB2_10_2	0,0042	0,0000	0,0019	0,0149	0,0032	0,0017	0,0065	0,0044	0,0000	**0,0078**	**0,0068**	0,0043	-0,0001	0,0020	0,0028		0,0032	0,0005	0,0017	0,0018	0,0027	0,0091	0,0066	0,0082	0,0004	0,0015	0,0006	0,0008	0,0003	0,0006	0,0005	0,0002	0,0015	0,0009	0,0097	0,0001
IND_09_1	0,0016	0,0040	0,0031	**0,0132**	0,0000	**0,0060**	0,0031	**0,0079**	**0,0058***	**0,0083***	**0,0108***	**0,0037***	**0,0040**	**0,0042**	**0,0110***	0,0052		0,0019	0,0011	0,0013	0,0013	0,0095	0,0062	0,0038	0,0000	0,0060	0,0007	0,0021	0,0046	0,0035	0,0017	0,0021	0,0023	0,0032	0,0012	0,0012
MAD_09_1	0,0017	-0,0002	0,0030	**0,0119***	0,0016	0,0007	0,0000	**0,0075**	0,0023	**0,0056***	**0,0071***	**0,0042**	**0,0036**	**0,0047***	**0,0051***	0,0023	0,0028		0,0009	0,0002	0,0007	**0,0130**	0,0012	0,0025	0,0026	0,0003	0,0003	0,0018	0,0022	0,0002	0,0000	0,0001	0,0013	0,0002	0,0019	0,0000
MAD_09_2	**0,0044***	-0,0031	0,0011	0,0063	-0,0011	0,0010	0,0006	0,0044	0,0015	**0,0072***	**0,0035***	**0,0024**	0,0026	**0,0034***	**0,0049**	0,0037	**0,0031**	**0,0027**		0,0000	0,0000	0,0065	0,0024	0,0038	0,0050	0,0005	0,0011	0,0000	0,0036	0,0013	0,0024	0,0005	0,0003	0,0004	0,0026	0,0003
MAD_10_1	0,0007	0,0000	0,0007	**0,0107**	0,0020	-0,0008	-0,0006	**0,0068**	0,0017	**0,0046***	0,0024	**0,0029**	0,0021	**0,0025**	**0,0041**	0,0034	**0,0031**	0,0013	0,0012		0,0003	0,0047	0,0034	0,0008	0,0052	0,0000	0,0000	0,0000	0,0012	0,0000	0,0007	0,0006	0,0000	0,0000	0,0001	0,0000
MAY_09_1	0,0022	-0,0011	0,0005	0,0065	-0,0001	0,0020	-0,0003	0,0049	0,0012	**0,0063***	**0,0061***	**0,0036***	0,0025	**0,0029***	0,0030	0,0049	**0,0044***	**0,0023**	0,0005	0,0013		**0,0104**	**0,0115**	0,0017	0,0009	0,0011	0,0001	0,0011	0,0014	0,0000	0,0008	0,0012	0,0002	0,0026	0,0000	0,0000
MAY_10_1	**0,0109***	**0,0079**	**0,0082***	**0,0162**	**0,0076***	**0,0068***	**0,0063**	**0,0106***	**0,0063***	**0,0116***	**0,0122***	**0,0098***	**0,0078***	**0,0036**	0,0034	**0,0118***	**0,0108***	**0,0108***	**0,0088***	**0,0067***	**0,0091***		**0,0274**	0,0091	**0,0110**	0,0098	0,0055	0,0010	0,0073	0,0046	0,0091	0,0033	0,0062	0,0039	0,0078	0,0019
NAM_11_1	0,0027	-0,0017	0,0040	**0,0130**	**0,0045**	0,0026	0,0009	**0,0093**	**0,0079**	**0,0098**	**0,0071**	0,0018	**0,0055**	**0,0102***	**0,0116***	**0,0091**	**0,0065***	0,0022	0,0033	**0,0040**	**0,0057**	**0,0181***		**0,0167**	0,0059	0,0042	0,0068	0,0095	0,0072	**0,0103**	0,0031	0,0009	0,0061	0,0041	**0,0201**	0,0037
RON_09_1	**0,0038**	-0,0006	0,0017	0,0063	0,0017	-0,0010	-0,0005	0,0036	0,0021	**0,0051***	**0,0046***	**0,0035***	0,0019	0,0019	0,0020	**0,0068**	**0,0048**	**0,0028**	**0,0031***	0,0018	0,0026	**0,0057***	**0,0088***		0,0000	0,0010	0,0000	0,0015	0,0022	0,0000	0,0010	0,0020	0,0004	0,0007	0,0001	**0,0114**
ROS_09_1	0,0023	-0,0043	0,0002	**0,0152**	-0,0007	0,0058	0,0050	0,0043	0,0028	0,0077	**0,0073**	0,0018	0,0024	-0,0009	0,0044	0,0021	-0,0005	0,0022	0,0042	0,0049	0,0024	**0,0096**	0,0082	-0,0017		0,0050	0,0000	0,0015	0,0004	0,0013	0,0006	0,0042	0,0001	0,0012	0,0000	0,0062
ROS_10_1	0,0009	-0,0008	0,0029	**0,0097**	0,0026	-0,0014	-0,0012	**0,0069**	0,0021	0,0032	**0,0065**	0,0020	0,0002	0,0017	**0,0055**	0,0018	**0,0059**	0,0007	0,0015	-0,0006	0,0022	**0,0072***	0,0038	0,0027	0,0062		0,0003	0,0000	0,0019	0,0000	0,0000	0,0014	0,0000	0,0024	0,0007	0,0000
ROS_10_2	0,0008	-0,0010	0,0022	**0,0132**	**0,0045**	-0,0005	0,0002	**0,0066**	0,0023	**0,0052***	0,0022	0,0019	0,0004	0,0000	**0,0043**	0,0020	**0,0052**	0,0022	**0,0045**	0,0011	**0,0037***	**0,0065***	**0,0069**	0,0015	-0,0013	0,0022		0,0000	0,0008	0,0000	-0,0010	0,0000	0,0000	0,0000	0,0003	0,0014
ROS_10_3	0,0011	-0,0005	0,0000	**0,0094**	0,0009	-0,0008	0,0015	**0,0040**	-0,0015	**0,0045***	**0,0051***	0,0015	0,0017	0,0015	**0,0039**	0,0034	**0,0044**	**0,0021**	0,0014	0,0003	**0,0019**	**0,0036***	**0,0055**	0,0014	0,0024	-0,0017	0,0017		0,0013	0,0000	0,0002	0,0001	0,0006	0,0005	0,0031	0,0005
RUN_09_1	0,0025	-0,0008	**0,0037**	**0,0099**	0,0025	0,0017	0,0017	0,0060	**0,0038**	**0,0086***	**0,0055***	**0,0034***	**0,0037**	**0,0044**	**0,0056***	0,0033	**0,0056***	**0,0029**	**0,0055***	**0,0032**	**0,0032**	**0,0114***	**0,0059**	**0,0038**	0,0032	0,0031	**0,0041**	**0,0034***		0,0002	0,0004	0,0005	0,0001	0,0023	0,0026	0,0027
RUN_09_2	0,0009	0,0004	0,0010	**0,0088**	0,0005	-0,0007	-0,0036	0,0035	-0,0010	**0,0036**	**0,0044***	0,0016	0,0000	-0,0006	-0,0001	0,0029	**0,0049**	0,0011	**0,0024**	0,0002	0,0001	**0,0043***	**0,0053**	0,0000	0,0016	-0,0008	0,0004	-0,0002	0,0008		0,0001	0,0000	0,0000	0,0000	0,0000	0,0003
RUN_10_1	0,0010	-0,0006	0,0007	**0,0074**	0,0007	-0,0008	0,0008	0,0041	0,0002	**0,0056***	**0,0039**	0,0006	0,0002	**0,0015**	**0,0033**	0,0016	**0,0032**	0,0006	**0,0024**	0,0012	0,0016	**0,0074***	**0,0032**	0,0017	0,0020	-0,0001	-0,0010	-0,0002	0,0020	0,0002		0,0000	0,0000	0,0035	0,0019	0,0000
RUN_10_2	**0,0044**	-0,0030	0,0014	**0,0106**	-0,0001	0,0011	0,0010	0,0023	0,0009	**0,0062***	-0,0001	0,0007	0,0011	0,0013	**0,0037**	0,0021	**0,0070***	**0,0028**	**0,0021**	0,0017	**0,0030**	**0,0066***	0,0015	**0,0031**	0,0045	0,0026	0,0013	0,0018	**0,0028**	0,0007	-0,0003		0,0000	0,0000	0,0030	0,0005
SEY_09_1	-0,0005	-0,0036	0,0005	0,0078	0,0003	-0,0027	-0,0002	0,0052	0,0009	**0,0054***	**0,0032***	0,0006	-0,0008	0,0015	**0,0038**	0,0026	0,0028	**0,0019**	0,0011	0,0003	0,0007	**0,0074***	0,0031	0,0016	0,0002	-0,0017	0,0008	0,0005	0,0013	-0,0003	-0,0002	0,0007		0,0003	0,0000	0,0011
SEY_10_1	**0,0041**	-0,0005	0,0026	**0,0118**	-0,0002	0,0014	0,0018	0,0050	0,0011	**0,0062***	**0,0056***	**0,0062***	0,0010	**0,0025**	0,0025	0,0042	**0,0058**	**0,0024**	0,0018	0,0015	**0,0034**	**0,0049***	**0,0062**	0,0016	0,0008	0,0022	**0,0035**	0,0009	**0,0051**	0,0003	**0,0032**	0,0018	0,0015		0,0000	0,0011
SEY_10_2	**0,0072**	-0,0026	0,0021	**0,0143**	0,0026	0,0014	0,0020	0,0032	0,0023	**0,0066**	**0,0102***	**0,0092**	**0,0098***	**0,0063**	**0,0108**	**0,0146**	**0,0092**	**0,0066**	**0,0083***	**0,0073**	**0,0054**	**0,0141***	**0,0139***	0,0049	0,0011	0,0074	**0,0093**	**0,0071**	**0,0076**	0,0028	**0,0079***	**0,0089***	0,0049	0,0025		0,0048
SEY_11_1	0,0027	0,0008	0,0019	0,0077	0,0006	-0,0009	0,0001	0,0042	0,0007	0,0046	**0,0079***	**0,0046**	0,0028	0,0034	0,0011	0,0019	0,0034	0,0003	0,0012	0,0003	0,0010	**0,0073**	0,0027	**0,0057**	0,0068	-0,0020	0,0034	0,0016	0,0024	-0,0001	-0,0005	0,0022	0,0012	0,0034	**0,0082**	

Figure legends

Figure 1. a: Geographic location of Swordfish tissue samples analysed in this study . The size of circles is proportional to number of swordfish sampled; the colour indicates the accuracy of the localisation data collected (dark grey for exact coordinates and light grey for 5° square position). This map also shows the main Indian Ocean currents (from Schott et la. 2009); SEC: South Equatorial Current; SECC: South Equatorial Counter Current; NEMC: Northeast Madagascar Current; AC: Agulhas Current; ACR: Agulhas Current Retroflexion; BC = Benguela Current; ITF: Indonesian Trough Flow.

b: Geographic location of identified sampling areas and associated area name (in bold) used for data spatial and temporal analyses (see also Table 1). Grey colours differentiate the areas one to each other. Lines indicate the biogeographic Longhurst provinces ans associated names in regular (from Longhurst, 1998).

Figure 2. Unrooted neighbor-joining tree showing the relationship between the ND2 sequences (n = 2001). White triangles are samples from the Pacific Ocean (5.5% of the samples), black circles from Atlantic Ocean (8% of the samples) and branches without symbol are from Indian Ocean (86.5% of the samples). Clade I and clade II names refer to the same nomenclature proposed in Alvarado-Bremer *et al.*, (2005a)

Figure 3. Neighbor-joining trees showing the relationship between sample sets on the basis of pairwise genetic distances estimated with (3a) ND2 sequences and (3b) microsatellite datasets.

Figure 4. Map of plotted frequencies of the main ND2 haplotypes, shared haplotype and private haplotypes per identified areas. Number of samples is shown in brackets.

Figure 5. Isolation-by-distance (5a) and Isolation-by-time (5b) graphs showing corrected pairwise genetic distances [Φst/(1- Φst) for mtDNA and Fst/(1-Fst) for microsatellite] plotted as a function of geographic distances or of time for Indian Ocean swordfish. Black diamonds are for mtDNA data and white squares for microsatellite data (all were not significant: Mantel tests with $p > 0.05$)

Figure 6. Exact sampling size and location for the South Africa (AFS) and Namibia (NAM) area by sampling sets (see table 1 for details).

Figure 1a

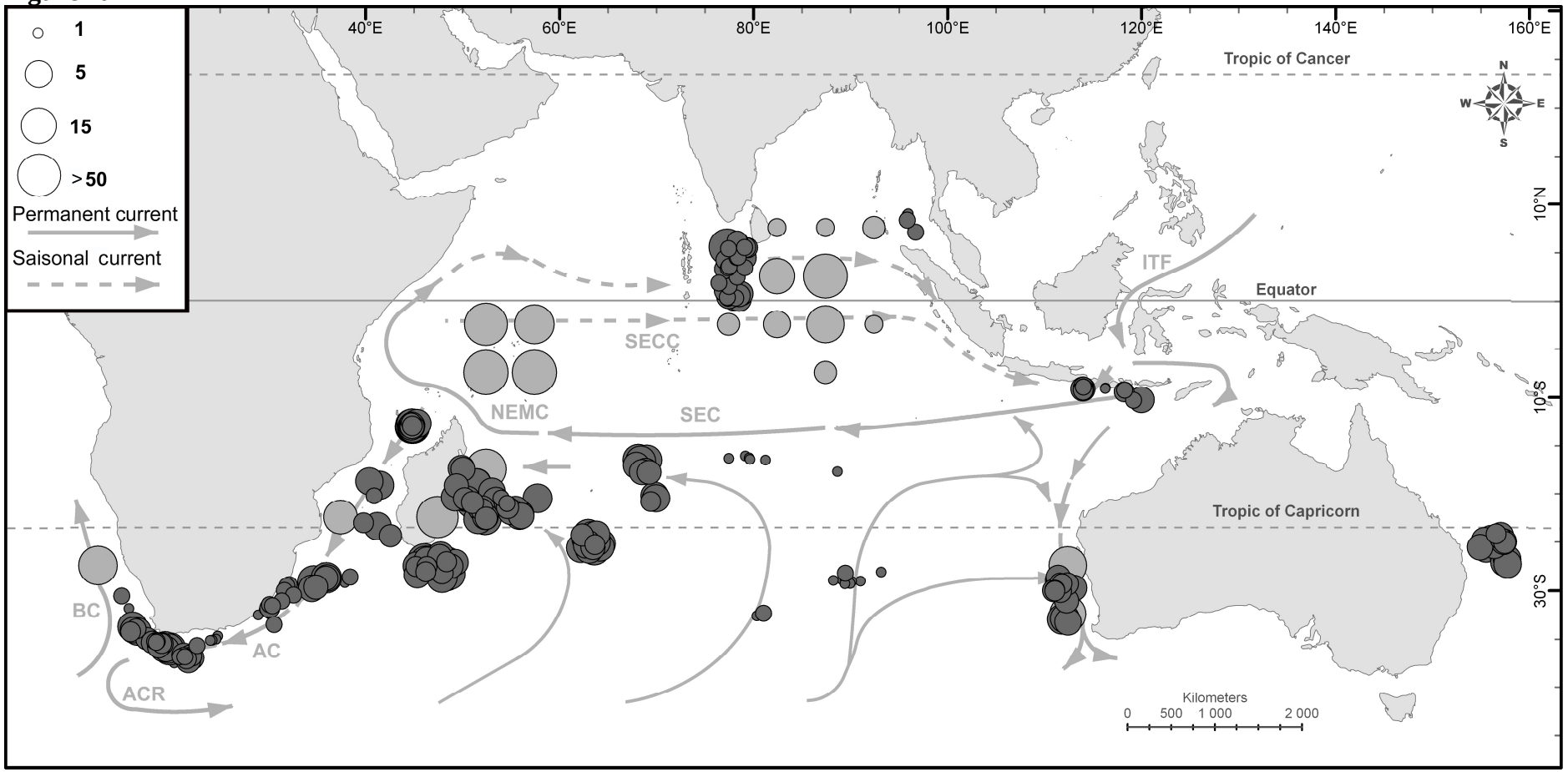

1
5
15
>50
Permanent current
Saisonal current
40°E
60°E
80°E
100°E
120°E
140°E
160°E
Tropic of Cancer
Equator
Tropic of Capricorn
10°N
10°S
30°S
N
W
E
S
ITF
SECC
NEMC
SEC
BC
AC
ACR
Kilometers
0 500 1 000 2 000

Figure 1b

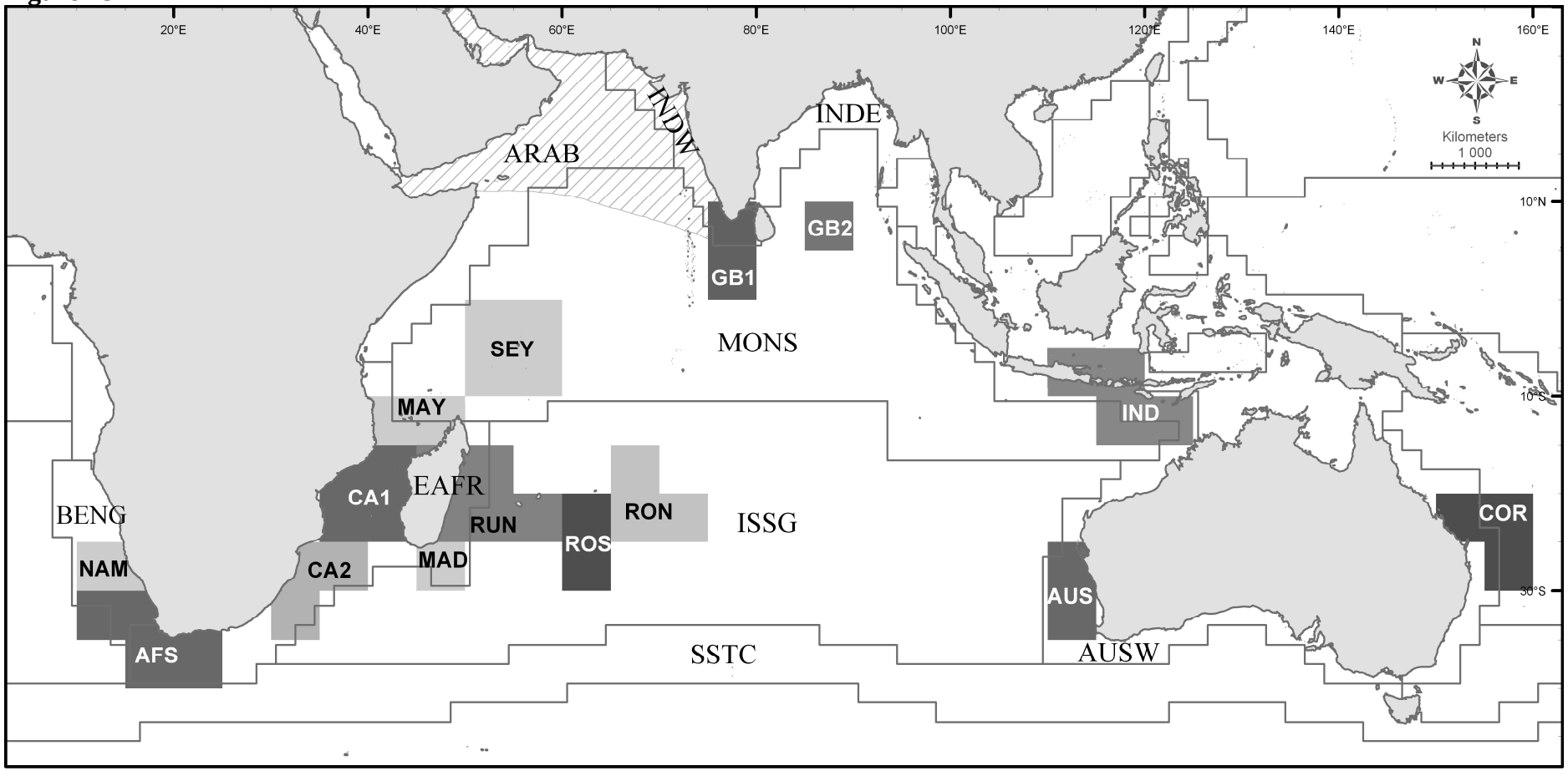

20°E
40°E
60°E
80°E
100°E
120°E
140°E
160°E
10°N
10°S
30°S
N
W
E
S
Kilometers
1 000
ARAB
INDW
INDE
GB1
GB2
SEY
MONS
MAY
IND
CA1
EAFR
BENG
RUN
RON
ROS
ISSG
COR
NAM
CA2
MAD
AUS
AFS
SSTC
AUSW

Figure 2

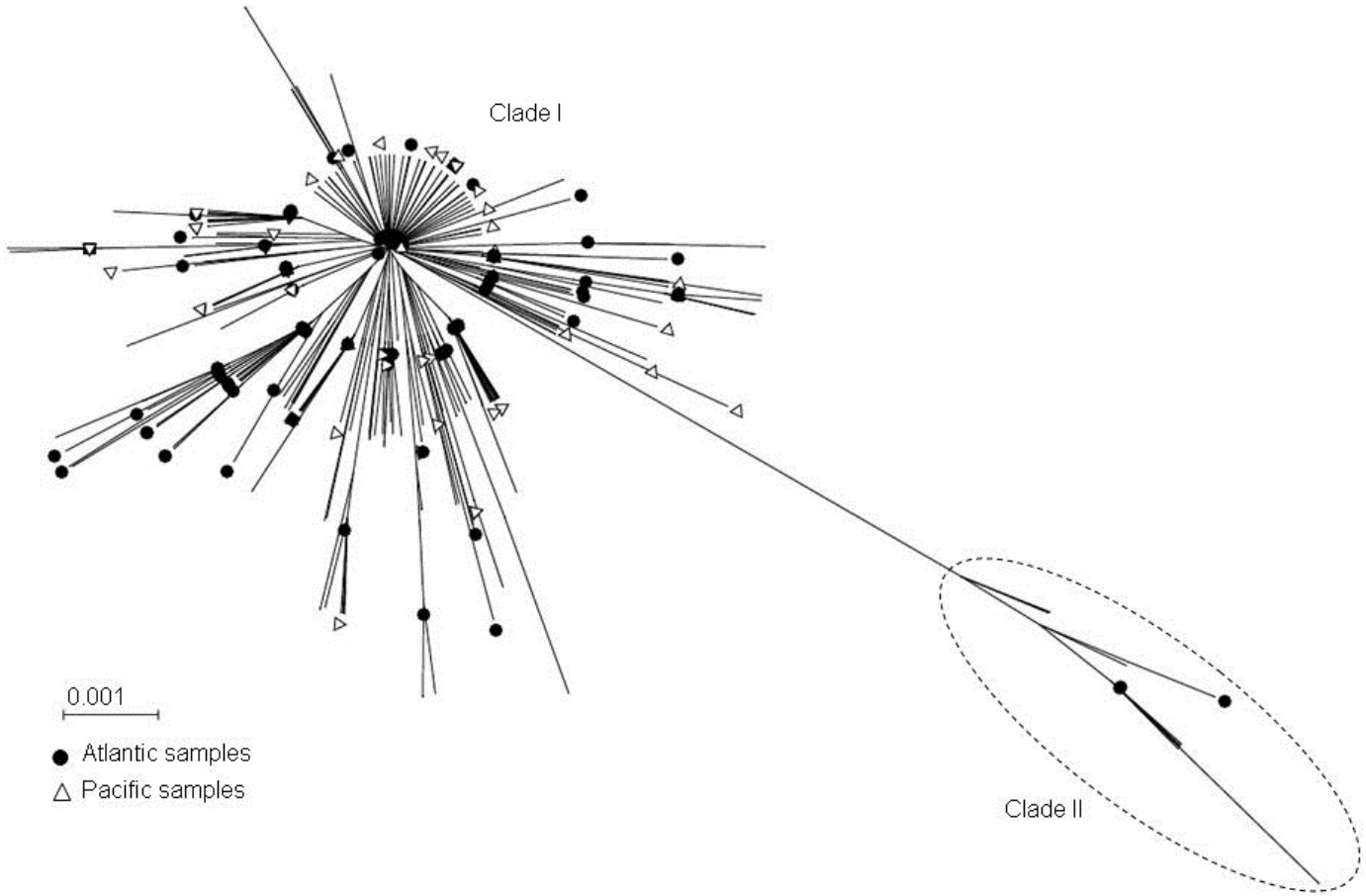
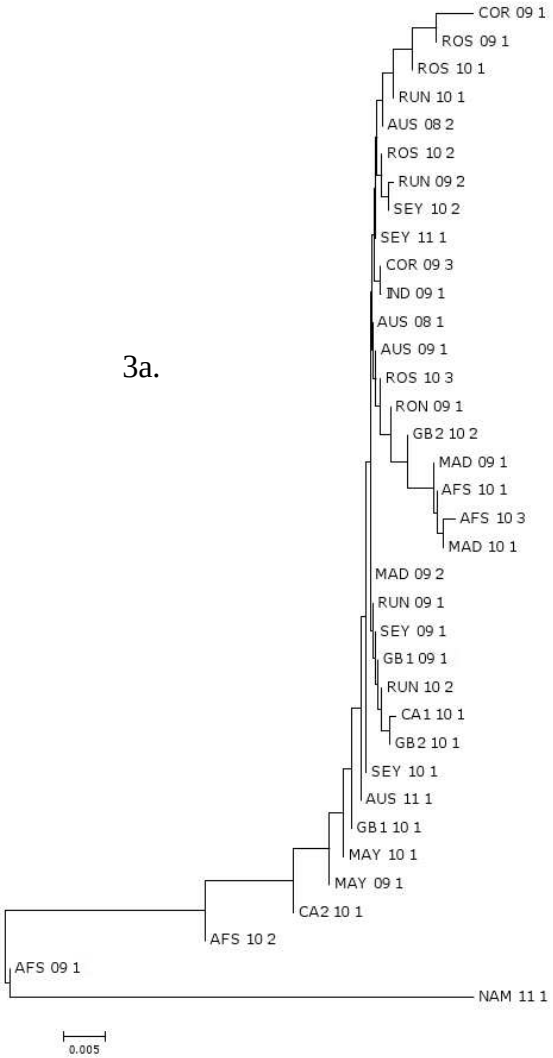
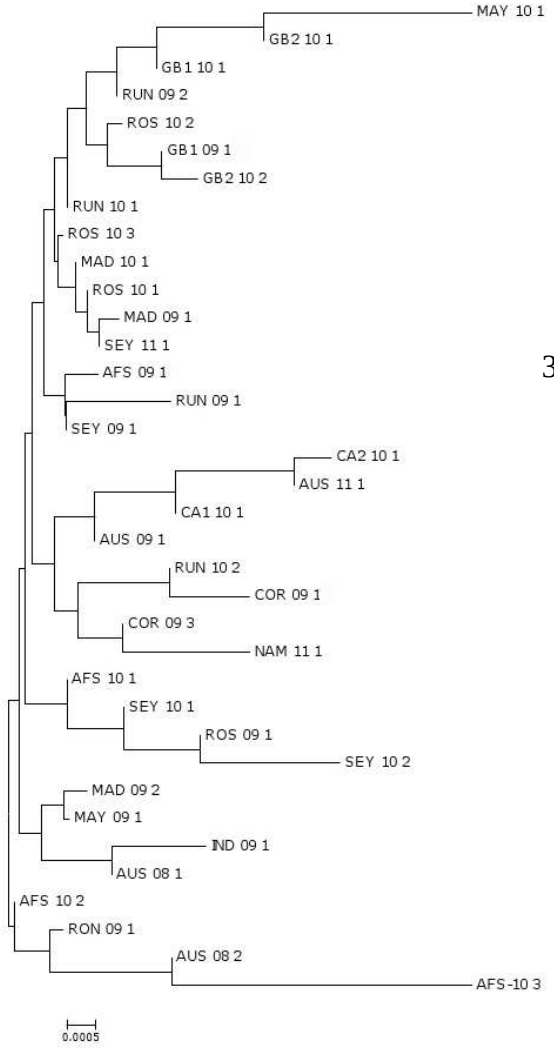


Figure 3



3a.



3b.

Figure 4

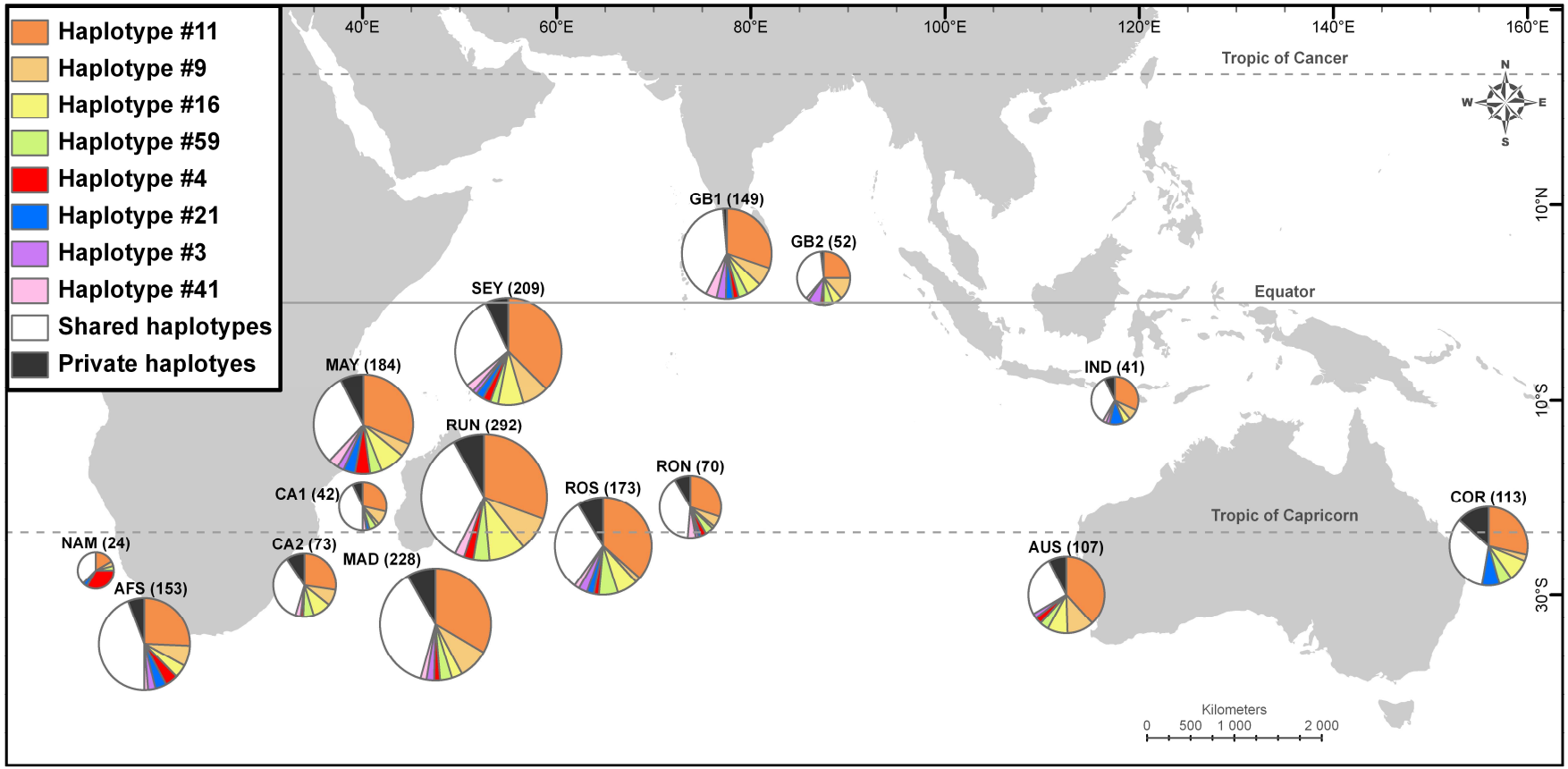
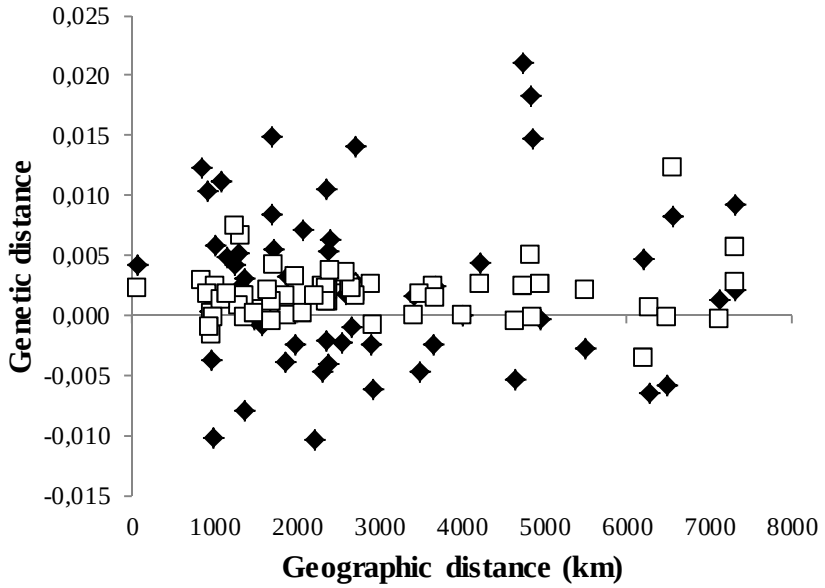

Haplotype #11
Haplotype #9
Haplotype #16
Haplotype #59
Haplotype #4
Haplotype #21
Haplotype #3
Haplotype #41
Shared haplotypes
Private haplotyes
40°E
60°E
80°E
100°E
120°E
140°E
160°E
Tropic of Cancer
Equator
Tropic of Capricorn
10°N
10°S
30°S
N
W
E
S
GB1 (149)
GB2 (52)
SEY (209)
MAY (184)
IND (41)
RUN (292)
CA1 (42)
ROS (173)
RON (70)
COR (113)
NAM (24)
CA2 (73)
MAD (228)
AFS (153)
AUS (107)
Kilometers
0 500 1 000 2 000

Figure 5

5a.



5b.

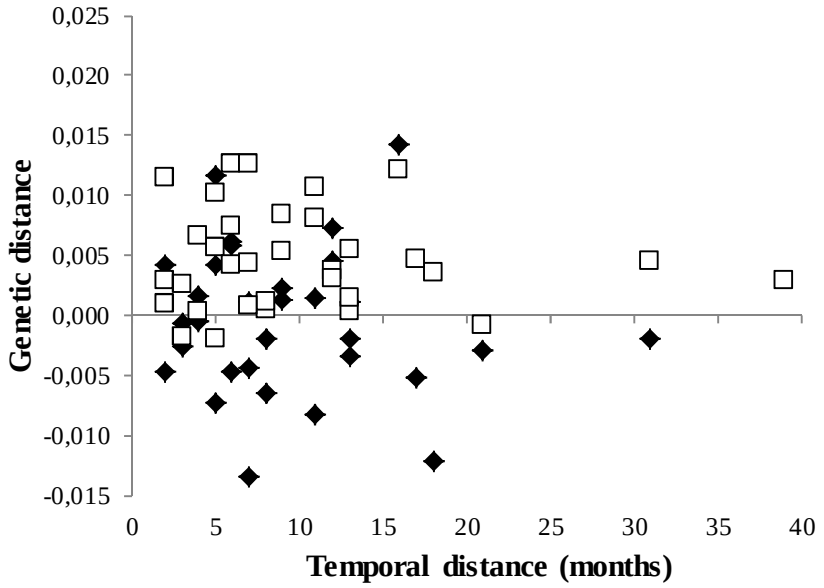
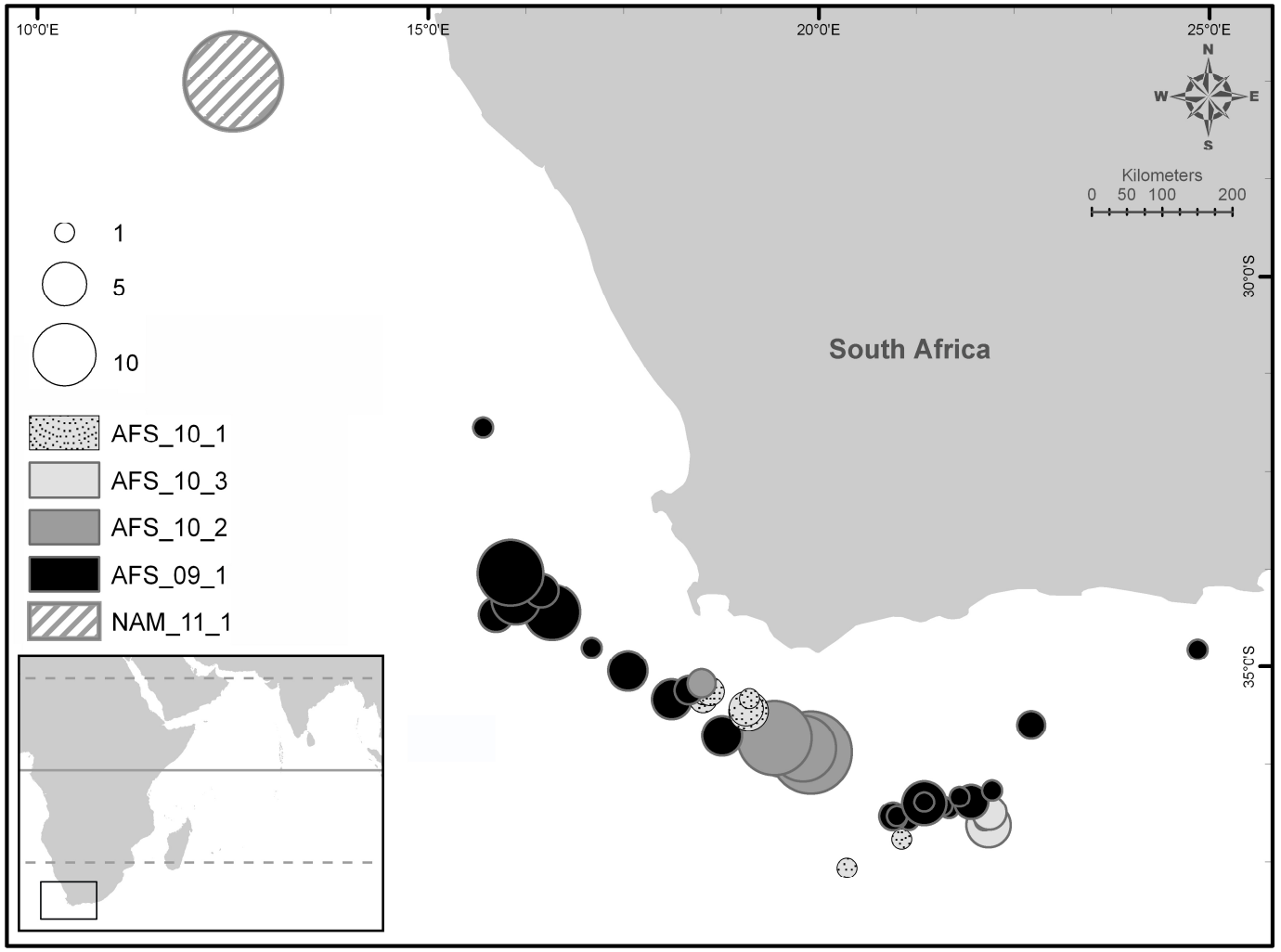


Figure 6


10°0'E
15°0'E
20°0'E
25°0'E
N
W
E
S
Kilometers
0 50 100 200
30°0'S
35°0'S
South Africa
1
5
10
AFS_10_1
AFS_10_3
AFS_10_2
AFS_09_1
NAM_11_1