HAL
open science

# Microsatellite analysis of albacore tuna (Thunnus alalunga): population genetic structure in the Nord-East Atlantic Ocean and Mediterranean sea 

C. A. Davies, E.M. Gosling, A. Was, D. Brophy, N. Tysklind

## - To cite this version:

C. A. Davies, E.M. Gosling, A. Was, D. Brophy, N. Tysklind. Microsatellite analysis of albacore tuna (Thunnus alalunga): population genetic structure in the Nord-East Atlantic Ocean and Mediterranean sea. Marine Biology, 2011, 158, pp.2727-2740. 10.1007/s00227-011-1772-x . hal-02282252

HAL Id: hal-02282252

## https://hal.science/hal-02282252

Submitted on 9 Sep 2019

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire HAL, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

# Microsatellite analysis of albacore tuna (Thunnus alalunga): population genetic structure in the North-East Atlantic Ocean and Mediterranean Sea 

C. A. Davies • E. M. Gosling • A. Was •<br>D. Brophy • N. Tysklind

Received: 5 March 2011/Accepted: 30 July 2011/Published online: 17 August 2011
© Springer-Verlag 2011


#### Abstract

Stock heterogeneity was investigated in albacore tuna (Thunnus alalunga, Bonnaterre 1788), a commercially important species in the North Atlantic Ocean and Mediterranean Sea. Twelve polymorphic microsatellite loci were examined in 581 albacore tuna from nine locations, four in the north-east Atlantic Ocean (NEA), three in the Mediterranean Sea (MED) and two in the south-western Pacific Ocean (SWP). Maximum numbers of alleles per locus ranged from 9 to 38 (sample mean, 5.2-22.6 per


[^0]locus; overall mean, $14.2 \pm 0.47 \mathrm{SE}$ ), and observed heterozygosities per locus ranged from 0.44 to 1.00 (overall mean: $0.79 \pm 0.19 \mathrm{SE}$ ). Significant deficits of heterozygotes were observed in $20 \%$ of tests. Multilocus $F_{\text {ST }}$ values were observed ranging from 0.00 to $\Theta=0.036$ and $\Theta^{\prime}=0.253$, with a mean of $\Theta=0.013$ and $\Theta^{\prime}=0.079$. Pairwise $F_{\text {ST }}$ values showed that the SWP, NEA and MED stocks were significantly distinct from one another, thus corroborating findings in previous studies based on mitochondrial DNA, nuclear DNA (other than microsatellites) and allozyme analyses. Heterogeneity was observed for the first time between samples within the Mediterranean Sea. GENELAND indicated the potential presence of three populations across the NEA and two separate populations in the Mediterranean Sea. Observed genetic structure may be related to migration patterns and timing of movements of subpopulations to the feeding grounds in either summer or autumn. We suggest that a more intensive survey be conducted throughout the entire fishing season to ratify or refute the currently accepted genetic homogeneity within the NEA albacore stock.

## Introduction

Waldman (1999) defines a "stock" as an exploitable population with some degree of genetic integrity. Other definitions of stock have less or no emphasis on genetic structure (Cadrin et al. 2005). Stocks can be delineated from observations relating to various aspects of life history (Griffiths 1997). Discrimination of stock components into genetic stocks can be undertaken by molecular methods, such as allozyme analysis and mitochondrial DNA studies, or by directly targeting variations in nuclear DNA composition. The stock structure of albacore (Thunnus
alalunga) has been identified globally by a variety of methods, primarily from information gathered directly from the fishery. Catch rates from each location and catch at length data (incorporated with information from ages determined from the calcareous structures) have been used to determine differences in growth rates and stock abundance in each ocean basin (ICCAT 1996; Miyake et al. 2004). In addition, conventional tag-recapture studies using plastic floy tags attached to individual fish have provided information on the migratory movements of albacore. It is considered that separate north and south stocks are present in both the Atlantic and Pacific Oceans as there has been no evidence to date of cross-equatorial migration from conventional tag-recapture studies, with the latitudinal differences observed in catch rates and seasonality of spawning (ICCAT 1996; Ramon and Bailey 1996). Therefore, fish observed in the northern and southern hemispheres are managed as separate units. Beardsley (1969) proposed that small numbers of albacore may undertake inter-oceanic migrations between the South Atlantic Ocean and the Indian Ocean; however, such claims remain to be substantiated through tagging studies, and hence, the Indian Ocean population is managed as a separate stock (Chen et al. 2005). Results from tagging surveys by Arrizabalaga et al. $(2002,2003)$ have shown that only very limited migration occurs between the North Atlantic Ocean and Mediterranean Sea, and genetic differences have been observed between the two regions using nuclear DNA (Nakadate et al. 2005). Consequently, the Mediterranean stock is managed as a separate unit (ICCAT 1996). In summary, based on information gathered from the fishery, six populations of albacore are recognised as stock units: Northern Atlantic, Southern Atlantic, Mediterranean, Indian, Northern Pacific and Southern Pacific (Miyake et al. 2004; ICCAT 2007).

Stock identification by genetic methods may indicate previously unidentified population structuring (Hoarau et al. 2004; Carlsson et al. 2006; Was et al. 2008; Kovach et al. 2010). Results from molecular genetic studies presently support the recognised subdivision of albacore populations into the six recognised stocks. Despite the lack of differentiation in mitochondrial DNA (mtDNA) (using restriction endonuclease analysis) observed between albacore sampled in the South Atlantic and North Pacific Oceans (Graves and Dizon 1989), Chow and Kishino (1995) showed differentiation between North and South Atlantic and Indo-Pacific albacore populations using PCR-restriction fragment length polymorphism (RFLP) analysis of the mtDNA ATPase gene. Further analysis of the mtDNA D-loop region of albacore in the Indo-Atlantic region by Yeh et al. (1997) showed that populations in the South Atlantic and Eastern Indian Oceans were genetically distinct. Investigations into the genetic structure of North Atlantic and Mediterranean
stocks, also using the mtDNA D-loop region (Viñas et al. 1999) as well as allozymes (Pujolar et al. 2003), showed genetic homogeneity between the two stocks. However, differences in morphometric characteristics, growth rates and reproductive areas had been previously reported for the two stocks (Megalofonou 2000). Viñas et al. (2004) conducted an additional study using the mtDNA control region in combination with nuclear DNA markers with their results indicating there was a small but significant difference between the two stocks. Nakadate et al. (2005) using nucleotide sequence variations of the glucose-6-phosphate dehydrogenase gene intron (G6PDH) and the mtDNA D-loop region corroborated their findings. Analysis of blood lectins (Arrizabalaga et al. 2004) indicated that the northeast Atlantic, South Atlantic and south-east Pacific populations were distinct but that South Atlantic and Indian Ocean populations were genetically similar.

Many of the previous studies address differences between stocks in different oceanic regions, with few investigating genetic heterogeneity within regions. Recently, Wu et al. (2009) studied albacore from three areas in the north-western Pacific Ocean (Taiwan, Japan and North of Hawaii) using analysis of mtDNA sequence data. Their findings showed that albacore tuna in the region constituted a single stock with no significant differences in geographic distributions. A preliminary study using microsatellites on albacore tuna revealed significant levels of differentiation between and within Atlantic and Pacific Oceans compared to mtDNA analyses of samples from the same areas (Takagi et al. 2001).

In view of the paucity of information on the genetic structure of albacore tuna within the North Atlantic Ocean (NEA) and Mediterranean Sea, the main objective of the present study was to analyse spatial, seasonal and temporal genetic heterogeneity using 12 microsatellite markers in albacore tuna collected in consecutive years from 2005 to 2007, from four NEA areas (waters off the south-west of Ireland, towards the southern Bay of Biscay along the Porcupine Ridge and off the northern coast of Africa near the Canary Islands), and from central (Tyrrhenian and Southern Adriatic Seas) and western (Balearic Sea) Mediterranean Sea regions. All albacore sampled with the exception of those collected from near the Canary Islands were juveniles.

## Materials and methods

## Sampling

A total of 14 samples $(N=581)$ of albacore were collected from NEA (West of Ireland, South Bay of Biscay and Canary Islands) and Mediterranean Sea (Med) using a variety of fishing methods (Table 1). All samples were
Table 1 Details of albacore tuna (Thunnus alalunga) samples

| Sample | Sample size | Location | Location name | Date | Survey vessel | Fishing method | Mean $\mathrm{LF}(\mathrm{~cm})$ | Mean weight (kg) | Maturity | Age (years)/number of fish |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Med_05 | 52 | $4000^{\prime}$ N $134^{\prime} \mathrm{E}$ | Western Mediterranean | Nov-05 | - | L | $63 \pm 2.6$ | $4.68 \pm 0.61$ | J | 3/22, 4/28, 5/2 |
| Med_06 | 50 | 39 49'N $1300{ }^{\prime} \mathrm{E}$ | Central Mediterranean | Nov-06 | - | L | $65 \pm 4.0$ | $5.06 \pm 0.97$ | J | $\begin{aligned} & \text { 3/19, 4/17, 5/10, 6/1 } \\ & \text { (no information for } 3 \text { fish) } \end{aligned}$ |
| Med_07 | 50 | $3949^{\prime} \mathrm{N} 1300{ }^{\prime} \mathrm{E}$ | Central Mediterranean | Dec-07 | - | L | $75 \pm 3.4$ | $7.90 \pm 1.10$ | J | 2/1, 3/8, 4/22, 5/16, 6/3 |
| CS1_05 | 38 | $4830^{\prime} \mathrm{N} 1038^{\prime} \mathrm{W}$ | Celtic sea | Sep-05 | MFV Maggie C | T | $56 \pm 5.7$ | - | J | 2/31, 3/5, 4/0, 5/1, 6/2 |
| CS2_05 | 50 | $4734^{\prime}$ N $1228^{\prime} \mathrm{W}$ | Celtic sea | Jul-05 | MFV Mellifont | T | $62 \pm 7.9$ | $5.62 \pm 2.07$ | J | 2/23, 3/37, 4/9, 5/2 |
| CS3_05 | 50 | $4821^{\prime} \mathrm{N} 1029^{\prime} \mathrm{W}$ | Celtic sea | Sep-05 | MFV Supreme 2 | P | $66 \pm 10.2$ | - | J | 2/13, 3/17, 4/18, 5/2 |
| CS1_06 | 57 | 47 32'N $930^{\prime} \mathrm{W}$ | Celtic sea | Aug-06 | MFV Ocean Dawn | T | $59.5 \pm 8.5$ | $5.00 \pm 2.60$ | J | $\begin{aligned} & \text { 2/35, 3/11, 4/7, 5/2 } \\ & \text { (no information for } 1 \text { fish) } \end{aligned}$ |
| BB1_06 | 67 | $4450^{\prime} \mathrm{N} 320^{\prime} \mathrm{W}$ | Bay of Biscay | Aug-06 | MFV Skipper | P | $74 \pm 12.1$ | $9.60 \pm 4.50$ | J | 2/13, 3/10, 4/17, 5/22, 6/3, 7/1, 8/1 |
| BB2_06 | 16 | $4336^{\prime} \mathrm{N} 223^{\prime} \mathrm{W}$ | Bay of Biscay | Sep-06 | - | T | $54 \pm 9.9$ | $1.40 \pm 0.20$ | J | 1/6, 2/8, $3 / 2$ |
| WI1_07 | 46 | $5219^{\prime} \mathrm{N} 123^{\prime} \mathrm{W}$ | West of Ireland | Sep-07 | MFV De Linn | T | $72 \pm 4.4$ | $8.03 \pm 1.69$ | J | $\begin{aligned} & \text { 3/7, 4/24, 5/11, 6/3 } \\ & \text { (no information for } 1 \text { fish) } \end{aligned}$ |
| WI2_07 | 50 | $5133^{\prime} \mathrm{N} 1351^{\prime} \mathrm{W}$ | West of Ireland | Sep-07 | MFV Teresa Mae | T | $67 \pm 5.0$ | - | J | 2/1, 3/30, 4/17, 5/2 |
| CAN_07 | 20 | $2700^{\prime} \mathrm{N} 1700^{\prime} \mathrm{W}$ | Canary Islands | Mar-07 | - | - | $106.8 \pm 7.6$ | - | A | - |
| Pac_03 | 18 | $2100{ }^{\prime} \mathrm{S} 16350{ }^{\prime} \mathrm{E}$ | SW Pacific | Jul-03 | - | - | $89 \pm 4.6$ | - | A | - |
| Pac_05 | 20 | $1400{ }^{\prime}$ S $13500^{\prime} \mathrm{W}$ | SW Pacific | Sep-05 | - | - | $98 \pm 4.6$ | - | A | - |

[^1]obtained from commercial fishing operations, which targeted aggregations of fish in summer feeding grounds. Fish were measured for fork length $\left(L_{F}\right)$ to the nearest centimetre and weighed to the nearest 10 g . Maturity was assigned on the basis of age and length with fish $<5$ years and with a $L_{F}<90 \mathrm{~cm}$ considered immature or juveniles (see Santiago and Arrizabalaga 2005). Sample details are shown in Table 1. A $5-\mathrm{mm}^{3}$ piece of white muscle was removed from behind the head in each individual and stored in $96 \%$ ethanol. Two south-west Pacific Ocean (Pac) sample sets from archived freeze-dried tissue (2003 and 2005) were acquired to serve as out-group samples.

Microsatellite analysis
Genomic DNA was extracted from muscle tissue ( $\sim 2 \mathrm{~mm}^{3}$ ) using the phenol-chloroform method of Sambrook et al. (1989). DNA was diluted 1:5 in sterile deionised water to give a concentration of 30-100 ng $\mu \mathrm{l}^{-1}$. The microsatellite loci developed for bluefin tuna were cross-amplified in albacore, and of those successfully amplifying, twelve were selected for analysis: Ttho4, Ttho6, Ttho7 (Takagi et al. 1999), Tth5 (McDowell et al. 2002), Tth4, Tth 14, Tth17, Tth185, Tth254, Tth1-31, Tth1229 and Tth16-2 (Clark et al. 2004). The reverse primer of each pair was end-labelled with fluorescent dye (700-IRD or $800-I R D$, Li-COR, Lincoln, NE, USA). Polymerase chain reaction (PCR) was carried out using a reaction volume of $10 \mu \mathrm{l}$, containing 0.17 U Taq polymerase, $1 \times$ reaction buffer (Bioline), $0.25 \mu \mathrm{M}$ of each primer, $0.2 \mu \mathrm{M}$ of mixed dNTPs, 0.2 mM MgCl 2 and $1 \mu \mathrm{l}$ of the 1.5 dilution of template DNA. Thermocycling procedures for each locus were exactly those in Takagi et al. (1999); McDowell et al. (2002), and Clark et al. (2004).

Amplification products were separated on $6 \%$ polyacrylamide gels using a Li-COR 4300 automated sequencer (Li-COR, Lincoln, NE, USA). PCR products were diluted $1: 5-1: 15$ with deionised water and $1 \mu \mathrm{l}$ of the dilution mixed 1:3 with bromophenol blue in formamide loading buffer. A sizing standard (50-350 base pairs, Li-COR, Lincoln, NE, USA) was run in the centre and at both ends of the gels to calibrate allele size. An internal reference sample consisting of individuals where allele sizes had been predetermined was included to ensure consistency in genotype scoring across runs. Fragment length polymorphisms were scored with GENE IMAGIR software (LiCOR, Lincoln, NE, USA).

## Data analysis

Allelic distribution, observed $\left(H_{\mathrm{O}}\right)$ and unbiased expected $\left(H_{\mathrm{E}}\right)$ heterozygosity estimates for the 14 samples were computed for each locus individually and as a multilocus
estimate using GENETIX 4.05.2 (Belkhir et al. 2002). Tests for conformance to Hardy-Weinberg equilibrium (HWE), single and multilocus $F_{\text {IS }}$ (Weir and Cockerham 1984), significance of heterozygote deficiency and linkage disequilibrium between pairs of loci were performed using GENEPOP v.4.0 (Rousset 2008) with specified Markov chain parameters (10,000 dememorisation steps, 100 batches, 5,000 iterations per batch). Sequential goodness of fit (SGoF) (CarvajalRodriguez et al. 2009) was employed in all multiple testing in order to reduce Type I errors. Deviations from HWE expectations were manually checked for the evidence of heterozygote or homozygote excess, and rare allele combinations. In locus-sample combinations where significant heterozygote deficiency was detected, the frequency of null alleles was estimated by the EM algorithm (Dempster et al. 1977) in the program FreeNA (Chapuis and Estoup 2007).

Global and pairwise $F_{\text {ST }}$ estimated using traditional $(\Theta)$ (Weir and Cockerham 1984) and heterozygosity-corrected estimators ( $\Theta^{\prime}$ ) (Hedrick 2005; Meirmans and Hedrick 2011) were employed to infer population differentiation. Two heterozygosity-independent methods were also employed to assess population structuring: Pairwise exact $G$ tests were performed in GENEPOP v.4.0; correspondence analysis (CA) was performed using the Adegenet package in R (Jombart 2008). For the latter analysis, all loci were included, plots were centred in the origin and missing data were replaced using mean $\chi^{2}$ distance. The first and second principle components (PC) with the highest eigenvalues were plotted to reveal the relative typology of the samples based on their multilocus allele distributions.

Microsatellite genotypes and sample spatial location data were analysed for all loci and samples in GENELAND package in R (Guillot et al. 2005, 2008). The geographical information was used to detect spatial delineation of genetic discontinuities, where the number of population units is treated as an unknown parameter. The number of populations ( $K$ ) was inferred by running the Markov chain Monte Carlo (MCMC) analysis using numbers of iterations varying from 100,000 to $1,000,000$. The maximum number of $K$ after the initial analysis was set at a minimum of 1 and a maximum of 10 . The MCMC analysis was run at 100,000 iterations with 100 burn-in generations. The analysis was run with correlated allele frequency models and true spatial and null allele models. Consistency across the best suite of parameters was assessed across ten independent runs.

## Results

Genetic diversity and HWE

A total of 581 fish from 14 locations in NEA, SWP and MED were genotyped at 12 microsatellite loci. All loci
Table 2 Summary of genetic variation in albacore tuna (Thunnus alalunga) for twelve microsatellite loci at 14 locations

| Pop | Ttho4 | Ttho6 | Ttho7 | Tth4 | Tth5 | Tth14 | Tth17 | Tth 185 | Tth254 | Tth1-31 | Tth12-29 | Tth16-2 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| MED_05 |  |  |  |  |  |  |  |  |  |  |  |  |
| $N$ | 52 | 52 | 52 | 51 | 52 | 52 | 52 | 52 | 52 | 52 | 52 | 52 |
| $N_{A}$ | 21 | 9 | 11 | 25 | 16 | 7 | 17 | 18 | 16 | 11 | 6 | 7 |
| $N_{E}$ | 10.052 | 3.671 | 5.485 | 11.309 | 7.748 | 2.749 | 5.859 | 7.988 | 9.089 | 5.175 | 2.569 | 2.439 |
| $H_{\mathrm{O}}$ | 0.827 | 0.673 | 0.885 | 0.882 | 0.885 | 0.519 | 0.846 | 0.827 | 0.712 | 0.673 | 0.596 | 0.500 |
| $H_{\text {E }}$ | 0.901 | 0.728 | 0.818 | 0.912 | 0.871 | 0.636 | 0.829 | 0.875 | 0.890 | 0.807 | 0.611 | 0.590 |
| $F_{\text {IS }}$ | 0.091* | 0.085 | -0.072 | 0.042 | -0.006 | 0.193** | -0.011 | 0.064 | 0.210*** | 0.175* | 0.034 | 0.178** |
| MED_06 |  |  |  |  |  |  |  |  |  |  |  |  |
| $N$ | 50 | 50 | 50 | 49 | 49 | 50 | 50 | 50 | 50 | 50 | 50 | 50 |
| $N_{A}$ | 21 | 9 | 9 | 22 | 17 | 5 | 18 | 17 | 17 | 16 | 8 | 8 |
| $N_{E}$ | 10.101 | 3.828 | 4.480 | 12.344 | 9.252 | 2.484 | 10.753 | 9.225 | 8.897 | 5.097 | 3.287 | 2.585 |
| $H_{\mathrm{O}}$ | 0.860 | 0.720 | 0.820 | 0.918 | 0.837 | 0.600 | 0.860 | 0.920 | 0.780 | 0.740 | 0.720 | 0.500 |
| $H_{\text {E }}$ | 0.901 | 0.739 | 0.777 | 0.919 | 0.892 | 0.597 | 0.907 | 0.892 | 0.888 | 0.804 | 0.696 | 0.613 |
| $F_{\text {IS }}$ | 0.056 | 0.036 | -0.046 | 0.011 | 0.072 | 0.006 | 0.021 | -0.022 | 0.134* | $0.067^{* * *}$ | -0.047 | 0.263*** |
| MED_07 |  |  |  |  |  |  |  |  |  |  |  |  |
| $N$ | 50 | 50 | 48 | 49 | 50 | 50 | 50 | 49 | 49 | 50 | 50 | 50 |
| $N_{A}$ | 21 | 7 | 11 | 21 | 16 | 6 | 17 | 16 | 23 | 13 | 9 | 6 |
| $N_{E}$ | 7.764 | 3.365 | 4.017 | 12.440 | 8.000 | 2.629 | 11.038 | 6.860 | 10.889 | 4.440 | 3.294 | 2.530 |
| $H_{\mathrm{O}}$ | 0.880 | 0.720 | 0.750 | 0.878 | 0.920 | 0.620 | 0.860 | 0.898 | 0.959 | 0.860 | 0.660 | 0.580 |
| $H_{\text {E }}$ | 0.871 | 0.703 | 0.751 | 0.920 | 0.875 | 0.620 | 0.909 | 0.854 | 0.908 | 0.775 | 0.696 | 0.605 |
| $F_{\text {IS }}$ | 0.000 | -0.014 | 0.012 | 0.056 | -0.413 | 0.010 | 0.064** | -0.041 | -0.046 | -0.100 | 0.038 | 0.051 |
| CS1_05 |  |  |  |  |  |  |  |  |  |  |  |  |
| $N$ | 38 | 38 | 38 | 36 | 38 | 38 | 37 | 36 | 38 | 38 | 38 | 38 |
| $N_{A}$ | 19 | 11 | 15 | 27 | 18 | 5 | 19 | 19 | 23 | 9 | 7 | 5 |
| $N_{E}$ | 9.110 | 3.297 | 5.730 | 18.000 | 9.286 | 2.337 | 11.904 | 12.284 | 13.248 | 4.143 | 2.664 | 2.657 |
| $H_{\mathrm{O}}$ | 0.921 | 0.579 | 0.816 | 0.972 | 0.842 | 0.711 | 0.838 | 0.861 | 1.000 | 0.868 | 0.632 | 0.605 |
| $H_{\mathrm{E}}$ | 0.890 | 0.697 | 0.825 | 0.944 | 0.892 | 0.572 | 0.916 | 0.919 | 0.925 | 0.759 | 0.625 | 0.624 |
| $F_{\text {IS }}$ | -0.021 | 0.182*** | 0.025 | -0.015 | 0.070 | -0.230 | 0.099 | 0.077 | -0.068 | -0.132 | 0.002 | 0.043 |
| CS2_05 |  |  |  |  |  |  |  |  |  |  |  |  |
| $N$ | 50 | 50 | 50 | 49 | 50 | 50 | 50 | 50 | 50 | 50 | 50 | 50 |
| $N_{A}$ | 21 | 11 | 16 | 27 | 21 | 7 | 21 | 21 | 18 | 11 | 8 | 6 |
| $N_{E}$ | 9.804 | 3.615 | 8.143 | 15.196 | 12.788 | 2.585 | 10.846 | 15.385 | 9.653 | 5.097 | 2.790 | 2.773 |
| $H_{\mathrm{O}}$ | 0.940 | 0.720 | 0.860 | 0.939 | 0.920 | 0.580 | 0.860 | 0.960 | 0.800 | 0.860 | 0.620 | 0.600 |
| $H_{\mathrm{E}}$ | 0.898 | 0.723 | 0.877 | 0.934 | 0.922 | 0.613 | 0.908 | 0.935 | 0.896 | 0.804 | 0.642 | 0.639 |
| $F_{\text {IS }}$ | -0.037 | 0.015 | 0.030 | 0.005 | 0.012 | 0.064 | 0.063 | 0.017 | 0.118* | -0.060 | 0.044 | 0.042 |

Table 2 continued

| Pop | Ttho4 | Ttho6 | Ttho7 | Tth4 | Tth5 | Tth14 | Tth17 | Tth185 | Tth254 | Tth1-31 | Tth12-29 | Tth16-2 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| CS3_05 |  |  |  |  |  |  |  |  |  |  |  |  |
| $N$ | 50 | 50 | 50 | 49 | 48 | 50 | 48 | 49 | 50 | 50 | 50 | 50 |
| $N_{A}$ | 21 | 10 | 14 | 24 | 21 | 6 | 23 | 22 | 25 | 12 | 7 | 4 |
| $N_{E}$ | 7.289 | 4.437 | 5.086 | 16.908 | 11.077 | 2.604 | 9.521 | 12.005 | 13.966 | 4.608 | 2.505 | 2.537 |
| $H_{\text {O }}$ | 0.900 | 0.720 | 0.800 | 0.878 | 0.833 | 0.640 | 0.833 | 0.837 | 0.980 | 0.800 | 0.720 | 0.640 |
| $H_{\mathrm{E}}$ | 0.863 | 0.775 | 0.803 | 0.941 | 0.910 | 0.616 | 0.895 | 0.917 | 0.928 | 0.783 | 0.601 | 0.606 |
| $F_{\text {IS }}$ | $-0.033$ | 0.081* | 0.014 | 0.078* | 0.094 | -0.029 | 0.079** | 0.098* | -0.046 | -0.012 | -0.188 | -0.046 |
| CS1_06 |  |  |  |  |  |  |  |  |  |  |  |  |
| $N$ | 57 | 57 | 57 | 55 | 56 | 57 | 57 | 57 | 57 | 57 | 57 | 57 |
| $N_{A}$ | 21 | 13 | 14 | 26 | 20 | 6 | 23 | 23 | 20 | 13 | 8 | 6 |
| $N_{E}$ | 9.038 | 3.893 | 6.377 | 14.439 | 9.664 | 3.165 | 14.188 | 11.301 | 10.830 | 5.967 | 2.861 | 2.814 |
| $H_{\mathrm{O}}$ | 0.842 | 0.649 | 0.825 | 0.964 | 0.929 | 0.561 | 0.877 | 0.895 | 0.825 | 0.860 | 0.754 | 0.614 |
| $H_{\mathrm{E}}$ | 0.889 | 0.743 | 0.843 | 0.931 | 0.897 | 0.684 | 0.930 | 0.912 | 0.908 | 0.832 | 0.651 | 0.645 |
| $F_{\text {IS }}$ | 0.062 | 0.135** | 0.031* | -0.026 | -0.027 | 0.188** | 0.065* | 0.027 | 0.100*** | $-0.024$ | -0.148 | 0.031* |
| BB1_06 |  |  |  |  |  |  |  |  |  |  |  |  |
| $N$ | 67 | 67 | 67 | 67 | 67 | 67 | 67 | 67 | 67 | 67 | 67 | 67 |
| $N_{A}$ | 20 | 11 | 19 | 28 | 21 | 4 | 20 | 22 | 27 | 17 | 7 | 7 |
| $N_{E}$ | 9.855 | 3.286 | 7.615 | 17.884 | 11.251 | 2.572 | 11.125 | 13.400 | 13.941 | 6.417 | 2.327 | 3.488 |
| $H_{\mathrm{O}}$ | 0.910 | 0.627 | 0.881 | 0.955 | 0.940 | 0.657 | 0.896 | 0.866 | 0.806 | 0.866 | 0.478 | 0.537 |
| $H_{\mathrm{E}}$ | 0.899 | 0.696 | 0.869 | 0.944 | 0.911 | 0.611 | 0.910 | 0.925 | 0.928 | 0.844 | 0.570 | 0.713 |
| $F_{\text {IS }}$ | 0.001* | 0.096 | 0.001* | -0.002 | -0.023 | -0.056 | 0.028* | 0.061 | 0.147*** | -0.048 * | 0.201* | 0.211** |
| BB2_06 |  |  |  |  |  |  |  |  |  |  |  |  |
| $N$ | 16 | 16 | 16 | 16 | 16 | 16 | 16 | 16 | 16 | 16 | 16 | 16 |
| $N_{A}$ | 17 | 8 | 9 | 15 | 15 | 5 | 14 | 14 | 18 | 10 | 5 | 5 |
| $N_{E}$ | 8.828 | 3.346 | 6.400 | 11.907 | 8.828 | 2.738 | 8.828 | 10.667 | 11.130 | 4.267 | 2.116 | 2.393 |
| $H_{\text {O }}$ | 0.875 | 0.625 | 0.813 | 1.000 | 0.938 | 0.813 | 0.938 | 0.875 | 0.938 | 0.688 | 0.438 | 0.438 |
| $H_{\mathrm{E}}$ | 0.887 | 0.701 | 0.844 | 0.916 | 0.887 | 0.635 | 0.887 | 0.906 | 0.910 | 0.766 | 0.527 | 0.582 |
| $F_{\text {IS }}$ | 0.046 | 0.140* | 0.069 | -0.060 | -0.025 | -0.250 | -0.025 | 0.067 | 0.002 | 0.060 | 0.202 | 0.278 |
| WI1_07 |  |  |  |  |  |  |  |  |  |  |  |  |
| $N$ | 46 | 46 | 46 | 46 | 45 | 46 | 46 | 46 | 46 | 46 | 46 | 46 |
| $N_{A}$ | 19 | 10 | 17 | 25 | 20 | 4 | 24 | 21 | 24 | 13 | 7 | 6 |
| $N_{E}$ | 6.551 | 4.157 | 6.107 | 17.782 | 11.066 | 2.411 | 15.223 | 12.824 | 12.447 | 4.853 | 2.519 | 2.427 |
| $H_{\text {O }}$ | 0.870 | 0.804 | 0.761 | 0.891 | 0.867 | 0.522 | 0.913 | 0.913 | 0.891 | 0.826 | 0.478 | 0.500 |
| $H_{\text {E }}$ | 0.847 | 0.759 | 0.836 | 0.944 | 0.910 | 0.585 | 0.934 | 0.922 | 0.920 | 0.794 | 0.603 | 0.588 |
| $F_{\text {IS }}$ | $-0.015$ | $-0.048$ | 0.101 | 0.067 | 0.058 | 0.119 | 0.034 | 0.021 | 0.042 | $-0.030$ | 0.186 | 0.127 |

Table 2 continued

| Pop | Ttho4 | Ttho6 | Ttho7 | Tth4 | Tth5 | Tth14 | Tth17 | Tth185 | Tth254 |  | Tth1-31 | Tth12-29 | Tth16-2 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| WI2_07 |  |  |  |  |  |  |  |  |  |  |  |  |  |
| $N$ | 50 | 50 | 50 | 49 | 50 | 50 | 49 | 50 | 50 |  | 50 | 50 | 50 |
| $N_{A}$ | 26 | 11 | 17 | 29 | 19 | 5 | 23 | 20 | 23 |  | 13 | 9 | 5 |
| $N_{E}$ | 8.929 | 3.362 | 8.532 | 15.540 | 8.503 | 2.525 | 13.527 | 11.655 | 13.812 |  | 5.482 | 2.607 | 2.438 |
| $H_{\mathrm{O}}$ | 0.860 | 0.580 | 0.940 | 0.878 | 0.880 | 0.660 | 0.878 | 0.880 | 0.920 |  | 0.940 | 0.540 | 0.460 |
| $H_{\text {E }}$ | 0.888 | 0.703 | 0.883 | 0.936 | 0.882 | 0.604 | 0.926 | 0.914 | 0.928 |  | 0.818 | 0.616 | 0.590 |
| $F_{\text {IS }}$ | 0.042 | 0.178** | -0.056 | 0.054* | 0.017 | -0.081 | 0.065 | 0.052 | 0.021 |  | -0.137 | 0.121 | 0.215 |
| CAN_07 |  |  |  |  |  |  |  |  |  |  |  |  |  |
| $N$ | 20 | 19 | 17 | 17 | 17 | 20 | 18 | 17 | 16 |  | 17 | 20 | 20 |
| $N_{A}$ | 14 | 7 | 14 | 17 | 13 | 4 | 17 | 12 | 15 |  | 8 | 5 | 3 |
| $N_{E}$ | 5.970 | 2.051 | 5.959 | 12.844 | 8.758 | 2.204 | 11.172 | 9.966 | 9.309 |  | 5.207 | 2.564 | 2.228 |
| $H_{\mathrm{O}}$ | 0.850 | 0.579 | 0.706 | 1.000 | 1.000 | 0.650 | 0.944 | 0.941 | 1.000 |  | 0.824 | 0.750 | 0.500 |
| $H_{\text {E }}$ | 0.833 | 0.512 | 0.832 | 0.922 | 0.886 | 0.546 | 0.910 | 0.900 | 0.893 |  | 0.808 | 0.610 | 0.551 |
| $F_{\text {IS }}$ | 0.005 | -0.103 | 0.181 | -0.054 | -0.099 | -0.165 | -0.009 | -0.016 | -0.088 |  | 0.011 | -0.205 | 0.118 |
| PAC_03 |  |  |  |  |  |  |  |  |  |  |  |  |  |
| $N$ | 18 | 18 | 18 | 18 | 18 | 18 | 18 | 18 | 18 |  | 18 | 18 | 18 |
| $N_{A}$ | 15 | 9 | 17 | 15 | 15 | 5 | 16 | 18 | 16 |  | 10 | 5 | 4 |
| $N_{E}$ | 7.281 | 3.340 | 9.127 | 11.172 | 10.983 | 2.582 | 9.529 | 12.706 | 11.172 |  | 6.113 | 3.057 | 2.464 |
| $H_{\mathrm{O}}$ | 1.000 | 0.556 | 0.833 | 0.833 | 0.944 | 0.722 | 0.944 | 1.000 | 0.889 |  | 0.944 | 0.556 | 0.444 |
| $H_{\text {E }}$ | 0.863 | 0.701 | 0.890 | 0.910 | 0.909 | 0.613 | 0.895 | 0.921 | 0.910 |  | 0.836 | 0.673 | 0.594 |
| $F_{\text {IS }}$ | -0.131 | 0.234** | 0.093 | 0.113* | -0.011 | -0.151 | -0.027 | -0.057 | 0.052 |  | -0.157 | 0.134 | 0.279 |
| PAC_05 |  |  |  |  |  |  |  |  |  |  |  |  |  |
| $N$ | 20 | 20 | 20 | 20 | 20 | 20 | 20 | 19 | 20 |  | 20 | 20 | 20 |
| $N_{A}$ | 18 | 7 | 15 | 16 | 16 | 4 | 14 | 17 | 15 |  | 9 | 6 | 4 |
| $N_{E}$ | 7.921 | 2.909 | 8.163 | 11.594 | 8.602 | 2.192 | 6.154 | 12.033 | 11.111 |  | 4.188 | 3.077 | 1.891 |
| $H_{\mathrm{O}}$ | 0.850 | 0.700 | 0.900 | 0.900 | 0.850 | 0.600 | 0.900 | 1.000 | 0.950 |  | 0.850 | 0.750 | 0.500 |
| $H_{\mathrm{E}}$ | 0.874 | 0.656 | 0.878 | 0.914 | 0.884 | 0.544 | 0.838 | 0.917 | 0.910 |  | 0.761 | 0.675 | 0.471 |
| $F_{\text {IS }}$ | 0.053 | -0.041 | 0.000 | 0.041 | 0.064 | -0.078 | -0.049 | -0.064 | -0.018 |  | -0.091 | -0.086 | -0.035 |
| All Pops | Tho4 | Ttho6 | Ttho7 | Tth4 | Tth5 | Tth14 | Tth17 | Tth185 | Tth254 | Tth1-31 | Tth12-29 | Tth16-2 | Total |
| Mean $N$ | 41.714 | 41.643 | 41.357 | 40.786 | 41.143 | 41.714 | 41.286 | 41.143 | 41.357 | 41.500 | 41.714 | 41.714 | 41.423 |
| SE $N$ | 4.398 | 4.426 | 4.466 | 4.393 | 4.431 | 4.398 | 4.431 | 4.501 | 4.505 | 4.484 | 4.398 | 4.398 | 1.238 |
| Mean $N_{\text {A }}$ | 19.571 | 9.500 | 14.143 | 22.643 | 17.714 | 5.214 | 19.000 | 18.571 | 20.000 | 11.786 | 6.929 | 5.429 | 14.208 |
| SE $N_{A}$ | 0.796 | 0.489 | 0.831 | 1.341 | 0.707 | 0.281 | 0.908 | 0.856 | 1.089 | 0.697 | 0.370 | 0.374 | 0.511 |
| Mean $N_{E}$ | 8.464 | 3.469 | 6.516 | 14.240 | 9.700 | 2.556 | 10.690 | 11.307 | 11.392 | 5.075 | 2.731 | 2.547 | 7.391 |

Table 2 continued

| All Pops | Ttho4 | Ttho6 | Ttho7 | Tth4 | Tth5 | Tth14 | Tth17 | Tth185 | Tth254 | Tth1-31 | Tth12-29 | Tth16-2 |
| :--- | :---: | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| TE $N_{E}$ | 0.359 | 0.152 | 0.420 | 0.699 | 0.397 | 0.066 | 0.715 | 0.596 | 0.487 | 0.194 | 0.093 | 0.094 |
| Mean $H_{\mathrm{O}}$ | 0.885 | 0.661 | 0.828 | 0.921 | 0.899 | 0.632 | 0.885 | 0.905 | 0.889 | 0.828 | 0.621 | 0.530 |
| SE $H_{\mathrm{O}}$ | 0.012 | 0.020 | 0.017 | 0.014 | 0.013 | 0.021 | 0.010 | 0.015 | 0.024 | 0.022 | 0.029 | 0.018 |
| Mean $H_{\mathrm{E}}$ | 0.879 | 0.703 | 0.838 | 0.928 | 0.895 | 0.605 | 0.900 | 0.908 | 0.910 | 0.799 | 0.628 | 0.601 |
| SE $H_{\mathrm{E}}$ | 0.006 | 0.017 | 0.011 | 0.003 | 0.004 | 0.010 | 0.008 | 0.006 | 0.004 | 0.007 | 0.013 | 0.014 |
| $F_{\text {IS }}$ | -0.007 | 0.059 | 0.012 | 0.008 | -0.005 | -0.045 | 0.016 | 0.003 | 0.023 | -0.036 | 0.012 | 0.118 |
| Mean $F_{\text {IS }}$ | - | - | - | - | - | - | - | - | - | - | - | - |
| SE $F_{\text {IS }}$ | - | - | - | - | - | - | - | - | - | - | - | - | $N$ number of individuals, $N_{A}$ number of alleles per locus, $N_{E}$ effective number of alleles per locus, $H_{O}$ observed heterozygosity, $H_{E}$ unbiased expected heterozygosity (gene diversity), $F_{I S}$ inbreeding coefficient (Weir and Cockerham 1984). The significance of $F_{\text {IS }}$ depicted by $* P<0.05,{ }^{* *} P<0.01$, *** $P<0.001$. The HWE significant after multiple testing is shown in bold

were moderately to highly polymorphic with a maximum of $9-38$ alleles per locus (mean 5.2-22.6; Table 2) with similar level of polymorphism across samples and effective numbers of alleles $\left(N_{\mathrm{E}}\right)$ ranged from 1.89 to 18 . Of the 301 alleles detected at the 12 loci, 43 were rare alleles occurring within a single sample with frequencies no higher than 0.006 . Observed heterozygosity values ranged from 0.44 for Tth16-2 to 1.00 for Tth4 and Ttho4. Mean multilocus observed heterozygosities were similar across all samples (0.74-0.82).

Ten locus-sample combinations significantly deviated from HWE after multiple testing (Table 2); however, only six of these combinations could be explained by heterozygosity deficiency, of which three were in locus Tth16-2. The estimate of null allele frequency in Tth16-2 ranged from 0.05 to 0.11 . There was no consistent pattern across samples or the other loci; hence, only locus Tth16-2 was removed for analyses assuming HWE. No significant linkage disequilibrium was found among any combination of loci across all samples, and no loci combination within samples was significant after correction for multiple testing, indicating no evidence of physical linkage between all pairs of loci tested among all sampled areas.

## Population differentiation between regions

Significant population structure was detected across samples, with three major clusters being identified; NEA, MED and SWP. Samples were consistently separated from each other for all analytical methods used. Global $F_{\text {ST }}$ values for all loci tested were significant (Table 3). Pairwise multilocus $F_{\mathrm{ST}}$ estimates and exact $G$ tests of genic proportions indicated that the two samples from the SWP (Pac_03 and Pac_05) were similar to each other but differed significantly from all samples from the MED and NEA with $F_{\text {ST }}$ estimates ranging for $\Theta$ between 0.007 and 0.036 and for $\Theta^{\prime}$ between 0.065 and 0.253 (Table 3). The correspondence analysis (CA) supports this as both SWP samples grouped separately from the northern hemisphere samples (Fig. 1). All three MED samples were found to be significantly distinct from all of the NEA samples based on pairwise $F_{\mathrm{ST}}$ estimates ( $\Theta$ ranging from 0.011 to 0.026 and $\Theta^{\prime}$ from 0.011 to 0.166 ) and exact $G$ tests (Table 3). The difference is also illustrated in the CA plot (Fig. 1), in which samples from the MED and NEA are clearly separated from each other.

Population differentiation within regions
Within the NEA out of 36 pairwise comparisons, only 5 $F_{\text {ST }}$ estimates and 9 exact $G$ test were significant after multiple testing correction (Table 3). These samples were obtained from feeding grounds covering approximately

Table 3 Multilocus pairwise estimates of differentiation $\left(\Theta\right.$ and $\Theta^{\prime}$ ) and significance of exact $G$ test for albacore tuna (Thunnus alalunga)

|  | MED_05 | MED_06 | MED_07 | CS1_05 | CS2_05 | CS3_05 | CS1_06 | BB1_06 | BB2_06 | WI1_07 | WI2_07 | CAN_07 | PAC_03 | PAC_05 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| MED_05 |  | 0.014 * | 0.008 * | 0.014 * | 0.019 * | 0.018 * | 0.024 * | 0.018 * | 0.026 * | 0.017 * | 0.020 * | 0.023 * | 0.025 * | 0.033 * |
| MED_06 | 0.124 |  | 0.002 | 0.012 * | 0.020 * | 0.015 * | 0.021 * | 0.017 * | 0.018 * | 0.013 * | 0.019 * | 0.024 * | 0.026 * | 0.034 * |
| MED_07 | 0.072 | 0.036 |  | 0.011 * | 0.021 * | 0.015 * | 0.020 * | 0.017 * | 0.020 * | 0.013 * | 0.018 * | 0.021 * | 0.026 * | 0.036 * |
| CS1_05 | 0.122 | 0.100 | 0.113 |  | 0.004 | 0.000 | 0.006 * | 0.000 | 0.000 | -0.002 | -0.002 | 0.001 | 0.014 * | 0.020 * |
| CS2_05 | 0.152 | 0.174 | 0.184 | 0.046 |  | 0.005 * | 0.006 * | 0.002 | 0.007 | 0.003 | 0.001 | 0.002 | 0.003 | 0.007 * |
| CS3_05 | 0.135 | 0.112 | 0.119 | 0.002 | 0.038 |  | 0.003 | 0.001 | 0.003 | 0.002 | 0.003 | 0.006 | 0.017 * | 0.019 * |
| CS1_06 | 0.149 | 0.162 | 0.148 | 0.029 | 0.041 | 0.024 |  | 0.007 * | 0.003 | 0.009 * | 0.004 | 0.007 | 0.011 * | 0.015 * |
| BB1_06 | 0.150 | 0.134 | 0.141 | 0.012 | 0.023 | 0.011 | 0.048 |  | 0.001 | 0.002 | 0.001 | 0.003 | 0.009 * | 0.015 * |
| BB2_06 | 0.157 | 0.130 | 0.155 | -0.011 | 0.047 | 0.003 | 0.034 | -0.004 |  | 0.008 | -0.001 | 0.002 | 0.009 | 0.014 * |
| WI1_07 | 0.166 | 0.125 | 0.132 | 0.004 | 0.019 | 0.008 | 0.036 | 0.021 | 0.039 |  | 0.000 | 0.002 | 0.014 * | 0.019 * |
| WI2_07 | 0.154 | 0.167 | 0.145 | 0.009 | 0.018 | 0.023 | 0.019 | 0.024 | 0.001 | -0.001 |  | 0.000 | 0.008 * | 0.014 * |
| CAN_07 | 0.150 | 0.158 | 0.162 | 0.026 | 0.015 | 0.051 | 0.019 | 0.036 | 0.001 | -0.002 | 0.016 |  | 0.009 | 0.014 * |
| PAC_03 | 0.189 | 0.211 | 0.194 | 0.132 | 0.046 | 0.128 | 0.094 | 0.105 | 0.073 | 0.115 | 0.088 | 0.082 |  | -0.005 |
| PAC_05 | 0.223 | 0.253 | 0.253 | 0.149 | 0.065 | 0.103 | 0.107 | 0.121 | 0.084 | 0.122 | 0.103 | 0.100 | -0.015 |  |

Tables correspond to pairs of $\Theta$ (above diagonal) and heterozygosity-corrected $\Theta^{\prime}$ (below diagonal). Significant values after multiple test correction are denoted with stars $\left(^{*}\right)$. The values have been shaded in grey for ease of interpretation: the darker the grey the higher the relative value among comparisons (within estimator). The lines represent the borders between samples in different basins: Mediterranean Sea (top and left), north-east Atlantic and Pacific (bottom and right). Differentiation values in grey font indicate exact $G$ test comparisons that were not significant after correction for multiple testing


Fig. 1 Sample correspondence analysis (CA) of albacore tuna (Thunnus alalunga) representing the first (PC1) and second (PC2) principal components of multilocus allele distributions. Eigenvalues corresponding to the selected components are shown in black in the histogram at the bottom right corner. Sample indicated by: $\mathrm{NEA}=($ open square $), \mathrm{Med}=($ filled circle $), \mathrm{SWP}=(\boxtimes)$
$2,500 \mathrm{~km}$ from south-west Ireland to the southern Bay of Biscay. There was evidence of genetic heterogeneity in pairwise comparisons involving the three samples: CS2_05, CS1_06 and BB1_06 (Table 3). Four significant pairwise $F_{\text {ST }}$ and four exact $G$ test comparisons indicated slight genetic heterogeneity between CS1_06 and other NEA samples (average $\Theta=0.006 ; \Theta^{\prime}=0.031$ ). Significant genetic differentiation was also detected with both methods between CS2_05 and CS3_05 ( $\Theta=0.005$;
$\left.\Theta^{\prime}=0.038\right)$. These three samples (CS2_05, CS1_06 and BB1_06) were caught early in the fishing season (July and August) (Table 1), while the other five juvenile NEA samples were caught between the end of September and October (Table 1).

All juvenile samples (CS1_05, CS2_05, BB2_06 and WI2_07) from the NEA were genetically undifferentiated from the adults collected from the Canary Islands (CAN_07), i.e. there were no significant differences in pairwise comparisons of $F_{\mathrm{ST}}$ values and exact tests for these five samples (Table 3).

The results of the GENELAND analysis are shown using a maximum of $K=10$, at 100,000 iterations, thinning at a rate of 100 , correlated allele frequency model, with 100 burn-in generations. GENELAND analysis consistently identified $K=5$ within the NEA and MED samples. The map of probable sample membership to a particular cluster is shown in Fig. 2 (Individual membership can be viewed in supplementary Figures). The southern Bay of Biscay samples (BB1_06 and BB2_06) group together. The only sample in this study which was obtained from an adult population of albacore in the North Atlantic (CAN_07) forms its own group. The majority of the remaining NEA (CS and WI) samples are classified as belonging together.

Pairwise $F_{\text {ST }}$ estimates and exact $G$ tests showed that the sample collected from the western side of the Mediterranean Sea in 2005 (Med_05) differed significantly from the two samples from the central region: Med_06 ( $\Theta=0.014$; $\left.\Theta^{\prime}=0.124\right)$ and Med_07 ( $\left.\Theta=0.008 ; \quad \Theta^{\prime}=0.072\right)$. Although the results from exact $G$ tests also indicated significant allele frequency heterogeneity among all three MED samples (Table 3), differentiation between the two samples from the central region of the Mediterranean Sea was not significant. The GENELAND analysis provides a


Fig. 2 Geographical locations of albacore tuna (Thunnus alalunga) sampling in Med_05 (X), Med_06 (filled circle), Med_07 (open circle), CS1_05 (filled triangle), CS2_05 (filled square), CS3_05 (filled diamond), CS1_06 (shaded right pointed triangle), BB1_06 (shaded triangle), BB2_06 (shaded square), WI1_07 (open diamond), WI2_07 (+) and CAN_07 (open square); the different colours indicate posterior probability of belonging to subpopulations $1-5$ detected in the GENELAND analysis (colours are arbitrary to differentiate between population groupings)
graphical representation of such significant heterogeneity between the western and central Mediterranean samples.

The two samples from the SWP (Pac_03 and Pac_05) did not differ for either $F_{\text {ST }}$ or exact $G$ test pairwise comparisons in either data sets.

## Discussion

## Genetic diversity and HWE

The present study used microsatellite markers to investigate the genetic structure of albacore tuna both within and among different oceanic regions. Twelve microsatellites were screened, all of which were developed for bluefin tuna (Takagi et al. 1999; McDowell et al. 2002; Clark et al. 2004). Three of the microsatellites used in the present study had previously been utilised by Takagi et al. (2001) to evaluate genetic variation within and among albacore samples from the North and South Atlantic and Pacific Oceans. Similar numbers of alleles were observed in the two studies at loci Ttho6 ( $N_{A}=18$ (this study) and $N_{A}=19$ (Takagi et al. 2001)). At Ttho-4 and Ttho7 in NE Atlantic samples, there were approximately twice as many alleles observed in this study (Mean $N_{A}=32$ and 26, respectively)
compared to Takagi et al. (2001) ( $N_{A}=11$ and 12 , respectively). Mean heterozygosities per locus were similar in both studies for all loci and areas sampled; heterozygosities were similar in range to studies on other species of tuna (Appleyard et al. 2001; Carlsson et al. 2004).

Population differentiation between regions

Multilocus pairwise comparisons of $F_{\mathrm{ST}}$ values were low, ranging from 0.000 (negative value shown in Table 2) to $\Theta^{\prime}=0.253(\Theta=0.036)$, with an average value of $\Theta^{\prime}=$ $0.071(\Theta=0.013)$. Despite relatively low $F_{\text {ST }}$ values, 55 out of 91 ( $60 \%$ ) were significant. Overall, results from pairwise $F_{\text {ST }}$ estimates and exact tests, and the CA plot (Table 3; Fig. 1) indicate that NEA, MED and SWP are strongly differentiated from one another. The largest $F_{\text {ST }}$ values were found between SWP and MED samples (SWP_05 and Med_07, $\Theta^{\prime}=0.253 ; ~ \Theta=0.036, P<$ 0.001 ) and $F_{\mathrm{ST}}$ between MED and NEA ranged from $\Theta^{\prime}=0.100$ to 0.166 and $\Theta=0.011$ to 0.026 (all significant after multiple testing correction). The finding of significant genetic differentiation between NEA and SWP albacore corroborates those of Chow and Ushiama (1995), where haplotype analysis of the mitochondrial ATPase gene indicated genetic heterogeneity between both the Atlantic and Pacific stocks but, showed homogeneity within both stocks. In addition to $F_{\mathrm{ST}}$ and CA results, the GENELAND analysis also supports genetic differentiation between NEA and MED albacore; this has also been reported by Arrizabalaga et al. (2004), Viñas et al. (2004) and Nakadate et al. (2005) for a variety of markers, such as blood lectins, mtDNA and nuclear markers. All these studies validate nonmolecular differences reported between NEA and MED albacore (Megalofonou 2000). There is now ample genetic evidence to support the justification of managing albacore in the Mediterranean Sea as a separate entity to albacore in the North Atlantic Ocean.

The science of landscape ecology is increasingly being combined with population genetics to explain differentiation between populations of a species (Manel et al. 2003). Isolation by distance and physical barriers to gene flow are two factors often proposed to explain differences within species across different geographic areas, for example, as the basis for the separation of bluefin tuna into two subspecies, one which inhabits the Atlantic Ocean (Thunnus thynnus thynnus) and the other the Pacific Ocean (T. $t$. orientalis) (Ward 1995). Landscape genetics can be applied to marine studies where both visible and invisible oceanographic features, such as benthic topography and currents, can lead to the segregation of marine populations with pelagic stages in their life history (Jørgensen et al. 2005; Karlsson and Mork 2005; Was et al. 2008; Kovach et al. 2010). The observed genetic distinctness of North Atlantic

Ocean and Mediterranean Sea albacore is particularly interesting in the light of the geological separation of the two regions in the late Miocene period ( $\sim 5.9$ million years ago) and reconnection during the Pliocenic period of the late Cenozoic period, some 5.33 million years ago (Patarnello et al. 2007). The Mediterranean Sea is a fully enclosed sea except for the narrow and deep connection with the North Atlantic Ocean, with the majority of biota having colonised the Mediterranean Sea from the Atlantic Ocean through this entrance (Almada et al. 2001; Domingues et al. 2005). Albacore are similar in morphology (Pujolar et al. 2003) and environmental preference (Beardsley 1969; Chow and Kishino 1995) to bluefin tuna (T. t. thynnus), and both are considered part of the "bluefin" tuna group that occupy cooler waters, yet bluefin tuna migrate out of the Mediterranean Sea through the straits of Gibraltar (Carlsson et al. 2006), whereas for albacore, Atlantic-Mediterranean migrations have been shown to be limited (Arrizabalaga et al. 2002, 2003). The comparative differences in behaviour of these two species raises questions as to why limited Atlantic-Mediterranean movement is observed in albacore when these fish (as a fast moving pelagic species tolerant of cooler waters) have the physiology to cross oceanographic features such as the AlmeriaOran front and the Straits of Gibraltar.

## Population differentiation within regions

Albacore in the North Atlantic Ocean is currently managed as a single stock, and no genetic structuring is recognised within the population (ICCAT 2007) in spite of studies that indicate otherwise (Hue 1979, 1980; Arrizabalaga et al. 2004). Although there have been no previous studies on albacore, a study on bluefin tuna by Carlsson et al. (2006) was able to determine whether individual bluefin tuna in a feeding aggregation in the North Atlantic belonged to either the eastern or western stock. The two stocks have been shown to migrate to feeding grounds at different times but are present for a few months as a mixed feeding aggregation (Carlsson et al. 2006). The results presented here indicate that there may be both spatial and seasonal structuring within the North Atlantic albacore, with the Bay of Biscay (BB1_06 and BB2_06, caught in August and September) samples separating from the Celtic Sea (CS1_06, caught in September) samples in 2006 and West of Ireland samples (WI1_07 and WI2_07, caught in September) separating from the Canary Islands sample (CAN_07, caught in March) in 2007. The observed structuring of albacore in a transient population in the NEA may be based on different timing of migration to feeding areas and the observation of genetic structuring may be dependent on the month the samples are collected during the fishing season. The identification of three subpopulation clusters within the north-
east Atlantic feeding aggregations (based on twelve microsatellite loci) indicates that management based on the whole population may mask issues with the health of subpopulations; therefore, caution must be used to prevent a genetic subpopulation (and hence the expression of available phenotypic plasticity) being exploited into possible extinction. This is fundamental to ensure the longevity of the populations/stocks within the whole catchment (Carvalho and Hauser 1994). Hue $(1979,1980)$ proposed that North Atlantic albacore are differentiated into at least two subpopulations with separate seasonally distinct migration routes (i.e. the "Classic" and the "Azores"); the fish that follow these separate migration routes can be characterised by observed differences in morphometric traits (head length vs. body length) and by the analysis of proteins from the eye lenses. Further information needs to be gathered to track the movement of the different components migrating into the feeding aggregations as well as collecting adult albacores from spawning grounds. Data on intra-oceanic migration pathways may be ascertained from archival tags, such as those used on larger fish (Sims et al. 2003). A further study including more intensive sampling throughout the fishing season would be needed to confirm or disprove the suggested structuring where different populations may be migrating to the feeding areas at different times. The combination of investigating migration pathway and timings with microsatellite data may provide further information in order to either refute or ratify genetic homogeneity within the North Atlantic stock.

Megalofonou (1990) and Cefali et al. (1986) cited in Megalofonou (2000) have shown that the distribution of albacore in the Mediterranean is discontinuous, with the highest concentrations found in the Tyrrhenian Sea in the Western Mediterranean Basin and the Ionian, Adriatic and Aegean Seas in the Eastern Mediterranean Basin. Previous studies have shown that oceanographic barriers appear to exist within the Mediterranean Sea, most notably the Almeria-Oran and the Siculo-Tunisian fronts, which separate the Mediterranean into the East and West basins. Carlsson et al. (2004) proposed possible heterogeneity of bluefin tuna within the Mediterranean, with the distinction being most evident between the Tyrrhenian and Ionian Seas (i.e. between the East and West basin separated by the Siculo-Tunisian front). Genetic heterogeneity between the East and West basins has been observed in other species, from those with sedentary and slow dispersal (sea grass, Posidonia oceanica (Arnaud-Haond et al. 2007) and cuttlefish, Sepia officinalis (Pérez-Losada et al. 2007)) to mobile species such as sea bass, Dicentrarchus labrax (Bahri-Sfar et al. 2000) and anchovy, Engraulis encrasicolus (Magoulas et al. 2006). In the current study, little difference in $F_{\text {ST }}$ values between the Tyrrhenian (Med_06) and Southern Adriatic Seas (Med_07) was found, indicating
homogeneity in albacore population genetic structure around the Italian peninsula. However, large differences were observed in both the $F_{\mathrm{ST}}$ and GENELAND analysis between samples from the Balearic Sea (Med_05) and those around the Italian peninsula, indicating possible heterogeneity within albacore in the Western Mediterranean basin. Such findings have not been reported in other studies on tuna. It is therefore possible that further heterogeneity in addition to that observed in the present study may exist in albacore within the Mediterranean Sea.

In conclusion, significant population structuring was observed in both North Atlantic and Mediterranean albacore, despite potentially high gene flow by larval dispersal, high fecundity, large population size (ICCAT 2007), high fishery mortality, and the extensive trans-oceanic feeding and spawning migrations undertaken by albacore tunas. This study highlights that albacore in North Atlantic Ocean and Mediterranean Sea need to be managed at a smaller scale where substructuring is indicated. However, in order to define boundaries, more exactly further work should be undertaken; this includes collecting reference material from spawning aggregations in the Eastern Atlantic Ocean (Beardsley 1969), and throughout the entire Southern Mediterranean Sea (Piccinetti and Piccinetti Manfrin 1993) should be included. At present, the North Atlantic albacore stock is managed as a single unit, with the Mediterranean stock as a separate entity (ICCAT 2007). Heterogeneity may exist within both stocks on the basis of different migration patterns, discontinuous distribution, morphometric traits and molecular data, which may have implications for stock management if one subpopulation contributes more to the effective population size than another. Bias in stock assessment could lead to the possible elimination of some subpopulations (Carvalho and Hauser 1994) by overfishing of recruits or spawning stock.

Acknowledgments The authors gratefully acknowledge the PhD sponsorship to CAD by Bord Iasciagh Mhara, Ireland, funded by the Irish Government and part-financed by the European Union under the National Development Plan 2000-2006 through the Supporting Measures in the Fisheries Sector. Our grateful thanks to all those involved in the sourcing, collection and processing of samples, especially fellow researchers at Instituto Tecnológico Pesquero y Alimentario (ATZI), Bord Iasciagh Mhara and Galway Mayo Institute of Technology. Many thanks to D.S., P.McG., A.L.M. and the two anonymous reviewers for their comments which have greatly improved earlier versions of this manuscript.

## References

Almada VC, Oliveira RF, Goncalves EJ, Almeida AJ, Santos RS, Wirtz P (2001) Patterns of diversity of the north-eastern Atlantic blenniid fish fauna (Pisces: Blenniidae). Glob Ecol Biogeogr. doi:10.1046/j.1466-822X.2001.00244.x

Appleyard SA, Grewe PM, Innes BH, Ward RD (2001) Population structure of yellowfin tuna (Thunnus albacares) in the western Pacific Ocean, inferred from microsatellite loci. Mar Biol. doi: 10.1007/s002270100578

Arnaud-Haond S, Migliaccio M, Diaz-Almela E, Teixeira S, van de Vliet S, Alberto F, Procaccini G, Duarte CM, Serrao EA (2007) Vicariance patterns in the Mediterranean Sea: east-west cleavage and low dispersal in the endemic grass Posionia oceania. J Biogeogr. doi:10.1111/j.1365-2699.2006.01671.x
Arrizabalaga H, Lopez-Rodas V, Oritz de Zarate V, Costas E, Gonzalez-Garces A (2002) Study on the Migrations and Stock Structure of Albacore (Thunnus alalunga) from the Atlantic Ocean and the Mediterranean Sea Based on Conventional Tag ReleaseRecapture Experiences. ICCAT Col Vol Sci Pap 54:1479-1494
Arrizabalaga H, Lopez-Rodas V, Costas E, Gonzalez-Garces A (2003) Estimating albacore movement rates between the North Atlantic and the Mediterranean from conventional tagging data. ICCAT Col Vol Sci Pap 55:280-291
Arrizabalaga H, Costas E, Juste J, Gonzalez-Garces A, Nieto B, Lopez-Rodas V (2004) Population structure of albacore Thunnus alalunga inferred from blood groups and tag-recapture analyses. Mar Ecol Prog Ser. doi:10.354/meps282245
Bahri-Sfar L, Lemaire C, Hassine OKB, Bonhomme F (2000) Fragmentation of sea bass populations in the western and eastern Mediterranean as revealed by microsatellite polymorphism. Proc R Soc B-Biol Sci. doi:10.1098/rspb.2000.1092
Beardsley F (1969) Proposed migrations of albacore, Thunnus alalunga, in Atlantic Ocean. Trans Am Fish Soc 98:589-590
Belkhir K, Borsa P, Chikhi L, Raufaste N, Bonhomme F (2002) GENETIX 4.04, logiciel sous Windows TM pour la génétique des populations. Laboratoire génome, populations, interactions: CNRS UMR 5000, Université de Montpellier II, Montpellier, France. http://www.univ-montp2.fr/\~genetix/genetix/genetix. htm
Cadrin SX, Friedland KD, Waldman JR (2005) Stock identification methods: applications in fishery science. Elsevier Academic Press, Oxford
Carlsson J, McDowell JR, Diaz-Jaimes P, Carlsson JEL, Boles SB, Gold JR, Graves JE (2004) Microsatellite and mitochondrial DNA analyses of Atlantic bluefin tuna (Thunnus thynnus thynnus) population structure in the Mediterranean Sea. Mol Ecol. doi:10.1111/j.1365-294X.2004.02336.x
Carlsson J, McDowell JR, Carlsson JEL, Olasdottir D (2006) Genetic heterogeneity of Atlantic bluefin tuna caught in the eastern North Atlantic Ocean south of Iceland. ICES J Mar Sci. doi:10.1016/ j.icesjms.2006.04.009

Carvajal-Rodriguez A, de Una-Alvarez J, Rolan-Alvarez E (2009) A new multitest correction (SGoF) that increases its statistical power when increasing the number of tests. BMC Bioinform. doi:10.1186/1471-2105-10-209
Carvalho GR, Hauser L (1994) Molecular genetics and the stock concept in fisheries. Rev Fish Biol Fisheries. doi:10.1007/ BF00042905
Cefali A, Potoschi A, De Metrio G, Petrosino G (1986) Biology and fishing of germon, Thunnus alalunga (Bonn. 1788), observed for a four-year period in the Gulf of Taranto. Oebalia N.S. 12:123-136
Chapuis MP, Estoup A (2007) Microsatellite null alleles and estimation of population differentiation. Mol Biol Evol. doi: 10.1093/molbev/msl191

Chen IC, Lee PF, Tzeng WN (2005) Distribution of albacore (Thunnus alalunga) in the Indian Ocean and its relation to environmental factors. Fish Oceanogr. doi:10.1111/j.1365-2419. 2004.00322.x

Chow S, Kishino H (1995) Phylogenetic relationships between tuna species of the genus Thunnus (Scombridae: Teleostei):

Inconsistent implications from morphology, nuclear and mitochondrial genomes. J Mol Evol. doi:10.1007/BF00173154
Chow S, Ushiama H (1995) Global population-structure of albacore (Thunnus alalunga) inferred by RFLP analysis of the mitochondrial atpase gene. Mar Biol. doi:10.1007/BF00350321
Clark TB, Ma L, Saillant E, Gold JR (2004) Microsatellite DNA markers for population-genetic studies of Atlantic bluefin tuna (Thunnus thynnus thynnus) and other species of genus Thunnus. Mol Ecol Notes. doi:10.1046/j.1471-8286.2004.00572.x
Dempster AP, Laird NM, Rubin DB (1977) Maximum liklihood from incomplete data via the EM algorithm. J R Stat Soc B 39:1-38
Domingues VS, Bucciarelli G, Almada VC, Bernardi G (2005) Historical colonization and demography of the Mediterranean damselfish, Chromis chromis. Mol Ecol. doi:10.1111/j.1365294X.2005.02723.x
Graves JE, Dizon AE (1989) Mitochondrial-DNA Sequence Similarity of Atlantic and Pacific Albacore Tuna (Thunnus alalunga). Can J Fish Aquat Sci. doi:10.1139/f89-110
Griffiths MH (1997) The life history and stock separation of silver knob, Argyrosomus inodorus, in South African waters. Fish Bull 95:47-67
Guillot G, Mortier F, Estoup A (2005) Geneland: A program for landscape genetics. Mol Ecol Notes. doi:10.1111/j.1471-8286. 2005.01031.x

Guillot G, Santos F, Estoup A (2008) Analysing georeferenced population genetics data with Geneland: a new algorithm to deal with null alleles and a friendly graphical user interface. Bioinformatics. doi:10.1093/bioinformatics/btn136
Hedrick PW (2005) A standardized genetic differentiation measure. Evolution. doi:10.1111/j.0014-3820.2005.tb01814.x
Hoarau G, Piquet AMT, van der Veer HW, Rijnsdorp AD, Stam W, Olsen JL (2004) Population structure of plaice (Pleuronectes platessa L.) in northern Europe: a comparison of resolving power between microsatellites and mitochondrial DNA data. J Sea Res. doi:10.1016/j.seares.2003.12.002
Hue SB (1979) Reserches sur L'heterogeneite du stock du germon T. alalunga du N E Atlantique par electrophorese. ICCAT Col Vol Sci Pap 8:265-271
Hue SB (1980) Summary of the Study on the Heterogeneity of the Stock of Albacore ( $T$. alalunga) in the Northeast Atlantic. ICCAT Col Vol Sci Pap 9:353-355
ICCAT (1996) Report of the final meeting of the ICCAT Albacore Research Program. Sukarrieta, Vizcaya
ICCAT (2007) Report of the 2007 ICCAT Albacore Stock Assessment Session, Madrid
Jombart T (2008) adegenet: a R package for the multivariate analysis of genetic markers. Bioinformatics. doi:10.1093/bioinformatics/ btn129
Jørgensen HBH, Hansen MM, Bekkevold D, Ruzzante DE, Loeschcke V (2005) Marine landscapes and population genetic structure of herring (Clupea harengus L.) in the Baltic Sea. Mol Ecol. doi:10.1111/j.1365-294X.2005.02658.x
Karlsson S, Mork J (2005) Deviation from Hardy-Weinberg equilibrium, and temporal instability in allele frequencies at microsatellite loci in a local population of Atlantic cod. ICES J Mar Sci. doi:10.1016/j.icesjms.2005.05.009
Kovach AL, Breton TS, Berlinsky DL, Maceda L, Wirgin I (2010) Fine-scale spatial and temporal genetic structure of Atlantic cod off the Atlantic coast of the USA. Mar Ecol Prog Ser. doi: 10.3354/meps08612

Magoulas A, Castilho R, Caetano S, Marcato S, Patarnello T (2006) Mitochrodrial DNA reveals a mosaic pattern of phylogeographical structure in Atlantic and Mediterranean populations of anchovy (Engraulis encrasicolus). Mol Phylogenet Evol. doi: 10.1016/j.ympev.2006.01.016

Manel S, Schwartz MK, Luikart G, Taberlet P (2003) Landscape genetics: combining landscape ecology and population genetics. Trends Ecol Evol. doi:10.1016/S169-5347(03)00008-9
McDowell JR, Diaz-Jaimes P, Graves JE (2002) Isolation and characterization of seven tetranucleotide microsatellite loci from Atlantic northern bluefin tuna Thunnus thynnus thynnus. Mol Ecol Notes. doi:10.1046/j.1471-8286.2002.00197.x
Megalofonou P (1990) Size distribution, Length-Weight Relationships, Age and Sex of Albacore Thunnus alalunga Bonn.in the Aegean Sea. ICCAT Col Vol Sci Pap 33:154-162
Megalofonou P (2000) Age and growth of Mediterranean albacore. J Fish Biol. doi:10.1111/j.1095-8649.2000tb00269.x
Meirmans PG, Hedrick PW (2011) Assessing population structure: (i)Fst(/i) and related measures. Mol Ecol Res. doi:10.1111/j. 1755-0998.2010.02927.x
Miyake MP, Miyabe N, Nakano H (2004) Historical Trends of Tuna Catches in the World. FAO Fisheries Technical Paper. No 467. Food and Agriculture Organization of the United Nations, 467, Rome, Italy
Nakadate M, Viñas J, Corriero A, Clarke S, Suzuki N, Chow S (2005) Genetic isolation between Atlantic and Mediterranean albacore populations inferred from mitochondrial and nuclear DNA markers. J Fish Biol. doi:10.1111/j.0022-1112.2005.00705.x
Patarnello T, Volckaert F, Castilho R (2007) Pillars of Hercules: is the Atlantic-Mediterranean transition a phylogeographical break? Mol Ecol. doi:10.1111/j.1365-294X.2007.03477.x
Pérez-Losada M, Nolte MJ, Crandall KA, Shaw PW (2007) Testing hypotheses of population structuring in the Northeast Atlantic Ocean and Mediterranean Sea using the common cuttlefish Sepia officinalis. Mol Ecol. doi:10.1111/j.1365-294X.2007.03333.x
Piccinetti C, Piccinetti Manfrin G (1993) Distribution des Larves de Thonnides en Mediterranee. ICCAT Col Vol Sci Pap 40:164172
Pujolar JM, Roldan MI, Pla C (2003) Genetic analysis of tuna populations, Thunnus thynnus thynnus and T. alalunga. Mar Biol. doi:10.1007/s00227-003-1080-1
Ramon D, Bailey K (1996) Spawning seasonality of albacore, Thunnus alalunga, in the South Pacific Ocean. Fish Bull 94:724-733
Rousset F (2008) GENEPOP'007: a complete re-implementation of the GENEPOP software for Windows and Linux. Mol Ecol Res. doi:10.1111/j.1471-8286.2007.01931.x
Sambrook J, Fritsch E, Maniatis T (1989) Molecular cloning: a laboratory manual. Cold Spring Harbor Laboratory Press, New York
Santiago J, Arrizabalaga H (2005) An integrated growth study for North Atlantic albacore (Thunnus alalunga Bonn. 1788). ICES J Mar Sci. doi:10.1016/j.icesjms.2005.01.015
Sims DW, Southall EJ, Richardson AJ, Reid PC, Metcalfe JD (2003) Seasonal movements and behaviour of basking sharks from archival tagging: no evidence of winter hibernation. Mar Ecol Prog Ser. doi:10.3354/meps248187
Takagi M, Okamura T, Chow S, Taniguchi N (1999) PCR primers for microsatellite loci in tuna species of the genus Thunnus and its application for population genetic study. Fish Sci 65:571-576
Takagi M, Okamura T, Chow S, Taniguchi N (2001) Preliminary study of albacore (Thunnus alalunga) stock differentiation inferred from microsatellite DNA analysis. Fish Bull 99:697-701
Viñas J, Santiago J, Pla C (1999) Genetic Characterisation and Atlantic-Mediterranean Stock Structure of Albacore Thunnus alalunga. ICCAT Col Vol Sci Pap 49:188-190
Viñas J, Alvarado Bremer JR, Pla C (2004) Inter-oceanic genetic differentiation among albacore (Thunnus alalunga) populations. Mar Biol. doi:10.1007/s00227-004-1319-5
Waldman JR (1999) The importance of comparative studies in stock analysis. Fish Res. doi:10.1016/S0165-7836(99)00075-2

Ward RD (1995) Population genetics of tunas. J Fish Biol. doi: 10.1111/j.1095-2649.1995.tb06060.x

Was A, Gosling E, McCrann K, Mork J (2008) Evidence for population structuring of blue whiting (Micromesistius poutassou) in the Northeast Atlantic. ICES J Mar Sci. doi:10.1093/ icesjms/fms187
Weir BS, Cockerham CC (1984) Estimating F-Statistics for the Analysis of Population-Structure. Evol 38:1358-1370

Wu GCC, Chiang HC, Chen KS, Hsu CC, Yang HY (2009) Population structure of albacore (Thunnus alalunga) in the Northwestern Pacific Ocean inferred from mitochondrial DNA. Fish Res. doi:10.1016/j.fishres.2010.03.015
Yeh SY, Treng TD, Hui CF, Penney AJ (1997) Mitochondrial DNA sequence analysis on Albacore Thunnus alalunga, meat samples collected from the waters off western South Africa and the Eastern Indian Ocean. ICCAT Col Vol Sci Pap 46:152-159


[^0]:    Communicated by T. Reusch.
    Electronic supplementary material The online version of this article (doi:10.1007/s00227-011-1772-x) contains supplementary material, which is available to authorized users.
    C. A. Davies ( $\triangle$ ) • D. Brophy

    Commercial Fisheries Research Group, Department of Life Sciences, Galway-Mayo Institute of Technology, Dublin Road, Galway, Ireland
    e-mail: carys.davies@bangor.ac.uk
    C. A. Davies • E. M. Gosling • A. Was

    Molecular Ecology Research Group, Department of Life Sciences, Galway-Mayo Institute of Technology, Dublin Road, Galway, Ireland

    Present Address:
    C. A. Davies

    School of Ocean Sciences, Bangor University, Menai Bridge, Anglesey LL59 5AB, UK
    A. Was

    Department of Fishery Resources, Sea Fisheries Institute, Kołłataja Street 1, 81-332 Gdynia, Poland
    N. Tysklind

    Molecular Ecology and Fisheries Genetics Laboratory, School of Biological Sciences, Bangor University, Deniol Road, Bangor, Gwynedd LL57 2UW, UK

[^1]:    - indicates no information/data; fishing method, $L$ pelagic longline, $P$ pair trawling, $T$ trolling; maturity based on size $J$ juvenile, $A$ adult

