

Use of genetic data to assess the uncertainty in stock assessments due to the assumed stock structure: the case of albacore (*Thunnus alalunga*) from the Atlantic Ocean

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Stock assessments can be problematic because of uncertainties associated with the data or because of simplified assumptions made when modeling biological processes (Rosenberg and Restrepo, 1995). For example, the common assumption in stock assessments that stocks are homogeneous and discrete (i.e., there is no migration between the stocks) is not necessarily true (Kell et al., 2004a, 2004b).

On the other hand, it is essential that the stock structure assumed during the assessment and management process corresponds to the real population structure of the resource. Otherwise, fishery management becomes inefficient (less productive populations may be overfished and collapse, while more productive populations may be underexploited [Allendorf et al., 1987; Begg et al., 1999]) and may affect biological attributes, such as growth, productivity, or genetic diversity (Ricker, 1981). In spite of this problem, current regulations on several fisheries are based on spatial schemes that do not necessarily reflect the real biological structure

of the populations (Pawson and Jennings, 1996; Stephenson, 1999; Ward, 2000). In these cases, the results of stock assessments may be biased and, in general, an important level of uncertainty exists in stock assessments (NRC, 1994; Turner, 1998) due to the assumed stock structure.

An assessment of the magnitude of this uncertainty is important so as to increase confidence in the assessment itself. Moreover, quantifying the uncertainty allows the evaluation of the relative effect of stock structure assumptions with respect to other assumptions about biological, fishery, or modeling parameters in the assessment. Knowing the relative importance of the effect of these underlying assumptions will allow management scientists to prioritize the types of research needed to better ground the stock assessments with real information.

In this note, we suggest a way to assess uncertainty in stock assessments that is due to assumptions of stock structure. The assessment is essentially based on a sensitivity analysis conducted by testing alter-

native stock structure hypotheses derived from available genetic, fishery, and biological information. The method is illustrated with albacore (*Thunnus alalunga*, Bonn. 1788) in the Atlantic Ocean.

Albacore is a highly migratory species distributed between latitudes 45°N and 45°S. Studies of albacore reproduction in the Atlantic Ocean have shown different spawning periods and areas in both hemispheres (Beardsley, 1969; Koto, 1969). Shiohama (1971) and Uozumi (1996), based on Japanese longline distribution studies, described an adult concentration area in each hemisphere. These findings, along with studies of larval concentration areas (Ueyanagi, 1971), support the existence of two separate populations, one in each hemisphere. Based on these studies, it is assumed within the International Commission for the Conservation of Atlantic Tunas (ICCAT) that there are two albacore management units in the Atlantic, separated by parallel 5°N. However, various authors have suggested the possibility that albacore move between the north and south Atlantic (reviewed in González-Garcés, 1997). Moreover, the continuous spatial distribution of catches around the equator also suggests this possibility (Fig. 1).

Recent studies have shown genetic differences between north and south Atlantic albacore (Takagi et al., 2001; Arrizabalaga et al., 2004), but it is still unclear whether the limit between both populations is at latitude 5°N or somewhere else. In fact, results from Arrizabalaga et al. (2004) are not concordant with the limit at latitude 5°N because a sample from the Gulf of Guinea (1°N, 15–16°W) was genetically more like the sample from the north Atlantic than the one from the south Atlantic. This observation may indicate that either the limit between both stocks may be located farther south than that currently assumed or that

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there may be some interchange between individuals of both stocks. An earlier statistical comparison of blood group frequencies in albacore found in the Gulf of Guinea (lat. 0°–9°S, long. 0°–8°W), northwest Atlantic (lat. 23°–31°N, long. 60°–70°W) and middle-north Atlantic (lat. 1°–34°N, long. 11°–40°W) in an earlier study (Suzuki, 1962) did not show differences between them, again indicating that the fish present in the Gulf of Guinea may belong to the northern population.

Materials and methods

Taking into account the above findings, we assessed the uncertainty in north and south Atlantic albacore stock assessments by means of a sensitivity analysis. This analysis consisted in assessing both stocks, either under alternative stock boundaries or by assuming certain migration rates between them.

Stock assessment under the assumption of alternative boundaries between stocks

Two alternative boundaries between albacore stocks were considered: at lat. 0°N and lat. 5°S. The catch-at-age within lat. 5°N–0°N and lat. 5°N–5°S was removed from the southern catch-at-age matrix and added to the northern one, by using available catch (ICCAT¹), size, and growth information (Bard, 1981; Sarralde et al., 2002). For each boundary, abundance and fishing mortality rates were estimated separately for each stock by virtual population analysis (VPA) by using the VPA-2box, vers. 3.0 program (Porch et al., 2001). This program assesses the abundance and mortality of one or two intermixing stocks by fitting age-structured population equations to fishery data. All stock assessment options were maintained as in the ICCAT 2001 report (ICCAT²) and variance of estimated parameters was computed by performing 400 nonparametric bootstraps of the abundance indices.

¹ ICCAT (International Commission for the Conservation of Atlantic Tunas). Website: <http://www.iccat.int/> (accessed 31 June 2005).

² ICCAT (International Commission for the Conservation of Atlantic Tunas). 2001. Report of the ICCAT SCRS albacore stock assessment session (Madrid, Spain; October 9 to 15, 2000). Collect. Vol. Sci. Pap. ICCAT, 52, p. 1283–1390. International Commission for the Conservation of Atlantic Tunas, Corazón de María 8, 28002 Madrid, Spain.

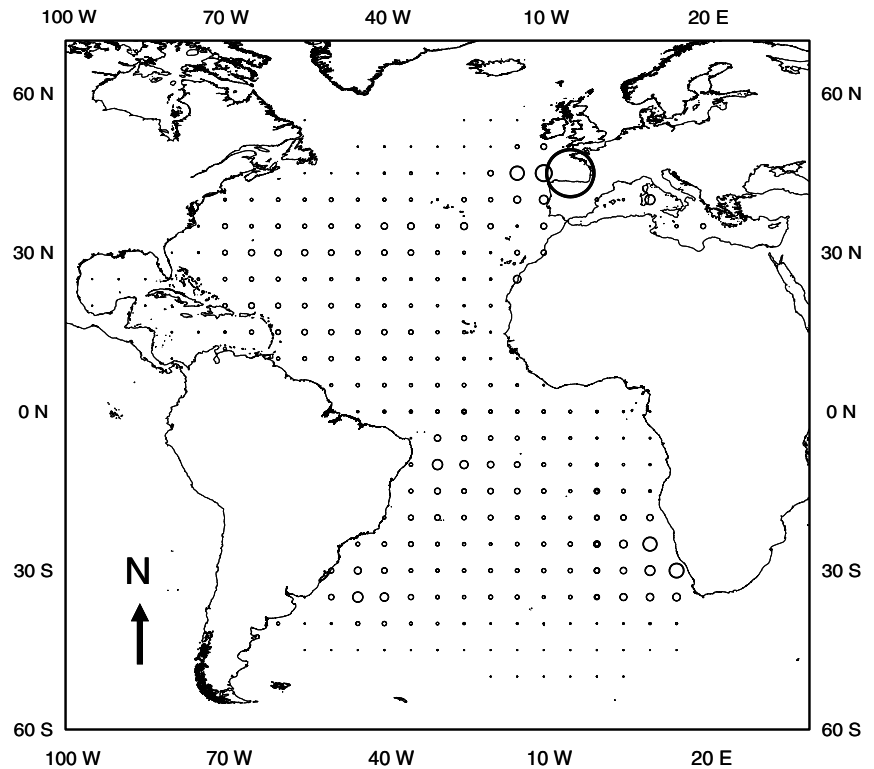


Figure 1

Spatial distribution of Atlantic and Mediterranean albacore (*Thunnus alalunga*) catches (ICCAT, 2001). The size of the circles is proportional to the square root of the total catch at each location.

Stock assessment under the assumption that there is migration between stocks

Blood group frequency data in Arrizabalaga et al. (2004) were used, with the assumption that the sample in the Gulf of Guinea was within the currently accepted range limit for both stocks, and therefore that it may be made up of a mixture of albacore belonging to the northern and southern populations. The proportion that each population would contribute to the mixture was calculated according to Cavalli-Sforza and Bodmer (1981) as

$$x_m = mx_A + (1-m)x_B, \quad (1)$$

where m = the fraction of population A in the mixture;
 x_m = the allelic frequency in the mixture; and
 x_A and x_B = the allelic frequencies in populations A and B, respectively.

The variance of m is given by

$$\sigma_m^2 = \frac{1}{(x_A - x_B)^2} \left[\sigma_{x_m}^2 + m^2 \sigma_{x_A}^2 + (1-m)^2 \sigma_{x_B}^2 \right], \quad (2)$$

where, $\sigma_{x_m}^2$, $\sigma_{x_A}^2$ and $\sigma_{x_B}^2$ are the variances of the allelic frequencies in the mixture and populations A and B,

respectively. When several diallelic loci are analyzed, the fraction of population A in the mixture can be computed as a weighted average:

$$\bar{m} = \frac{\sum \frac{m}{\sigma_m^2}}{\sum \frac{1}{\sigma_m^2}} \quad (3)$$

Using three lectins, for which the positive lectin binding proportion in the Gulf of Guinea was intermediate between the proportions for the northern and southern populations as described in Arrizabalaga et al. (2004), we obtained m values shown in Table 1. The weighted mean proportion indicated that 79% of the fish present in the Gulf of Guinea would belong to the northern Atlantic population, and this result was used to formulate plausible migration hypotheses for the two stocks. The mean historical (1975–99) catch around the equator (between lat. 5°N and lat. 5°S) has been 1218 metric tons (t) per year, and therefore 974 t would belong to fish from the North Atlantic population and 244 t to fish from the South Atlantic population. In reference to the average total catch in each stock (38,960 t and 27,111 t in the northern and southern stocks, respectively), these quantities would imply that about 2.5% of the fish from the North Atlantic and 0.9% from the South Atlantic are present in the Gulf of Guinea every year. Assuming that albacore in this area are migrating from one stock to the other, these percentages would, in broad terms, represent the yearly transfer rates between stocks.

Several scenarios were established and tested. Scenario number 1 reflects the above situation (2.5% and 0.9% annual migration rates from north to south and south to north, respectively). However, high variances for mixing proportions were obtained because no diagnostic loci was detected, and those precision estimates could, in fact, be overestimated because not all fish were sampled from different schools in the study of Arrizabalaga et al. (2004). This overestimation may indicate that annual migration rates vary considerably from those in scenario 1. Thus, a range of alternative migration scenarios were explored in which additional biological or fishery aspects were taken into account. Scenarios 2, 3, 7, and 8, reflected the situation in which migration occurs only in one direction (5% yearly from north to south and south to north in scenarios 2 and 3, respectively, and 10% from north to south and south to north in scenarios 7 and 8, respectively). Because no fishing effort targeting albacore exists in the equatorial area, the real migration rate may be higher than the one inferred from catches in that area. Accordingly, in scenario 4, twice the migration rates of scenario 1 (5% from north to south and

Table 1

Proportion of albacore (*Thunnus alalunga*), with a given blood group in the North Atlantic, Gulf of Guinea, and South Atlantic determined with three different lectins (Con A: *Concanavaline A*; WGA: *Triticum vulgare*; ECA: *Eritrina cristagally*; from Arrizabalaga et al., 2004) and estimated mixing proportions in the Gulf of Guinea. m =proportion of northern origin fish in the Gulf of Guinea sample; \bar{m} =weighted average proportion. Standard deviation of m and \bar{m} is given in parentheses.

Lectin	Con A	WGA	ECA
North Atlantic	0.2500	0.4500	0.0500
Gulf of Guinea	0.2174	0.3913	0.0435
South Atlantic	0.0357	0.2857	0
m	0,8478 (0,5553)	0,6427 (0,7794)	0,8695 (1,2006)
\bar{m}		0,7900 (0,4232)	

1.8% from south to north) were adopted. In scenario 5, migration was considered to be limited to the adult fraction of the stock (ages 5–8+), as size distributions in this area indicated, and finally in scenarios 6 and 9, high rates of migration (5% and 10%, respectively) in both directions were chosen. Although these scenarios are believed to be representative of the true nature of mixing between the stocks, it should be stressed that they represent only some of many different possible mixing scenarios.

All scenarios were tested by assuming an overlap migration model (fish return back to the area of origin for spawning) and using the VPA-2box program (Porch et al., 2001). No diffusive migration was considered because it is not consistent with observed genetic differentiation. Results for all scenarios were compared (in terms of spawning stock biomass trends and the small sample bias-adjusted version of the Akaike information criteria ([AICc, Hurvich and Tsai, 1995]) with the base case where no migration was assumed to occur between stocks.

Results

Stock assessment under the assumption of alternative boundaries between stocks

Best fits for northern and southern stocks were obtained by assuming different stock boundaries, at lat. 5°S and lat. 5°N, respectively. However, estimated abundance and fishing mortalities, with the assumption of any of the alternative stock limits, showed minor differences with respect to the base case (Table 2). The effect of considering the limit in lat. 0°N or in lat. 5°S was practically the same because most of the catch in the equatorial area happens in the Northern Hemisphere (between lat. 5°N and lat. 0°N). All coefficients of variation (CV) were below 15%, except for the F_{5+}^{87-99} in the south Atlantic, which were between 15% and 30%.

Table 2

Results of model fits for alternative boundaries between stocks of albacore (*Thunnus albacore*). Instantaneous fishing mortality (F) and abundance (N , in millions of individuals) estimates are averaged by age groups (subscripts) and time periods (superscripts). Corresponding mean coefficients of variation are given within parentheses. n = number of data points; p = number of estimated parameters; AICc = adjusted Akaike information criteria (Hurvich and Tsai, 1995).

Limit	North Atlantic albacore			South Atlantic albacore		
	5°N	0°N	5°S	5°N	0°N	5°S
–logL	66.68	66.74	66.52	80.85	81.98	82.20
Deviance	117.04	117.01	116.92	61.95	61.97	62.02
n	117.00	117.00	117.00	62.00	62.00	62.00
p	14.00	14.00	14.00	12.00	12.00	12.00
AICc	149.15	149.12	149.04	92.31	92.34	92.39
F_1^{75-86}	0.11 (0.2%)	0.11 (0.23%)	0.11 (0.19%)	0.00 (0.75%)	0.00 (0.86%)	0.00 (0.92%)
F_1^{87-96}	0.16 (3.87%)	0.16 (4.27%)	0.16 (3.97%)	0.01 (6.84%)	0.01 (6.87%)	0.01 (6.63%)
F_{2-4}^{75-86}	0.39 (0.19%)	0.37 (0.22%)	0.37 (0.18%)	0.11 (0.8%)	0.11 (1.02%)	0.11 (1.12%)
F_{2-4}^{87-99}	0.44 (10.44%)	0.41 (10.91%)	0.4 (9.9%)	0.2 (8.44%)	0.2 (8.95%)	0.21 (8.46%)
F_{5+}^{75-86}	0.3 (0.21%)	0.3 (0.24%)	0.3 (0.19%)	0.16 (0.86%)	0.15 (1.12%)	0.15 (1.24%)
F_{5+}^{87-99}	0.2 (11.48%)	0.21 (13.97%)	0.22 (11.17%)	0.3 (18.46%)	0.26 (29.39%)	0.25 (22.42%)
N_1^{75-86}	10.37 (0.19%)	10.6 (0.22%)	10.67 (0.18%)	8.23 (0.87%)	8.17 (1.05%)	8.16 (1.14%)
N_1^{87-96}	8.76 (3.94%)	9.02 (4.33%)	9.12 (4.16%)	7.55 (8.6%)	7.37 (8.52%)	7.3 (9%)
N_{2-4}^{75-86}	12.51 (0.15%)	12.87 (0.18%)	12.97 (0.15%)	13.64 (0.78%)	13.68 (0.99%)	13.69 (1.09%)
N_{2-4}^{87-99}	9.07 (7.97%)	9.47 (8.5%)	9.62 (7.99%)	11.96 (7.97%)	11.56 (8.14%)	11.61 (8.33%)
N_{5+}^{75-86}	3.29 (0.17%)	3.35 (0.2%)	3.36 (0.16%)	4.31 (0.83%)	4.37 (1.07%)	4.41 (1.19%)
N_{5+}^{87-99}	1.65 (7.87%)	1.81 (8.4%)	1.85 (7.67%)	3.57 (10.04%)	3.57 (10.19%)	3.59 (10.12%)

Stock assessment under the assumption of migration between stocks

Fits under several migration scenarios were more parsimonious than under the assumption of no migration between stocks (Table 3). Scenarios 1 ($p_{NS}=0.025$, $p_{SN}=0.009$), 2 ($p_{NS}=0.05$, $p_{SN}=0$), 3 ($p_{NS}=0$, $p_{SN}=0.05$), 4 ($p_{NS}=0.05$, $p_{SN}=0.018$), 6 ($p_{NS}=0.05$, $p_{SN}=0.05$), and 7 ($p_{NS}=0.1$, $p_{SN}=0$) showed lower AICc values than in the base case (BC).

Spawning stock biomass (SSB) values and trends under scenarios 1, 2, 3, 4, 5, 6, and 7 were similar to the ones observed in the base case, especially in the second half of the study period (except for the SSB of the southern stock over the last two years, which showed more variability, Fig. 2). In contrast, scenarios 8 and 9 showed a very different pattern in the last half of the series. In the north Atlantic, after the decline of the SSB during the beginning of the 1980s, the recovery was much more effective under these two scenarios, reaching higher values at the end of the 1990s than in the 1970s. Meanwhile, the SSB values for the southern stock were only slightly lower than those under the assumption of no migration, and under scenario 9 they were higher than in the base case over the last two years (Fig. 2).

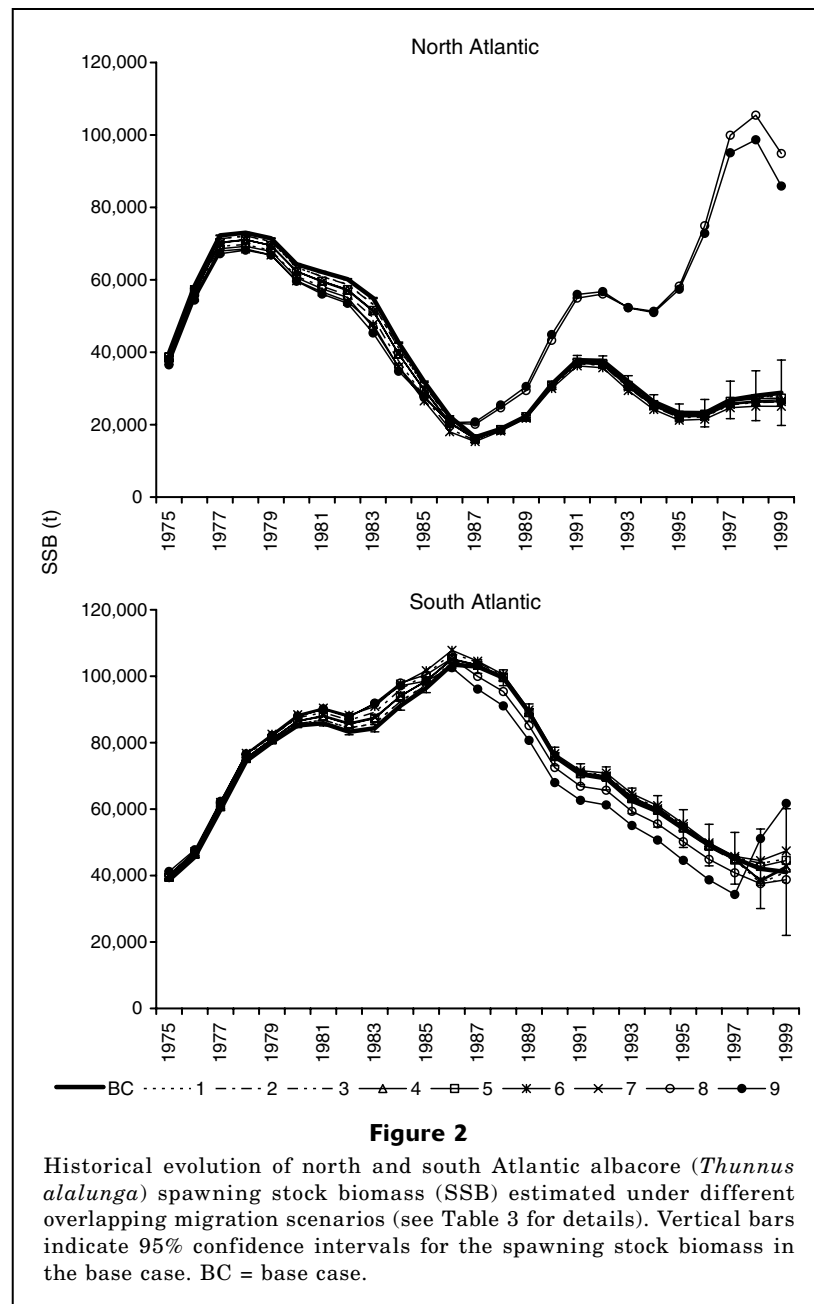
Table 3

Considered overlap migration scenarios and associated results of model fits for albacore (*Thunnus alalunga*). $n = 179$; $p = 25$; AICc = adjusted Akaike information criteria (Hurvich and Tsai, 1995); BC = base case; p_{NS} = annual migration rate from north to south; p_{SN} = annual migration rate from south to north.

Scenario	p_{NS}	p_{SN}	Age range (yr)	AICc
BC	0	0	1–8+	18.76
1	0.025	0.009	1–8+	13.74
2	0.05	0	1–8+	15.12
3	0	0.05	1–8+	18.03
4	0.05	0.018	1–8+	13.10
5	0.05	0.018	5–8+	19.41
6	0.05	0.05	1–8+	17.67
7	0.1	0	1–8+	12.77
8	0	0.1	1–8+	37.58
9	0.1	0.1	1–8+	46.81

Discussion

The method used to assess the uncertainty in the stock assessments that is due to the assumed stock structure



is based on a simple sensitivity analysis conducted by testing alternative stock structure hypotheses. When plausible hypotheses are generated from the cumulated knowledge on the biology and fisheries of the species, the effect of these hypotheses on the assessment results can be studied. However, it is also important to consider a range of alternative hypotheses so that they produce significantly different results in the assessment, in reference to the base case. The wide range of results allows us to discern the level of migration that is of concern for assessment purposes and shows the level of migration that is not likely to be realistic, given the available catch and effort data. However, several other sources of

uncertainty should be taken into account at this stage. The analysis could be extended to future biomass projections under different management strategies in order to indicate those management strategies that are more robust to violation of stock structure assumptions. This kind of study should run parallel to other studies where additional sources of uncertainty (e.g., in biological parameters or fishery data) are quantified because this approach would show their relative importance so that research could be prioritized with the goal of providing improved information on stock status.

In the case of Atlantic albacore, recent genetic studies indicate that, either the limit between both popula-

tions is not at lat. 5°N, but farther south, or that some amount of migration exists between them. Because no diagnostic loci were found by Arrizabalaga et al. (2004), the estimated proportions from each stock in the Gulf of Guinea sample could not be precisely determined and the true nature of mixing between north and south Atlantic albacore has yet to be fully determined. In spite of this uncertainty, the present exercise has made it possible to explore the response of biomass trends in different plausible discrete-stock scenarios and stock-mixing scenarios.

Although it is not possible to determine where the real limit lies between populations, we can conclude from our knowledge about the current low level of reported equatorial catch and the size structure of this catch, that assuming the population limit is 0°N or 5°S, instead of 5°N (as currently assumed), our perception about the stock status does not change significantly. On the other hand, several migration scenarios fitted the observed catch-at-age and abundance indices better than the scenario of no migration. In all these scenarios, SSB trends were very similar and values did not differ significantly from the ones in the base case; therefore it can be concluded that, although some rate of migration between stocks likely exists, the perception that we have about stock status, assuming there is no migration, is quite realistic. In other words, uncertainty in northern and southern Atlantic albacore stock assessments associated with the assumed stock structure does not seem to be important, given current biological knowledge and fishery data.

The highest variations in SSB were observed for northern Atlantic albacore in scenarios with high migration rates from south to north, showing high levels of SSB at the end of the study period. However, the observed difference in SSB levels with respect to the base case in the South Atlantic was not that pronounced, showing that northern Atlantic albacore biomass is more sensitive to biomass input from the south than vice versa. This result occurs because the minimum level of SSB in the north Atlantic in 1987 coincides in time with the maximum SSB in the southern stock, which is an order of magnitude higher. In this case, a migration rate of 10% from south to north would imply the input of approximately half the biomass present in the north at that moment, leading to a more rapid recovery of historic levels than under the null migration assumption. However, the existence of such important migration rates from south to north seems unlikely given the observed catch-at-age and abundance indices for both stocks.

The present analysis allows for the increase in confidence levels regarding stock assessment results for northern and southern Atlantic albacore obtained within ICCAT, assuming that stocks are separated at lat. 5°N and that there is no migration between them. This information is essential in order that the catch- and effort-related management measures that are in force for Atlantic albacore remain effective. Nevertheless, additional hypotheses, such as migration between North Atlantic and

Mediterranean albacore, or between South Atlantic and Indian Ocean albacore, should be investigated further as future research findings are made available. Moreover, it should be noted that migration between stocks could vary among years, and a yearly based assessment of genetic mixture, based on DNA analysis, would be more useful for quantitative stock assessments.

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