Investigating natal origins and trans-oceanic migrations in albacore tuna (*Thunnus alalunga*) from the southwest Indian Ocean using otolith chemistry

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Abstract:

Variation in otolith elemental fingerprints was investigated in albacore tunas (*Thunnus alalunga*) sampled in the southwest Indian Ocean (SWI) and along the Atlantic coast of South Africa (SA). A total of 72 otoliths were selected, from 46 adult fish captured around the Reunion Island (SWI) and 26 juvenile and sub-adults sampled at two locations off the South African coast (SA-N and SA-S, n = 13 per location). LA-ICP-MS was used to assess the signatures in 15 chemical elements at all otolith cores (to investigate potential differences in fish spawning origin among regions) and along all otolith edges (to characterize the chemical signatures of fish capture areas). Among the 15 chemical elements analysed, only Mg, P, Zn, Sr, Ba, B and Cu were above detection limits and significantly contributed to the variation in otolith composition. Based on differences in these elements, two groups of distinct multi-elemental signatures, denoting potentially discrete spawning origins (SpO), were identified at the otolith cores using hierarchical clustering based on Euclidian distances. Each of the two potential SpO contributed to the tuna sampled in all three areas, suggesting a common origin in some fish caught in the Atlantic and in the Indian Ocean and important trans-oceanic migrations between these two Oceans. The possible location of the two spawning areas is discussed based on the signatures recorded on the otolith edges before the final capture of the fish, in both oceans. This study was part of a collaborative project on the population structure of tuna, billfish and sharks of the Indian Ocean (PSTBS-IO).

1-Introduction

Albacore tuna (*Thunnus alalunga*) is a circumglobal, highly migratory species found throughout tropical, subtropical, and temperate regions of the world's oceans. Commercial catches of the species represent around 5% in weight of the global tuna catches in 2019 (ISSF,

2021). The species is currently managed as six separate stocks that occur in the north and south Pacific, the north and south Atlantic, the Indian Ocean and Mediterranean Sea (ISSF, 2021). The most recent stock assessment of albacore in the Indian Ocean indicated that the stock is not overfished but is likely to be subject to overfishing, but the results were highly uncertain (Langley, 2019).

Albacore is distributed from ~5°N to 40°S in the Indian Ocean. There is geographical repartition by latitude where immature albacore are predominantly caught in areas south of 30°S and mature albacore are predominantly caught between 10°S and 25°S, both with seasonal north-south movement (Chen et al., 2005; Nikolic et al., 2014; Nikolic et al., 2017). The separation of mature, spawning, and immature albacore life history stages roughly coincides with the boundaries of the three oceanic current systems in the Indian Ocean: the monsoon-driven current in the north of 10°S, the subtropical gyre between 10°S and 30°S and the Circumpolar Current south of 30°S (Chen et al., 2005, Durmeea et al., 2016). The spawning is predominantly occurring between 15° and 25°S (IOTC, 2008; IOTC, 2019).

Larval, genetic and morphometric studies have suggest for long the existence of two populations, separated by 90°E longitude (Stequert & Marsac 1989; Penney et al., 1998; Yeh et al., 1995). More recent studies, based on genetic markers (Montes et al., 2012), blood groups (Arrizabalaga et al., 2014), or larval drift modelling (Nikolic et al., 2020), have also indicated population structuring in the area, and possible exchanges of individuals between the south Atlantic Ocean and at least the south Indian Ocean. Determining the number of populations present in the Indian Ocean and the potential links between its (sub)populations is key for improving management measures across fishing zones.

Over the last few decades, otolith microchemistry has emerged as a very powerful tool for assessing lifetime migrations and population structure in marine fish (Sturrock et al. 2012), mainly because it is capable of gathering reliable information even from fish early life stages, which are often the most difficult to capture and track at sea (Hazen et al. 2012). Otoliths are small calcified structures located in the inner ear of the fish. They grow continually throughout life and are formed by the deposition of calcium carbonate crystals within a protein matrix (Pannella, 1971). As the otolith material accretes, it incorporates trace elements from the environment (Kalish, 1989; Campana, 1999, Elsdon et al., 2008). Therefore, their chemical signatures provide fingerprints of the water masses successively inhabited by the fish, acting as natural tags (Campana et al., 2000; Elsdon & Gillanders, 2003; Darnaude & Hunter, 2017) that

can be used to reconstruct the environmental history of sampled individuals or identify migratory and life-history patterns within populations (Walther et al. 2017). So far, otoliths have been successfully used to identify natal origins, population structure and movements of a wide variety of large pelagic fish (e.g., Artetxe-Arrate et al., 2019, Fraile et al., 2016; Rooker et al., 2016, Baumann et al., 2015). The objectives of the PSTBS-IO project concerned the entire Indian Ocean, but based on the samples collected, we focused on the south-western area of the Indian Ocean. In this context, the main objectives of this study were:

- To characterise the chemical signatures recorded in the otolith of *T. alalunga* during its adult life in the south west (SW) Indian Ocean and during its juvenile life in two different nursery areas of the south eastern Atlantic (South Africa) which could be used by this adult population,
- To identify the likely number of spawning zones for the fish captured in all these areas and their respective chemical signatures,
- To provide information about the lifetime migration patterns of the species and the potential connectivity between the two Oceans.

2-Material and Methods

2-1 Sampling

Among the 72 tuna specimens included in this study (Figure 1, Table 1), 46 were collected around the French Reunion island in the south west Indian Ocean (SWI), during 3 sampling events: in February 2018 (n=13), in May 2018 (n=13) and in December 2018 (n=20). All the others (n = 26) were sampled in the south east Atlantic Ocean in March-April 2018, at two sites along the shores of South Africa (SA): off Saldanha Bay in the north (SA-N, n = 13), where water masses are mainly under the influence of the Benguela current (which flows in a north west direction along the eastern coast of South Africa), and off Hout Bay (SA-S, n = 13), which is located farther south and bordered by the Agulhas current (which flows in a south west direction along the west coast of southern Africa and around the southerly tip).

Location	N	Sampling dates	FL (cm)	*Estimated age range (years)
south west Indian Ocean (SWI-Feb 18)	13	February 2018	96-104	7-10
south west Indian Ocean (SWI-May 18)	13	May 2018	98-113	7-15+
south west Indian Ocean (SWI-Dec 18)	20	December 2018	96-116	7-15+
South Africa – Hout Bay (SA-S)	13	March-April 2018	63-85	2-5
South Africa – Saldanha Bay (SA-N)	13	March-April 2018	63-85	2-5

Table 1. Number, sampling period, size range and estimated ages of fish for each of the sampling locations SWI, and SA.* The ranges in ages are for male and females combined (Xu et al. 2014).

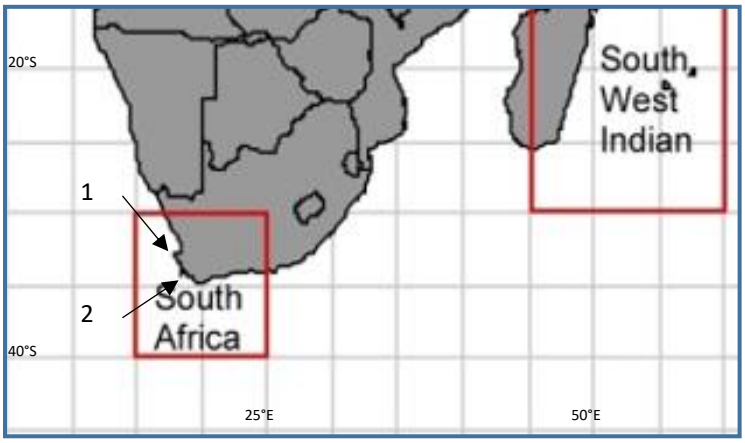

Figure 1. Sampling locations, referred to as southwest Indian Ocean (SWI, La Réunion Island), South Africa (1 SA-N- South Africa North: Saldanha Bay; 2 SA-S South Africa South: Hout Bay).

All fish were collected from longline fleets and ranged from 63 to 116 cm in size (fork length, FL, Table 1). They spanned multiple age-classes and life stages. Indeed, given the length at 50% maturity for females is 85 cm FL (Dhurmeea et al., 2016), the South African specimens (63-85 cm FL) were either juveniles or sub-adults of 2-5 years of age, while south west Indian Ocean ones were all adults (96-116 cm FL) above 7 years old.

2-2 Otolith preparation

All materials for otolith handling, preparation and analysis were decontaminated in 4% ultrapure nitric acid baths, rinsed with ultrapure (18.2 MQ) water and dried under a Class 100 laminar flow hood. For each individual fish, the left otolith was cleaned from adherent tissues, rinsed with distilled water then sonicated for 5 min in ultrapure water and dried under a laminar flow hood. It was then embedded in epoxy resin (Araldite 2020) polymerized in an oven at 35 °C for 24 h and transversal sections (of 1 mm thick on average) including the nucleus were made using a precision saw (Bluehler®, Isomet 1000). The posterior face of the otolith sections was then polished using 1200, 2400 and 4000 grit dry abrasive papers until the core was

reached. The sections were then sonicated for 5 min in ultrapure water, dried under a class 100 laminar flow hood and attached to a clean microscope slide for further processing.

2-3 Trace element analyses

Element concentrations in the otoliths were measured using Laser Ablation ICP-MS (Thermo fisher- Element2 XR coupled to a Geolass Q+ 193 nm laser) at the AETE-OSU OREME laboratory of the Montpellier University (France). For each otolith, the concentrations were measured along a transect from the core to the edge. A pre-ablation transect was used to clean the otolith surface (pulse rate 4 Hz, energy 15 J cm^{-2} and spot diameter 80 µm), and then the ablation transect was analyzed for measuring the chosen elements (pulse rate 7 Hz, energy 15 J cm^{-2} and spot diameter 50 µm). For calibration and quality control, a glass reference material (NIST 612 - National Institute of Standard and Technology, USA) was analysed at the beginning, after every 5 samples and at the end of each session. Another reference material (MACS 3, United States Geological Survey, USA) was analysed at the beginning and at the end of each session to check the accuracy. To remove residual sample gas that could interfere with the analysis, the laser chamber was purged for 30 seconds before analysing each sample. Fifteen chemical elements were measured. Calcium was used as the internal otolith standard, and results were given as ratios to Ca. All raw data were processed using the elementR package for R (Sirot et al., 2017). 6 elements were retained for further analysis (B, Mg, P, Zn, Sr and Ba) as they were above the detection limit. Percentage relative standard deviations (% RSD) based on replicate measurements of the MACS 3 standards reflect the level of precision achieved for each element ranging from 35% (P) to 3% (Sr).

Elemental ratios in the otolith core can be affected by egg yolk composition (Brophy 2004; Ruttenberg et al., 2005; Mcdonald et al., 2008). Consequently, the value centred on the otolith primordium was removed from our analyses, in order to avoid any maternal influence on otolith composition. Instead, the mean of the next three points, between 10 and 40 microns after the core (or 'near-core signature') was chosen to reflect fish spawning origin(s), i.e. the characteristics of the water mass(es) encountered during the first weeks of larval drift at sea. The last point of the transect was chosen to reflect the signature of the fish final capture area.

2-4 Statistical analyses

Differences in otolith fingerprints between fish natal origins and final capture areas were investigated separately, using the multi-elemental signatures from the otolith ‘near-core’ and ‘edge’ areas respectively.

For all datasets, a Principal Component Analysis (PCA) using the R package FactoMineR was made to identify the main chemical elements responsible for data separation. The 'near core' signatures in these key elements were then used to identify the most likely number of spawning origins in our sample, i.e. the number k of separate fish groups with distinct otolith 'near-core' signatures, by agglomerative hierarchal clustering (Ward's method). Lastly a combination of univariate and multivariate statistical tests was used to investigate the differences in single and multi-element signatures among capture locations and potential spawning origins. As the assumptions for normality and homoscedasticity were not met for all elements, a PERMANOVA test was first performed, followed, when relevant, by separate Kruskal Wallis tests and Pairwise Wilcoxon tests for each element. All statistical analyses were performed using the R software version 3.6.0 (R development Core Team, 2019) taking $\alpha < 0.05$ as the threshold for statistical significance. Data normality and homoscedasticity were checked using Shapiro-Wilk and Box M tests, respectively.

3-Results

3-1 Capture locations fingerprints

For otolith edge signatures, only six elements (P, B, Ba, Sr, Zn and Mg) were above detection limits and therefore included in the analyses. The first two dimensions of the PCA explained 60% of the total variation in otolith edge signatures, which were driven by differences in all these elements (Fig.2). Otolith fingerprints were different (PERMANOVA, $p < 0.05$) for all three capture locations, although some overlap was observed between them, especially for the fish captured at the SWI and at the SA-S sites.

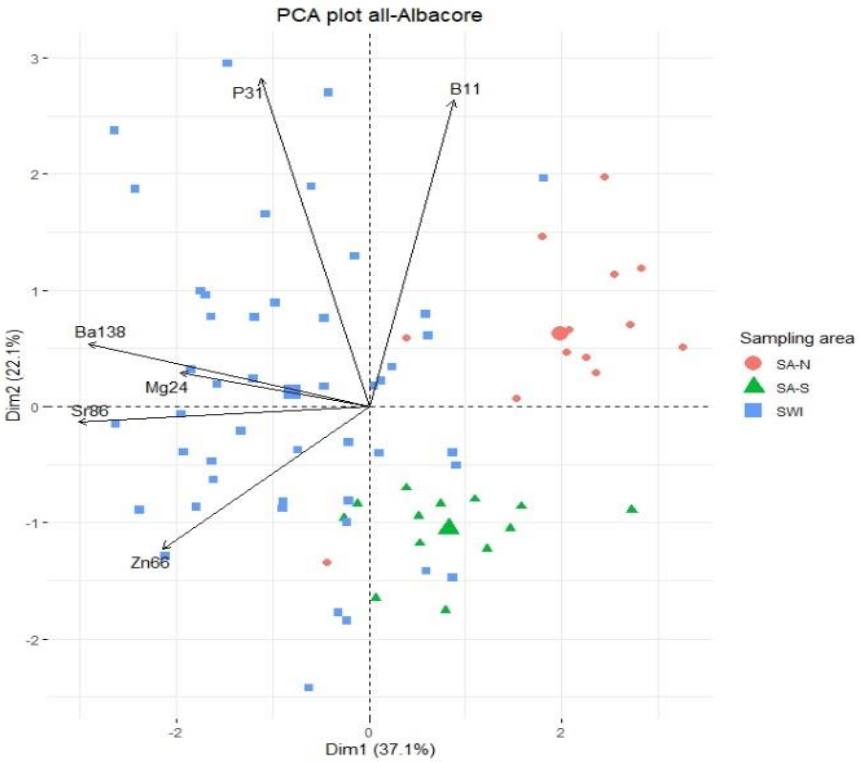

Figure 2. PCA plots of individual (fish) and variable (chemical elements) projection on the first plane of the PCA (60%) made with the otolith edge signatures. Individuals are coded by their sampling region (SWI 3 sampling events, SA-N and SA-S). For the variables, the length of the arrow reflects the % of contribution to the total inertia.

The edge signatures for the adult fish sampled in SWI differed significantly ($p<0.05$) from those measured in all the fish sampled in SA (irrespective of the site), being significantly enriched in Ba, Sr and Mg (Fig. 3). For the fish captured in South Africa, edge signatures differed ($p<0.05$) according to the capture site, with significantly higher values of B and P in the fish from SA-N (Fig.3).

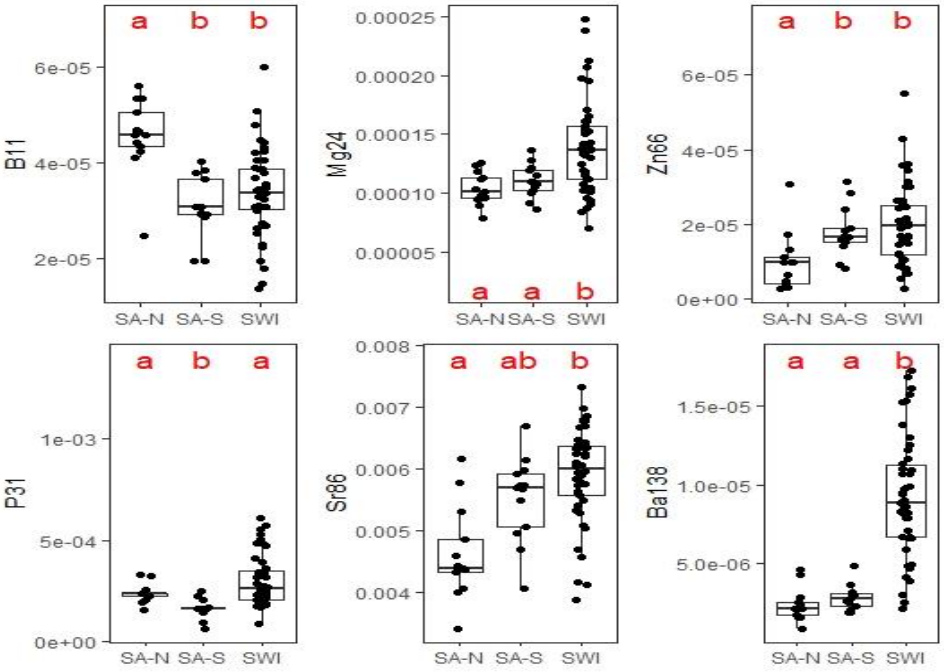

Figure 3: Edge elemental signatures (black dots) of the 72 albacores analysed and corresponding boxplots. Letters in red indicate groups with significantly distinct signatures ($p<0.05$).

3-2 Fish spawning origin (near-core fingerprints)

For near core signatures, seven elements (the six mentioned above plus Cu) were above detection limits and were therefore included in the analyses. The first two dimensions of the PCA explained 49% of the total variation in otolith near core signatures, which overlapped for all sampling locations except the two SA sites (Fig. 4). Among the elements successfully measured in this part of the otoliths, only Sr, Zn, B and P significantly contributed to inter-individual variation in near-core signatures and were retained for further investigation of fish spawning origin.

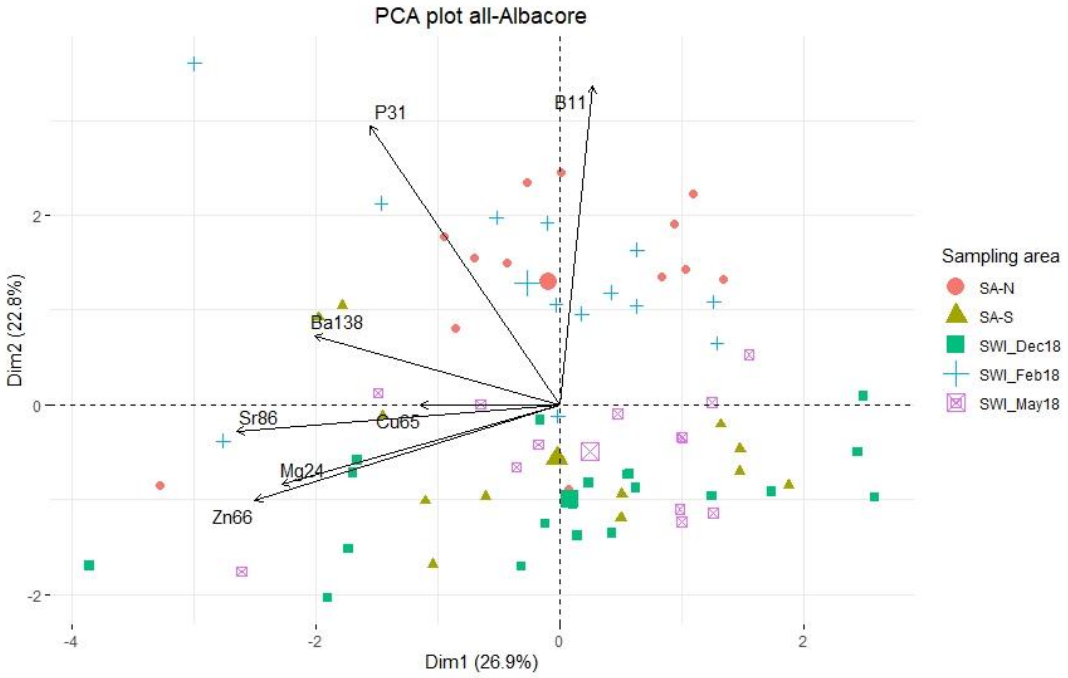

Figure 4. Projections for individuals (fish) and variables (chemical elements) on the first plan of the PCA (% of the total inertia explained: 49%) made on otolith near core signatures. Fish are coded by their sampling region (SWI with 3 sampling events, SA-N and SA-S). For each chemical element, the length of the arrow reflects the % of contribution to the total inertia.

The hierarchical clustering method based on the signatures of these elements identified two groups of fish of potentially distinct spawning origins (SpO), i.e. with different multi-elemental signatures (PERMANOVA, p = 0.07): SpO-1 mainly regrouping the fish from the SA-N and those captured in February in SWI and SpO-2 regrouping most of the fish from the SA-S, and those fished in December and in May in SWI (Fig. 5).

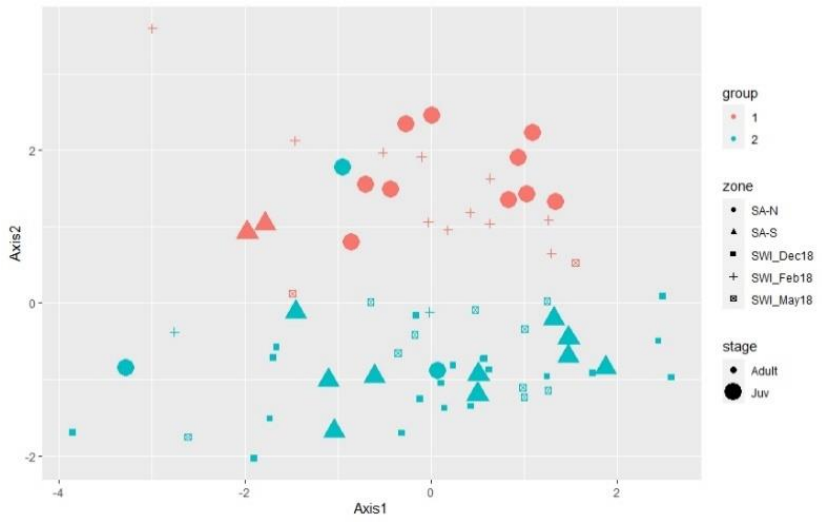

Figure 5. Projection of the clusters representing fish with near-core chemical signatures on the first plane of the PCA made with the near-core multi-elemental (Sr, Zn, B, P) signatures of the otolith of the 72 albacores, from SWI and SA areas. Colours on the graph represent the similar signatures for each fish and symbols represent the region of capture (large symbols=juveniles, small ones= adults).

In particular, the fish form SpO-1 had significantly higher near-core values for B than those of SpO-2, and the same trend (although just not significant) was observed for their signature in P (Fig. 6).

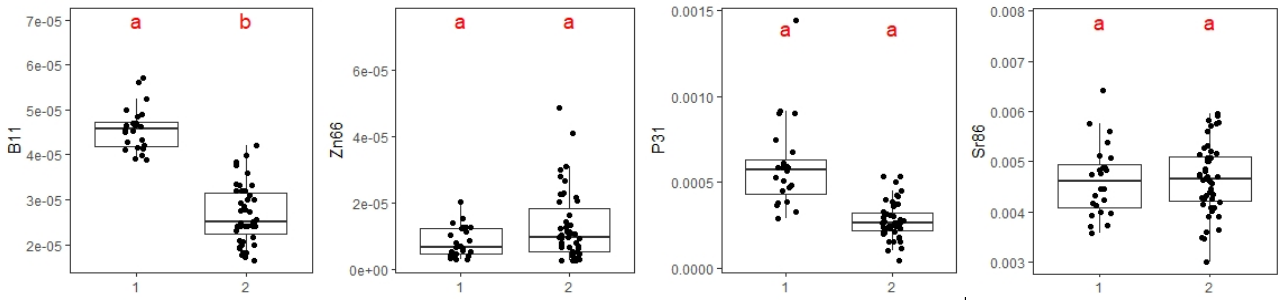

Figure 6. Near-core elemental signatures (black dots) of the 72 albacores analysed from their spawning origins and corresponding boxplots. Letters in red indicate groups with significantly distinct signatures ($p<0.05$).

Overall, SpO-2 was the main spawning source for all the individuals sampled (66%), providing 15-100% of the fish analysed irrespective of the region (Tab. 2). However, the two SpO apparently contributed to the stocks exploited in each of the 3 regions investigated, with different proportions depending on the site, but also, less expectedly, on the sampling date (Fig. 5, Tab.2). Thus, if 83% of the fish sampled in SA-N originated from SpO-1, and 85% of those from SA-S from SpO-2, the situation was more complicated for the fish sampled in SWI. Indeed, the spawning origin of these later varied according to the season of capture: SpO-2 was the main source for SWI-May (92%) and SWI-Dec (100%) samples, while most of the SWI-Feb samples (85%) originated from SpO-1. Therefore, SpO1 was the main spawning source only for SWI-Feb and SA-N samples, representing 85% and 83% of the fish sampled in each of these areas respectively.

	SA-N	SA-S	SWI-Feb18	SWI-May18	SWI-Dec18
SpO 1	83%	15%	85%	8%	0%
SpO 2	17%	85%	15%	92%	100%

Table 2. Relative proportion (%) of sub-adult and adult albacore individuals from each spawning origin analysed (total number of fish tested = 72, LJFL = 63-116 cm), for each of the 5 sampling events in the Atlantic and Indian Oceans.

Discussion

This study provides important information regarding the spawning origin and the lifetime migrations of the *T. alalonga* exploited in the Indian Ocean.

The first important finding regards the significant differences in multi-elemental signatures observed between all three capture locations. Of course, the edges of the otoliths in the SWI and SA samples were deposited at very different life stages (2 years versus 15 years) so ontogeny could explain some of the differences between SWI and SA capture locations. However, this does not explain the differences observed between the two South African zones sampled, as their fish were collected at the same period and at very similar sizes and ages. This proves that otolith microchemical signatures in this species largely reflect differences in ocean composition, allowing to discriminate between the contrasted water masses inhabited by its juvenile and the mature individuals in the Indian ocean (Fig.4). Indeed, immature albacore tunas in this part of the world are mainly distributed in areas south of 30°S that are under the influence of the Circumpolar Current, while mature ones are mainly concentrated at latitudes between 10°S and 25°S, i.e. under the influence of the subtropical gyre (Chen et al., 2005, Durmeea et al., 2016). Moreover, the two areas belong to different biogeochemical provinces in the Global Ocean, of contrasted bathymetries, chlorophyll a concentrations, surface temperatures and salinities (Longhurst, 2007; Reygondeau et al., 2018). This also applies to the difference in chemical fingerprints observed for the SA-N site, which belongs to a third separate province extending into the South-East Atlantic and under the influence of the Benguela Current.

The second important finding regards the high level of connectivity identified between the sampling sites from the Atlantic and the Indian Ocean. The cores from the otoliths investigated here could have been deposited as much as 15 years apart, so the water masses inhabited by the fish during their first weeks of life could be very different even if they were spawned in the same location. However, the fact that spawning origin differed drastically between the fish from SA-N (83% of SpO-1) and SA-S (85% of SpO-1), when they had similar sizes and ages, suggests once more that the two groups of distinct otolith signatures identified might rather reflect spatial differences in water masses composition than inter-annual variations in oceanic characteristics. Spawning areas for the species have been identified both in the central Atlantic Ocean and along the eastern shore of Madagascar (Beardsley, 1969; Bard, 1982; Nikolic et al., 2017). These spawning sites are equidistant from the South African coast, with similar geostrophic surface currents connecting them to this area. Because SpO-1, which provided most

of the fish caught in SA-N exhibited the higher concentrations in B and P, and high B values were measured on the edge of the otolith of the SA-N fish, we can hypothesize that this spawning origin might be that located in the Atlantic Ocean. SpO-2, characterized by low signatures in all elements and providing most of the fish sampled in SA-S and in the SWI, could correspond to the Indian Ocean spawning site located east of Madagascar. This is all the more plausible as the currents in the area connect to the SWI capture locations for a large part of the year. Finally, as the same spawning origin was identified for *T. alalonga* specimens caught on both sides of the African continent, in the fish caught in SA-N and those caught SWI-Feb (SpO-1) and, to a lesser extent for the fish caught in SA-S and those caught SWI-Dec and SWI-May (SpO2), our results clearly advocate for the existence of a non-negligible connectivity between the stocks of the species fished in the Atlantic and in the Indian Oceans. They confirm previous findings indicating possible larval drifts between the Indian and the Atlantic Oceans for this species, in both directions (Nikolic et al. 2020).

These preliminary results will need to be confirmed by the analysis of a larger number of samples, collected in several successive years (at least three) in each of the three regions investigated here. In addition, we suggest collecting albacore tunas from any other location in the Indian and the Atlantic Oceans where the juveniles of the species are caught, its adults are known to spawn or where its larvae have been reported. These samples could be used to validate that the spawning origin clusters found in this study do correspond to spatially distinct spawning zones. Additionally, an investigation on the distribution of biogeochemical tracers of the Indian Ocean and Atlantic Ocean water masses (through literature and sampling) would provide highly valuable information for the interpretation of the elemental composition of otoliths.

Acknowledgements

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